Chapter 7
New Biogeochemical Proxies in Seep Bivalves

Xudong Wang, Steffen Kiel, and Dong Feng

Abstract Reduced compounds dissolved in seeping fluids, such as methane and hydrogen sulfide, are the main energy sources in submarine cold seep systems, where they nourish the unique chemosynthesis-based ecosystems. Chemosymbiotic bivalves are the dominant macrofauna in many of these ecosystems and have been extensively studied due to their large biomass (hundreds of individuals per square meter), their symbiotic relationships with chemotrophic bacteria (methanotrophic bivalves: methane-oxidizing bacteria; thiotrophic bivalves: sulfur-oxidizing bacteria), and because they are unique archives of biogeochemical processes. In this chapter, we briefly introduce the advancements in seep bivalve research worldwide and then summarize the trophic modes and geographic distribution of seep bivalves in the South China Sea. Thereafter, the biogeochemical processes, such as the enzymatic strategy and energy transfer of seep bivalves, are generalized by integrating the trace elements and stable isotope data of the soft tissues and their corresponding calcareous shells of seep bivalves. Overall, we highlight the past contributions and current knowledge in this field and outline opportunities and future directions to expand this area of research.

7.1 Introduction

Since the discovery of hydrothermal vents and cold seeps in the 1980s (Corliss et al. 1979; Paull et al. 1984), the widespread chemosynthetic ecosystems on the seabed have revolutionized our understanding of life on Earth (Fisher 1995; Dubilier

X. Wang (✉) · D. Feng
College of Marine Sciences, Shanghai Ocean University, Shanghai 201306, China
e-mail: xd-wang@shou.edu.cn

D. Feng
e-mail: dfeng@shou.edu.cn

S. Kiel
Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden
e-mail: Steffen.Kiel@nrm.se

D. Chen and D. Feng (eds.), *South China Sea Seeps*,
https://doi.org/10.1007/978-981-99-1494-4_7

et al. 2008). Within chemosynthetic environments, the high abundance of reduced compounds, such as hydrogen sulfide (H_2S) and methane (CH_4), serve as energy sources for carbon-fixing microbes. These microbes, in turn, form the base of the food web of dense biological communities and make significant contributions to primary production in the deep sea, deep-marine biodiversity, and marine geochemical cycles (Baker et al. 2010).

Deep-sea cold seeps are chemosynthetic ecosystems that host highly productive communities and thus enhance regional diversity on continental margins (Levin et al. 2016). Due to their ubiquity and dominance in cold seep ecosystems, chemosymbiotic bivalves—in particular bathymodiolin mussels and vesicomyid clams—have attracted the attention of researchers since the discoveries of these ecosystems. They were first investigated in the Gulf of Mexico with respect to their biogeochemical behavior (Paull et al. 1985; Childress et al. 1986; Cordes et al. 2009) and were subsequently found and studied at virtually all active cold seeps worldwide (Nankai accretionary wedge: Fiala-Médioni et al. 1993; Håkon Mosby mud volcano: Gebruk et al. 2003; pockmarks on the West African margin: Olu-Le Roy et al. 2007; Concepción methane seep area off Chile: Sellanes et al. 2008; New Zealand: Thurber et al. 2010; Marmara Sea: Ritt et al. 2012; North Atlantic and Mediterranean Sea: Duperron et al. 2013; Gulf of Cadiz: Rodrigues et al. 2013; Pacific coast of Costa Rica: Levin et al. 2015; Guaymas Basin: Portail et al. 2015; Arctic: Åström et al. 2019; Krishna-Godavari Basin: Peketi et al. 2022). After nearly 40 years of research, the understanding of the unique symbiotic relationships between seep-inhabiting bivalves and chemotrophic bacteria and the related biogeochemical processes has grown considerably (Fisher 1995; Dubilier et al. 2008; Petersen and Dubilier 2009; Lorion et al. 2013; Decker et al. 2014; Petersen et al. 2016).

Encouraging progress has also been made in discovering and understanding seep-inhabiting bivalves in the South China Sea (SCS) in the last 20 years through a large amount of investment in capital and technology. To date, three active cold seep regions (Site F, Haima and Yam) with seabed manifestations of significant gas seepage and active biological activity have been identified in the SCS, and bivalves represent the dominant macrofauna at these sites. The species, their trophic modes, and their distribution in the SCS are shown in Table 7.1 and Fig. 7.1. Among the chemosymbiotic bivalves, there are five mussel species (*Bathymodiolus aduloides* and *Gigantidas platifrons*, Hashimoto and Okutani 1994; *Gigantidas securiformis*, Okutani et al. 2003; *Gigantidas haimaensis*, Xu et al. 2019; *Nypamodiolus samadiae*, Lin et al. 2022), and one clam species (*Archivesica marissinica*, Chen et al. 2018) has been found. In addition, seven bivalve species with heterotrophic or unknown feeding strategies were found in (or near) site F and Haima seep (Han et al. 2008; Jiang et al. 2019; Ke et al. 2022).

Anatomically, chemosymbiotic bivalves are composed of soft tissue (gill, mantle, foot, siphons, etc.) and a calcareous shell, making them a unique archive for a diversity of research questions (Fig. 7.2). Soft tissue preserves information of the microenvironment that the bivalve inhabits and allows the reconstruction of biogeochemical processes, but it only provides an "instantaneous snapshot" of the brief time immediately before sampling. In contrast, the calcareous shell can provide insights

Table 7.1 Bivalve species from the cold seep ecosystems in the South China Sea

Species	Trophic modes	Distribution	References
Gigantidas platifrons	Methanotroph	Site F, Haima, Yam	Hashimoto and Okutani (1994)
Gigantidas haimaensis		Haima	Xu et al. (2019)
Gigantidas securiformis		Yam	Okutani et al. (2003); Kuo et al. (2019)
“Bathymodiolus” aduloides	Thiotroph	Site F, Haima	Hashimoto and Okutani (1994)
Nypamodiolus samadiae		Haima	Lin et al. (2022)
Archivesica marissinica			Chen et al. (2018)
Vesicomya rhombica	Unknown		Jiang et al. (2019)
Spinosipella xui			
Malletia sp.			Ke et al. (2022)
Propeamussium sp.			
Acharax sp.		Near Site F	Han et al. (2008)
Conchocele sp.			
Lucinoma sp.			Personal observation

into various environmental conditions during the entire lifetime of the bivalve and can potentially preserve this information for a long time and thus provide insights into evolutionary processes over geological timescales. Therefore, chemosymbiotic bivalves are excellent model organisms—their soft tissues and calcareous shell can be used to explore current and past biogeochemical processes, respectively (Wang et al. 2022a, b).

