A relict oasis of living deep-sea mussels *Bathymodiolus* and microbial-mediated seep carbonates at newly-discovered active cold seeps in the Gulf of Cádiz, NE Atlantic Ocean

Luis Somoza1 · José Luis Rueda2 · Francisco J. González1 · Blanca Rincón-Tomás3,4 · Teresa Medialdea1 · Olga Sánchez-Guillamón2 · Michael Hoppert3 · Juan T. Vázquez2 · Pedro Madureira5 · Esther Santofimia1 · Enrique López-Pamo2 · Desirée Palomino2 · Jose Eugenio Ortiz6 · Lorena Blanco1,6 · Maria del Carmen Fernández-Puga7 · L. M. Fernández-Salas8 · Joachim Reitner9

Received: 5 June 2021 / Accepted: 12 November 2021 / Published online: 23 December 2021 © The Author(s) 2021

Abstract

Extensive beds of the deep-sea mussel *Bathymodiolus mauritanicus* (currently also known as *Gigantidas mauritanicus*) linked to active cold seeps related to fissure-like activity on Al Gacel mud volcano, Gulf of Cádiz, were filmed and sampled for the first time during the oceanographic expedition SUBVENT-2 aboard R/V Sarmiento de Gamboa. Al Gacel mud volcano is one of up to 80 fluid venting submarine structures (mud volcanoes and mud volcano/diapir complexes) identified in the Gulf of Cádiz as result of explosive venting of hydrocarbon-enriched fluids sourced from deep seated reservoirs. This mud volcano is a cone-shaped edifice, 107 m high, 944 m in diameter constituted by mud breccias and, partially covered by pavements of seep carbonates. Extensive beds of this deep-sea mussel were detected at the northern flank at 810–815 m water depth associated with bacterial mats around intermittent buoyant vertical bubble methane plumes. High methane concentrations were measured in the water column above living mussel beds. Other chemosymbiotic species (*Siboglinum* sp., *Solemya elarraichensis*, *Isorropodon* sp., *Thyasira vulcolutre* and *Lucinoma asaphus*) were also found in different parts of Al Gacel mud volcano. Al Gacel mud volcano may currently represent one of the most active mud volcanoes in the Gulf of Cádiz, delivering significant amounts of thermogenic hydrocarbon fluids which contribute to foster the extensive chemosynthesis-based communities detected. This finding is of paramount importance for linking extremophile bivalve populations along the North Atlantic, including cold seeps of the Gulf of México, hydrothermal vents of the Mid-Atlantic Ridge and now, detailed documented at the Gulf of Cádiz.

Keywords Deep-sea mussels · Chemosynthesis-based habitats · *Bathymodiolus mauritanicus* · Cold seeps · Seep carbonates · Mud volcanoes · Gulf of Cádiz

Introduction

Bathymodioline deep-sea mussels (Mytilidae, Bathymodiolinae) are one of the dominant macroorganisms of chemosynthesis-based communities in hydrothermal vents on spreading ridges and back-arc basins and in cold-water seeps along subduction zones across the globe (Miyazaki et al. 2010; Laming et al. 2018). Although initially viewed as oases within a barren deep ocean, hydrothermal vents and methane seep chemosynthesis-based communities are now recognized to interact with surrounding ecosystems on the seafloor and with the water column, and to affect global biogeochemical cycles (Levin et al. 2016).

Deep-sea mussels within the subfamily Bathymodiolineae are among the most iconic fauna to colonize deep-sea reducing habitats (cold seeps and hydrothermal vents) globally (e.g. Cosel 1982; Laming et al. 2018). Within this subfamily, the different *Bathymodiolus* (over 20 species) and *Gigantidas* species (ca. 10 species) can occur in both cold seeps and hydrothermal vents, with some species displaying different morphology but showing little genetic differentiation, which may indicate the high adaptability...
of some bathymodioline species to deep-sea reducing environments (Miyazaki et al. 2010). According to the “Evolutionary stepping stone hypothesis”, the ancestors of bathymodioline deep-sea mussels exploited resources from organic-fall habitats (e.g. sunken wood, whale carcasses) in their progressive adaptation to deep-sea reducing environments (Distel et al. 2000; Jones et al. 2006). These changes of habitat preferences resulted in adaptive trends in shell lengths (related to the availability of space and energy, and physiological trade-offs) and in the successive colonization of greater water depths (Lorion et al. 2013). During this process, these singular bivalves established symbiosis with chemosynthetic bacteria like sulfide and methane oxidizers, as an effective feeding strategy and tolerance to toxic hydrogen sulfide (Miyazaki et al. 2010; Rodrigues et al. 2010). Fueled by energy derived from chemosynthetic symbioses, their contribution to ecosystem productivity is conspicuous, with many bathymodioline species forming dense and extensive aggregates and beds (Petersen and Dubilier 2009).

The first report of methanotrophic deep-sea mussels, living in the vicinity of cold seeps and consuming methane as the principal component of natural gas, was made by Childress et al. (1986) at the Gulf of México. Populations of other deep-sea mussels have been reported from some of the most important deep-sea cold-seep areas (around the world (Fig. 1a), including the Gulf of México (e.g. MacDonald et al. 1990), Western Africa (Olu-Le Roy et al. 2007), the Caribbean Arc-Barbados accretionary Prism (Cosel and Olu 1998), the Japanese Arc (Miyazaki et al. 2010), Papua New Guinea (Cosel and Janssen 2008) and recently, along the Costa Rica margin (McCowin et al. 2020), among others. In some of these areas, deep-sea mussels may also play an important role as ecosystem engineers, both through the formation of spatially heterogeneous biogenic reefs and in redistributing reduced-fluid emissions (Laming et al. 2018).

Bathymodiolus mauritanicus (currently assigned to Gigantidas mauritanicus according to Xu et al. 2019) was firstly caught as by-catch by commercial bottom trawlers along the African margin off Banc d’Arguin, Mauritania, and they were presumably associated with potential cold seeps occurring there (Cosel 2002). This species displays morphological similarities with the Bathymodiolus childressi clade (Childress et al. 1986) and were included in the same morphological “group” by Cosel (2002). Later on, phylogenetic studies made by Olu-Le Roy et al. (2007) pointed out some connectivity along the equatorial belt between the species originally described as Bathymodiolus mauritanicus living in the West Africa margin seep sites along the eastern Atlantic (Cosel 2002; Génio et al. 2008) and Bathymodiolus childressi occurring in the western Atlantic, especially in seep sites of the Barbados Prism (Cosel and Olu 1998) and the Gulf of México (Childress et al. 1986). Miyazaki et al. (2010) include both deep-mussel species in the same hierarchical phylogenetic group 1–1, supporting the hypothesis that these bathymodioline species living on deep-sea cold seeps at both sides of the Atlantic Ocean could have been differentiated from amphi-Atlantic species and treated like that in further studies (Coykendall et al. 2019). Recent phylogenetic reconstruction based on three mitochondrial genes and two nuclear genes revealed that B. mauritanicus belongs to the Gigantidas genus (Xu et al. 2019) as it was already previously suggested by Jones et al. (2006). Some studies have revealed Bathymodiolus and Gigantidas species differentiation has not a single pattern and that habitat specific biotic and oceanographic characteristics play an important role, leading to deep-sea mussel population divergence at seeps and vents (Laming et al. 2018).

