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Geo-Biological Coupling of Authigenic Carbonate Formation and Autotrophic Faunal Colonization at Deep-Sea Methane Seeps II. Geo-Biological Landscapes

Takeshi Naganuma

Additional information is available at the end of the chapter

Abstract

Deep-sea methane seeps are typically shaped with authigenic carbonates and unique biomes depending on methane-driven and methane-derived metabolisms. Authigenic carbonates vary in $\delta^{13}C$ values due probably to $\delta^{13}C$ variation in the carbon sources (directly carbon dioxide and bicarbonate, and ultimately methane) which is affected by the generation and degradation (oxidation) of methane at respective methane seeps. Anaerobic oxidation of methane (AOM) by specially developed microbial consortia has significant influences on the carbonate $\delta^{13}C$ variation as well as the production of carbon dioxide and hydrogen sulfide for chemoautotrophic biomass production. Authigenesis of carbonates and faunal colonization are thus connected. Authigenic carbonates also vary in Mg contents that seem correlated again to faunal colonization. Among the colonizers, mussels tend to colonize low $\delta^{13}C$ carbonates, while gutless tubeworms colonize high-Mg carbonates. The types and varieties of such geo-biological landscapes of methane seeps are overviewed in this chapter. A unique feature of a high-Mg content of the rock-tubeworm conglomerates is also discussed.

Keywords: lithotrophy, chemoautotrophy, thiotrophy, methanotrophy, stable carbon isotope, $\delta^{13}C$, isotope fractionation, $\Delta^{13}C$, calcite, dolomite, anaerobic oxidation of methane (AOM), sulfate-methane transition zone (SMTZ), *Lamellibrachia* tubeworm, *Bathymodiolus* mussel, *Calyptogena* clam

1. Introduction

Aristotle separated the world into two realms, *nature* and *living things* (originally animals), the latter having structures, processes, and functions of spontaneous formation and voluntary

movements [1]. He argued the difference in the manner similar to "living organisms produce stones (e.g., calculi, shells, and other bio-mineralized materials [2]), but stones do not generate living things". However, in the view of modern science, which has an origin in the Democritean atomism that Aristotle rejected, stones may sustain, not to say generate, life as exemplified by the biological term "lithotrophy." Etymologically, the term was coined from the Greek words *líthos* and *tréphō* that correspond to English words of "stone" and "nourishment," respectively. Therefore, lithotrophy is interpreted as "stone-eating," and the corresponding organisms, that is, lithotrophs, are "stone-eaters."

Lithotrophy or stone-eating is a figurative expression and is biologically interpreted as "living on inorganic sources." For instance, human and animals feed on organic foods and thus are not lithotrophs (but organotrophs). Lithotrophs in this chapter are defined as the organisms that derive life-sustaining energy from redox processes of inorganic materials such as hydrogen sulfide and methane. It should be noted that methane in this argument is taken as semi-inorganic (and semi-organic) as discussed in the former chapter.

It should also be noted that the term "chemoautotrophy" takes the place of lithotrophy in this chapter, because chemoautotrophy (a.k.a., chemosynthesis) is more widely used in general and provides a clearer idea about energy sources in reference to light-driven photoautotrophy (a.k.a. photosynthesis). Autotrophy indicates the inorganic carbon source, that is, CO_2, for organic (biomass) production in both photoautotrophy and chemoautotrophy (Note 1). Methane, CH_4, serves as an energy source and occasionally as a carbon source via "methanotrophy," part of which is regarded as a variety of autotrophy as explained later.

Authigenic formation of *líthos* (stones and rocks) at methane seeps is associated with the generation of inorganic sources that feed living organisms via chemoautotrophic and methanotrophic metabolisms. In addition, their metabolisms in turn facilitate the formation of authigenic carbonates. These rock-forming (geological) and biomass-producing (biological) processes are interwoven, and they literally, more than metaphorically, interweave to form "conglomerates" of rocks and organisms [3].

Authigenic carbonates and associated unique faunas thus represent the typical landscape of methane seeps. Methane seeps are formed by various settings as reviewed in the former chapter, and a variety of carbonates and faunas (and rock-fauna conglomerates) are formed, accordingly. This chapter provides an overview of the types of authigenic carbonates and faunas based on chemoautotrophy and methanotrophy. Profiles of a stable carbon isotope signature ($\delta^{13}C$) of authigenic carbonates and faunal tissues are summarized. In addition, high-magnesium (Mg) contents of the conglomerate carbonates, which are potentially associated with certain geo-biological processes, will be discussed.

2. Backgrounds for landscapes of deep-sea methane seeps

Landscapes of deep-sea methane seeps are characterized by unique and exotic biological communities based on microbial chemo(thio)autotrophic and methanotrophic biomass production, not on photosynthesis (photo-autotrophy), in the dark. Representatives of the methane seep biota are mussels, clams, and gutless tubeworms (**Figure 1**). The landscapes are also featured

Figure 1. Landscape of a methane seep at 1100 m depth, off Hatsushima Island, Sagami Bay, Central Japan. The *Bathymodiolus* Kenk and Wilson, 1985 mussels and *Lamellibrachia* Webb, 1969 tubeworms colonize the authigenic carbonate rocks. The *Calyptogena* Dall, 1891 clams are half-buried in the sediment to move around carbonate rocks to exploit available sulfide. Photo by JAMSTEC.

by occurrences of authigenic carbonate rocks that take forms of seafloor pavements, cementations, and slabs buried in sediments (**Figure 1**). The biological processes (biomass production, production and consumption of methane, etc.) and carbonate-forming processes are interrelated in rather a complex manner, and the interrelationships and the involved processes will be outlined from a geochemical point of view, with particular respect to stable carbon isotopes.

In addition to abiogenic carbonates, some organisms such as mollusks and foraminiferas produce carbonate as protective shells through the process of biomineralization. Biomineralized carbonates, particularly dolomite, are also produced by microorganisms as exemplified by *Desulfovibrio brasiliensis* Warthmann et al., 2005 [5], for dolomite formation or dolomitization [4–6] and *Bacillus subtilus* (Ehrenberg, 1835) John, 1872, possessing the *etfa* gene (involved in energetic electron transfer) for $CaCO_3$ deposition [7], although it is uncertain whether they are actually involved in carbonate formation in methane seeps. Carbonate formation in methane seeps is likely facilitated by the conversion of CH_4 to HCO_3^-, that is, oxidation of methane, which is mediated by microorganisms. Oxidation of methane is done both aerobically and anaerobically, and anaerobic oxidation of methane (AOM) coupled with sulfate reduction (sulfate respiration) produces sulfide, HS^-, that supports chemo(thio)autotrophic biomass production in the dark.

2.1. Stable carbon isotope deviation ($\delta^{13}C$) and fractionation ($\Delta^{13}C$)

Methane, CH_4, is often geochemically characterized by the ratio of stable isotopes of $^{13}C/^{12}C$ and $^2H/^1H$ or D/H (D stands for deuterium). The ratios are generally expressed as deviations (depletion or enrichment; δ) from the reference standard ratios such as the Vienna Pee Dee Belemnite (VPDB) with the $^{13}C/^{12}C$ ratio of 0.0112372 for $\delta^{13}C$, and the Vienna Standard Mean Ocean Water (VSMOW) with the $^2H/^1H$ (D/H) ratio of 0.00015576 for δ^2H (δD) as well as the $^{18}O/^{16}O$ ratio of 0.00200520 for $\delta^{18}O$. The unit of ‰ (per mil) instead of % (percent) is generally

used for these deviations. For example, if a $^{13}C/^{12}C$ ratio of 0.0101135 is determined for biogenic methane, its $\delta^{13}C$ is −100‰, as calculated as $(0.0101135/0.0112372 − 1) \times 1000$.