In this chapter, we compile the latest elemental and isotopic data from soft tissues and calcareous shells of diverse seep bivalves in the SCS. The trace element contents and stable isotope compositions of bivalves are outstanding indicators for evaluating their living environment, physiological functions, pathways of energy, and food sources. Together with the understanding of important biogeochemical processes of deep-sea cold seeps, we discuss the variations in geochemical composition in seep-inhabiting bivalves and provide new insights based on recent findings.

7.2 Tissue Element Compositions

Only limited studies have reported trace elements in the gill, mantle and shell of the bathymodiolin mussel *G. platifrons* (Wang et al. 2017; Zhou et al. 2020), systematic comparative studies (inter- and intraspecific comparison and comparison between soft tissues and shells) are still sparse. Generally, trace element contents are ranked in decreasing order, Zn > Fe > Cu > Sr > Ag > As > Al > Mn > Ba > Pb ≈ Cd > Ni

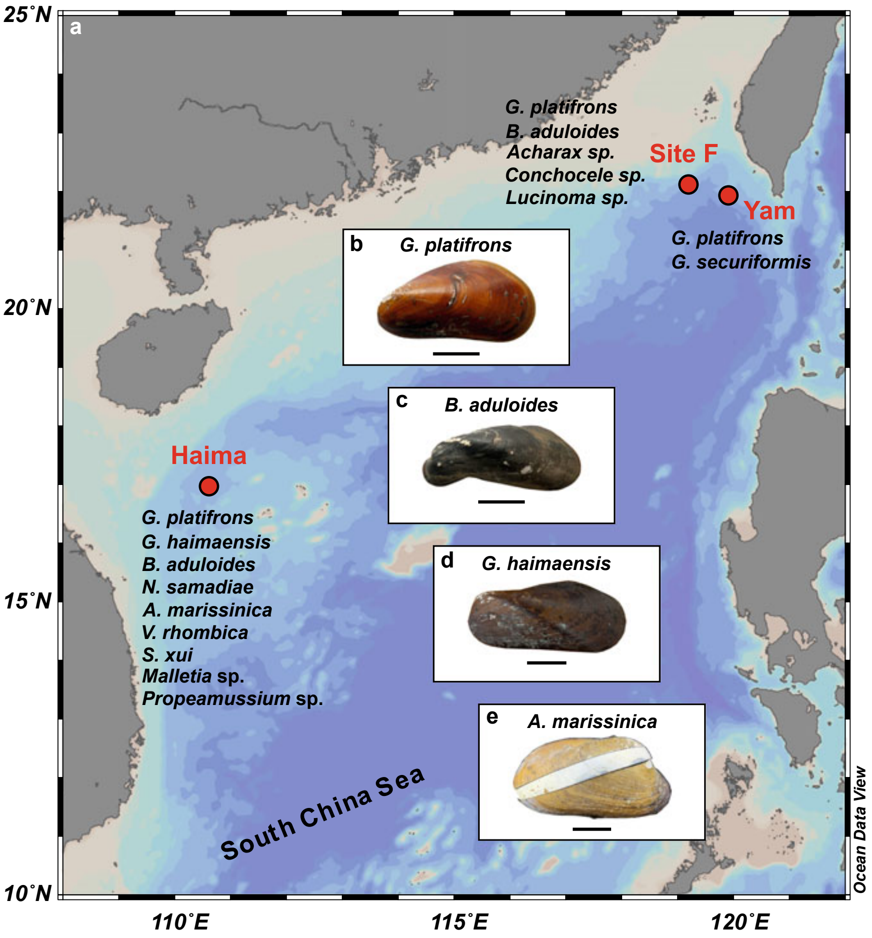

Fig. 7.1 Distribution of known bivalves in cold seep ecosystems in the South China Sea thus far. **a** The active seep sites—Site F, Haima and Yam—are highlighted by red circles. Representative seep bivalves are shown in **b** *Gigantidas platifrons*; **c** *Bathymodiolus aduloides* (modified from Feng et al. 2015); **d** *Gigantidas haimaensis*; and **e** *Archivesica marissinica* (modified from Wang et al. 2022a, b, c). Scale bars in **b**–**e** are 3 cm. See Table 7.1 for the abbreviations

> Co, and it seems that the contents of transition metal elements (e.g., Zn, Fe, Cu) in soft tissues are much higher than those in corresponding shells, indicating that bivalves may have strong physiological requirements for these elements (Fig. 7.3). Undoubtedly, through more measurements over a larger geographic area, longer timespan, and more specimens than species, the interactions among trace elements, the local environments and the physiology of bivalves may be further verified.