This study provides, for the first time, images and data of dense beds of living deep-mussels B. mauritanicus (currently assigned to Gigantidas mauritanicus) associated with cold seeps sourced from one of the most active mud volcano, Al Gacel MV, of the Gulf of Cádiz (GoC), NE Atlantic. Furthermore, this study suggests that the GoC was an area of formerly widespread populations of Bathymodiolus mauritanicus associated with a past higher activity of cold seeps, which has now waned, persisting in some isolated areas, such as Al Gacel MV that currently represent a relict oasis for this deep-mussel species (Fig. 1). The importance of this fact reconsider questions on the past fast spreading of the populations of B. mauritanicus colonizing active cold seeps at both sides of the Atlantic Ocean.

Mud volcanoes and mud volcano/diapir complexes: the largest manifestations of cold seeps

Cold seeps are seafloor manifestations of fluid migration including methane and other hydrocarbons, brine, hydrogen sulfide, and sometimes carbon dioxide from the subsurface to the seabed and into the water column, occurring worldwide on both passive and tectonically-active continental margins (Ceramicola et al. 2018). Mud volcanoes (MVs) and mud volcano/diapir complexes (MVDs) are the largest seafloor expressions of cold seeps generated by the vertical and jointly migration of overpressured fluids (gas and water) and extrusion of mud-breccia sediments (Kopf 2002; Ceramicola et al. 2018). These fluid venting submarine structures occur globally in a wide variety of geological environments such as convergent margins as the GoC (Somoza et al. 2002, 2003; Wulff-Barreiro 2009; Palomino et al. 2016), the Calabrian accretionary prism (Ceramicola et al. 2014), the Barbados accretionary prism (Deville and Guerlais 2009) and the Caspian Basin (Blouin et al. 2020) but also in relation to sedimentary-related overpressures as
A relict oasis of living deep-sea mussels Bathymodiolus

Due to the high volume of emissions and the deep roots of MVs, these structures are considered one of the most important global mechanisms for degassing of deeply buried, methane-oversaturated sediments (Dimitrov 2002). The main sink for methane in subseafloor MVs is the anaerobic oxidation of methane (AOM) mediated by archaea, operating most likely in cooperation with sulphate-reducing bacteria (SRB) (Boetius et al. 2000; Reitner et al. 2005a, b).

At cold seeps, a recent review of existing data estimated that 0.02 Gt of methane-C is consumed annually in the sediment metabolized by microbial action, with an additional 0.02 Gt methane-C escaping annually into the hydrosphere
mit is located at 775 m depth (Fig. 2). Flanks generally have structure with a diameter at its base of 944 m, whose sum-to 250 m high. Al Gacel MV is a 107 m high cone-shaped is smaller in size, when compared to the large MVs located middle Moroccan MV field (MMF) (León et al. 2012). This MV Al Gacel MV is located on the north-eastern side of the mid-

Cold seeps fueled by deep hydrocarbon reservoirs

Al Gacel MV is located on the north-eastern side of the middle Moroccan MV field (MMF) (León et al. 2012). This MV is smaller in size, when compared to the large MVs located at the MMF, such as Yuma and Ginsburg MVs that are up to 250 m high. Al Gacel MV is a 107 m high cone-shaped structure with a diameter at its base of 944 m, whose summit is located at 775 m depth (Fig. 2). Flanks generally have smooth slopes ranging from 2 to 20°, rarely up to 30°, and display several terrace levels on the southern flank interpreted as mudflow lobes. The summit forms a high reflective internal dome interpreted as active fluid venting.

High-resolution multichannel seismic data of Al Gacel MV revealed that the formation of this MV is related to the eruption of hydrocarbon-enriched sediments sourced from a subsurface reservoir. This MV stands over vertical fractures that act as a feeder complex connecting the MV to the gas reservoir by fracturing the hosting Pliocene–Quaternary sedimentary units. The feeder complex is rooted in a seismic unit interpreted as the hydrocarbon reservoir characterized by high amplitude acoustic anomalies linked to the surface expression of MV by hydro-fractures that source with hydrocarbon-enriched fluids on the surface of the mud volcano (Fig. 2c). The top of the reservoir is located at 1.4 s two-way travel time (TWT).

Methods

In March 2014, the R/V Sarmiento Gamboa with the ROV Luso explored more than eleven MVs in the Moroccan margin of the GoC (Somoza and UTM-CSIC, 2018b). The ROV Luso is instrumented with high definition camera (1024 × 1024 pixel digital still camera), 2 robotic manipulators for biological/geological samples, CTD (conductivity, temperature and depth measurements) with fluorescence, turbidity and CO2, CH4 and O2 sensors and 4 Niskin bottles for water samples. Subsamples of 20 and 500 mL were taken immediately on board for CH4 and CO2 analyses, respectively, preserved with saturated mercuric chloride and stored in darkness. More than 107 h of video imagery were recorded from the mud volcanoes. Targets et al. Gacel mud volcano were selected using previous information from multibeam bathymetry and gravity cores during the MVS-EIS cruise (Somoza and UTM-CSIC, 2018a) on board the R/V Hesperides. Different B. mauritanicus specimens were sampled for further biosignature analysis of their shells. Furthermore, their gills were inspected to characterize their chemosynthetic symbionts, by 16S rRNA gene metabarcoding sequencing, and light and electron microscopy (Supplementary Material). Detailed information about the geophysical, sampling, mineralogical, and biogeochemical techniques can be found in the Supplementary Material.

Seafloor observations of living beds of Bathymodiolus mauritanicus and carbonate seeps

Visual observations made during two ROV transects across the summit and flanks of Al Gacel MV allowed to map the distribution of chemosynthesis and non-chemosynthesis-based habitats on the seafloor (Fig. 3a). Chemosynthesis-based habitats were mainly formed by: (i) beds of living Bathymodiolus mauritanicus, sometimes covered by microbial mats, in the N flank; (ii) Pockmark-like circular depressions, 10–50 m in diameter, completely covered by dead shells of B. mauritanicus and other typical cold seep species along the SE flank; and (iii) Dense populations of Siboglinum sp. worms at the bottom of pockmarks (1–2 m in diameter) located on the summit of Al Gacel MV (Rincón-Tomás et al. 2019, 2020) (Fig. 3a).

Extensive beds of living B. mauritanicus (Bathymodiolus beds) generally form linear aggregations (up to 10 m in length) and scattered sub-circular clumps surrounded by intermittent gas bubbling areas (diffuse to focused venting areas). These were identified at the northern flank of Al Gacel MV at 810–820 m (Figs. 3a and 4). These Bathymodiolus beds displayed average seafloor coverages up to 20%, with densities reaching 280 individuals m−2. Similar abundances of large (up to 8 cm shell length) and small size individuals (< 2 cm) have been detected in collected mussel clumps using the ROV manipulators, with the small size individuals being more common in the interior part of the clumps. The living Bathymodiolus beds showed peaks of methane concentration (Fig. 2b).