These deviation parameters ($\delta^{13}C$, $\delta^{2}H$ (δD) and $\delta^{18}O$) are regarded as the indicative of dynamics (origins, sources, processes, pathways, sinks, changes, etc.) of methane and carbonates as shown in **Figure 3** of the former chapter, with careful cautions for interpretations required. For example, methane that has high $\delta^{13}C$ and $\delta^{2}H$ values (enriched in ^{13}C and ^{2}H) is generally regarded as abiotic origins (geothermal and thermogenic sources); however, the "enriched" methane may also be interpreted as "leftover" or residual of methane oxidation that removes lighter isotopes (^{1}H and ^{12}C) faster and leaves heavier isotopes (^{2}H and ^{13}C) behind, or isotope fractionation (discrimination), resulting in the isotopically "enriched" (heavy) residual methane, as discussed later.

The product of methane oxidation (carbon dioxide, CO_2) and the derived carbonate rock ($CaCO_3$) contain no hydrogen isotopes but stable oxygen isotopes, ^{16}O and ^{18}O, of geochemical interest. The deviation (depletion or enrichment) parameter $\delta^{18}O$ of carbonates is indicative of oxygen dynamics (origins, sources, processes, pathways, sinks, etc.) but is more readily influenced by temperature, fluid inclusion, diagenesis, and so on, than $\delta^{13}C$ [8]. Therefore, this chapter deals mainly with $\delta^{13}C$ that may serve as a "signature" of carbon dynamics as
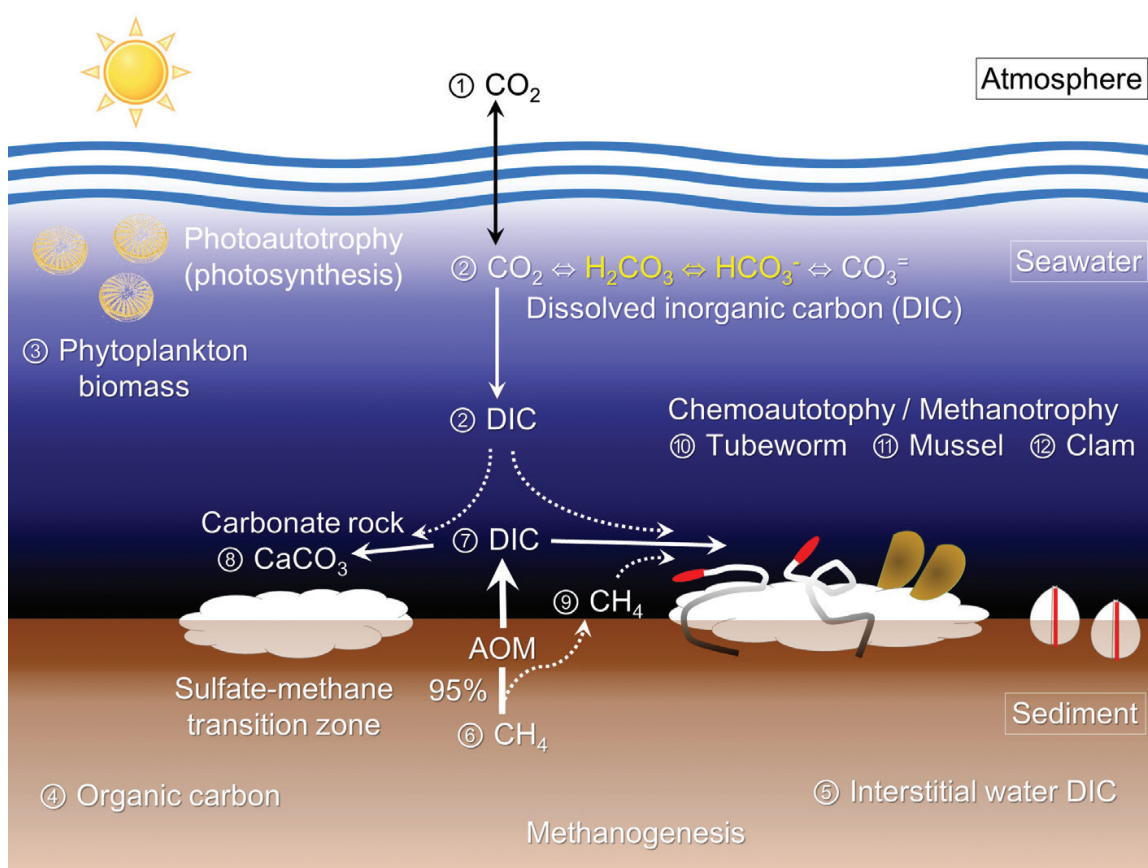

Figure 2. An illustrated general view of carbon dynamics with reference to the processes occurring at a methane seep. Numbers in circles from 1 to 12 correspond to the numbers in **Tables 2** and **3**.

	Carbon species	Form	$\delta^{13}C$ (‰)	Reference
1	CO_2	Gas (atmospheric)	-8.00	[9]
2	DIC	ca. 90% HCO_3^-	0.00	[9]; Bjerrum plot [13] Figure 1.1.2, p.5
3	Organic C	Phytoplankton biomass	-22.0	[9]
4	Organic C	Sedimentary	-27.0 to -22.0	In general [9]
			-30.0 to -22.0	Methane seeps [23, 24, 26, 144]
			-80.0 to -47.0	Brine seep at Florida Escarpment [27, 28]
5	CO_2	Interstitial water	-50.0 to -5.00 (DIC)	[25, 40, 145]
			-38.0 to +11.0 (DIC) -21.0 to +1.00 (CO_2)	[26]
				[26]
			-27.5 (CO_2)	[33]
6	CH_4	Sedimentary	-100.0 to -40	In general [32]
			-101.3 to -27.2	[23, 26, 31, 33]
7	post-AOM CO_2	CH_4-derived (oxidized)	Not found	
8	$CaCO_3$	Authigenic carbonate	-60.0 to +26.0	[50, 56]
9	post-AOM CH_4	Residual (unoxidized)	Possibly -27.2	Eel River Basin [33]
10	Tubeworm	Soft tissue	-55.0 to -18.0	[23, 31, 41–48]
	(*Lamellibrachia*)	Tube (chitin + protein)	-28.1 to -19.9	[24, 41–44]
11	Mussel	Soft tissue	-76.0 to -36.4	[27, 31, 49, 146, 147]
	(*Bathymodiolus*)	Shell ($CaCO_3$)	-6.80 to -2.60	[27, 147]
12	Clam	Soft tissue	-69.2 to -32.5	[23, 43, 44, 146]
	(*Calyptogena*)	Shell ($CaCO_3$)	-2.00 to +0.35	[23, 43, 144, 148, 149]

Table 1. Stable carbon isotope ratio deviation, $\delta^{13}C$ (‰), of different carbon species and forms involved in the carbon dynamics associated with methane seepage.

depicted in **Figure 2** and summarized in **Table 1**, and fractionation parameters ($\Delta^{13}C$) in the processes and pathways of carbon dynamics (focusing on methane dynamics) is also discussed later and summarized in **Table 2**.

