

Abstract

Previous work in the mud volcanoes from the Gulf of Cadiz revealed a high number of chemosymbiotic species, namely bivalves and siboglinid polychaetes. In this study we give an overview of the distribution and life styles of those species in the Gulf of Cadiz, determine the role of autotrophic symbionts in the nutrition of selected species using stable isotope analyses ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$) and investigate the intra-specific variation of isotope signatures within and between study sites. Twenty siboglinid and nine bivalve chemosymbiotic species have been identified and were found living in fifteen mud volcanoes during our studies. Solemyids bivalves and tubeworms of the genus *Siboglinum* are the most widespread, whereas other species were found in a single mud volcano (e.g. "*Bathymodiolus*" *mauritanicus*) or restricted to deeper mud volcanoes (e.g. *Polybrachia* sp., *Lamelisabella denticulata*). Species distribution suggests that different species may adjust their position within the sediment according to their particular needs and intensity and variability of the chemical substrata supply. Isotopic values found for selected species are in accordance with values found in other studies, with thiotrophy as the dominant nutritional pathway, and with methanotrophy and mixotrophy emerging as secondary strategies. The heterogeneity in terms of nutrient sources (expressed in the high variance of nitrogen and sulphur values) and the ability to exploit different resources by the different species may explain the high diversity of chemosymbiotic species found in the Gulf of Cadiz. This study increases the knowledge of the chemosymbiotic species in the Gulf of Cadiz, highlight the relevance of seep chemoautolithotrophic production in this area and provide a starting point for future trophic ecology studies.

1 Introduction

The finding that hydrothermal vent tubeworms have a significantly depleted $\delta^{13}\text{C}$ signature, very distinct from the values of other typical deep-sea invertebrates led Rau

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and Hedges (1979) to postulate that these worms rely on some non-photosynthetic food source. Later this finding was repeated for several cold seep invertebrates, and confirmed by the observation that they host symbiotic chemoautotrophic bacteria. In this symbiotic relationship, the invertebrate host facilitates the access to inorganic carbon, oxygen and reduced sulphur-compounds, and in exchange it uptakes the bacterial metabolic byproducts or digests symbiont tissue for its nutrition (Fisher, 1990; MacAvoy et al., 2002). The carbon source for thiotrophic and metanotrophic bacteria is different with the former using pore water dissolved inorganic carbon (DIC) and the latter using CH₄ (Fisher, 1990; Conway et al., 1994; MacAvoy et al., 2002).

The different carbon fixation pathways involve distinct isotopic fractionation (e.g. carbon, sulphur and nitrogen) which makes stable isotope approaches particularly useful for elucidating the nutritional status of organisms in vent and seep environments (Conway et al., 1994; Van Dover and Fry, 1994). Carbon isotopic values have been used to differentiate animals with thiotrophic symbionts from those with methanotrophic symbionts (Brooks et al., 1987; Kennicutt et al., 1992) and to identify the methane pool as either thermogenic or biogenic (Sassen et al., 1999). Chemoautotrophs tend to have lower $\delta^{15}\text{N}$ values than heterotrophs or marine phytoplankton and the $\delta^{34}\text{S}$ values of animals hosting thiotrophic bacteria are depleted relative to those with methanotrophic symbionts and heterotrophs (Brooks et al., 1987). In fact, values of $\delta^{34}\text{S}$ below 5‰ can be used to infer a thiotrophic mode of nutrition (Vetter and Fry, 1998) reflecting the isotopic signature of the sulphide source (Fisher, 1995). Stable isotope signatures can therefore provide information on food resource use and partitioning, both inter-specifically and intraspecifically (Levesque et al., 2003).

Previous work in the Gulf of Cadiz mud volcanoes (South Iberian Margin) found a high number of chemosymbiotic species, namely bivalves and siboglinid polychaetes (Rodrigues et al., 2008; Hilário and Cunha 2008; Hilário et al., 2010; Oliver et al., 2011); and studies on the faunal assemblages in the area show high biodiversity and high variability in structure, composition and density, which are likely to result from a combination of biogeographic, historical and environmental factors (Cunha et al., 2012).

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Especially relevant for the distribution of chemosynthetic species is the variability in the fluid sources and transport mechanisms determining the intensity of the fluxes and the geochemistry of the porewater and sediments.

The Gulf of Cadiz is an extensive cold seepage area including over 40 mud volcanoes at depths between 200 and 4000 m (Pinheiro et al., 2003; Van Rensbergen et al., 2005). The molecular and isotopic composition of the hydrocarbon gases present in the different mud volcanoes reveal a predominance of thermogenic sources with varying degrees of thermal maturity (Mazurenko et al., 2002, 2003; Stadnitskaia et al., 2006; Hensen et al., 2007; Nuzzo et al., 2008) and, in some cases, partial recycling of thermogenic methane and other hydrocarbons mediated by anaerobic oxidation of methane (AOM)-related methanogenic archaea in the shallow sediments (Nuzzo et al., 2009). Differences in both fluid geochemistry and composition of the microbial assemblages responsible for the AOM activity have major consequences in the quantity and chemical composition of the hydrocarbons reaching near-surface sediments or the water column offering a multitude of physicochemical niches that can be exploited by species with different anatomical features, physiology and symbiotic associations.

Symbiotic bivalves in the Gulf of Cadiz include members of five of the six families known to host chemoautotrophic bacteria: Solemyidae, Lucinidae, Thyasiridae, Vesicomysidae, and Mytilidae (Génio et al., 2008; Rodrigues et al., 2008; Oliver et al., 2011). These bivalves have different anatomical organization particularly in relation to the structure of the gill which in all of them are modified to house the symbionts (reviewed by Taylor and Glover, 2010), and also very different life habits ranging from deep sediment burrowers to epifaunal baysate species. Bathymodiolin mussels (family Mytilidae) further differ from the other chemosymbiotic bivalves in the way that they are capable of co-hosting sulphur- and methane-oxidizers symbionts and that they keep their filter feeding ability (Fisher et al., 1993; Duperron et al., 2008).