Otherwise, pockmark-like circular depressions with diameters from meters to tens of meters harbouring shell graveyards with abundant shells of typical cold seep bivalves (mainly of B. mauritanicus and Lucinoma asaphus) were detected at the southeastern flank of Al Gacel MV at 790 m depth (Fig. 3a). Live individuals of other typical cold seep bivalves as Solemya elarraichensis (large and small-size individuals) and Isorropodon sp., as well as recent remains of B. mauritanicus, were collected from the muddy bottoms of the south-eastern flank of Al Gacel MV at 773 m depth.

Large seep carbonate build-ups (up to 2–3 m wide) forming pavements and blocks were frequently detected and scattered around the summits of the MV. These seep carbonates were colonized by deep-sea gorgonians
A relict oasis of living deep-sea mussels *Bathymodiolus*

A relict oasis of living deep-sea mussels *Bathymodiolus* 1 3 (Swiftia), antipatharians (*Bathypathes, Leiopathes, Stichopathes*), bamboo corals (*Chelidonisis, Acanella*) and demosponges (Fig. 3a). These habitat-forming species conformed complex habitats that were located in areas with high concentrations of carbon dioxide (Fig. 3c). Otherwise muddy bottoms of the flanks contained abundant graveyards of scleractinian corals (*Desmophyllum pertusum, Dendrophyllia*) and stony octocorals (*Corallium*). Cementation by seep carbonates of sediments (sizes of 20–30 cm) underlying by dense populations of siboglinids appear at the center of unit pockmarks, of ca. 1–2 m in diameter. Recent data from the same expedition suggested that these dense siboglinid populations may favour the formation of hotspots of seep carbonates on the seafloor by the action of symbionts sulphide-oxidizing bacteria by isolating these highly hydrogen sulfide toxic acidic environments not compatible with carbonate formation (Rincón-Tomás et al. 2019). At the basal part of Al Gacel MV, muddy bottoms with some patches containing graveyards of scleractinian corals and small seep carbonates were also colonized by hexactinellid sponges (*Pheronema, Hyalonema*) and gorgonians (*Radicipes* on soft bottoms, *Swiftia* on dispersed seep carbonates (Fig. 3a).
Methane concentrations derived from cold seeps

The ROV observations of gas bubbles venting from the seafloor at some *Bathymodiolus* beds (Fig. 4b), together with the vigorous release of methane upon push-core recovery collected from this MV confirmed that the interstitial gas concentrations are at (or near to) saturation close to the seafloor. Seafloor bubbling was recorded at *Bathymodiolus* beds and sometimes directly on mussel clumps with bacterial mats (available ROV video footage can be found in Supplementary Material). In these bubbling areas above the *Bathymodiolus* beds, methane concentrations measured in the water sampled with ROV Niskin bottles reached up to 97.6 nM at 1 m above the seabed.

Chemistry of interstitial fluids of the extruded muds

A 137-cm-long gravity core (TG03, location in Fig. 2b) recovered from the summit of Al Gacel MV (762 m depth), displayed a 120-cm lower sediment layer consisting of a mud breccia matrix of dark greenish-grey colour (GLEY 1 4/5GY after Munsell Colour Chart code) with a strong hydrogen sulfide smell and a 14 cm top oxidizing sediment layer with abundant planktonic foraminifera. High contents of elemental organic sulfur and other sulfide compounds (dimethylsulfide and 1,4-dimethyltretasulfide) were detected.
A relict oasis of living deep-sea mussels *Bathymodiolus*

in mud-breccia sediments between 80 and 100 cm below seafloor (Table S1, Supplementary Material). Pore-water analyses of the gravity core TG03 displayed higher barium (Ba), boron (B) and lithium (Li) concentrations than seawater, with at least one order of magnitude higher at the top of the core, and increasing their concentrations in deeper core sediments (Table S1, Supplementary Material).

### Carbon and oxygen stable isotopes of *Bathymodiolus* shells and seep carbonates

Carbon and oxygen stable isotope compositions were analyzed for shells of live *B. mauritanicus* individuals and for seep carbonates (Fig. 5). Thus, shells contained slight negative δ^{13}C values ranging from −4.3‰ VPDB in large-size individuals to −2.4‰ VPDB in small-size individuals and low positive δ^{18}O values (3.0–3.3‰ VPDB).

Otherwise, carbonates at the summit of Al Gacel MV have high negative δ^{13}C values ranging from −29.7 to −16.4‰ VPDB but low positive δ^{18}O values (3.2–3.7‰ VPDB) similar to those in shells of living *B. mauritanicus* (Fig. 5). In contrast, seep carbonates collected along the flanks of the Al Gacel MV have slighter negative δ^{13}C values (−9.2 to −8.3‰ VPDB) in comparison with those seep carbonates collected from the summit but higher positive δ^{18}O values (5.0–5.3‰ VPDB) (Fig. 5).

### Biomarkers of the hydrocarbon-enriched extruded muds

Analyses of n-alkanes of sub-seafloor sediments composed of mud breccia collected on the core TG03 at the summit of Al Gacel MV (Fig. 6), showed distribution ranging from n-C15 to n-C35 with predominance of n-C21 and abundant presence at n-C29 and minor at n-C31 (Fig. 6a). Pristane/
phytane ratio ranging from 0.3 to 1.1 is commonly an indicator of anoxia in reducing environments, although as well these values could also be interpreted as indicators of the high input of archaeal microorganisms, potentially methanogens, due to the nature of this type of environments. The carbon preference index (CPI) from 2.2 to 4.6 suggests a deep thermal maturation of the organic matter. Fatty acids were also detected with a distribution ranging from the C\textsubscript{14} isomer to the C\textsubscript{32} homologue with maxima at C\textsubscript{16} and C\textsubscript{18} (Fig. 6b) indicate a bacterial origin and recent participation of microorganisms in the mineralization process.

**Endosymbiotic bacteria of living *Bathymodiolus mauritanicus***

Bacterial symbionts have been identified in most bathymodioline deep-sea mussel species, and they provide some-to-all of the host nutrition (Duperron 2010). At many hydrothermal vents, cold seeps and organic fall habitats, these symbiotic associations can sustain dense aggregations of deep-sea mussels. Analysis of 16S rRNA gene sequences recovered from 2 different specimens revealed the bacterial community from the *B. mauritanicus* gills collected et al. Gacel MV (Fig. 7). Bacterial DNA was highly abundant in both specimens, obtaining up to 40,000 sequence reads in both cases (see detailed description in Supplementary Material. Methanotrophic bacteria were the most abundant organisms isolated in the gills, but the presence of Verrucomicrobia and thiotrophic bacteria was also detected. Marine Methylo-trophic Group-1 was the main group of methane-oxidizers, representing 99.99% of the methanotrophs in mussel-3 and 99.94% of the methanotrophs in mussel-4. *Methylo-tenera* sp., MMG-2 and MMG-3 bacterial taxa were also found within the methanotrophic bacteria.