2.1.1. $\delta^{13}C$ values before and after methanogenesis

Taking atmospheric CO_2 as the starting material of methanogenesis, its $\delta^{13}C$ value is currently estimated at about −8‰ (**Table 1**) [9] with an estimate of a decrease rate of 0.05–0.06‰ year^{-1} [10], possibly due to the input of lighter carbon (^{12}C) into atmosphere by artificial fossil fuel combustion, that is, the so-called "Suess effect" [11]. Air-to-seawater transport prefers lighter $^{12}CO_2$ to heavier $^{13}CO_2$ and thus decreases its $\delta^{13}C$ by 2‰ ($\Delta^{13}C$ of −2‰, **Table 2**) [12]. Part of

Process	Carbon isotope fractionation process	$\Delta^{13}C$ (‰)	Reference
$1 \rightarrow 2$	Air-to-sea transfer of CO_2	−2.00	[12]
$2 \rightarrow 1$	(Sea-to-air transfer of CO_2)	(−10.0)	[12]
2	Hydration of CO_2 (^{13}C-enrichment in HCO_3^-)	+8.00	[14]
$2 \rightarrow 3$	HCO_3^- to CO_2 by carbonic anhydrase	+10.0	[15]
$2 \rightarrow 3$	Photoautotrophy (photosynthesis in seawater)	−29.0 to −11.0	[16–19]
$3 \rightarrow 4$	Diagenesis (shallow burial)	−4.00 to −5.00	[22, 150]
	Diagenesis (deep burial)	few	[150]
$4 \rightarrow 5$	Anaerobic oxidation (organic C to CO_2)	Not found	
$4 \rightarrow 6$	Methanogenesis (organic C to CH_4)	−61.5 to −31.1	Peatland [29]
		−83.0 to −72.0	From methanol [30]
$6 \rightarrow 7$	AOM	−29.00	With nitrate (not sulfate) [36]
$7 \rightarrow 8$	Carbonate authigenesis (from CO_2 or DIC)	Almost 0	In general [9]
		+0.08, +19.44	Certain seep cases [28]
$7 \rightarrow 10$	Chemoautotrophy	−33.0 to −24.0	Calvin-Benson cycle [151]
		−11.0 to −10.0	Reductive TCA cycle [152, 153]
	Biomineralization (shell formation)	A few; +10.0	To DIC; to food [154]

Table 2. Stable carbon isotope fractionation, $\Delta^{13}C$ (‰), during geo-biological processes of carbon dynamics associated with methane seepage.
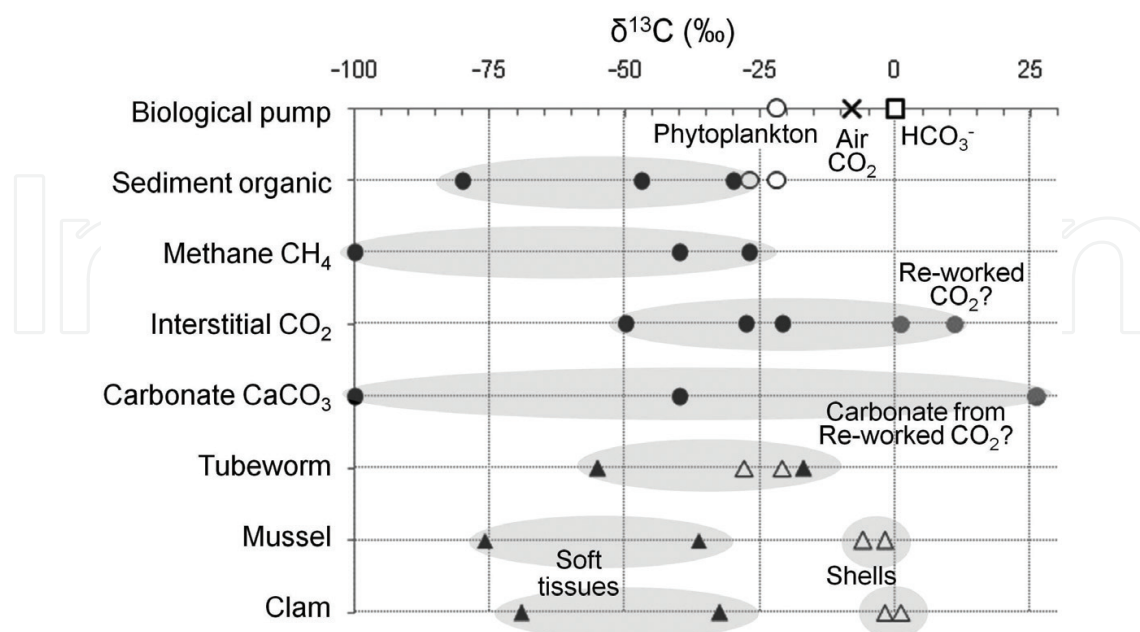

Figure 3. A schematized view of $\delta^{13}C$ variability from atmospheric CO_2 to authigenic carbonate and autotrophic fauna. The $\delta^{13}C$ values are taken from **Table 2**.

CO_2 in seawater will be hydrated toward a chemical equilibrium of CO_2-H_2CO_3-HCO_3^--CO_3^{2-} (virtually CO_2-HCO_3^--CO_3^{2-}), and these are collectively termed "dissolved inorganic carbon" (ΣDIC or simply "DIC"). Among DIC, HCO_3^- is the predominant ion form at seawater pH of 8.00 [13]. Fractionation between ^{12}C and ^{13}C also occurs during hydration of CO_2 into HCO_3^-, back-conversion (by carbonic anhydrase) from HCO_3^- to photosynthetically available CO_2, and photosynthesis mainly by phytoplankton that assimilate CO_2 via C3 pathway (Calvin-Benson cycle, **Table 2**) [14–19]. After all fractionations together, $\delta^{13}C$ of eventually (photosynthetically) produced biomass is generally taken as −22.0‰ [9].

About 0.50% of the photosynthetically produced organic matter is buried in the sediment [20], where the process is often termed as "biological pump" shown in **Figure 3** [21]. The $\delta^{13}C$ values of the "biologically pumped" sedimentary organic matter decreases from −22.0‰ in shallow (fresh) to −27.0‰ in deep (old) layers, due to diagenetic fractionation [22]. Almost the same $\delta^{13}C$ values, −22.0 to −30.0‰, of sedimentary organic matter from methane seepstwere reported [23–26]. However, very depleted $\delta^{13}C$ values, as low as −47.0 to −80.0‰, of sedimentary organic matter were also reported from the methane seep at the base of Florida Escarpment in the Gulf of Mexico [27, 28], which may be associated with "brine" seepage from very old organics or organics of non-photosynthetic origins.

Strong fractionation occurs during methanogenesis, for example, as strong as $\Delta^{13}C$ of >−60.0‰ in a Finnish peatland [29] and >80‰ from methanol in the laboratory [30]. Therefore, methane generated from sedimentary organic matter often shows depleted $\delta^{13}C$ values, as low as −40.0 to −100‰ [26, 31–33]. Care should be taken to such cases that even biogenic methane may be enriched (having high $\delta^{13}C$ values) due to microbial oxidation as described subsequently and thus mistakenly regarded as abiogenic (thermogenic) methane [34].

2.1.2. $\delta^{13}C$ values after anaerobic oxidation of methane

In methane oxidation, heavier methane ($^{13}CH_4$) is less preferably oxidized, and therefore $\delta^{13}C$ of the resultant CO_2 is depleted by 5.00 to 30.0‰, that is, $\Delta^{13}C$ of $CH_4 \rightarrow CO_2$ is generally −5.00 to −30.0‰ [34]. A decrease in $\delta^{13}C$, or $\Delta^{13}C$, during aerobic microbial methane oxidation is reported to be −15.0 to −30.0‰ [35]. AOM with nitrate (not sulfate) is reported to result in $\Delta^{13}C$ of about −30.0‰ [36]. Although $\Delta^{13}C$ of "AOM with sulfate" has not been determined, it would not be too far from these fractionation values.