Siboglinid polychaetes are represented in the Gulf of Cadiz by a high diversity of frenulates (Hilário et al., 2010). Frenulata, the most speciose clade of siboglinids, live in a variety of reducing environments including shelf and slope sediments, cold seeps,

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hydrothermal vents and organic falls with their tube spanning oxic-anoxic boundaries (Hilário et al., 2011). The anterior end of the tube remains in the top layer of the sediment or extends into the oxygenated bottom water and oxygen is absorbed by a gill-like structure. Hydrogen sulphide and, in the case of *Siboglinum poseidoni* that harbours methane-oxidizing endosymbionts (Schmaljohann and Flügel, 1987), methane are transported across the posterior tube and body wall into the trophosome, a specialized tissue where the endosymbiotic bacteria are housed (reviewed by Hilário et al., 2011). In addition to the nutrition provided by their symbionts species of the genus *Siboglinum* can take up and metabolise dissolved organic compounds at a rate sufficient to sustain respiration but not enough for growth and reproduction (Southward and Southward, 1981).

In this study we give an overview of the distribution of chemosymbiotic species in the Gulf of Cadiz and determine the role of autotrophic symbionts in the nutrition of selected species using stable isotope analyses ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$). Furthermore, we assess intra and interspecific differences in stable isotope signatures between species occurring at the same and different sites and discuss them in the light of species morphology and sediment geochemistry.

2 Material and methods

Chemosymbiotic species were obtained from macrofaunal samples collected during 14 cruises carried out between 2000 and 2009 from numerous locations in the Gulf of Cadiz using a variety of quantitative and non-quantitative sampling gears and processed on board accordingly (Rodrigues et al., 2011a). Chemosymbiotic bivalves and siboglinid tubeworms were sorted and identified; *Siboglinum* and *Polybrachia* specimens were ascribed to species according to Hilário et al. (2010) or given new code-names when needed for more recently collected. Specimens from the largest and more abundant species (five bivalve and seven tubeworm species) were dissected on board

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and the different tissues were frozen and kept at -80°C until further processing for stable isotope analysis.

The samples were freeze-dried and homogenized with a mortar-and-pestle grinding tool and aliquots were separated for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ analyses. The ground sample for carbon analysis was acidified with HCl (1M) until no further bubbling occurred; the sample was re-suspended in distilled water, centrifuged and the supernatant was discarded, finally the sample was dried at 60°C and re-grinded. The ground sample for sulphur analysis was re-suspended in distilled water, shaken for 5 min, centrifuged and the supernatant was discarded; this procedure was repeated 3 times and finally the sample was dried at 60°C and re-grinded.

The samples were analyzed at the ISO-Analytical laboratory (UK) using the method EA-IRMS (elemental analysis – isotope ratio mass spectrometry).

The isotope compositions are reported relative to standard material and follow the same procedure for all stable isotopic measurements (follow equation).

$$\delta^x E = \left[\left(\frac{{}^x E / {}^y E}{\text{sample}} \right) / \left(\frac{{}^x E / {}^y E}{\text{standard}} \right) - 1 \right] \times 100$$

where E is the element analyzed (C, N or S), x is the molecular weight of the heavier isotope, and y the lighter isotope ($x = 13, 15, 34$ and $y = 12, 14$ and 32 for C, N and S, respectively). The standard materials to which the samples are compared are the marine limestone fossil, Pee Dee Belemnite (PDB) for carbon (Craig, 1953); atmospheric air for nitrogen (Mariotti, 1983). and trillite from the Canyon Diablo iron meteorite (CTD) for sulphur (Krouse, 1980).

Isotopic signatures of methane and gas hydrates for some of the studied mud volcanoes are available from the literature (Stadnitskaia et al., 2006; Hensen et al., 2007; Nuzzo et al., 2009).

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3 Results

3.1 Species distribution

Chemosymbiotic species were identified in 15 mud volcanoes (MVs) with 11 bivalve species (including two mixotrophic) occurring at 13 MVs and 20 siboglinid species at 14 MVs (Table 1 and Fig. 1). The majority of the samples collected from a total of 24 MVs in the Gulf of Cadiz yielded fragmented or empty siboglinid tubes and bivalve shells but these were not considered herein.

The solemyid *Solemya elairrachensis* was the most widespread chemosymbiotic bivalve occurring at eight MVs in the shallower El Arraiche field (Mercator, Gemini, Kidd) and in the Carbonate Province (Meknès, Yuma, Ginsburg, Darwin and Sagres). Another solemyid *Acharax gadirae* was found in seven MVs at greater depths in the Carbonate Province (Yuma, Ginsburg, Jesus Baraza) and Deep Field (Capt. Arutyunov, Sagres, Carlos Ribeiro and Porto), with both solemyid species co-occurring at three mud volcanoes. The thyasirids were represented by two chemosymbiotic species occurring in MVs of the Deep Field – *Thyasira vulcolutre* (Capt. Arutyunov, Sagres and Carlos Ribeiro) and *Spinaxinus sentosus* (Capt. Arutyunov) – and two mixotrophic species occurring mostly at shallower depths: *Axinulus croulinensis* (Mercator, Meknès and Capt. Arutyunov) and *Thyasira granulosa* (Mercator and Meknès). The three vesicomyid species were found always at depths greater than 1000 m: two small *Isorropodon* species, *I. megadesmus* (Capt. Arutyunov and Darwin MVs) and *I. perplexum* (Capt. Arutyunov) and the larger *Christenoconcha regab* (Bonjardim MV). Lucinids and mytilids were each represented by a single species in only one MV (*Lucinoma aspheus* at Mercator MV and “*Bathymodiolus mauritanicus*” at Darwin MV respectively).

The unidentaculate Frenulata genus *Siboglinum* was found in all the 14 MVs. From the nine *Siboglinum* species, *Siboglinum* lb has the widest distribution in the Gulf of Cadiz, being present in seven MVs from approximately 350 to 3060 m depth (Fig. 1). *Siboglinum* la is present in three MVs and three other species are found in two different MVs. The four remaining *Siboglinum* species are only found in one MV. It is

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worth noticing the presence of the methanotrophic species *Siboglinum* cf. *poseidoni* (Rodrigues et al., 2011b) in the Capt. Arutyunov MV.

With the exception of one species of *Polybrachia*, multitentaculate species are only present in MVs below 1300 m depth. Only three of the eleven species are found in more than one MV: *Polybrachia* sp.1 is found in Mercator and Bonjardim, *Polybrachia* Va in Carlos Ribeiro and Semenovich, and one species of an undermined genus (Undetermined IIa) in Carlos Ribeiro and Porto MVs (Fig. 1). The species *Lamelisabella denticulata* and *Spirobrachia tripeira* form conspicuous clumps of dark long tubes covering continuously the crater of Porto MV. The tubes of *Bobmarleya gadensis* are less conspicuous and more regularly spaced but were also observed forming a continuous field in the crater of Carlos Ribeiro MV.