Light and electron microscopy images revealed the presence of bacteria organized in bacteriocytes inside the gills, as shown in Fig. 8. These bacteriocytes are localized surrounding the blood lacuna of the gills’ filaments. The bacteria display a characteristic system of inner membranes typical of methanotrophic bacteria.

**Discussion**

**Influence of the type of hydrocarbon fluids and associated salt brines during the life of fossil and present deep-sea mussels**

Geochemical, isotopic and seismic data pointed out to thermogenic gas as the origin of cold seeps where *B. mauritanicus* occur at present in Al Gacel MV. In support of this data, the acquired seismic section displayed signals of the occurrence of deep hydrocarbon-enriched fluids migrating upwards throughout hydro-fractures (Fig. 2c). MVs are edifices built up by periodic violent mud-breccia eruptions triggered by overpressured hydrocarbon fluids stored in deep-seated reservoirs. Nevertheless, during dormant...
periods, these conduits favor a continuous leakage of enriched-hydrocarbon fluids and may relict brine waters from the subsurface to the seafloor (Kopf 2002; Dimitrov 2002). Therefore, based on ROV images, it could be possible to support that some linear *B. mauritanicus* beds of Al Gacel MV are located along seafloor fissures formed on the
surface of the MV that favor continuous leakage from sub-surface hydrocarbon reservoirs with diffuse to focused fluid venting along with time and space. Analyses of n-alkanes of the mud breccia extruded at the summit of Al Gacel MV showed values from n-C15 to n-C35 with a predominance of C21 and the low carbon preference index (CPI) indicate the maturity of the organic matter, pointing out the thermogenic origin of the fluids rising from the sub-surface hydrocarbon reservoirs. The concretionary carbonate δ¹³C values (Fig. 5) most likely indicate varying degrees of mixing between δ¹³C-depleted bicarbonate produced by thermogenic methane oxidation (predominant at the summit) and δ¹³C-enriched carbon dioxide produced by methanogenesis (prevailing on the flanks). Carbon isotopes values of the B. mauritanicus shells ranging between −2.41 and −4.27‰ VPDB are interpreted to be results of the mix between several carbon sources: methane anaerobic oxidation, fermentation of organic matter and seawater.

The fact that most depleted carbon isotopes values are found in B. mauritanicus suggests the progressive influence of thermogenic gases in the construction of the shells during the life of the deep-sea mussels. Otherwise, high concentrations of Ba, B and Li (up to 18.89 nM, 1170 µM and 46 µM respectively) together with low values of redox potential (−200 mV), at 1.30 m below seafloor, suggest that reducing fluids rising to surface enriched in these elements, probably related to salt brines or as results of the dehydration of smectite in depth and transformation to illite (Hensen et al. 2007). In contrast, pore-water fluids are depleted in Mg and K. These mineralized fluids could explain the origin of circular depression filled by graveyards of deep-sea mussel shells as formerly originated by brine pools surrounded by deep-sea mussels as identified in the Gulf of México (MacDonald et al. 1990), where seep carbonates are enriched in Ba, Sr and Li from the methane seeps (Sun et al. 2021).

**Symbioses as a mechanism for adaptation of deep-sea mussels to cold seeps**

Thus, while symbioses may explain why bathymodioline deep-sea mussels are so productive in deep-sea reducing habitats, species survival over successive generations by the repeated colonization of nascent, chemo synthetically active habitat, depends more upon the adaptive characteristics of their lifecycle as a whole (Laming et al. 2018). 16S rRNA gene metabarcoding sequencing and visual analysis of the gills have been used to reveal the presence of methanotrophic symbionts in the gills of two B. mauritanicus specimens (Figs. 7, 8). The OTUs recovered from Illumina MiSeq sequencing show the high abundance of Marine Methylothrophic Group I (99.99% and 99.94% of the methanotrophic bacteria detected in mussel-3 and mussel-4, respectively), which has been reported to include many sequences closely related to bathymodioline deep-sea mussel endosymbionts (Ruff et al. 2013). These deep-sea mussels have reduced digestive systems and their nutrition mostly relies on their chemosynthetic bacteria, organized in bacteriocytes inside their gills (Duperron et al. 2005). Figure 8 shows the localization of these bacteriocytes surrounding the blood lacuna of the gills’ filaments. The bacterium from those gills illustrated in Fig. 8C displays inner membranes, a typical feature of type I methanotrophs, like Marine Methylothrophic Group I bacteria (Garrity et al. 2006). Detected sequences related to thiotrophic bacteria can also indicate a dual-symbiosis of the B. mauritanicus specimens (Fig. 7), even though their presence was not abundant and no visualization of these bacteria within the gills was possible. Nevertheless, B. mauritanicus has been previously identified as dual symbiotic mussel with the dominance of methanotrophic bacteria (Rodrigues et al. 2013).

**Potential influence of the reactivation of seepage activity in the Al Gacel mud volcano: comparison with other cold seeps**

Occurrence of hemipelagic sediment overlying mud breccia sediments suggests that Al Gacel MV is now likely in the quiescence phase in terms of mud extrusion. However, the dense populations of B. mauritanicus aligned in fractures, indicate an active fluid venting related to the formation or reactivation of seabed fissures connecting with deep-seated reservoirs of thermogenic fluids. At present, methane concentration seems to control the present distribution of benthic habitat types on their surface from chemosynthetic-based fauna living surrounding seeps to non-chemosynthetic species colonizing seep carbonates. Methane concentrations detected in Al Gacel MV are much higher than those registered in other MVs of the GoC such as Captain Arutyunov MV, located northwards of Al Gacel MV, with average values of 2–8 nM in vertical profiles and 20 nM near-bottom (Sommer et al. 2009) or at St Petersburg MV, located northwards of Captain Arutyunov MV, with values ranging from 12.8 nM (seafloor) to 14.29 nM (near-bottom at the MV summit) (Sierra et al. 2017). Other MVs in the Eastern Mediterranean Sea (e.g., Napoli, Milano and Amsterdam) seem to display even higher near-bottom methane concentrations (400–2000 nM), indicating a more intensive degassing related to fluid circulation in fault systems (Charlou et al. 2003).