In contrast, the contents of rare earth elements (REEs) in seep bivalve soft tissues of the SCS have been well studied (Wang et al. 2020). The aerobic oxidation of methane is thought to be largely dependent upon the use of REEs, but to date, the

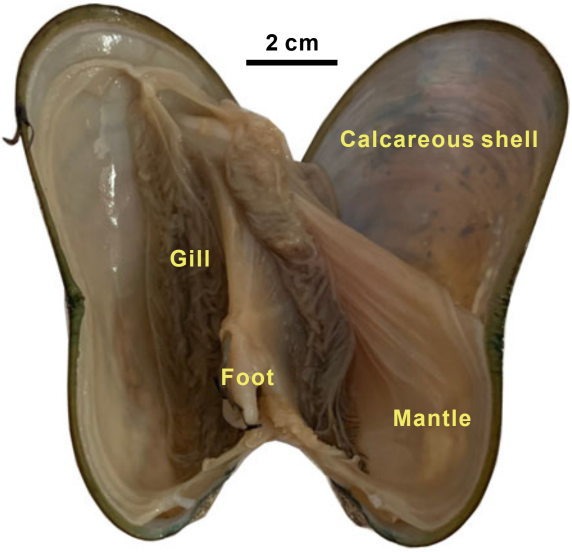

Fig. 7.2 Anatomy of *Gigantidas haimaensis*. Typical features of bivalves include the calcareous shell and soft tissues, such as the gill, mantle and foot

effects of this process on their abundance in bacteria or organisms living in symbiosis with methanotrophs remain to be evaluated. Wang et al. (2020) selected *G. platifrons* (methanotroph) and *B. aduloides* (thiotroph) from Site F and *G. haimaensis* (methanotroph) and *A. marissinica* (thiotroph) from the Haima seep site to compare the effects of different regions and different trophic modes on the contents and patterns of REEs in seep bivalves. They showed that the soft tissues of all methanotrophic bivalves had significant lanthanum (La) enrichment, whereas such a pattern was not observed in thiotrophic bivalves (Fig. 7.4). These results demonstrate that methanotrophic bivalves prospering at methane seeps display distinctive La enrichments linked to the enzymatic activities of their symbionts and that methanotrophic bacteria efficiently fractionates REE distributions in organisms and possibly in the environment.

7.3 Tissue Isotope Compositions

It is well recognized that measuring the carbon, nitrogen, and sulfur isotope compositions of the macrofauna inhabiting cold seeps is one of the most powerful approaches to identifying their food and energy sources, as well as the determination of complex trophic interactions, including symbiosis and heterotrophy (Paull et al. 1985; Childress et al. 1986; Brooks et al. 1987; Carlier et al. 2010; Decker and Olu 2012; Demopoulos et al. 2019; Ke et al. 2022). Indeed, it is possible to distinguish consumers that assimilate carbon through chemosynthesis (more ^{13}C- and ^{15}N-depleted) from those that rely on photosynthetic primary production (Paull et al. 1985; Brooks et al. 1987). This is because methane is much more ^{13}C-depleted (usually $\delta^{13}C_{CH4} < -40‰$; Whiticar 1999) than dissolved inorganic carbon (DIC)

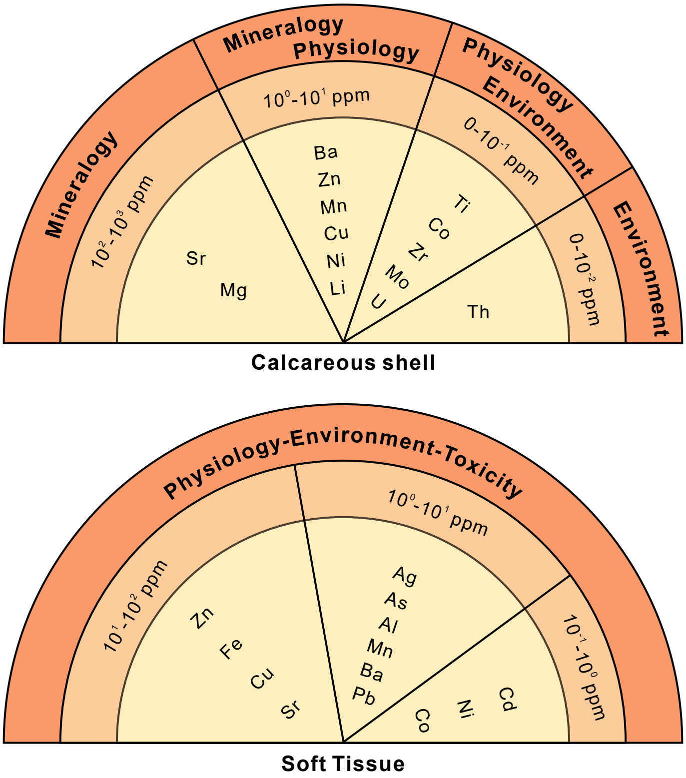

Fig. 7.3 General overview of trace elements analyzed in the shell and soft tissue of seep bivalves, their approximate concentrations, and the factors potentially controlling their behavior (summarized based on data from Wang et al. 2022a)

in the water column ($\delta^{13}C_{DIC} \approx 0‰$), and methane is assimilated by bacteria with only a small carbon isotopic fractionation (Alperin et al. 1988). Within cold seep areas, methane is mainly consumed in the surface sediment by anaerobic oxidation of methane (AOM) coupled with sulfate reduction and produces DIC and sulfide (Boetius et al. 2000), which generates a high microbial biomass (usually a consortium of anaerobic methanotrophic archaea and sulfate-reducing bacteria) and thus can provide a significant supply of methane-derived carbon to heterotrophic bacteria and higher-level consumers (Boetius et al. 2000). The $\delta^{13}C$ signatures of symbiotic and heterotrophic seep-related metazoans indicate whether they preferentially rely on methanotrophically or thiotrophically derived carbon (Childress et al. 1986; Brooks et al. 1987) because the net $\delta^{13}C$ fractionation between a consumer and its diet is small (typically < 1‰; Vander Zanden and Rasmussen 2001; McCutchan et al. 2003). Methanotrophic bacteria are usually more ^{13}C-depleted than thiotrophic bacteria that fix DIC from the water column (Paull et al. 1985). However, $\delta^{13}C$ values of symbiotic species that exclusively rely on thiotrophic bacteria may also be strongly