Theoretically, $\delta^{13}C$ values of the resultant DIC forms (CO_2, HCO_3^-, and CO_3^{2-}) after AOM are depleted and actually determined to be −41.0‰ for DIC (virtually HCO_3^-) in interstitial water, compared with $\delta^{13}C$ −24.0‰ of sedimentary organic matter [25]. It should be remembered that $\Delta^{13}C$ of $CO_2 \rightarrow HCO_3^-$ is about +8.00‰ [14] (**Table 2**), leading to a generally accepted idea and the fact that $\delta^{13}C$ of DIC in non-seep, non-vent seawater is −2.00‰ or roughly 0‰. Returning to seep-methane-derived DIC, $\delta^{13}C$ −41.0‰ of DIC would possibly correspond to $\delta^{13}C$ −49.0‰ of CO_2. However, such a theoretical view is often challenged by reality. An example of sequential $\delta^{13}C$ values from sedimentary organic matter (−22.0%) and biogenic methane (−68.0‰) to CO_2 (−20.0‰ to +1.00‰) and DIC (−38.0 to +11.0‰) [26] is tough to be elucidated.

Common name	Functional name	Autotrophy	$\Delta^{13}C$ from DIC (‰)	Reference
Calvin-Benson cycle	C3; Reductive pentose phosphate cycle	Photo (O/A), Chemo, Methanol	−33.0 to −24.0	[151]
Hatch-Slack pathway	C4 carbon fixation	Photo (O)	−16.0 to −10.0	[151]
CAM pathway	Crassulacean acid metabolism pathway	Photo (O)	−20.0 to −10.0	[151]
Reverse Krebs cycle	Reverse tricarboxylic acid (rTCA) cycle	Photo (A), Chemo	−11.4, −10.0	[152, 153]
Wood-Ljungdahl pathway	Reductive acetyl CoA pathway	Chemo (Methanogenesis)	−36.0	[152]
3-Hydroxypropionate pathway		Photo (A), Chemo	−14.0 + 3	[155, 156]
3-Hydroxypropionate/4-hydroxybutyrate cycle		Chemo	+2.50	[157]
Dicarboxylate/4-hydroxybutyrate cycle		Chemo	Not found	

Photo, oxygenic (O), and anoxygenic (A) photosynthesis or photoautotrophy; Chemo, chemoautotrophy; and, Methano, methanotrophy.

Table 3. Pathways and fractionation factors, $\Delta^{13}C$ (‰), of autotrophic CO_2 assimilation.

2.1.3. $\delta^{13}C$ values of authigenic carbonates and autotrophic faunas

Generally, fractionation in $\delta^{13}C$, that is, $\Delta^{13}C$, from DIC to carbonates is regarded to be zero [9]. Therefore, authigenic carbonates in methane seeps should have depleted $\delta^{13}C$ values, as authigenesis starts with oxidation of depleted methane and proceeds with the resultant depleted CO_2, as typically shown by the $\delta^{13}C$ values of around −50‰ in the matrices, nodules, and cements of authigenic seep carbonates [37–39]. However, again, theories are challenged by unexpectedly high $\delta^{13}C$ values (**Figure 3**), for example, as high as +16 and +24‰ in carbonates of the Eel River Basin seeps [37, 40]. The involvement of ordinary (non-seep, non-vent) DIC and "leftover" DIC that had not been incorporated into earlier carbonate authigenesis (therefore enriched), as well as "re-worked" DIC that had been generated from leftover (enriched) CH_4, is imaginable.

The seep methane and derived CO_2 after AOM will also be incorporated into faunal biomass via thioautotrophic or methanotrophic biomass production by symbiotic bacteria, respectively. As the source methane and CO_2 are depleted in $\delta^{13}C$, the biomass $\delta^{13}C$ should be depleted accordingly. The observed $\delta^{13}C$ values in soft tissue of the gutless tubeworms are within the range from −55.0 to −18.0‰ [23, 31, 41–48]. The $\delta^{13}C$ values of tubeworm soft tissue are relatively higher (enriched) compared with those in the soft tissue of mussels and clams inhabiting the same seeps (**Table 1**; **Figure 3**) [46, 47, 49, 50], which may be related to the possible dual CO_2-fixation pathways (C3 pathway and rTCA cycle, **Table 3**) in seep tubeworms as predicted for the endosymbiont of the vent tubeworm *Riftia pachyptila* Jones, 1981, by metaproteomics [51]. Hard tissues such as shells of mussels and clams show generally higher $\delta^{13}C$ values than those in soft tissues, some of which are close to that of ordinary DIC (**Table 1**; **Figure 3**).

3. Authigenic carbonate rocks

Authigenic carbonates have recently been recognized as an important "carbon sink" in the global carbon cycling next to marine carbonates and organic matters [52], and the authigenesis occurs mainly at methane seeps via anaerobic oxidation of methane (AOM). In other words, methane seeps are often accompanied by authigenic carbonate rocks, that is, carbonate rocks that are formed in situ (autochthonously) in the seabed of methane seeps. The process generates structurally and compositionally multi-staged carbonates that are explained by not simply geochemical but biogeochemical or even microbial involvements [53]. The process may be accelerated due possibly to microbial involvements, as shown by "fresh" ages of authigenic carbonates, as fresh as 195 years old to almost zero for the carbonates exposed on the shelf slope of the Gulf of Mexico [126]; otherwise, from 53,400 to 1700 years old (53.4–1.70 kiloyears ago, ka) in the Gulf of Mexico, 45.5–3.00 ka in the Cong Fan, and 1.60–1.10 ka in the Black Sea [54], as well as 6.40–0.80 ka in the Hydrate Ridge [55].

A simplified mechanism of carbonate rock formation, or authigenesis, is as follows: methane is oxidized (mainly anaerobically with sulfate in the sediment) to generate DIC (CO_2-HCO_3^--CO_3^{2-}), which will react with Ca^{2+} and Mg^{2+} to precipitate $Ca(Mg)CO_3$. The precipitates will grow into aggregates and conglomerates of visible sizes. The real processes are not that simple [56], and they often take the forms of slabs in the sediment and pavements on the sediment, as well as half-buried aggregates with wide-ranged $\delta^{13}C$ values. Modes of carbonate occurrence are regarded as affected not only by microorganisms but also by carbonate-dwelling macro-fauna such as tubeworms and mussels [57].

Gutless tubeworms are occasionally incorporated in aggregates (**Figure 1**), as they require physically hard substrates for settlement and chemically aerobic-anaerobic boundaries, at which carbonates are exactly deposited though anaerobic oxidation of methane (AOM) with sulfate. Sulfide, an AOM byproduct, is aerobically oxidized by symbiotic bacteria (of the host tubeworms) with O_2 to obtain metabolic energy for thioautotrophic chemosynthesis; the symbionts are localized inside of the host cells and are termed "endosymbionts." The gutless tubeworms, therefore, colonize the hard substrates that lay in the zone where sulfide and O_2 coexist, that is, exactly the zone of carbonate deposition, almost overlapping the sulfate–methane transition zone (SMTZ).

Mussels that harbor thioautotrophic and/or methanotrophic symbiotic bacteria are epibenthic and colonize the carbonate rocks that extrude the sediment for settlement (**Figure 1**). By contrast, clams depending on bacterial thioautotrophy are semi-endobenthic and live half-buried in the sediment between and around carbonate rocks (**Figure 1**).

Types of authigenic carbonate rocks are generally grouped into calcites (as well as aragonites) and dolomites. Calcite is further divided into high- and low-Mg calcite according to their Mg contents. Interrelations between carbonate rock types and seep faunal types, that is, between calcites-dolomites and mussels-clams-tubeworms, are hypothesized as discussed later.