**Glacial to interglacial variability driven the formation of seep carbonates**

Carbon isotope composition from seep carbonates collected in other MVs (e.g. Las Negras and Mvseis MVs) sampled during the SUBVENT cruise (Fig. 1) shows similar depleted δ¹³C values ranging from −30 and −15‰ VPDB, similar...
to seep carbonates from the summit of Al Gacel MV. The origin of seep carbonates resulting from microbial-mediated oxidation of methane is supported by their negative carbon isotope signatures ranging from $-56.2$ to $-8.4\%$ VPDB, similar to other seep carbonates reported in the GoC (Díaz-del-Río et al. 2003; Magalhães et al. 2012). Otherwise, the oxygen isotope composition of the seep carbonates is controlled by a combination of factors, including the carbonate mineralogy and chemistry, the temperature of precipitation and the pore-water isotopic composition. At present, the near-bottom water temperature measured with the ROV sensor et al. Gacel MV was 9.9–10 °C and salinities of 35.6–36.0 psu. According to Magalhães et al. (2012), seep carbonates with heavier isotopic compositions, up to 5.9%e VPDB (Fig. 5), must have been formed from pore water fluids with an assumed temperature of formation of 4 °C. Regional palaeoceanographic reconstructions point to 4 °C as the minimum sea bottom water temperature possible to occur during glacial periods (Voelker et al. 2006). Therefore, we interpret that seep carbonates collected et al. Gacel MV flanks and at other MVs having enriched $\delta^{18}O$ values > 5%e VPDB were formed during past colder glacial conditions. In contrast, the seep carbonates formed at the summit of Al Gacel MV displaying $\delta^{18}O$ values around 3%e VPDB associated with living B. mauritanicus and aggregates of Siboglinids (Fig. 5) are formed at present seabed temperature conditions by active seeps (Rincón-Tomás et al. 2019).

**Potential causes of the demise of deep-sea mussel populations in the Gulf of Cádiz: variability in tectonic stress, sea-level changes and/or oceanic bottom-current circulation from glacial to interglacial times**

Cold seeps provide habitats that are frequently ephemeral and fragmented as those fueled by active fluid venting, separated sometimes by wide areas with typical deep-sea oligotrophic conditions (Levin et al. 2016). The wide occurrence of B. mauritanicus shells reported in the GoC (Fig. 1b) in contrast to live records of this deep-sea mussel suggests a dramatic demise of its populations. Therefore, surrounding Al Gacel MV, small clumps of B. mauritanicus have been reported from Darwin MV (1115 m depth) together with extensive mussel graveyards at Ginsburg (910 m), Student (955 m) and Yuma (975 m) MVs by Génio et al. (2008) (Fig. 1). Furthermore, B. mauritanicus shells were also detected in Las Negras MV during the SUBVENT expedition (Somoza et al. 2014) and even further north in Almazán MV (at 829 m depth) within the Spanish margin of the GoC (Rueda et al. 2012). Imprints of past extensive cold seeps during glacial times as documented by empty shells of che- mosymbiotic bivalves is rather common in MVs from the Mediterranean Sea to the Arctic Ocean (Ivanov et al. 2010; Taviani et al. 2013; Rovere et al. 2014; Ambrose et al. 2015). In the Mediterranean Sea, large populations of Bathymodiolus sensu lato seem to have disappeared from this basin, leaving Idas modiolaeformis as the sole bathymodioline species at present (Taviani 2011).

In the Gulf of Cádiz, the fate of large B. mauritanicus populations might follow a similar trend to that occurred with the fossil giant cold-water coral reefs associated with the formation of carbonate seeps on MVs (Rincón-Tomás et al. 2019). A progressive decrease in the rate of release of thermogenic hydrocarbon fluids and associated formation of seep carbonates could represent an important factor conspiring in the onset/demise of B. mauritanicus populations in the Gulf of Cádiz. The cessation of reducing conditions can cause populations of chemosymbiotic-based bivalves to collapse entirely. Thus, large pool-like structures, ranging 20–50 m in diameter, filled up with large numbers of B. mauritanicus shells observed along the southern flanks of Al Gacel MV could be interpreted as relics of large pockmarks or even brine pools as well as imprints of past intense hydrocarbon seepage. This type of circular aggregations of living deep-sea mussels has been reported in highly active seeps of the Gulf of México (Smith et al. 2000) and the Gabon margin (Ondreas et al. 2005).

Tectonics and global climate changes are the main drivers controlling the activity of seafloor seepage. In the Gulf of Cádiz and Alborán Sea, the release of the huge reservoirs of deep hydrocarbons is tectonically controlled by the convergence between the African-Eurasia plates within the Gibraltar Arc generating extrusion of up to 84 mud volcanoes and mud volcano/diapir complexes (e.g. Somoza et al. 2021a). At global scale, intensifications of seafloor seepage have been related to the increasing destabilization of subsurface hydrates caused by two of these factors: (i) Decrease in hydrostatic pressure during sea-level lowstands (e.g. Teichert et al. 2003 among others) and/or (ii) Warming by incursions of extreme warm bottom waters during deglacial-interglacial times reported into the Arctic by a massive inflow of Atlantic waters since the last glacial (El bani Altuna et al. 2021) and other cases as in the north South China Sea margin reporting intensification of seepage during the last interglacial period (Chen et al. 2019).

In the GoC, the massive outflow of warm Mediterranean waters through the Gibraltar Strait has been related to seafloor morphologies collapses and pockmarks interpreted to be caused by massive destabilization of subsurface hydrates (Gardner et al. 2001). Otherwise, the demise of giant cold water coral reefs along the NW African coast, including the GoC, has been related to the abrupt decrease of bottom-water temperature caused by the onset of inflow of Antarctic-sourced waters along the NW African margin during deglacial (Rincón-Tomás et al. 2019) up to 6 °C at present conditions between Mediterranean and Antarctic waters (Somoza et al. 2021b).
We suggest that the demise of deep-sea mussel populations in the GoC could be associated with the reduction of seafloor seepage in most of the mud volcanoes. Thus, we hypothesize that this reduction in seafloor seepage might be caused by (i) a decreasing in mud volcanoes activity associated with diminishing tectonic stress along the African-Eurasian plate boundary; (ii) a reduction in the destabilization of buried subsurface hydrates bearing within the mud volcanoes associated with both global oceanic circulation or by sea-level changes during deglacial and interglacial times i.e. by an abrupt decrease in the bottom water temperature related to the onset of incursions of Antarctic sourced waters into the Northern Hemisphere along the NW African during deglacial times and/or by the increase in hydrostatic pressure by sea-level rise during highstands.

Conclusion

Based on the available published information, we remark that the extensive beds of *B. mauritanicus* documented in this study could be considered a hot-spot of deep-sea chemosynthesis-based fauna for the NE Atlantic. Moreover, it could represent a relict of formerly widespread deep-sea mussel populations that colonized different cold seeps of the Gulf of Cádiz, but nowadays are restricted to very few cold seeps, with those of Algcace MV harbouring the best and most complex beds of this deep-sea mussel in the GoC and the NE Atlantic.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1007/s12542-021-00594-3.

Acknowledgements

We thank the captain and crew of the R/V Sarmiento de Gamboa during the SUBVENT-2 expedition. Thanks are also given to the acoustic, mechanics and seismic technicians of the UTM-CSIC (Unidad de Tecnología Marina, Consejo Superior de Investigaciones Científicas (CSIC). Special thanks to the EMEPC Team for their professional and enthusiastic work operating the ROV-“Luso”. This research has been granted by the SUBVENT (CGL2012-39524-C02) and EXPLOSEA (CTM2016-75947-R) research projects funded by the Spanish Minister for Science and Innovation. Special congratulations to Prof. Joachim Reitner for his fruitful scientific career linking geology and biology aspects of the fossil extreme life in Earth. Finally, we thank the interesting and helpful corrections and comments provided by four reviewers on a previous version of this manuscript.