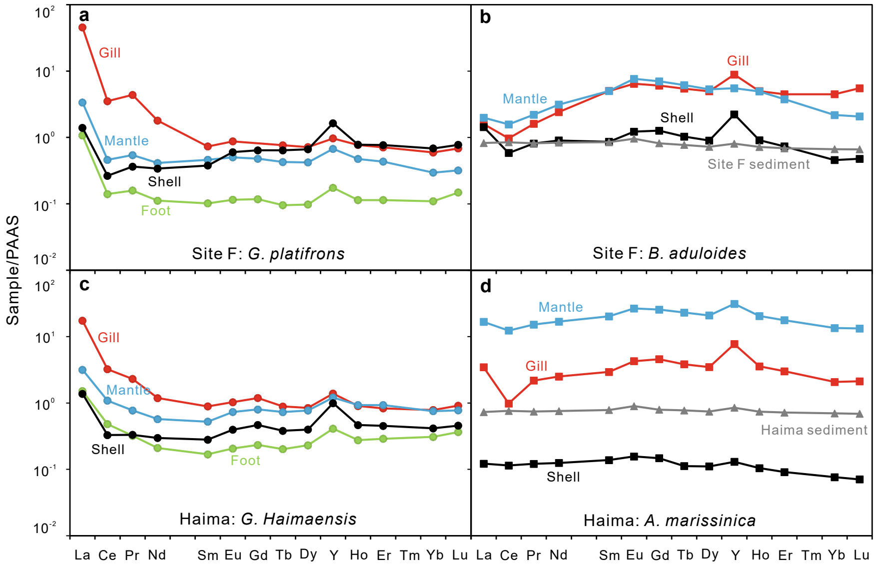

Fig. 7.4 REE + Y patterns normalized to the Post-Archean Australian Shale (PAAS; Pourmand et al. 2012) for seep bivalves in the South China Sea (data from Wang et al. 2020). Abbreviations: (1) *G. platifrons* = *Gigantidas platifrons*; (2) *B. aduloides* = *Bathymodiolus aduloides*; (3) *G. haimaensis* = *Gigantidas haimaensis*; (4) *A. marissinica* = *Archivesica marissinica*

modified when the DIC originates from a diversity of sources, including byproducts of methane oxidation (Lösekann et al. 2008).

Sulfur stable isotopes are useful in discriminating organic matter (OM) from the water column (by phytoplankton) or from reduced sediments (by chemosynthetic microorganisms). In general, the $\delta^{34}S$ values of seawater sulfate are quite homogeneous at ~+21‰. Carbon fixation by phytoplankton results in only a small negative fractionation of sulfur isotopes, resulting in a narrow range in the sulfur isotope composition of oceanic particulate OM (+17‰ < $\delta^{34}S$ < +21‰; Peterson and Fry 1987). Therefore, benthic organisms that depend exclusively on phytoplanktonic production show $\delta^{34}S$ values with similar signatures because sulfur isotopes do not significantly fractionate between trophic levels (McCutchan et al. 2003). In contrast, dissimilatory sulfate reduction by bacteria within the sediment results in strong fractionation (−25‰ < $\delta^{34}S$ < +5‰; Carlier et al. 2010). Consequently, organisms that assimilate these reduced compounds exhibit low $\delta^{34}S$ values as well. To some extent, additional $\delta^{34}S$ analyses may allow differentiation between the input of photosynthetic and chemosynthetic material for seep-related organisms (Brooks et al. 1987; MacAvoy et al. 2005).

The carbon, nitrogen, and sulfur isotopes of *G. platifrons*, *B. aduloides* and *A. marissinica* from cold seeps in the SCS have been investigated (Fig. 7.5; Feng et al. 2015; Zhao et al. 2020; Ke et al. 2022). According to the observations of the available data, some general patterns emerge:

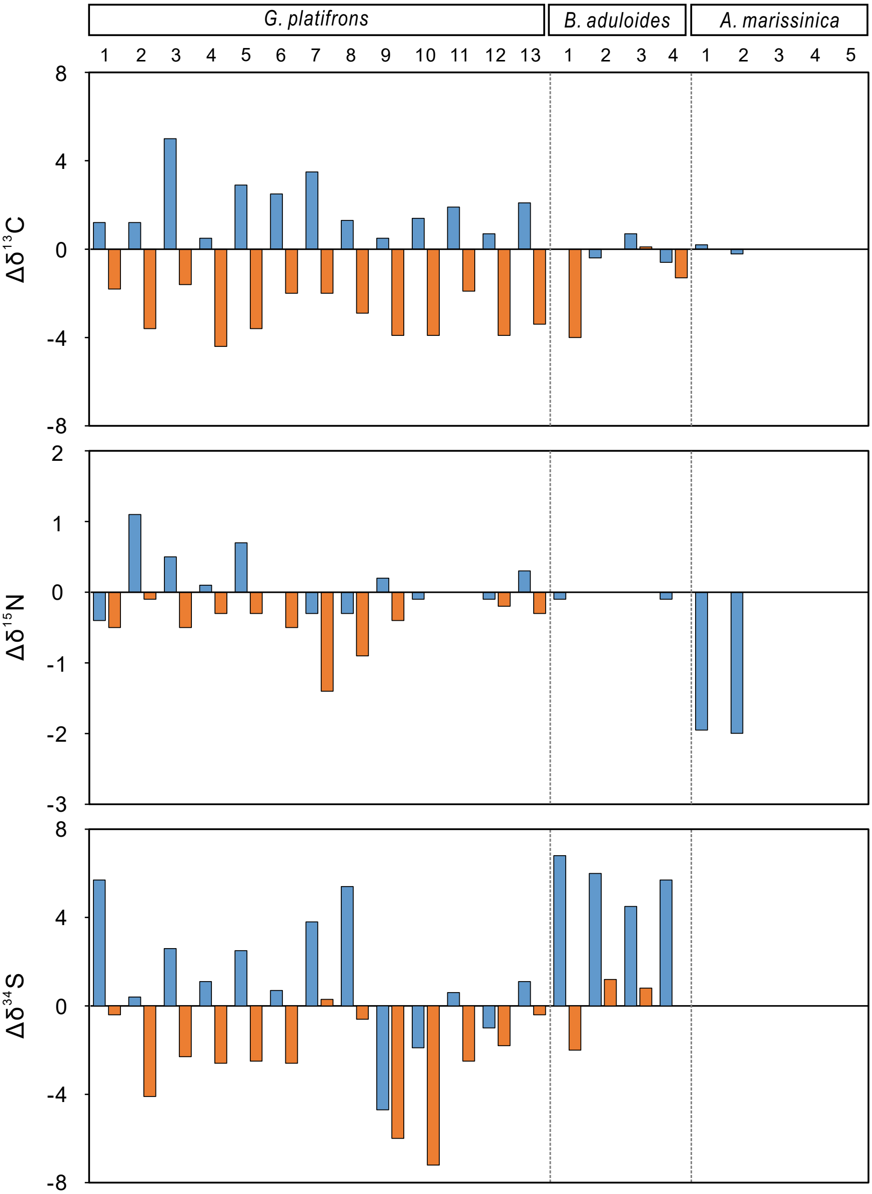

Fig. 7.5 Differences (Δ) in $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values among the gill, mantle and foot of seep bivalves (data from Feng et al. 2015, 2018 and unpublished). Blue rectangle: $\delta^{xx}C/N/S_{\text{gill-mantle}}$; orange rectangle: $\delta^{xx}C/N/S_{\text{gill-foot}}$. Abbreviations: *G. platifrons* = *Gigantidas platifrons*; *B. aduloides* = *Bathymodiolus aduloides*

(1) Carbon and sulfur isotopic compositions of seep bivalve soft tissues are related to their respective trophic modes. The carbon isotope values of methanotrophic bivalves (−77.6‰ to −51.2‰) are obviously lower than those of thiotrophic bivalves (−37.7‰ to −33.0‰), while the sulfur isotope values show the opposite trend (methanotrophic bivalves: +1.4‰ to +19.3‰; thiotrophic bivalves: −12.9‰ to +14.6‰).

(2) The characteristics of the carbon isotope signatures of different soft tissue parts of methanotrophic bivalves are consistent ($\delta^{13}C_{Mantle} < \delta^{13}C_{Gill} < \delta^{13}C_{Foot}$), which has implications for the carbon transmission process in *G. platifrons*.

(3) It is suggested that different nitrogen sources are used by bivalves, in which the main nitrogen source of *B. aduloides* is organic nitrogen from the sediments, while *G. platifrons* mainly uses NH_4^+ (Sun et al. 2017; Wang et al. 2022a, b, c). However, it remains unclear whether different nitrogen sources are responsible for the rather stable nitrogen isotope signature of *B. aduloides* (+1.1‰ to + 1.2‰) and the lower and highly variable nitrogen isotope signature of *G. platifrons* (−0.9‰ to +1.3‰). Obviously, the nitrogen isotope signature archived by seep bivalves should be further explored.

7.4 Element and Isotope Compositions of Shells

By comparison, prospecting and investigation of the calcareous shells of these bivalves lags behind that of their soft tissue. Generally, due to some inherent methodological and physiological limitations related to the shell (the record of the whole life process – years to decades of accumulation, the high degree of mixing with seawater, bulk shell sampling methods, etc.), it seems that the shell reflects some insignificant geochemical signals that inevitably blend the information of seawater and carbonate. For example, trace element concentrations ranked in decreasing order for calcareous shells of *G. haimaensis* and *A. marissinica* are Sr > Mg > Ba > Zn ≈ Mn > Cu > Ni > Li ≈ Ti > Co ≈ Zr ≈ Mo ≈ U > Th, obviously because carbonate is rich in trace elements, such as Sr, Mg and Ba (Fig. 7.3; Wang et al. 2022a). However, few studies have demonstrated that shells, similar to soft tissue, can potentially be used to reconstruct biogeochemical processes (Feng et al. 2018; Wang et al. 2020). Although the REE contents of the shells are lower than those of the corresponding soft tissues, characteristic of La enrichment is also observed in the methanotrophy-related shells (Fig. 7.4). In addition, generally consistent characteristics between the carbon, nitrogen and sulfur isotopic information contained in the shell organic matter (SOM) and its corresponding soft tissue mantle are present (Fig. 7.6). In contrast to the quickly degrading soft tissue, the bivalve shell has a high preservation potential, including its original mineralogy. Hence, the geochemical signal in the shell can be used as a fingerprint of food chains, as well as to track early evidence of microbial life and to reconstruct the chemosynthetic behavior among different types of ecosystems in the geologic past (Feng et al. 2018; Wang et al. 2020).