Extreme ^{13}C depletion is seen in the authigenic carbonates, when they are formed from depleted DIC (CO_2-HCO_3^--CO_3^{2-}) via AOM against biogenic-depleted methane having $\delta^{13}C$ values as

low as −125‰ [58]. On the other hand, enriched DIC is derived from oxidation (probably aerobic oxidation after AOM) of residual ^{13}C-enriched methane and yields ^{13}C-enriched carbonates accordingly. Therefore, the δ^{13}C ranges of authigenic carbonates are relatively greater than those of seep mussels, clams, tubeworms, and so on.

3.1. Authigenic calcite and aragonite

Among the carbonates, calcite/aragonite and dolomite are often seen in the methane seep environs. Calcite and aragonite are the carbonate polymorphs used in many marine organisms (mollusks, brachiopods, foraminiferans, corals, etc.); they have the same chemical formula ($CaCO_3$) but are different in crystal structures [59]. Aragonite is about 1.50 times as soluble (unstable) as calcite in seawater. Calcite that has lower contents of impurity magnesium, Mg, is more stable than high-Mg calcite. Therefore, the stability order on the deep seafloor is generally low-Mg calcite, high-Mg calcite, and aragonite.

Despite the stability next to low-Mg calcite, high-Mg calcite is often seen in the methane seep environs, with occasional association with tubeworm settlement. By contrast, low-Mg calcite is associated with mussel colonization. The formation and occurrence of less stable high-Mg calcite has not yet been fully elucidated. It may be associated with the attachment and growth of colonies of tubeworms and will probably provide a platform to investigate mineral-animal (and bacteria) interaction from a geo-biological point of view.

3.2. Authigenic dolomites

Dolomite, $CaMg(CO_3)_2$ in an ideal chemical formula, is formed by replacing calcium ions of calcite with magnesium ions. Or, high-Mg calcite may be regarded as an intermediate form of dolomitization. Once there was a paradox about dolomitization at low temperatures, that is, at physiological temperatures, it was solved by the laboratory experiment using sulfur-reducing (sulfate-respiring) bacteria [4–6].

Authigenic dolomite in methane seeps has rarely been studied, and an example from the naturally exhumed fossil seep in Greece showed depleted δ^{13}C values as low (light, depleted) as −8.00 to −29.0‰, maybe indicative of dolomite formation at the AOM zone in the sediment [60]. Authigenic dolomite in drill-cores from the oil fields in the Santa Barbara Basin, off California, showed δ^{13}C values of −16.0 to +9.00‰; lighter values are also indicative of dolomite formation in the relatively shallower zone of AOM with sulfate reduction, while heavier values may come from the relatively deeper zone of methanogenesis [61].

4. Autotrophic faunas: Tubeworms, mussels, and clams

Methane seeps and hydrothermal vents, as well as organic falls such as whale carcasses, are located not too far from each other, particularly along the Pan-Pacific "Ring of Fire." Similarities in taxonomic structures and energetic metabolisms (including chemoautotrophy and methanotrophy) between seep and vent fauna have been studied. While the importance of the β-diversity, that is, site-specific diversity, among the seeps and vents worldwide has been pointed out [62],

faunal assemblages in the semi-enclosed Guaymas Basin in the Gulf of California (six seeps and four vents without topo-/geographic barriers) share species compositions [63]. In the same but a greater way, the ring-of-fire-type array of seeps and back-arc basin vents in the active margins (convergent margins) contribute to biogeographic connectivity of vent and seep faunas but does not support the "stepping stone" hypothesis by whale carcasses [64].

The gutless tubeworms that represent the exotic seep/vent faunas had already been known (but only sporadically sampled) since the beginning of the twentieth century, before the massive colonies were discovered in association with deep-sea volcanism at the Galápagos Rift in 1977 [65]. It took 4 years to propose that the gutless tubeworms (polychaetes) depend for their nutrition on sulfide−/sulfur-oxidizing chemoautotrophic (thiotrophic or thioautotrophic) biomass production by endosymbiotic bacteria in their specialized sac-like tissue, trophosome [66]. The trophosome is a natural "culture vessel" of, for example, not-yet-cultured thiotrophic gamma-proteobacterial *Candidatus* Endoriftia persephone in the case of the giant vent tubeworm *R. pachyptila* Jones, 1981 [67], and has still been enthusiastically investigated from not only biological but also biomedical and biotechnological points of view [68].

It also took 3–4 years after the first discovery of methane seeps in the Gulf of Mexico [69] for scientists to reveal that seep mussels depend not on thiotrophic but on methanotrophic endosymbionts in gills [70, 71]. In 1987, methanotrophic symbiosis was also found in a non-vent, non-seep gutless tubeworm (*Siboglinum poseidoni* Flügel and Langhof, 1983 from polychaetes) from the sediment of the central Skagerrak strait [72, 73] and some other vent/seep mussel species, but not for clams [74]. While many bivalve and gastropod mollusks have chemo−/methanotrophic symbionts [75], this chapter focuses on bivalve mussels (*Bathymodiolus* Kenk and Wilson, 1985) and clams (*Calyptogena* Dall, 1891) from seep (and vent) habitats.

Symbiosis with more than one symbiotic species in one host, which is dual or multiple symbiosis, is known for gutless tubeworms; an example is the vent-dwelling tubeworm that hosts multiple thiotrophic species as endosymbionts [76]. In addition, dual symbiosis with both thio- and methanotrophic endosymbionts has been known for the seep mussels (*Bathymodiolus* spp.) in, for example, the Gulf of Mexico [77] and off-Congo passive margins [78], as well as other invertebrates (mostly gutless oligochaetes) dwelling non-vent, non-seep habitats (Note 2).

In addition to thiotrophy and methanotrophy, in 2011, hydrogenotrophy (chemoautotrophy based on hydrogen oxidation) appeared as the third way of a vent mussel (and possibly for seep mussels) [79].

4.1. Thiotrophy and methanotrophy

Photosynthesis and chemoautotrophy differ in energetic processes but share the CO_2-fixing pathways, for example, the best-known Calvin-Benson cycle (reductive pentose phosphate cycle). Currently, eight autotrophic CO_2-fixing pathways, including Calvin-Benson cycle, are known for life even in the dark chemoautotrophy (**Table 3**) [80]. Dual pathways are widely known in chemoautotrophy-based macro-organisms, such as siboglinid (formerly known as vestimentiferan and pogonophoran) tubeworms, of hydrothermal vents and methane seeps [48].

In addition to a variety of CO_2-fixation pathways, a battery of energetic pathways with diverse reductants and oxidants (electron donors and acceptors) is also known for chemoautotrophy [81, 82]. The most representative one in the methane seeps is the oxidation of sulfide. If chemoautotrophy is based on sulfide oxidation, it is correspondingly termed "thiotrophy" or "thioautotrophy." While aerobic oxidation of sulfide is most common, anaerobic oxidation of sulfide with nitrate, $HS^- + NO_3^- \rightarrow HSO_4^- + N_2$ (Note 3), (nitrate reduction, nitrate respiration, or denitrification), is possible, although its occurrence in methane seeps is not necessarily evident.

Both aerobic and anaerobic oxidation of H_2 can also provide an energetic basis for chemo-autotrophy. Aerobic oxidation of H_2 with O_2 has recently been recognized as widespread among the hydrothermal vent chemoautotrophy [79, 83]. H_2 is also oxidized anaerobically with CO_2, which corresponds to the autotrophic CO_2 respiration, or autotrophic hydrogenotrophic methanogenesis, and represented by the thermophilic species of *Methanothermobacter thermoflexus* (Kotelnikova et al. 1994) Boone 2002 and *M. thermautotrophicus* (Zeikus and Wolfe 1972) Wasserfallen et al. 2000. However, in a non-thermophilic environment such as artificial anaerobic digesters, non-autotrophic CO_2 respirers dominate the microflora [84], which gives an implication for considering CO_2 respirers in the "cold" methane seeps.