3.2 Stable isotope signatures

Stable isotope values were obtained for five bivalve species and seven siboglinid species (Table 2). Although analyses were carried out in the gill and foot tissues no significant differences in the isotopic values of both tissues were observed and therefore only the average results per specimen are presented. Chemosymbiotic bivalves presented $\delta^{13}\text{C}$ average values between -54.8 and -27.2‰ ; the most depleted $\delta^{13}\text{C}$ values were measured in "*Bathymodiolus*" *mauritanicus* from Darwin MV and the least depleted for *Acharax gadirae* from Sagres MV. There was a clear segregation between the mytilid and the other families (Solemyidae, Lucinidae and Thyasiridae) (Fig. 2, Table 2) that never showed $\delta^{13}\text{C}$ values below -36.8 . Despite some overlap of individual values the different species showed distinct average $\delta^{13}\text{C}$ signatures. The overall $\delta^{15}\text{N}$ range for the chemosymbiotic bivalves (10.5‰) was lower than the $\delta^{13}\text{C}$ range (27.5‰) $\delta^{15}\text{N}$ values varied between -1.2 and 7.0‰ with *Solemya elarraichensis*, *Lucinoma asapheus* and *Thyasira vulcolutre* showing higher average values than "*B.*" *mauritanicus* and *A. gadirae* (Fig. 2, Table 2). The $\delta^{34}\text{S}$ values were the most variable with an overall range of 45.3‰ . "*B.*" *mauritanicus* presented lighter $\delta^{34}\text{S}$ signatures and a relatively narrow range (values between 11.5 and 17.7‰). Thyasirids and solemyids

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showed more depleted signatures and much wider $\delta^{34}\text{S}$ ranges, especially *A. gadirae* (−25.7 and 11.9‰) (Fig. 2, Table 2).

$\delta^{13}\text{C}$ values for Siboglinidae worms varied between −49.8‰ (*Siboglinum* Id from Capt. Arutyunov MV) and −33.1‰ (*Siboglinum* Ib, Gemini MV). Values of $\delta^{13}\text{C}$ lower than −40‰ were found for *Siboglinum* cf. *poseidoni* and *Siboglinum* Id, both in the Capt. Arutyunov MV, and for one *Lamelisabella denticulata* from Porto MV. Most of the species presented $\delta^{15}\text{N}$ values lower than 6 ‰ except *Siboglinum* Ib that for the specimens in the shallow Gemini and Lazarillo de Tormes MVs presented values ranging from 8.2 to 12.2‰. Similarly, these two specimens also presented relatively high values of $\delta^{34}\text{S}$ (6.5 and 5.7‰). The lowest value of $\delta^{34}\text{S}$ (−16.8‰) was found in the specimen of *Siboglinum* If from Meknès MV (Fig. 2, Table 2).

3.3 Intra-specific variation within and between study sites

The $\delta^{13}\text{C}$ values for *Acharax gadirae* specimens collected from six different mud volcanoes ranged from −27.2 to −34.7‰, with a clear separation of values from specimens collected above (−27.2 to −29.3‰ in Ginsburg, Yuma, Jesus Baraza and Sagres MVs) and below 2000 m (−31.6 to −34.7‰ in Carlos Ribeiro and Porto MVs). Within the same site variability was much smaller (1.3‰ in four specimens from Yuma MV). *Solemya elarraichensis* presented small intraspecific variation between sites (2.0‰) and negligible variation within the same site (0.2 to 0.6‰). The $\delta^{13}\text{C}$ signatures for the thyasirid *Thyasira vulcolutre* varied by 2.7‰, between specimens from Sagres and Carlos Ribeiro MVs but most of the variation was observed among specimens from Carlos Ribeiro (range of 2.4‰). “*Bathymodiolus*” *mauritanicus* showed the greatest variability within the same site (7.1 ‰ in Darwin MV).

The intraspecific range of $\delta^{15}\text{N}$ values in different sites varied from 3.0‰ (*T. vulcolutre*) to 6.1‰ (*A. gadirae*). Within the same site *S. elarraichensis* showed ranges of 2, 0.5 and 0.4‰ in the Gemini, Meknès and Darwin MVs, respectively. The four specimens of *A. gadirae* collected in the Yuma MV showed the widest range of $\delta^{15}\text{N}$ values

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within the same species and site for all studied species (3.8‰). The $\delta^{15}\text{N}$ ranges were 0.5‰ in Capt. Arutyunov MV and 2.4‰ in Carlos Ribeiro MV for *T. vulcolutre* and 3.0‰ in Darwin MV for "*B.*" *mauritanicus*.

Isotopic signatures of $\delta^{34}\text{S}$ measured in *A. gadirae* showed a wide range (37.6‰) with high variability within the same site (14.2‰ in Yuma MV) and between different sites (more than 20‰). In *S. elarraichensis* the $\delta^{34}\text{S}$ overall range was lower: 26.1‰ as well as within the same volcano (2.2, 10.6 and 3.0‰ in Gemini, Meknès and Darwin MVs respectively). *Thyasira vulcolutre* presented $\delta^{34}\text{S}$ ranges of 13.4‰ in Capt. Arutyunov MV and 29.8‰ in Carlos Ribeiro MV (comparable to the overall range for the species). The six specimens of "*B.*" *mauritanicus* all from Darwin MV varied by 5.2‰.

Intra-specific variation of isotopic signatures could only be examined for one species of Frenulata, *Siboglinum* lb. The $\delta^{13}\text{C}$ values varied from -35.9‰ in the Lazarillo de Tormes MV to -33‰ in the Sagres MV; $\delta^{15}\text{N}$ values from 0.2‰ (Sagres MV) to 12.2‰ (Gemini MV) and the $\delta^{34}\text{S}$ from -8.4 (Sagres MV) to 6.5‰ (Gemini MV). Within Yuma MV, ranges of 1.5 and 3.5‰ were registered for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

4 Discussion

4.1 Distribution and life styles

The combination of form and function studies are essential to understand the ways in which chemosymbiotic species have evolved to exploit their environment and to understand their current distribution. Because the association between an eukaryote and its symbionts can be seen as an adaptation to bridge oxic-anoxic interfaces (Cavanaugh, 1994) the chemistry profile of the sediments is expected to play a role in determining which species are able to inhabit a particular site (Dando et al., 2008).