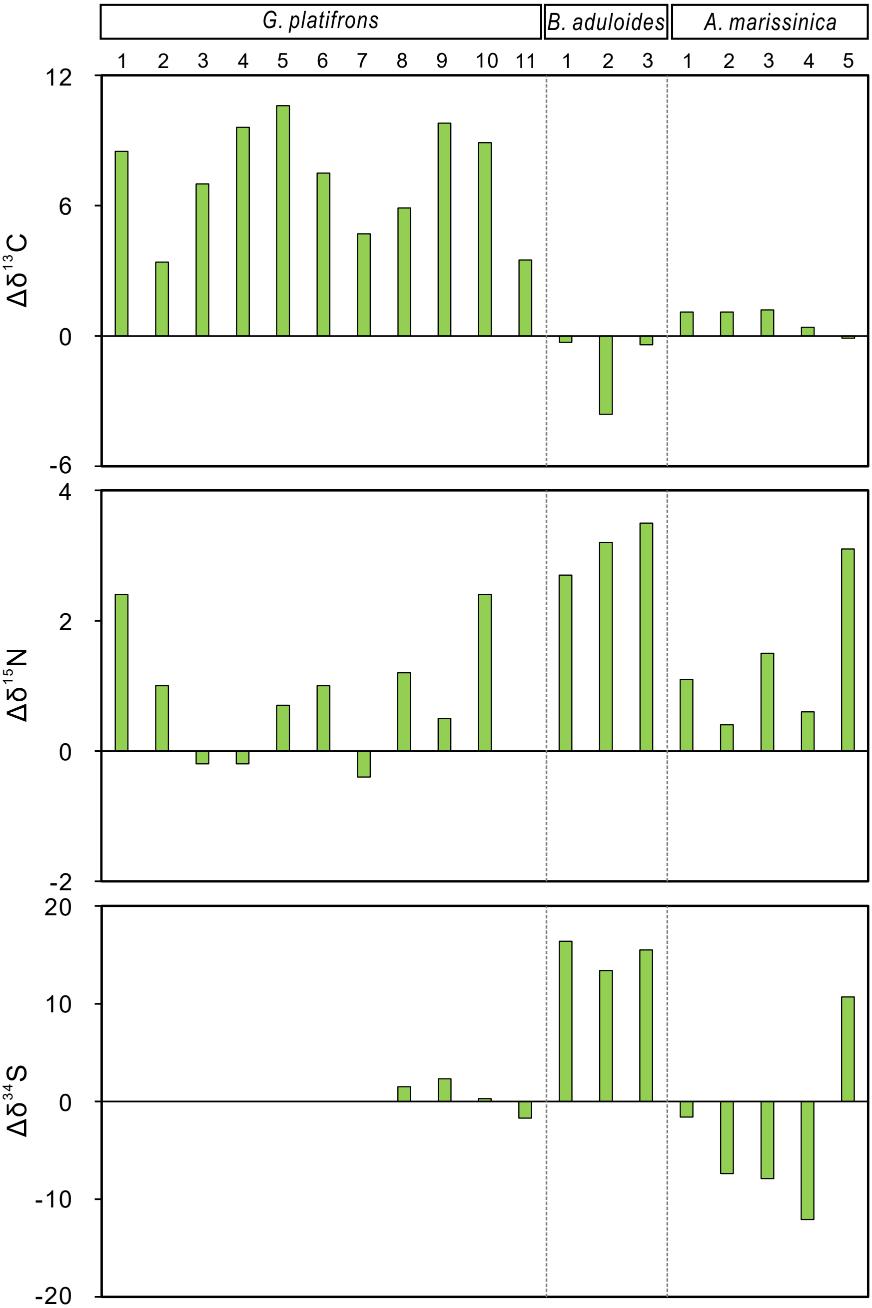

Fig. 7.6 Differences (Δ) in $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values between the organic shell matrix and mantle of seep bivalves (data from Feng et al. 2018). Abbreviations: *G. platifrons* = *Gigantidas platifrons*; *B. aduloides* = *Bathymodiolus aduloides*; *A. marissinica* = *Archivesica marissinica*

7.5 Summary and Perspective

Research on seep bivalves in the South China Sea (SCS) has acquired a series of profound understandings that have spurred the wave of the development of cold seeps in China in the last 20 years. Studies on the elemental geochemistry, especially rare earth elements of seep bivalves, have further verified the catalysis of light rare earth elements on the aerobic oxidation of methane and provided an excellent example for exploring the coupling (enzymatic) relationship between life activities and trace elements. At the same time, by investigating the carbon, nitrogen, and sulfur isotopes of seep bivalves, temporally and spatially integrated trophic estimates used to understand and define trophic linkages among species and communities are provided.

However, it must be admitted that our knowledge of the geochemical behavior of seep bivalves is restricted since the study of the seep bivalves of the SCS is still in the initial stage of discovery and research. The existing issues include but are not limited to the following: (1) there is a large gap in the research on different species of seep bivalves. Intensive studies on the geochemical characteristics of seep bivalves focus on *G. platifrons*, *G. haimaensis* and *A. marissinica*, while few studies have been conducted on other species. The trace element data of soft tissues are particularly scarce. (2) The mechanism that controls the behavior of carbon, nitrogen, and sulfur isotopes in chemosymbiotic bivalves remains understudied. In addition to the interaction between host and symbiotic bacteria, facultative filter feeding among seep bivalves remains a hard-to-define factor that may obstruct predictions of the behavior of carbon, nitrogen, and sulfur isotopes in these bivalves. (3) Due to the technical difficulties of sampling the deep sea, species of nondominant bivalves are typically found only as bycatch rather than as the result of focused and systematic sampling. Promising in this respect is the Haima cold seep as it covers a vast area, and Yam is a recently discovered seep area, allowing the discovery and research of new species of bivalves.

The exploration of seep bivalves is of great significance to both biology and geology because the combination of soft tissue and calcareous shells makes them excellent model organisms to bridge contemporary earth surface processes (present) and the sedimentary record (fossil). Future research on seep bivalves should strengthen the combination of biology and geology (especially geochemistry) and further apply this research approach to all seep macrofauna, which is expected to decode the 'vital effect' of symbiotic organisms and their overprint on geological records. We believe that future research on seep bivalves (and all seep macrofauna) in the South China Sea cold seeps will continue to expand our knowledge of the biological activities in this unique ecosystem, and we look forward to the advancement of knowledge in the fields of life evolution, symbiotic relationships and beyond.

Acknowledgements Funding was provided by the National Natural Science Foundation of China (Grant: 42106059), Shanghai Sailing Program (Grant: 21YF1416800) and Chenguang Program of Shanghai Education Development Foundation and Shanghai Municipal Education Commission (Grant: 22CGA58).