Methanotrophy, feeding methane as "food" or "fuel," may be placed between autotrophy and heterotrophy, because methane can be placed between inorganic and organic matter [85]. For most methanotrophs, methane serves as the dual sources for metabolic energy (catabolism, dissimilation) and biomass production (anabolism, assimilation). In this context, if methane is taken as half-organic and half-inorganic, methanotrophs are accordingly regarded as half-autotrophs and half-heterotrophs. However, the "type X" (or type Ib) methanotrophs and Verrucomicrobia-related methanotrophs are known to possess the CO_2-fixing enzyme, RuBisCO, and assimilate CO_2 via the Calvin-Benson cycle [86], and they are probably more widespread than previously presumed [87, 88].

Anaerobic oxidation of methane (AOM) is also a form of methanotrophy that is conducted by more than one microbial species, that is, archaeal-bacterial consortia, as described earlier. Both archaeal methanogens and bacterial sulfate-respirers (sulfate-reducing bacteria) are reported to assimilate CH_4-derived (CH_4-oxidized) CO_2 autotrophically via the Calvin-Benson cycle [89].

4.2. Tubeworms

The gutless tubeworms, or siboglinid veriforms, represent the most enigmatic and intriguing organisms of the seep fauna in terms of body plan, morphology, life cycle, metabolisms, endosymbioses, and so on [90]. The first specimen of the gutless tubeworms was dredge-sampled in 1900 during the Siboga Expedition (1899–1900) from 462 m deep, off Selayar Island, Flores Sea, Indonesia [91], where methane seepage is presumed to occur in the active margin [92], and was later described as the new species *S. weberi* Caullery, 1944 [93], with proposals of the new genus *Siboglinum* Caullery, 1914, and the new family Siboglinidae [94] (Note 4).

Thereafter, siboglinid worms, typically >10-mm long and <1-mm wide, were collected sporadically from various oceanographic sites. Due to their unique and enigmatic body plan with

Year	Species	Genus	Family	Order	Class	Phylum
Current	236 accepted [158]	32 accepted [158]	Siboglinidae [94]	(Sabellida) [159]	(Polychaeta) [160])	(Annelida) [158])
2015	*Lamellibrachia sagami* Kobayashi, Miura and Kojima, 2015 [96]					
1997			Siboglinidae [94, 161, 162]			
1985	*Escarpia spicata Jones, 1985, Escarpia laminata* Jones, 1985 [104]	*Escarpia* [104]				Vestimentifera
1981	*Riftia pachyptila* Jones, 1981 [163]	*Riftia* [163]				Pogonophora
1975	*Lamellibrachia luymesi* van der Land and Nørrevang, *1975* [103]					
1969				Vestimentifera		
1964	*Lamellibrachia barhami* Webb, 1969 [164]	*Lamellibrachia* [164]	Lamellibrachiidae			
1944	*Siboglinum weberi* Caullery, 1944 [93]					Pogonophora
1937				Pogonophora		
1933			Sabellidae			
1914		*Siboglinum* [94]	Siboglinidae [94]			

Other marine gutless worms (mostly belonging to the subclass Oligochaeta, class Clitellata) are not listed. Only accepted highest taxa, that is, accepted parents, as well as representative species and genera, are listed with accepted references. Current supra-taxa are also listed but in parentheses. Currently (as of May 2018), the family Siboglinidae is the highest taxon (parent) of all the vent/seep gutless tubeworms.

Table 4. Taxonomic changes in positions and statuses of "gutless tubeworms" (mostly belonging to the class Polychaeta) that inhabit hydrothermal vents and methane seeps.

no mouth, no anus, and no digestive tract, their way of living was interpreted to depend on dissolved organic matter absorbed from somewhere of body surface including the anterior "beard"; they were often called "beard worms." The interpretation was based on the common belief that animals are heterotrophic. The heterotrophic animal view is still correct even now in a strict sense (that siboglinid worms depend eventually on organic matter produced by symbiotic bacteria), but the less-defined phrase "autotrophic animal" was advocated for siboglinid worms in a broad sense [66].

The gutless siboglinid worms often host a single thiotrophic endosymbiont species. A non-vent, non-seep gutless tubeworm (*S. poseidoni* Flügel and Langhof, 1983) harbors a methanotrophic symbiont [72, 73] probably of one species. However, gutless tubeworms may occasionally possess a single but probably methanotrophic endosymbiont, or thiotrophic but multiple endosymbionts. For example, the sediment-dwelling *Oligobrachia mashikoi* Imajima, 1973, hosts a symbiont that bears the genes of methanotroph-related 16S rRNA and CO_2-fixing enzyme RuBisCO, suggesting the possible involvement of a CO_2-fixing methanotroph, that is, "type X" or type Ib methanotroph [95]. Another sediment-dwelling worm (*S. poseidoni*) also has a methanotrophic endosymbiont [73]. Regarding multiple symbioses, some individuals of *Lamellibrachia* sp., currently described as *Lamellibrachia sagami* Kobayashi et al. [96], from the off-Hatsushima seep, Sagami Bay, central Japan, were reported to have four distinct thiotroph-like symbionts in their trophosome tissue [97–100], and *L. anaximandri* Southward, Andersen and Hourdez, 2011, despite vent-dwelling, also hosts multiple thiotrophic species as endosymbionts [76].

Due to their unique and enigmatic body plan, their taxonomic position and status have been confused and subject to not a few, not minor changes (**Table 4**), and still investigated by modern phylogenetic and phylogenomic approaches [101, 102]. As to their physiology, the "giant tubeworm" or *R. pachyptila* that inhabits hydrothermal vents is probably the most popular, well known, and well studied. The methane seep counterparts would be *L. luymesi* van der Land and Nørrevang [103] and *Escarpia laminata* Jones, 1985, inhabiting the base of Florida escarpment in the Gulf of Mexico [104], which are known to have extreme longevities as long as possibly >300 years [105–107].

The giant tubeworm *R. pachyptila* grows quickly to >2 m high as far as the worm can uptake sulfide emitted from the vents (**Figure 4A**). By contrast, the seep tubeworm *L. luymesi* may also grow over 2 m long (not high) only slowly over >200-year longevity [108], as well as *E. laminata* may grow over 300 years [107]. Individual worms of the colonies of *Lamellibrachia* Webb 1969 often look "trimmed" within the limits of seeped methane/sulfide (**Figure 4B**). Not only trimmed, their bodies are often twisted to crawl on seafloor and even buried in the sediment. It has been pointed out that the posterior extension, or "root," of *Lamellibrachia* worms functions to "sip" sulfide from the sulfate–methane transition zone (SMTZ) in the sediment [109] as well as to "dump" sulfate and protons (H+) to SMTZ [110]. Sulfate dumped into or below SMTZ will facilitate anaerobic oxidation of methane (AOM) with sulfate, and sulfide will be regenerated from the dumped sulfate and protons via AOM.

A whole process including symbiotic thiotrophy (aerobic oxidation of sulfide) and AOM in sediment may be viewed as an "extended symbiosis" that circulates the regeneration of

sulfide and sulfate as if it functions as a "coffee percolator" (Note 5). The H_2S/SO_4^{2-} percolator is driven by methane supplies, eventually leading to the generation of CO_2-HCO_3^--CO_3^{2-} from methane and thus to authigenesis of carbonates. The *Lamellibrachia* worms are often associated with carbonates and even incorporated in carbonates occasionally to form conglomerates as discussed later (**Figure 5**).