Solemyds, lucinids and thyasirids bivalves are sediment dwellers whose burrows span oxic-anoxic interfaces in the seafloor. Whereas solemyds form "U"- or "Y"-shaped burrows (Stewart and Cavanaugh, 2006), lucinids and thyasirids maintain an anterior

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inhalant connection to the surface (Taylor and Glover, 2000; Dufour, 2005) and produce long ramified burrows. In some thyasirids the length and number of burrows show a negative relationship with the concentration of hydrogen sulphide in the sediment (Dufour and Felbeck, 2003) and it has been proposed that lucinids and thyasirids are able to “mine” insoluble sulphides (Dando et al., 1994, 2004). Details of sulphur acquisition strategies are available for some lucinid and thyasirid species but both groups exhibit such a diversity of morphologies and live in such a wide variety of habitats that it is likely that they utilize a number of different behaviours and chemical pathways to acquire reduced sulphur from the environment (Taylor and Glover, 2000; Dufour, 2005). Regarding Vesicomidae most species live shallowly burrowed in sediment usually with the posterior half of the shell protruding (Krylova and Sahling, 2010) and the sulphide uptake is through the foot that protrudes into the sediment, while oxygen uptake is through the gill (Goffredi and Barry, 2002; Taylor and Glover, 2010). Finally, bathymodiolin mussels (family Mytilidae) are mostly epibenthic and live attached by byssal threads to hard substrates, sometimes forming tight aggregates. Their reliance on chemosynthetic symbionts located in their gills implies that reduced compounds are needed in the surrounding fluid, as they do not have access to the anoxic sediment (Duperron, 2010). Bathymodiolin mussels occur in a broad range of environments which may be attributed to their nutritional flexibility: they are capable of hosting multiple symbioses obtaining from chemosynthetic symbionts including the co-occurrence of sulphur- and methane-oxidizers in addition to receiving nutrition from filter feeding (Fisher et al., 1993; Duperron et al., 2008).

Frenulata are generally described as tubeworms that extend over oxic-anoxic boundaries in the sediment, with the anterior end on the top layer of the sediment and the posterior tube body buried in the sediment. However this simplified description hides the variety of morphologies of different species that can show wide ranges of sizes (length and width), depth penetration in the sediment and tube thickness, all important features that may influence the ability to exploit different sources of nutrients.

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In the Gulf of Cadiz the methane-sulphate transition zone, where most microbial activity occurs, is in most cases more than 30 cm below the seafloor and often at 80 cm or more. An exception is Capt. Arutyunov MV where high methane concentrations were measured near the surface (Hensen et al., 2007). Burrowing bivalves and frenulates with long bodies were expected in mud volcanoes with wider redox boundaries, living in sediments where high sulphide concentrations are deep below the sediment interface. This holds true for frenulate species, for example the long frenulates *Lamellisabella denticulata*, *Spirobrachia tripeira* and *Bobmarleya gadensis* have only been found in MVs (Porto, Bonjardim and Carlos Ribeiro, respectively) where high sulphide concentrations are deep (~ 50 cm) below the seafloor (Hensen et al., 2007; Nuzzo et al., 2008) and the presence of gas hydrates reservoirs is likely to ensure fluxes capable of sustaining larger biomasses. In Capt. Arutyunov MV geochemical gradients are steep but highly variable; the sediments are frequently disturbed by gas hydrate dissociation and sustain very high densities of smaller frenulates (*Siboglinum* spp.). At shallower MVs, only the slim *Siboglinum* species and also *Polybrachia* sp.1 (at Mercator MV only) are found but always in more modest abundances (Cunha et al. 2012). The presence of small frenulates in MVs with a variety of geochemical settings, suggests that smaller and shorter species may demand less concentration of reduced compounds, allowing them to exploit lower concentrations that diffuse to the upper sediment.

The only epibenthic chemosymbiotic bivalve known in the Gulf of Cadiz, "*Bathymodiolus*" *mauritanicus* was found in dense aggregations inhabiting the narrow fissures between the large carbonate slabs that pave the crater of Darwin MV; aggregations of small (young) individuals are rare suggesting a strong intraspecific competition for the limited amount of favorable habitat where higher concentrations of reduced compounds reach the seafloor. Unlike many other cold seeps, chemosymbiotic bivalves in the Gulf of Cadiz are predominantly burrowing species that are found in a variety of MVs with very different geochemical settings. Solemyids are widespread but were always found at very low densities. Thyasirids are represented by several species; the juveniles and the smaller mixotrophic species and may occur in relatively high densities and are

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often found closer to the sediment surface while the larger species, *Thyasira vulcolutre* is only found at the deeper (more active) MVs. The small vesicomimid *Isoorropodon megadesmus* is one of the dominant species found in the near surface of gas saturated sediments in Capt. Arutyunov MV (Cunha et al., 2012). Also for the vesicomimids, the larger species (*Cristineconcha regab*) was only found in one of the deeper MVs. These distributions suggest that different species and/or ontogenic phases may adjust their position within the sediment according to their particular needs and intensity and variability of the chemical substrata supply.

4.2 Methanotrophy vs. thiotrophy

Overall the isotopic signatures of the chemosymbiotic species indicate the prevalence of a thiotrophic mode of nutrition for most species with the exception of *S. cf. poseidoni* and "*B.*" *mauritanicus*. The presence of microbial symbionts was confirmed in most of the studied species with molecular characterization and Fluorescent in situ hybridization (Rodrigues et al., 2010, 2011b, 2012, 2013; Rodrigues and Duperron, 2011). The isotopic signatures of the two bivalve tissues analysed (foot and gill) did not show significant differences in any of the studied species, which as suggested in previous studies (Cary et al., 1989) is an indication of a high degree of carbon flow from the bacterial symbiont to the host.

Carbon isotopic values have been used to identify the source of methane as either thermogenic ($\delta^{13}\text{C} \leq -64\text{‰}$ when purely thermogenic) or biogenic ($\delta^{13}\text{C} \geq -50\text{‰}$ when purely biogenic) methane (Schoell, 1980). The $\delta^{13}\text{C}$ signature of the species harbouring methanotrophic symbionts, *S. cf. poseidoni* and *Siboglinum* Id from Capt. Arutyunov MV, and "*B.*" *mauritanicus* from Darwin MV (Rodrigues et al., 2011b, 2013) are consistent with the inferred thermogenic origin of methane in the Capt. Arutyunov MV in particular, and the Gulf of Cadiz in general (Nuzzo et al., 2008).