References

Alperin MJ, Reeburgh WS, Whiticar MJ (1988) Carbon and hydrogen isotope fractionation resulting from anaerobic methane oxidation. Glob Biogeochem Cycle 2(3):279–288

Åström EKL, Carroll ML, Sen A et al (2019) Chemosynthesis influences food web and community structure in high-Arctic benthos. Mar Ecol-Prog Ser 629:19–42

Baker MC, Ramirez-Llodra EZ, Tyler PA et al (2010) Biogeography, ecology, and vulnerability of chemosynthetic ecosystems in the deep sea. In: McIntyre AD (ed) Life in the World's Oceans. Wiley-Blackwell Publishing, Oxford, pp 161–182

Boetius A, Ravenschlag K, Schubert CJ et al (2000) A marine microbial consortium apparently mediating anaerobic oxidation of methane. Nature 407(6804):623–626

Brooks JM, Kennicutt MC II, Fisher CR et al (1987) Deep-sea hydrocarbon seep communities: evidence for energy and nutritional carbon sources. Science 238(4830):1138–1142

Carlier A, Ritt B, Rodrigues CF et al (2010) Heterogeneous energetic pathways and carbon sources on deep eastern Mediterranean cold seep communities. Mar Biol 157(11):2545–2565

Chen C, Okutani T, Liang Q et al (2018) A noteworthy new species of the family Vesicomyidae from the South China Sea (Bivalvia: glossoidea). Venus 76(1–4):29–37

Childress JJ, Fisher CR, Brooks JM et al (1986) A methanotrophic marine molluscan (Bivalvia, Mytilidae) symbiosis: mussels fueled by gas. Science 233(4770):1306–1308

Cordes EE, Bergquist DC, Fisher CR (2009) Macro-ecology of Gulf of Mexico cold seeps. Annu Rev Mar Sci 1:143–168

Corliss JB, Dymond J, Gordon LI et al (1979) Submarine thermal springs on the Galápagos Rift. Science 203(4385):1073–1083

Decker C, Olu K (2012) Habitat heterogeneity influences cold-seep macrofaunal communities within and among seeps along the Norwegian margin—part 2: contribution of chemosynthesis and nutritional patterns. Mar Ecol 33(2):231–245

Decker C, Zorn N, Potier N et al (2014) Globin's structure and function in vesicomyid bivalves from the Gulf of Guinea cold seeps as an adaptation to life in reduced sediments. Physiol Biochem Zool 87(6):855–869

Demopoulos AWJ, McClain-Counts JP, Bourque JR et al (2019) Examination of *Bathymodiolus childressi* nutritional sources, isotopic niches, and food-web linkages at two seeps in the US Atlantic margin using stable isotope analysis and mixing models. Deep-Sea Res I-Oceanogr Res Pap 148:53–66

Dubilier N, Bergin C, Lott C (2008) Symbiotic diversity in marine animals: the art of harnessing chemosynthesis. Nat Rev Microbiol 6(10):725–740

Duperron S, Gaudron SM, Rodrigues CF et al (2013) An overview of chemosynthetic symbioses in bivalves from the North Atlantic and Mediterranean Sea. Biogeosciences 10(5):3241–3267

Feng D, Cheng M, Kiel S et al (2015) Using *Bathymodiolus* tissue stable carbon, nitrogen and sulfur isotopes to infer biogeochemical process at a cold seep in the South China Sea. Deep-Sea Res I-Oceanogr Res Pap 104:52–59

Feng D, Peckmann P, Li N et al (2018) The stable isotope fingerprint of chemosymbiosis in the shell organic matrix of seep-dwelling bivalves. Chem Geol 479:241–250

Fiala-Médioni A, Boulègue J, Ohta S et al (1993) Source of energy sustaining the *Calyptogena* populations from deep trenches in subduction zones off Japan. Deep-Sea Res I-Oceanogr Res Pap 40:1241–1258

Fisher CR (1995) Toward an appreciation of hydrothermal-vent animals: their environment, physiological ecology, and tissue stable isotope values. In: Humphris SE, Zierenberg RA, Mullineaux LS, Thomson RE (eds) Seafloor hydrothermal systems: physical, chemical, biological, and geochemical interactions. Geophysical Monographs Series 91. Blackwell, Washington, DC, pp 297–316 (Geophysical Monograph Series)

Gebruk AV, Krylova EM, Lein AY et al (2003) Methane seep community of the Håkon Mosby mud volcano (the Norwegian Sea): composition and trophic aspects. Sarsia 88(6):394–403

Han XQ, Suess E, Huang YY et al (2008) Jiulong methane reef: Microbial mediation of seep carbonates in the South China Sea. Mar Geol 249(3–4):243–256

Hashimoto J, Okutani T (1994) Four new mytilid mussels associated with deepsea chemosynthetic communities around Japan. Venus 53:61–83

Jiang J, Huang Y, Liang Q et al (2019) Description of two new species (Bivalvia: Vesicomyidae, Verticordiidae) from a cold seep in the South China Sea. Nautilus 133(3–4):94–101

Ke Z, Li R, Chen Y et al (2022) A preliminary study of macrofaunal communities and their carbon and nitrogen stable isotopes in the Haima cold seeps, South China Sea. Deep-Sea Res Part I-Oceanogr Res Pap 184:103774

Kuo M-Y, Kang D-R, Chang C-H et al (2019) New records of three deep-sea bathymodiolus mussels (Bivalvia: Mytilida: Mytilidae) from hydrothermal vent and cold seeps in Taiwan. J Mar Sci Technol 27(4):352–358

Lin Y-T, Kiel S, Xu T et al (2022) Phylogenetic placement, morphology and gill-associated bacteria of a new genus and species of deep-sea mussel (Mytilidae: Bathymodiolinae) from the South China Sea. Deep-Sea Res Part I-Oceanogr Res Pap 190:103894

Levin LA, Mendoza GF, Grupe BM et al (2015) Biodiversity on the rocks: macrofauna inhabiting authigenic carbonate at Costa Rica methane seeps. PLoS ONE 10(7):e0131080