Funding

Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. Ministerio de Ciencia e Innovación, Project EXPLOSEA (CTM2016-75947-R). Luis Somoza, Ministerio de Ciencia, Innovación y Universidades, Project SUBVENT (CGL2012-39524-C02). Luis Somoza.

Open Access

This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Ambrose, W.G., Jr., G. Panieri, A. Schneider, A. Plaza-Faverola, M.L. Carroll, E.K.L. Åström, W.L. Locke, and J. Carroll. 2015. Bivalve shell horizons in seafloor pockmarks of the last glacial-interglacial transition: A thousand years of methane emissions in the Arctic Ocean. *Geochemistry, Geophysics, Geosystems* 16 (12): 4108–4129.

Blouin, A., N. Sultan, A. Pierron, P. Imbert, and J.P. Callot. 2020. Evolution model for the Absheron Mud Volcano: from stratified sediments to fluid mud generation. *Journal of Geophysical Research: Earth Surface* 25(12): e2020JF005623.

Boetius, A., K. Ravenschlag, C.J. Schubert, D. Rickert, F. Widdel, A. Gieseke, R. Amann, B.B. Jørgensen, U. Witte, and O. Pfannkuche. 2000. A marine microbial consortium apparently mediating anaerobic oxidation of methane. *Nature* 407: 623–626.

Boetius, A., and F. Wenzhöfer. 2013. Seafloor oxygen consumption fuelled by methane from cold seeps. *Nature Geoscience* 6(9): 725–734.

Bohrmann, G., M. Ivanov, J.P. Foucher, V. Spiess, J. Bialas, J. Greinert, and M. Zillmer. 2003. Mud volcanoes and gas hydrates in the Black Sea: New data from Dvurechenskii and Odessa mud volcanoes. *Geo-Marine Letters* 23(3): 239–249.

Ceramicola, S., S. Dupré, L. Somoza, and J. Woodside. 2018. Cold seep systems. In *Submarine geomorphology*, eds. A. Micalef, S. Krastel, and A. Savini, 367–387. New York: Springer.

Ceramicola, S., D. Praeg, A. Cova, D. Accettella, and M. Zecchin. 2014. Seafloor distribution and last glacial to postglacial activity of mud volcanoes on the Calabrian accretionary prism, Ionian Sea. *Geo-Marine Letters* 34: 111–129.

Charlou, J.L., J.P. Donval, T. Zitter, N. Roy, P. Jean-Baptiste, J.P. Foucher, and M.S. Party. 2003. Evidence of methane venting and geochemistry of brines on mud volcanoes of the eastern Mediterranean Sea. *Deep Sea Research Part I: Oceanographic Research Papers* 50(8): 941–958.

Chen, F., X. Wang, N. Li, J. Cao, G. Bayon, J. Peckmann, and D. Feng. 2019. Gas hydrate dissociation during sea-level hightstand inferred from U/Th dating of seep carbonate from the South China Sea. *Geophysical Research Letters* 46(23): 13928–13938.

Childress, J.J., C.R. Fisher, J.M. Brooks, M.C. Kennicutt, R. Bidigare, and A. Anderson. 1986. A methanotrophic marine molluscan symbiosis: Mussels fueled by gas. *Science* 233: 1306–1308.

Cosel, R. von. 1982. Marine Mollusken der Kapverdischen Inseln. Übersicht mit zoogeographischen Anmerkungen. *Courier Forschungsinstutit Senckenberg* 52: 35–76.

Cosel, R. von. 2002. A new species of bathymodioline mussel (Mollusca, Bivalvia, Mytilidae) from Mauritania (West Africa), with comments on the genus *Bathymodiolus* Kenk & Wilson, 1985. *Zoosystema* 24: 259–271.

Cosel, R. von., and R. Janssen. 2008. *Bathymodiolus* mussels of the *Bathymodiolus* (s. 1) childressi clade from methane seeps near Edison Seamount, New Ireland, Papua New Guinea (Bivalvia: Mytilidae). *Archiv für Molluskenkunde* 137: 195–224.
Deville, E., and S.H. Guerlais. 2009. Cyclic activity of mud volcanoes: Evidences from Trinidad (SE Caribbean). Marine and Petroleum Geology 26(9): 1681–1691.

Diaz-del-Río, V., L. Somoza, J. Martínez-Frías, M.P. Mata, A. Delgado, F.J. Hernández-Molina, R. Linares, J.A. Martin-Rubí, A. Maestro, M.C. Fernández-Puga, R. León, E. Llave, T. Medialdea, and J.T. Vázquez. 2003. Vast fields of hydrocarbon-derived carbonate chimneys related to the accretionary wedge/olistostrome of the Gulf of Cádiz. Marine Geology 195: 177–200.

Dimitrov, L.I. 2002. Mud volcanoes—The most important pathway for degassing deeply buried sediments. Earth-Science Reviews 59: 49–76.

Distel, D.L., A.R. Baco, E. Chuang, W. Morrill, C. Cavanaugh, et al. 2000. Do mussels take wooden steps to deep-sea vents? Nature 403: 725–726.

Duperron, S. 2010. The diversity of deep-sea mussels and their bacterial symbioses. In The vent and seep biota, ed. S. Kiel, 137–167. Dordrecht: Springer.

Dupré, S., J. Mascle, J.P. Foucher, H. Harmegnies, J. Woodside, and C. Pierre. 2014. Warm brine lakes in craters of active mud volcanoes, Meses caldera off NW Egypt: Evidence for deep-rooted thermogenic processes. Geo-Marine Letters 34(2–3): 153–168.

El bani Altuna, N., T.L. Rasmussen, M.M. Ezat, et al. 2021. Deglaciar bottom water warming intensified Arctic methane seepage in the NW Barents Sea. Communications Earth and Environment 2: 188. https://doi.org/10.1038/s43247-021-00264-x.

Gardner, J. M., P. R. Vogt, and L. Somoza. 2001. The possible affect of the Mediterranean Outflow Water (MOW) on gas hydrate dissociation in the Gulf of Cádiz. In AGU Fall Meeting Abstracts 2001, OS12B-0418.

Garrity, G.M., J.A. Bell, and T. Liburn. 2006. Class I Alphaproteobacteria class nov. In Bergey’s manual® of systematic bacteriology, volume two: The Proteobacteria (Part C), eds. J.T. Staley, D.J. Brenner, and N.R. Krieg. 1–574. Boston, Mass.: Springer.

Génois, L., S.B. Johnson, R.C. Vrijenhoek, M.R. Cunha, and L. Watling. 2016. Hydrothermal vents and methane seeps: Rethinking the sphere of influence. Frontiers in Marine Science 3: 7.