Average $\delta^{13}\text{C}$ values for *S. cf. poseidoni* and *Siboglinum* Id were less depleted than values previously reported for *S. poseidoni* collected in Norwegian fjords which is known to harbour methane-oxidizing bacteria (Schmaljohann and Flügel, 1987;

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Table S1). Nevertheless the values here reported are compatible with methanotrophic nutrition and molecular studies have already showed the occurrence of methane oxidizing bacteria *S. cf. poseidoni* from the Capt. Arutyunov MV (Rodrigues et al., 2011b). However, it is arguable that the average of $\delta^{34}\text{S}$ value (above 6‰) found in *S. cf. poseidoni* may indicate thiotrophy. Because of their small size and morphological similarity it is possible that co-occurring juveniles of *Polybrachia* sp. 2 may have been pooled together in the analysis, which complicates the interpretation of the results.

The isotope signatures of “*B.*” *mauritanicus*, highly depleted $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values higher than 5‰, can be taken as evidence for methanotrophy. However, molecular studies revealed the occurrence of a dual symbiosis with the presence two phylotypes of methane-oxidising bacteria and a less abundant phylotype of a sulphur-oxidising bacterium (Rodrigues et al., 2013). Isotopic values for mytilids are variable and dependent of their nutrition, symbionts, life cycle and site location. $\delta^{13}\text{C}$ values for “*B.*” *mauritanicus* (species confirmed as part of the “childressi” group (Génio et al., 2008)) are in accordance with values previously reported for *B. childressi*, that also harbour a dual symbiosis but $\delta^{34}\text{S}$ are much higher in “*B.*” *mauritanicus* probably due to the dominance of methano-oxidizing bacteria (Rodrigues et al., 2013) (Table S1).

The isotope values of other bivalve and siboglinid species are consistent with use of seawater CO_2 fixed via sulphide oxidation and are in line with values reported for other species elsewhere. The $\delta^{13}\text{C}$ values measured in *L. asapheus* are in the range of values reported for lucinids from other locations that are known to harbour thiotrophic symbionts (Table S1). The stable carbon isotope composition of *T. vulcolutre* is similar to that registered for other *Thyasira* species (*T. methanophila* and *T. sarsi*; Table S1) and indicates that the autotrophic bacteria make a substantial contribution to the nutrition of the host. Chemoautotrophy is usually considered to be more important in the nutrition of thyasirids than of lucinids (Van Dover and Fry, 1989), which also seems to be the case in the Gulf of Cadiz, since *T. vulcolutre* have more depleted values of $\delta^{13}\text{C}$ than *L. asapheus*. However, more depleted values may reflect local isotopic signatures of methane due to assimilation of pore water bicarbonate derived

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from microbial sulphate reduction coupled to methane oxidation (Scott et al., 2004; Becker et al., 2011). Methane isotopic signature is considerably less depleted at shallower MVs (higher thermal maturity of methane; Nuzzo et al., 2009) where *L. asphaeus* occurs than in the deeper MVs where *T. vulcolutre* is found.

5 4.3 Resource partitioning

The high diversity of chemosymbiotic species found in the Gulf of Cadiz may be explained by a combination of historical and contemporary factors (Cunha et al., 2012). The number of species coexisting in a single MV may be as high as nine (e.g. Capt. Arutyunov MV) and in most cases with no apparent zonation pattern, which suggests that there is resource partitioning. This may occur by means of differentiated life styles, differentiated metabolic pathways and strategies or by a combination of these. If chemical resource partitioning occurs, consistent differences in isotope values between species may be expected (Becker et al., 2011). Co-occurrence of phylogenetically close species is particularly interesting and in the Gulf of Cadiz it may be observed both for thyasirids and solemyids.

Overall *Solemya elarraichensis* presented more depleted $\delta^{13}\text{C}$ and more enriched $\delta^{15}\text{N}$ signatures than *Acharax gadirae*, which are probably a consequence of metabolic and morphological differences between the two species. Symbionts of co-generics of both species are known to use different forms of the enzyme ribulose 1,5-bisphosphate carboxylase/oxygenase (RubisCO) for CO_2 fixation. Whereas symbionts of *Solemya* species present RubisCO form I (Scott et al., 2004), symbionts of *Acharax* present the form II of the enzyme (Duperron et al. 2012), which has lower discrimination factors against $^{13}\text{C}\text{O}_2$. Previous studies have shown that the difference in discrimination against ^{13}C isotopes by the two forms of RubisCO can explain the disproportion in the ^{13}C values of the chemoautotrophic symbiosis between two groups of chemosymbiotic invertebrates: the “-30 ‰” group with a form I RubisCO and the “-11 ‰ group” expressing a form II (Robinson and Cavanaugh, 1995).

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When compared with other taxa that also present form II RubisCO (e.g. vent vestimentiferans) the values found for *A. gadirae* are more depleted, but are in accordance with the values found for the bivalves *Calyptogena magnifica* and *Calyptogena pacifica* (Southward et al., 1994; Fisher, 1995), which suggests that bivalves expressing RubisCO form II may have other factors than this enzyme structure and kinetics contributing to the carbon fractionation.

It is worth noticing that within our samples of *A. gadirae*, specimens from deeper MVs presented more depleted $\delta^{13}\text{C}$ values and in the same range of values found for *S. elarraichensis*. Oliver et al. (2011) ascribed *Acharax* specimens from Porto and Carlos Ribeiro mud volcanoes to the new species *A. gadirae* but because of the small size of the available specimens the same authors raised the possibility of the existence of a different species in these mud volcanoes, which could also explain the difference in the isotopic signatures.

When compared with previous data, the values of $\delta^{13}\text{C}$ of *S. elarraichensis* and those of *A. gadirae* from the deeper mud volcanoes were similar to those found for other species of the same genera (Table S1). However, several differences were found in the $\delta^{15}\text{N}$ values between solemyid species, suggesting that they are using different chemical species of nitrogen, tapping different pools of nitrogen, or discriminating differently after acquisition of their nitrogen source. Furthermore, it's likely that the $\delta^{15}\text{N}$ range reflects a dilution of the very ^{15}N ammonium values occurring at the sediment water interface (Lee and Childress, 1996; Carlier et al., 2010).