The tubeworm soft tissue that contains an amount of endosymbiotic thiotrophic bacteria is relatively higher (more enriched) in $\delta^{13}C$ than soft tissues of mussels and clams of the same
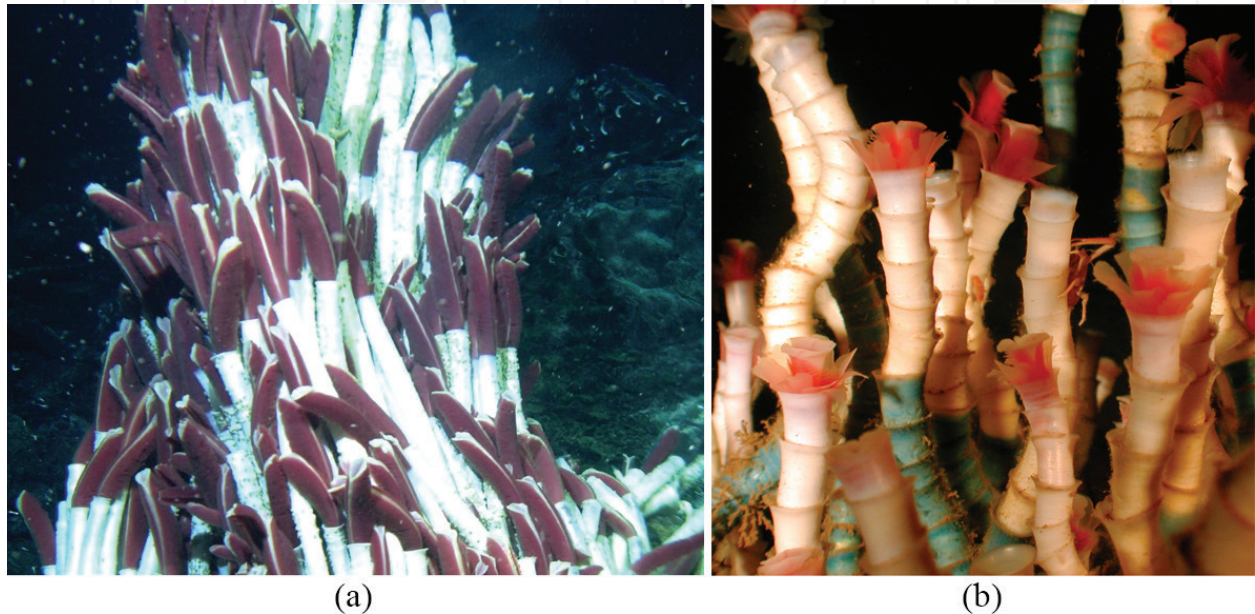
Figure 4. The gutless tubeworms of a hydrothermal vent and a methane seep. (A) *Riftia pachyptila* Jones, 1981, inhabiting a vent site of the East Pacific rise at 2500 m depth [167]. (B) *Lamellibrachia luymesi* van der Land and Nørrevang [103], from a methane seep at 550 m depth in the Gulf of Mexico. The blue-stained tube indicates approximately 14 months of growth [168]. Photograph by Charles R. Fisher.

Figure 5. The seep tubeworm *Lamellibrachia sagami* Kobayashi et al. [96], being embedded in authigenic carbonate formed in the off-Hatsushima methane seep at 1100 m depth, Sagami Bay, Central Japan. The width of the photograph corresponds to 7 cm. Photograph by the author.

seep (**Figure 3**) [46]. Tubes of the worms show intermediate $\delta^{13}C$ values compared with those of soft tissues, with a weak tendency of $\delta^{13}C$ becoming heavier toward the posterior end of the tubes [104]. This may be associated with the phenomenon that lower (more depleted) $\delta^{13}C$ values are seen in the tubeworm-associated high-Mg carbonates than those colonized by *Bathymodiolus* mussels [39, 50, 57, 111].

4.3. Mussels

The mussels belonging to the genus *Bathymodiolus* Kenk and Wilson, 1985, represent the vent and seep fauna as well and harbor endosymbiotic bacteria eventually in their gills. While juveniles of vent mussels host epi-symbionts almost everywhere on their surfaces, endosymbiotic colonization becomes restricted to gill tissue during the mussel growth [112], and even adults are subject to continued bacterial colonization attacks throughout their lifetimes [113]. Although the process was observed with vent *Bathymodiolus* mussels, it may similarly occur to the seep *Bathymodiolus* mussels, as it is known for the shallow-water tropical lucinid clam *Ctena orbiculata* (Montagu, 1808) cited as its synonym *Codakia orbiculata* (Montagu, 1808) [114].

Their endosymbionts are thiotrophs or methanotrophs or both. The vent mussel *B. thermophilus* Kenk and Wilson, 1985, in the East Pacific Rise has only thiotrophic symbionts [66, 115], while the seep mussel *B. childressii* Gustafson, Turner Lutz and Vrijenhoek, 1998, in the Gulf of Mexico hosts only methanotrophic symbionts [70]. A vent *Bathymodiolus* species in a western Pacific harbors a CO_2-fixing methanotroph, that is, "type X" or type Ib methanotroph [116].

Dual symbiosis, in which a single host harbors both thiotrophic and methanotrophic bacteria, has been described for seep mussels from the Gulf of Mexico (*B. brooksii* Gustafson, Turner, Lutz and Vrijenhoek, 1998) [71], off Congo passive margins [78] and other seep mussels, as well as vent mussels. A vent *Bathymodiolus* mussel is known to harbor hydrogen-oxidizing autotrophic bacteria [79], which process is now regarded as probably more widely and ubiquitously distributed in deep-sea environments [83].

The small mytilid mussel, *Idas* sp., inhabiting carbonate crusts at the off-Nile fan seep harbors six endosymbionts probably of thiotrophs, methanotrophs, and previously unrecognized roles [117]. Similarly, *B. heckerae* Turner, Gustafson, Lutz and Vrijenhoek, 1998, inhabiting the "asphalt" seep in the Gulf of Mexico [118, 119] harbors multiple endosymbiotic bacterial species, one of which belongs probably to the genus *Cycloclasticus* Dyksterhouse, Gray, Herwig, Lara and Staley, 1995 [120]. The symbiotic *Cycloclasticus* appeared to degrade and derive carbon and energy from short-chain alkanes such as ethane and butane [121], despite lack of genes responsible for the degradation of polyaromatic hydrocarbons that are seen in other *Cycloclasticus* species [122].

Overall, it can be said that the seep mussels possess high plasticity and flexibility in harboring and depending on a variety of endosymbionts and their energetic metabolisms: from single via dual to multiple symbioses with thiotrophs and methanotrophs via hydrogenotrophs to asphalt-degrading heterotrophs. This symbiotic plasticity may facilitate evolution and ubiquity of these mussel species [123–125].

The *Bathymodiolus*, as well as *Idas*, mussels attach and settle on hard substrates such as basalts in hydrothermal vents and carbonates in methane seeps, like tubeworms do. However,

	Modern carbonate in the off-Hatsushima methane seep, Sagami Bay		Miocene carbonate (17.2–14.4 Ma), Hayama Group, Miura Peninsula	
	With tubeworms	Without tubeworms	With fossil tubes	Without fossil tubes
$\delta^{13}C$	−28.0 to −27.0‰	−34.0 to −33.0‰	Not determined	
$CaCO_3$ (%)	34.0–43.0	52.0–86.0	39.0–40.0	66.0–67.0
$MgCO_3$ (%)	12.0–15.0	<0.10	14.0–15.0	<0.10
FeO_2 (%)	4.00–6.00	5.00–15.0	4.00–5.00	28.0–29.0
SiO_2 (%)	28.0–31.0	<0.10–37.0	28.0–29.0	<0.10
AlO_2 (%)	9.00–10.0	<0.10–12.0	9.00–10.0	<0.10

Table 5. Comparison of $\delta^{13}C$ values (‰) and compositions of selected chemical species (weight-to-weight %) in modern and Miocene carbonates with reference to the presence/absence of living tubeworms or fossil worm tubes [3, 100, 165, 166].