González, F.J., L. Somoza, R. León, T. Medialdea, T. Torres, J.E. Ortiz, R. Linares, J. Martínez-Frías, and R. Merinero. 2012. Fer - nodules associated with hydrocarbon seeps: A new discovery in the Gulf of Cádiz (NE Atlantic) mud volcanoes. Journal of Shellfish Research 27(1): 1–9.

González, F.J., L. Somoza, R. León, T. Medialdea, T. Torres, J.E. Ortiz, R. Linares, J. Martínez-Frías, and R. Merinero. 2012. Ferramanganese nodules and micro-hardgrounds associated with the Cadiz Contourite Channel (NE Atlantic): Palaeoenvironmental records of fluid venting and bottom currents. Chemical Geology 310(311): 56–78.

González, F.J., L. Somoza, R. Linares, J. Martínez-Frías, J.A. Martín Rubí, T. Torres, J.E. Ortiz, and V. Díaz del Río. 2007. Fe-Mn nodules associated with hydrocarbon seeps: A new discovery in the Gulf of Cádiz (eastern central Atlantic). Episodes 30(3): 187.

Hensen, C., M. Nuzzo, E. Hornibrook, L.M. Pinheiro, B. Bock, V.H. Magalhães, and W. Brückmann. 2007. Sources of mud volcano fluids in the Gulf of Cadiz—Indications for hydrothermal imprint. Deep-Sea Research Part I: Oceanographic Research Papers 54(11): 1890–1911.

Hensen, C., M. Nuzzo, E. Hornibrook, L.M. Pinheiro, B. Bock, V.H. Magalhães, and W. Brückmann. 2007. Sources of mud volcano fluids in the Gulf of Cadiz—Indications for hydrothermal imprint. Deep-Sea Research Part I: Oceanographic Research Papers 54(11): 1890–1911.

Jones, W.J., Y.J. Won, P.A.Y. Maas, P.J. Smith, R.A. Lutz, and R.C. Vrijenhoek. 2006. Evolution of habitat use by deep-sea mussels. Marine Biology 148: 841–851.

Kopf, A. 2002. Significance of mud volcanism. Reviews of Geophysics 40(2): 1005.

Laming, S.R., S.M. Gaudron, and S. Duperron. 2018. Lifecycle ecology of deep-sea chemosymbiotic mussels: A review. Frontiers in Marine Science 5: 282.

León, R., L. Somoza, T. Medialdea, J.T. Vázquez, F.J. González, N. López-González, D. Casas, M.P. Mata, M.C. Fernández-Puga, C.J. Giménez-Moreno, and V. Díaz-del-Río. 2012. New discoveries of mud volcanoes on the Moroccan Atlantic continental margin (Gulf of Cádiz): Morphostructural characterization. Geo-Marine Letters 32: 473–488.

Levin, L.A., A.R. Baco, D.A. Bowden, A. Colaco, E.E. Cordes, M.R. Cunha, and L. Watling. 2016. Hydrothermal vents and methane seeps: Rethinking the sphere of influence. Frontiers in Marine Science 3: 7.

Lorion, J., S. Kiel, B. Faure, M. Kawato, S.Y. Ho, B. Marshall, S. Tsuchida, J. Imiyazaki, and Y. Fujiiwara. 2013. Adaptive radiation of chemosymbiotic deep-sea mussels. Proceedings of the Royal Society (Biological Sciences) 280: 20131243.

MacDonald, I.R., N.L. Guinasso, J.F. Reilly, J.M. Brooks, W.R. Calender, and S.G. Gabrielle. 1990. Gulf of Mexico seep communities: VI. Patterns in community structure and habitat. Geo-Marine Letters 10: 244–252.

Magalhães, V.H., L.M. Pinheiro, M.K. Ivanov, E. Kozlova, V. Blinova, J. Kolganova, C. Vasconcelos, J. McKenzie, S.M. Bernasconi, A.J. Kopf, V. Díaz del Río, F.I. Gonzalez, and L. Somoza. 2012. Formation processes of methane-derived authigenic carbonates from the Gulf of Cádiz. Sedimentary Geology 243(244): 155–168.

McCowin, M.F., C. Feehery, and G.W. Rouse. 2020. Spanning the depths and depth-stratified: Three new species of Bathymodiolo- dus (Bivalvia, Mytilidae) at seeps along the Costa Rica margin. Deep-Sea Research Part I: Oceanographic Research Papers 164: 103322.

Miyazaki, J.I., L. de Oliveira Martins, Y. Fujita, H. Matsumoto, and Y. Fujiiwara. 2010. Evolutionary process of deep-sea Bathymodioulus mussels. PLoS ONE 5(4): e10363.

Olu-Le Roy, K., R. von Cosel, S. Hourdez, S.L. Carney, and D. Jollivet. 2007. Amphi-Atlantic cold-seep Bathymodioulus species complexes across the equatorial belt. Deep Sea Research Part I: Oceanographic Research Papers 54(11): 1890–1911.

Ondreas, H., K. Olu, Y. Fouquet, J.L. Charlou, A. Gay, B. Dennielou, J.P. Donval, A. Fiti, T. Nadalig, P. Cochonat, E. Cauquil, J.F. Bourillet, M. Le Moigne, and M. Sibuet. 2005. ROV study of a giant pockmark on the Gabon continental margin. Geo-Marine Letters 25: 281–292.

Palomino, D., N. López-González, J.T. Vázquez, L.M. Fernández-Salas, J.L. Rueda, R. Sánchez-Leal, and V. Díaz-del-Río. 2016. Multidisciplinary study of mud volcanoes and diapirs and their relationship to seepages and bottom currents in the Gulf of Cádiz continental slope (northeastern sector). Marine Geology 378: 196–212.

Petersen, J.M., and N. Dubhiér. 2009. Methanotrophic symbioses in marine invertebrates. Environmental Microbiology Reports 1: 319–335. https://doi.org/10.1111/j.1758-2229.2009.00081.x.

Reitner, J., J. Peckmann, A. Reimer, G. Schurmann, and V. Thiel. 2005a. Methane-derived carbonate build-ups and associated microbial communities at cold seeps on the lower Crimean shelf (Black Sea). Facies 51: 66–79.

Reitner, J., J. Peckmann, M. Blumenberg, W. Michaelis, A. Reimer, and V. Thiel. 2005b. Concretionary methane-seep carbonates and associated microbial communities in Black Sea sediments. Palaeogeography, Palaeoclimatology, Palaeoecology 227: 18–30.
Rincón-Tomás, B., J.P. Duda, L. Somoza, F.J. González, D. Schneider, T. Medialdea, E. Santofimia, E. López-Pamo, P. Madureira, M. Hoppert, and J. Reitner. 2019. Cold-water corals and hydrocarbon-rich seepage in Pompeia Province (Gulf of Cádiz)—Living on the edge. Biogeosciences 16: 1607–1627.