Nitrogen isotope values measured in both chemosymbiotic bivalves and frenulate tubeworms showed a wide range of values, including one species with $\delta^{15}\text{N}$ values above 6‰ (value indicated by Levin and Michener (2002) as upper limit for the presence of chemoautotrophic symbionts). These relatively high values were found in *Siboglinum* lb collected from three of the shallowest mud volcanoes are probably related to the fact that these animals can explore different sources of nitrogen since in addition to the nutrition provided by their symbionts they may be capable of take up and metabolise dissolved organic compounds (Southward and Southward, 1981).

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Furthermore, because of the shallower depth they may have access to organic nitrogen derived from superficial waters. On the contrary, low $\delta^{15}\text{N}$ values indicate that organic nitrogen is of local origin, presumably resulting from the activity of autotrophic bacteria (Levin, 2005; MacAvoy et al., 2008), and are possible due to assimilation of isotopically light nitrate or ammonium by the symbionts or, in the case of the very negative values, possibly fixation of N_2 (Fisher, 1995). As proposed by other authors (Carlier et al., 2010) we hypothesize that the inter-specific variations of $\delta^{15}\text{N}$ found in these study may result from species-specific types of symbionts characterized by different fractionation factor occurring during the assimilation of dissolved inorganic nitrogen, and that in the particular case of frenulate tubeworms, different species may have different degrees of access and abilities to exploit dissolved organic compounds.

In general, there was considerably less intra-specific variation between specimens collected from the same volcano than from different MVs which is plausibly explained by a higher variation in the composition of hydrocarbon pools at larger spatial scales (from one MV to another). These differences maybe lower at shallow MVs as high thermal maturity of the gases is consistent with more limited differences in carbon isotopic composition (Nuzzo et al., 2009). However, there were relevant intra-specific differences in the isotopic signatures of chemosymbiotic species both within and between MVs. The observed intra-specific variation in the $\delta^{13}\text{C}$ may result from the assimilation of DIC of diverse origins depending on the MV, and in variable proportions, but also from the variable $\delta^{13}\text{C}$ fractionation occurring during DIC fixation by endosymbionts, with the isotopic fractionation depending on the growth rate, and therefore on the size of each individual as reported for other studies (Carlier et al., 2010).

Similar arguments can be used to explain the differences in the $\delta^{34}\text{S}$ signatures. There is little fractionation between sulphide and sulphate or organic sulphur as a result of sulphide oxidation by chemoautolithotrophic bacteria (reviewed in Canfield, 2001). Therefore, $\delta^{34}\text{S}$ values of animals with chemoautolithotrophic sulphur-oxidizing symbionts reflect their reduced sulphur source (MacAvoy et al., 2005) and probably the relative abundance of reduced compounds available. $\delta^{34}\text{S}$ values were highly variable

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among individuals of the same species either in different MVs or within the same MV reflecting high variability in the sulphide pool on a very small spatial scale. According to Becker et al., (2011) this pattern of high variability is consistent with the cycling of sulphate and sulphide between chemosymbiotic invertebrates and sediment microbial consortia. It is known that in the Gulf of Cadiz, the environmental setting variations and AOM activity are reflected by very diverse microbial community compositions and that the three microbial consortia known to perform this reaction (ANME-1, -2, and -3) are active with different distribution patterns (Vanreusel et al., 2009). It is therefore probable that a diversity of sulphide sources is available locally for exploitation by the chemosymbiotic metazoans.

5 Conclusions

The number of chemosymbiotic species found in the Gulf of Cadiz is high when compared with other seep locations such as the mud volcanoes in Eastern Mediterranean Sea and the Gulf of Guinea (Hilário et al., 2010; Oliver et al., 2011). Here we report for the first time on the distribution and life styles of these species and study their nutritional patterns. Our results highlight the relevance of seep chemoautolithotrophic production in this area and provide a starting point for future trophic ecology studies.

In the Gulf of Cadiz the thiotrophy is the dominant nutritional pathway, with methanotrophy and mixotrophy emerging as secondary strategies. We found a wide span of $\delta^{13}\text{C}$ isotopic signatures that nevertheless are relatively consistent within species resulting from specific metabolic pathways. Contrastingly the highly variable $\delta^{34}\text{S}$ values are most likely the result of the high variability of the sulphide pool at local and regional scales. The diversity and the distribution of chemosymbiotic species in the Gulf of Cadiz reflect the environmental heterogeneity in terms of nutrient sources, but also an assortment of life-styles that allows resource partitioning at local and regional scales. Future time-series sampling of chemosymbiotic species coupled with geochemical measurements should be undertaken to better understand the interplay between temporal and

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spatial variations of environmental parameters and symbiont dynamics in the studied species.

Supplementary material related to this article is available online at:

<http://www.biogeosciences-discuss.net/9/17347/2012/>

[bgd-9-17347-2012-supplement.pdf](#)

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Table 1. Sampling details of specimens collected for stable isotope analysis. Different quantitative and non-quantitative samplers were used. Station code is composed by the cruise name and station number as used in PANGAEA database (www.pangaea.de)

MV	Station Code	Depth	Latitude	Longitude	Species code
Mercator	TTR15_AT569	358 m	35°17.92' N	06°38.72' W	B.L1, B.S1
Gemini	M2007_15	444 m	35°09.60' N	06°49.47' W	S.S1
	M2007_19	430 m	35°06.44' N	06°59.92' W	B.S2, B.S3, S.S2
Kidd	TTR14_AT528	489 m	35°25.30' N	06°43.97' W	B.S4
Lazarillo de Tormes	M2006_38A	494 m	35°19.09' N	06°46.40' W	S.S3
Meknès	TTR15_AT586	701 m	34°59.15' N	07°04.38' W	B.S5, B.S6, S.S4
Yuma	TTR14_AT524	960 m	35°24.97' N	07°05.46' W	B.A1
	TTR16_AT604	1030 m	35°25.82' N	07°06.33' W	B.A2, B.S7
	TTR16_AT605	975 m	35°25.05' N	07°05.45' W	B.A3, B.A4, S.S5
Ginburg	TTR16_AT607	983 m	35°22.68' N	07°04.98' W	B.A5
Jesus Baraza	TTR12_AT391	1105 m	35°35.44' N	07°12.26' W	B.A6
Darwin	TTR16_AT608	1115 m	35°23.53' N	07°11.47' W	B.B1, B.B2
	TTR17_AT664	1128 m	35°23.52' N	07°11.48' W	B.S8, B.B3, B.B4
Captain Arutyunov	JC10_032	1109 m	35°23.52' N	07°11.51' W	B.S9, B.B5, B.B6
	TTR14_AT544	1330 m	35°39.71' N	07°20.01' W	S.S6
	TTR14_AT546	1345 m	35°39.69' N	07°20.05' W	S.S7
	MSM01/03_190#1	1322 m	35°39.66' N	07°19.97' W	S.S8
	MSM01/03_217#1	1321 m	35°39.64' N	07°20.05' W	B.T1
Sagres	MSM01/03_225	1320 m	35°39.71' N	07°20.02' W	B.T2
	TTR17_AT667	1562 m	36°02.20' N	08°05.54' W	B.A7, B.S10, B.T3, S.S9
	Carlos Ribeiro	TTR16_AT615	2200 m	35°47.24' N	08°25.27' W
JC10_057		2175 m	35°47.25' N	08°25.32' W	B.T6
Bonjardim	MSM01/03_157	2200 m	35°47.27' N	08°25.36' W	B.T7
	MSM01/03_169	2199 m	35°47.26' N	08°25.36' W	B.T8, B.A8
	TTR15_AT597	3061 m	35°27.56' N	09°00.03' W	S.P1
Porto	MSM01/03_145	3860 m	35°33.70' N	09°30.44' W	B.A9, S.L1