Bathymodiolus mussels tend to colonize ^{13}C-enriched carbonates, compared with tubeworm association with ^{13}C-depleted high-Mg carbonates [39, 50, 57, 111].

4.4. Clams

The "giant white clams" or the vesicomyid clams belonging to the genes *Calyptogena* Dall, 1891, also represent the fauna of both hydrothermal vents and methane seeps. They are mostly dependent on endosymbiotic bacterial thiotrophs for their nutrition, not on methanotrophs [74]. However, a thyasirid clam, *Axinulus hadalis* Okutani et al. [126], living within (but a few meters deeper from) the deepest methane seep community [127], was reported to have dual endosymbionts, which were speculated to be thio- and hydrogenotrophs, that is, sulfur- and hydrogen-oxidizing chemoautotrophs, respectively [128].

The *Calyptogena* clams are semi-endobenthic and live half-buried in the sediment between and around carbonate rocks. Therefore, the clams are not associated with carbonate rocks for living, although they occur in close vicinities. This may be confirmed by the difference in $\delta^{13}C$ values of the clam shells and carbonate rocks, which would reflect different carbon sources despite their habitat vicinities [129].

5. Conglomerates of carbonates and tubeworms

Authigenic carbonates "grow" in the zone anaerobic oxidation of methane (AOM) and sulfate–methane transition zone (SMTZ) in the sediment of methane seeps, as shown by low $\delta^{13}C$ values. Similarly, the gutless tubeworms such as *Lamellibrachia* species grow toward posterior rather than anterior to "percolate" (exploit and regenerate) sulfide in the horizon of AOM zone overlapped with SMTZ, also as indicated by the tendency of lower $\delta^{13}C$ toward the posterior end of the tube [24]. Sipping of sulfide and dumping of sulfate at the root (posterior end) of the tubeworms may change the local pH and thus affect the conditions for favored

formation calcite to aragonite [57, 130]. These growths of authigenic carbonates and auto-trophic tubeworms occur concomitantly near the posterior of worm tubes [130] and often intercalate each other to form mineral-animal "conglomerates" (**Figure 5**). Although detailed observation suggested that a nodular high-Mg calcite is formed before tubeworm settlement [130], the coupling of high-Mg calcite and tubeworm colonization has not been elucidated.

The conglomerates of calcite and *L. sagami* in the off-Hatsushima methane seep, Sagami Bay, central Japan, were studied with reference to $\delta^{13}C$ and Mg contents and were compared with those from the past authigenic carbonate formed in the Miocene, 17.2–14.4 million years ago (Ma), from the Hayama Group, Miura Peninsula, central Japan. The two sites, that is, modern and past methane seeps, are only <50.0 km distant, and the data from the modern and past carbonates revealed that the high content (~15.0%) presence of Mg in relatively high $\delta^{13}C$ (<30.0‰ against >30.0‰) calcite is closely associated with conglomeration with tubeworms in both modern and fossil specimens (**Table 5**) [3, 100, 131].

6. Conclusive remarks

Authigenic carbonates and autotrophic faunas provide unique and typical landscapes of methane seeps (**Figures 1** and **2**). The carbonates and faunas are formed and maintained not independently but interactively via microbial activities of methanogenesis, anaerobic (and aerobic) oxidation of methane, anaerobic respirations such as sulfate reduction, and carbonate (particularly dolomite) formation. During these microbial processes, the stable carbon isotope ratios ($\delta^{13}C$ values) do shift with respective ranges of isotopic fractionation ($\Delta^{13}C$, **Tables 2** and **3**). Not only microorganisms but also macro-fauna may contribute to form and shape authigenic carbonate rocks. In the case of rock-tubeworm conglomerates, tubeworms actively recycle sulfide and sulfate in sediment, resulting in the acceleration of "growth" of the conglomerates.

Acknowledgements

Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Notes

(Note 1) In the strict sense, chemolithoautotrophy should be used instead of lithotrophy or chemoautotrophy; however, the term is only used by experts in rather a narrow area of microbiology and sounds too technical for non-expert audience.

(Note 2) Endosymbiosis is widespread in non-vent, non-seep organisms [123]. Chemoautotrophic bacterial endosymbiosis was characterized with the gutless oligochaetes *Inanidrilus leukodermatus* (Giere, 1979) from 5-m-deep sediment in a Bermuda inlet [135] and *Olavius crassitunicatus* Finogenova, 1986, from 270- to 359-mdeep sediment in the Peruvian passive margin [136], as well as a marine nematode *Astomonema* sp. from coral reef sediments in the Bahamas [137]. Multiple endosymbiosis of the gutless oligochaete *Olavius algarvensis* Giere, Erséus and Stuhlmacher, 1998, was subject to genetically and biochemically dissected by metaproteomics [138] that revealed unusual pathways, for example, use CO and H_2 for energetic metabolism [139]. Animal-bacterial chemo−/methanotrophic symbioses have recently been recognized as more widespread and ubiquitous in anaerobic sediments, besides vents, seeps, and organic falls, than previously presumed [140]. A microbiome of an individual of the gutless oligochaete *I. exumae* Erséus, 2003, differs markedly from those of other 22 individuals [141], which also demonstrates the symbiotic plasticity that may facilitate the adaption and evolution of this group of the gutless tubeworms.

(Note 3) Anaerobic oxidation of sulfide with nitrate, which is anaerobic thiotrophy (thioautotrophy) based on nitrate-respiration, is seen in bacterial species belonging to the genus *Beggiatoa* Trevisan, 1842 [132]. This energetic metabolism was once expected for the endosymbiont of the hydrothermal vent tubeworm (*R. pachyptila* Jones, 1981) [133], but the possibility was denied later [134].

(Note 4) Maurice Jules Gaston Corneille Caullery (1868–1958), a French zoologist, studied the first specimen of the "beard worm" and proposed the new family Siboglinidae and new genus *Siboglinum* Caullery, 1914, presumably named after the Dutch "Siboga" Expedition (1899–1900), during which the specimen was dredge-sampled. "Siboga" was the name of the vessel, which originally was a 50-m-long gunboat owned by the government of the Dutch East Indies [142]. Caullery described the new family Siboglinidae in 1914 based on the simultaneously proposed new genus *Siboglinum*. The type species of the genus, *S. weberi* Caullery 1944, was described subsequently 30 years later, in 1944. It is reasonably considered that the specific epithet "*weberi*" was named after the leader of the "Siboga" expedition, Max Carl Wilhelm Weber, a German-Dutch zoologist.

(Note 5) The sulfide/sulfate "percolator" in the seep system can be viewed as "extended symbiosis" between gutless host tubeworms, thiotrophic endosymbionts, and sulfate-consuming AOM microbial consortia. In these relationships, biologically true symbiosis is postulated only between host worms and internal thiotrophs, and the involvement of external AOM consortia is regarded as "extended". By contrast, true endosymbiosis of a host worm and two bacterial symbionts, that is, dual symbiosis of sulfur-oxidizing and sulfate-reducing bacteria is seen in the gutless oligochaete worm *Olavius algarvensis* Giere, Erséus and Stuhlmacher, 1998, and *Olavius crassitunicatus* Finogenova, 1986, that host multiple (more than dual) endosymbionts [136, 143].

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