Rincón-Tomás, B., F.J. González, L. Somoza, K. Sauter, P. Madureira, T. Medialdea, J. Carlsson, J. Reitner, and M. Hoppert. 2020. Siboglinidae tubes as an additional niche for microbial communities in the Gulf of Cádiz—A microscopical appraisal. Microorganisms 8(3): 367.

Rodrigues, C.F., A. Hilário, and M.R. Cunha. 2013. Chemosymbiotic species from the Gulf of Cádiz (NE Atlantic): Distribution, life styles and nutritional patterns. Biogeosciences 10: 2569–2581.

Rodrigues, C.F., G. Webster, M.R. Cunha, S. Duperron, and A.J. Weightman. 2010. Chemosynthetic bacteria found in bivalve species from mud volcanoes of the Gulf of Cádiz. FEMS Microbiology Ecology 73(3): 486–499.

Rovere, M., F. Gamberi, A. Mercorella, H. Rashed, A. Gallerani, E. Leidi, M. Marani, V. Funari, and G.A. Piniert. 2014. Venting and seepage systems associated with mud volcanoes and mud diapirs in the southern Tyrrhenian Sea. Marine Geology 347: 153–171.

Rueda, J.L., J. Urra, S. Gofas, N. López-González, L.M. Fernández-Salas, and V. Díaz del Río. 2012. New records of recently described chemosymbiotic bivalves for mud volcanoes within the European waters (Gulf of Cádiz). Mediterranean Marine Science 13: 262–267.

Ruff, S.E., J. Arndt, K. Knittel, R. Amann, G. Wegener, A. Ramette, and A. Boetius. 2013. Microbial communities of deep-sea methane seeps at Hikurangi continental margin (New Zealand). PLoS ONE 8(9): e72627.

Sierra, A., D. Jiménez-López, T. Ortega, R. Ponce, M.J. Bellanco, R. Rodríguez, A. Lobato, A. Maestro, J.T. Vázquez, T. Medialdea, E. Santofimia, E. López-Pamo, P. Madureira, and J.T. Vázquez. 2021b. The interactive role of hydrocarbon seeps, hydrothermal vents and intermediate Antarctic/Mediterranean water masses on the distribution of some vulnerable deep-sea habitats in mid latitude NE Atlantic Ocean. Oceans 2 (2): 351–385.

Somoza, L., J.I. Rueda, O. Sánchez-Guillamón, T. Medialdea, B. Rincón-Tomás, F.J. González, D. Palomino, F. Madureira, E. López-Pamo, L.M. Fernández-Salas, E. Santofimia, R. León, E. Marino, M.C. Fernández-Puga, and J.T. Vázquez. 2021a. Submarine active faults and morpho-tectonics around the Iberian Margins: Seismic and tsunami hazards. Frontiers in Earth Science 9: 519.

Somoza, L., J.I. Rueda, O. Sánchez-Guillamón, T. Medialdea, B. Rincón-Tomás, F.J. González, D. Palomino, F. Madureira, E. López-Pamo, L.M. Fernández-Salas, E. Santofimia, R. León, E. Marino, M.C. Fernández-Puga, and J.T. Vázquez. 2021b. The interactive role of hydrocarbon seeps, hydrothermal vents and intermediate Antarctic/Mediterranean water masses on the distribution of some vulnerable deep-sea habitats in mid latitude NE Atlantic Ocean. Oceans 2 (2): 351–385.

Taviani, M. 2011. The deep-sea chemosynthetic microbial world as experienced by the Mediterranean metazoans through time. In Advances in stromatolite geobiology, eds. J. Reitner, N.V. Queric, and G. Arp. Lectures in earth sciences 131: 277–295.

Taviani, M., L. Angeletti, A. Ceregato, F. Fogliani, C. Foglia, and F. Trincardi. 2013. The Gela Basin pockmark field in the strait of Sicily (Mediterranean Sea): Chemosymbiotic fauna and carbonate signatures of postglacial to modern cold seepage. Biogeosciences 10(7): 4653–4671.

Teichert, B.M.A., A. Eisenhauer, G. Bohrmann, A. Haase-Schramm, B. Bock, and P. Linke. 2003. U/Th systematics and ages of authigenic carbonates from Hydrate Ridge, Cascadia Margin: Recorders of fluid flow variations. Geochimica et Cosmochimica Acta 67(20): 3845–3857.

Voelker, A.H., S.M. Lebreiro, J. Schönfeld, I. Cacho, H. Erlenkeuser, and F. Abrantes. 2006. Mediterranean outflow strengthening during northern hemisphere coolings: A salt source for the glacial Atlantic? Earth and Planetary Science Letters 245(1–2): 39–55.

Wulff-Barreiro, E. 2009. Affluence of data on volcanism in the Gulf of Cádiz. Data Science Journal 8: 105–112.

Xu, T., D. Feng, J. Tao, and J.W. Qiu. 2019. A new species of deep-sea mussel (Bivalvia: Mytilidae: Gigan tididae) from the South China Sea: Morphology, phylogenetic position, and gill-associated microbes. Deep Sea Research Part I 146: 79–90.

Authors and Affiliations

Luis Somoza1 · José Luis Rueda2 · Francisco J. González1 · Blanca Rincón-Tomás3,4 · Teresa Medialdea1 · Olga Sánchez-Guillamón5 · Michael Hoppert3 · Juan T. Vázquez2 · Pedro Madureira5 · Esther Santofimia1 · Enrique López-Pamo2 · Desirée Palomino2 · Jose Eugenio Ortiz5 · Lorena Blanco1,6 · Maria del Carmen Fernández-Puga7 · L. M. Fernández-Salas8 · Joachim Reitner9

1 Marine Geology Division, Geological Survey of Spain (IGME-CSIC), Rios Rosas 23, 28003 Madrid, Spain
2 Instituto Español de Oceanografía (IEO-CSIC), Centro Oceanográfico de Málaga, 29640 Fuengirola, Málaga, Spain
3 Institutt for Mikrobiologi und Genetik, Georg-August University Göttingen, Grisebachstr. 8, 37077 Göttingen, Germany
4 Institute for General Microbiology, Christian-Albrechts-University Kiel, Am Botanischen Garten 1, 24118 Kiel, Germany
5 Estrutura de Missão para a Extensão da Plataforma Continental (EMEPC), Rua Costa Pinto 165, 2800-516 Lisboa, Portugal
606 L. Somoza et al.
A relict oasis of living deep-sea mussels *Bathymodiolus*

6 Escuela de Ingeniería de Minas y Energía, Universidad Politécnica de Madrid, Madrid, Spain

7 Departamento Ciencias de la Tierra, Facultad de Ciencias del Mar y Ambientales/INMAR, Universidad de Cádiz (UCA), Av. República Saharaui s/n, 11510 Puerto Real Cádiz, Spain

8 Instituto Español de Oceanografía (IEO-CSIC), Centro Oceanográfico de Cádiz, Muelle de Levante (Puerto Pesquero), 11006 Cádiz, Spain

9 Department of Geobiology, Georg-August University Göttingen, Goldschmidtstr. 3, 37077 Göttingen, Germany