Table 2. Stable isotope values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ (mean and standard error – SE) for the different specimens here studied. Species codes according to Table 1.

Species code	Species name	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		$\delta^{34}\text{S}$	
		Mean	SE	Mean	SE	Mean	SE
	Bivalvia						
B.A1	<i>Acharax gadirae</i>	-28.0	0.3	0.3	0.3	-9.2	1.2
B.A2	<i>Acharax gadirae</i>	-29.3	0.6	-2.3	0.3	-12.3	1.4
B.A3	<i>Acharax gadirae</i>	-28.3	0.3	1.2	0.2	-0.4	0.9
B.A4	<i>Acharax gadirae</i>	-29.2	0.1	1.5	0.4	1.9	0.7
B.A5	<i>Acharax gadirae</i>	-28.8	0.6	-3.4	0.3	-5.4	1.0
B.A6	<i>Acharax gadirae</i>	-28.2	0.4	-0.1	0.1	-17.3	0.2
B.A7	<i>Acharax gadirae</i>	-27.2		-1.5		-5.3	
B.A8	<i>Acharax gadirae</i>	-34.7	0.3	2.7	0.2	-25.7	1.7
B.A9	<i>Acharax gadirae</i>	-31.6	0.3	-1.4	0.2	11.9	1.9
B.S1	<i>Solemya elarraichensis</i>	-34.0	0.4	4.8	0.3	-10.7	1.9
B.S2	<i>Solemya elarraichensis</i>	-32.0	0.5	5.1	0.4	-4.2	0.5
B.S3	<i>Solemya elarraichensis</i>	-32.3	0.3	7.1	0.5	-6.4	1.4
B.S4	<i>Solemya elarraichensis</i>	-32.9	0.8	4.2	0.3	-9.4	1.3
B.S5	<i>Solemya elarraichensis</i>	-33.0	0.9	5.7	0.2	-21.8	4.0
B.S6	<i>Solemya elarraichensis</i>	-32.4	0.4	5.2	0.2	-11.2	2.0
B.S7	<i>Solemya elarraichensis</i>	-33.5	1.1	2.0	0.4		
B.S8	<i>Solemya elarraichensis</i>	-32.7		4.3		-0.8	
B.S9	<i>Solemya elarraichensis</i>	-33.2	0.2	3.9	0.2	2.2	1.0
B.S10	<i>Solemya elarraichensis</i>	-33.2	0.7	4.4	0.2	4.3	0.3
B.B1	<i>"Bathymodiolus" mauritanicus</i>	-54.3		-0.7		17.2	
B.B2	<i>"Bathymodiolus" mauritanicus</i>	-51.4	0.4	-0.4	0.1	16.6	0.0
B.B3	<i>"Bathymodiolus" mauritanicus</i>	-54.8		1.8		11.5	
B.B4	<i>"Bathymodiolus" mauritanicus</i>	-50.0	0.7	0.5	0.1	11.6	0.6
B.B5	<i>"Bathymodiolus" mauritanicus</i>	-47.7		-0.5		17.7	
B.B6	<i>"Bathymodiolus" mauritanicus</i>	-49.5	2.1	-1.2	0.3	17.7	
B.L1	<i>Lucinoma asapheus</i>	-29.8	0.4	4.4	0.3	-16.0	2.5
B.T1	<i>Thyasira vulcolutre</i>	-34.9	0.6	4.1	0.9	-14.0	2.4
B.T2	<i>Thyasira vulcolutre</i>	-34.9	0.0	3.6	1.3	-0.6	0.6
B.T3	<i>Thyasira vulcolutre</i>	-34.1	0.2	2.1	0.7	-8.4	0.5
B.T4	<i>Thyasira vulcolutre</i>	-36.8	0.4	2.6	1.4	1.0	0.5
B.T5	<i>Thyasira vulcolutre</i>	-34.6	1.8	2.7	2.2	2.2	0.0
B.T6	<i>Thyasira vulcolutre</i>	-35.4	1.0	4.8	0.9		
B.T7	<i>Thyasira vulcolutre</i>	-34.4	0.3	3.4	0.7	-27.6	1.7
B.T8	<i>Thyasira vulcolutre</i>	-35.3	0.4	5.1	0.8	-21.9	
	Siboglinidae – Frenulata						
S.S1	<i>Siboglinum lb</i>	-34.6		8.7		6.5	
S.S2	<i>Siboglinum lb</i>	-33.1		12.2			
S.S3	<i>Siboglinum lb</i>	-35.9		8.2		5.7	
S.S9	<i>Siboglinum lb</i>	-33.0		0.2		-8.4	
S.S4	<i>Siboglinum lf</i>	-38.7		-1.3		-16.8	
S.S5	<i>Siboglinum la</i>	-38.2		3.0		1.1	
S.S6	<i>Siboglinum cf. poseidoni</i>	-41.0		2.7		3.6	
S.S7	<i>Siboglinum cf. poseidoni</i>	-44.5		3.6		-8.2	
S.S8	<i>Siboglinum ld</i>	-49.8		4.2		6.0	
S.L1	<i>Lamelisabella denticulata</i>	-43.7		-0.6		-7.7	
S.P1	<i>Polybrachia sp.1</i>	-36.9		-1.1		2.5	