Levin LA, Mendoza GF, Grupe BM (2016) Methane seepage effects on biodiversity and biological traits of macrofauna inhabiting authigenic carbonates. Deep-Sea Res II-Top Stud Oceanogr 137:26–41

Lorion J, Kiel S, Faure BM et al (2013) Adaptive radiation of chemosymbiotic deep-sea mussels. Proc R Soc B-Biol Sci 280(1776):20131243

Lösekann T, Robador A, Niemann H et al (2008) Endosymbioses between bacteria and deep-sea siboglinid tubeworms from an Arctic cold seep (Haakon Mosby Mud Volcano, Barents Sea). Environ Microbiol 10(12):3237–3254

MacAvoy SE, Fisher CR, Carney RS et al (2005) Nutritional associations among fauna at hydrocarbon seep communities in the Gulf of Mexico. Mar Ecol-Prog Ser 292:51–60

McCutchan JH Jr, Lewis WM Jr, Kendall C et al (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102(2):378–390

Okutani T, Fujikura K, Sasaki T (2003) Two New Species of Bathymodiolus (Bivalvia: Mytilidae) from Methane Seeps on the Kuroshima Knoll off the Yaeyama Islands, Southwestern Japan. Venus 62:97–110

Olu-Le Roy K, Caprais J-C, Fifis A et al (2007) Cold-seep assemblages on a giant pockmark off West Africa: spatial patterns and environmental control. Mar Ecol 28(1):115–130

Paull CK, Hecker B, Commeau R et al (1984) Biological communities at the Florida Escarpment resemble hydrothermal vent taxa. Science 226(4677):965–967

Paull CK, Jull AJT, Toolin LJ et al (1985) Stable isotope evidence for chemosynthesis in an abyssal seep community. Nature 317(6039):709–711

Peketi A, Mazumdar A, Sawant B et al (2022) Biogeochemistry and trophic structure of a cold seep ecosystem, offshore Krishna-Godavari basin (east coast of India). Mar Pet Geol 138:105542

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Ann Rev Ecol Syst 18:293–320

Petersen JM, Dubilier N (2009) Methanotrophic symbioses in marine invertebrates. Environ Microbiol Rep 1(5):319–335

Petersen JM, Kemper A, Gruber- Vodicka H et al (2016) Chemosynthetic symbionts of marine invertebrate animals are capable of nitrogen fixation. Nat Microbiol 2(1):16195

Portail M, Olu K, Escobar-Briones E et al (2015) Comparative study of vent and seep macrofaunal communities in the Guaymas Basin. Biogeosciences 12(18):5455–5479

Pourmand A, Dauphas N, Ireland TJ (2012) A novel extraction chromatography and MC-ICP-MS technique for rapid analysis of REE, Sc and Y: revising CI-chondrite and Post-Archean Australian Shale (PAAS) abundances. Chem Geol 291:38–54

Ritt B, Duperron S, Lorion J et al (2012) Integrative study of a new cold-seep mussel (Mollusca:Bivalvia) associated with chemosynthetic symbionts in the Marmara. Deep-Sea Res I Oceanogr Res Pap 67:121–132

Rodrigues CF, Hilario A, Cunha MR (2013) Chemosymbiotic species from the Gulf of Cadiz (NE Atlantic): distribution, life styles and nutritional patterns. Biogeosciences 10(4):2569–2581

Sellanes J, Quiroga E, Neira C (2008) Megafauna community structure and trophic relationships at the recently discovered concepción methane seep area, Chile, ~36°S. ICES J Mar Sci 65(7):1102–1111

Sun J, Zhang Y, Xu T et al (2017) Adaptation to deep-Sea chemosynthetic environments as revealed by mussel genomes. Nat Ecol Evol 1(5):0121

Thurber AR, Kröger K, Neira C et al (2010) Stable isotope signatures and methane use by New Zealand cold seep benthos. Mar Geol 272(1–4):260–269

Vander Zanden MJ, Rasmussen JB (2001) Variation in δ^{15}N and δ^{13}C trophic fractionation: implications for aquatic food web studies. Limnol Oceanogr 46(8):2061–2066

Wang F, Wu Y, Feng D (2022a) Different nitrogen sources fuel symbiotic mussels at cold seeps. Front Mar Sci 9:869226

Wang X, Li C, Zhou L (2017) Metal concentrations in the mussel *Bathymodiolus platifrons* from a cold seep in the South China Sea. Deep-Sea Res I Oceanogr Res Pap 129:80–88

Wang X, Barrat J-A, Bayon G et al (2020) Lanthanum anomalies as fingerprints of methanotrophy. Geochem Perspect Lett 14:26–30

Wang X, Fan D, Kiel S et al (2022b) Archives of short-term fluid flow dynamics and possible influence of human activities at methane seeps: evidence from high-resolution element geochemistry of chemosynthetic bivalve shells. Front Mar Sci 9:960338

Wang X, Guan H, Qiu J-W et al (2022c) Macro-ecology of cold seeps in the south China Sea. Geosyst Geoenviron 1(3):100081

Whiticar MJ (1999) Carbon and hydrogen isotope systematics of bacterial formation and oxidation of methane. Chem Geol 161(1–3):291–314

Xu T, Feng D, Tao J et al (2019) A new species of deep-sea mussel (Bivalvia: Mytilidae: *Gigantidas*) from the South China Sea: morphology, phylogenetic position, and gill-associated microbes. Deep-Sea Res I Oceanogr Res Pap 146:79–90

Zhao Y, Xu T, Law YS et al (2020) Ecological characterization of cold-seep epifauna in the South China Sea. Deep-Sea Res I Oceanogr Res Pap 163:103361

Zhou L, Cao L, Wang X et al (2020) Metal adaptation strategies of deep-sea *Bathymodiolus* mussels from a cold seep and three hydrothermal vents in the West Pacific. Sci Total Environ 707:136046