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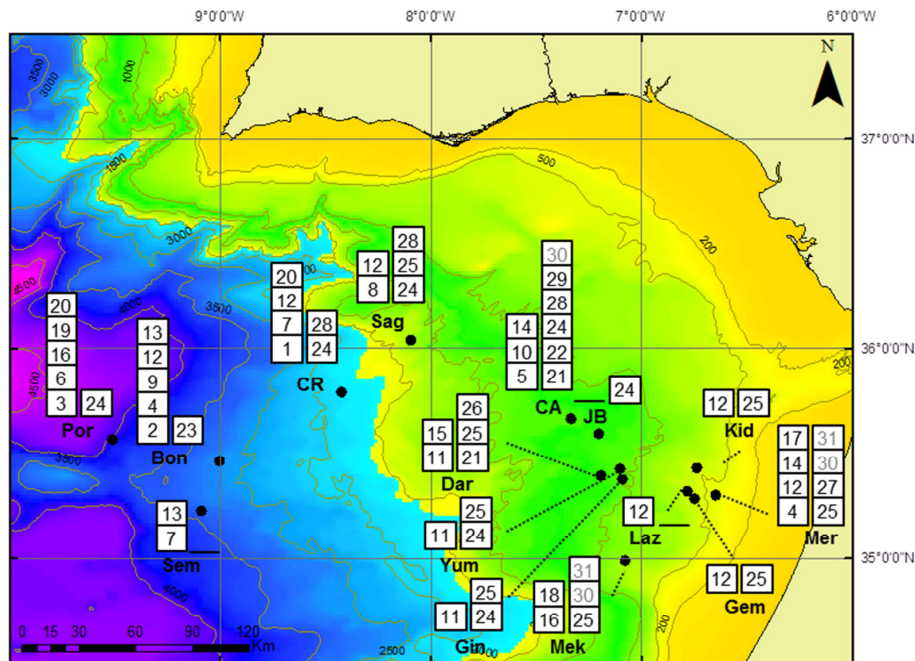


Fig. 1. Map of the Gulf of Cadiz showing the chemosymbiotic species distribution. Siboglinidae species: 1. *Bobmarleya gadensis*; 2. *Lamelisabella* sp.; 3. *Lamelisabella denticulata*; 4. *Polybrachia* sp.1; 5. *Polybrachia* sp.2; 6. *Polybrachia* sp.3; 7. *Polybrachia* Va; 8. *Polybrachia* Vb; 9. *Polybrachia* Vc; 10. *Siboglinum* cf. *poseidoni*; 11. *Siboglinum* Ia; 12. *Siboglinum* Ib; 13. *Siboglinum* Ic; 14. *Siboglinum* Id; 15. *Siboglinum* Ie; 16. *Siboglinum* If; 17. *Siboglinum* sp.1; 18. *Siboglinum* sp.2; 19. *Spirobrachia tripeira*; 20. Undetermined IIa. Bivalvia species; 21. *Isorropodon megadesmus*; 22. *Isorropodon perplexum*; 23. *Christineconcha regab*; 24. *Acharax gadirae*; 25. *Solemya (Petrasma) elarraichensis*; 26. “*Bathymodiolus*” *mauritanicus*; 27. *Lucinoma asapheus*; 28. *Thyasira vulcolutre*; 29. *Spinaxinus sentosus*; 30. *Axinulus croulinensis* (mixotrophic species); 31. *Thyasira granulosa* (mixotrophic species).

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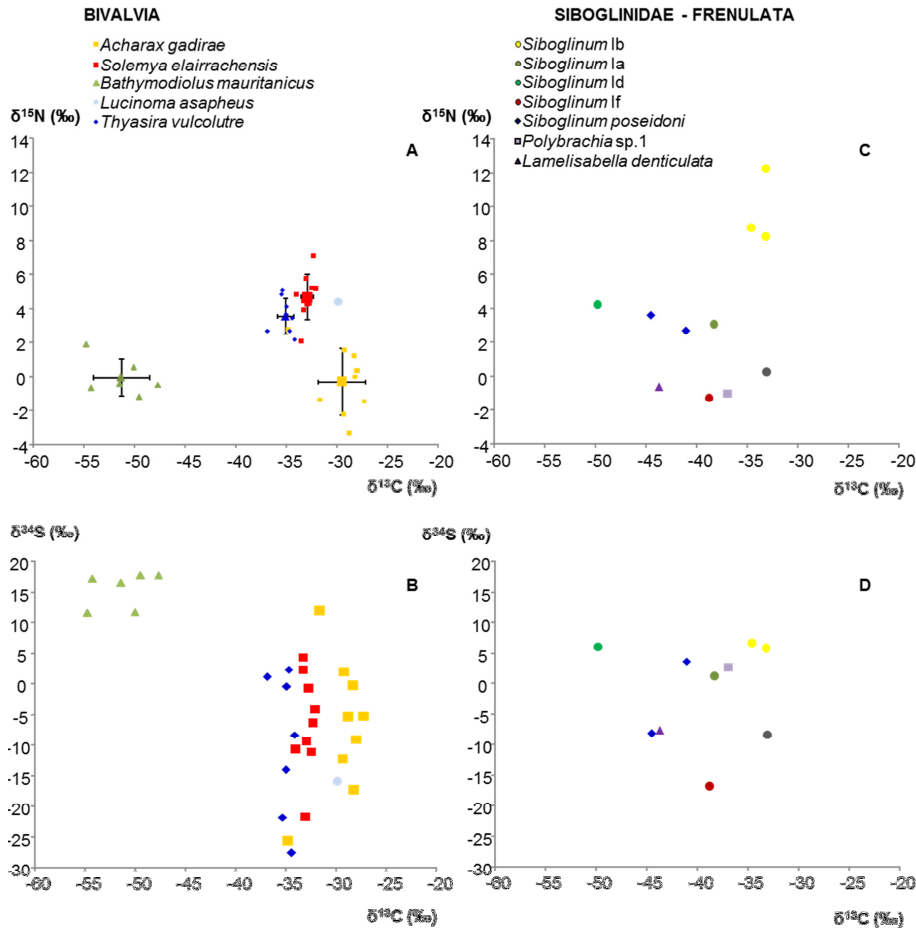


Fig. 2. Mean values (after Table II) of $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ vs. $\delta^{34}\text{S}$ for Bivalvia (**A, B**) and Frenulata (**C, D**) species from the Gulf of Cadiz. Mean values of species and respective standard error are also represented in A.