Deep sea vents and seeps: with a little help from my little friends – life fueled by gas release from the seabed

Sir: I saw a film on YouTube that the deep-sea can be crowded with marine life where gas escapes. Why is that?

Fig. 1: A hydrothermal vent ecosystem at 2000 m water depth in the Guaymas Basin, Gulf of California © Image is taken by Andreas Teske from the submarine ALVIN; Woods Hole Oceanographic Institution. The vent center is covered with tube worms of the genus *Riftia* and yellow and white microbial mats formed by sulfur-oxidizing bacteria.

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Deep sea vents and seeps

Storyline

The deep ocean is the largest biome on Earth, it covers an area of 60% of our planet's surface, and has an average depth of 3800 m. It is characterized by permanent darkness below 200 m, since most sunlight is attenuated by water. Life in the deep sea is adapted to cold temperatures and to high pressure, due to the weight of the water. For a long time, the deep sea was considered a desert, and an extreme environment, limiting the expansion of life. Indeed, large mobile life like fish, squids, and crabs are rare. This is because most of the deep sea is energy-starved. There is not enough sunlight for algae to grow, hence the food web depends on detritus, leftover algal material that sinks down to the seafloor. But already 40 years ago, scientists found some ecosystems in the deep sea that are different. Where gas escapes from the seabed, some amazingly rich oases of life form. Myriads of mussels, shrimps and alien-like giant tube worms gather around so called "hot vents" and "cold seeps". Why there, and how can marine life occupying these special oases tap into deep energy sources that allow higher biomasses than in coastal waters?

In the early days of the discovery of these oases of life, this was a real mystery. Geologists and biologists studied these habitats by submersible dives and later by robots with cameras. The scientists found that the deep-sea oases are rather small in space, often only a few meters or hundreds of meters across. In their vicinity, they often found marine life that filter particles from seawater, like sea anemones, sponges, deep-sea corals and sea lilies. At the center of the oases, the scientists found gas escaping from the seafloor, often from mineral structures covered by thick mats of microorganisms. Basically, two types of gas-emitting deep-sea habitats were recognized. One was associated with mid-ocean ridges, where new seafloor is born from ocean plates drifting apart. In such areas, "Hot vents" were identified that emit very hot seawater full of gas and particles, looking like a flare of smoke rising from a chimney. These systems are hence called "Black smokers". Hot vents form when hot magma from the Earth interior comes in contact with seawater. In complex chemical reactions at very high temperatures, the seawater interacts with newly formed rocks, and energy-rich gases such as hydrogen and methane but also reduced sulfur species and metals get emitted. The fluids are often as hot as 400°C. The other type of gas-emitting deep-sea ecosystem teaming with life is called a "cold seep". Its gas is mostly made of methane, other volatile hydrocarbons and sulfide. Cold seeps are found around the margins of all continents. They especially occur in areas with a high ocean productivity, where a lot of organic matter gets buried in the seabed. Over very long timescales of millions of years, this matter is transformed either by heat or by microorganisms to methane, in a process called methanogenesis. Methane is also called "swamp gas", for the reason that it is formed from putrefaction of plant detritus by unique microorganisms, called methanogens, in stagnant water bodies. These can produce enormous amounts of methane gas as a waste product from their metabolism. With time, the gas accumulates in the seafloor and forms bubbles, even at the high pressure prevailing. Eventually, the light, methane-rich cold fluids are pressed out under the weight of sediments and water. When it is cold enough on the seafloor, the gas forms layers of frozen clathrates – ice-like crystalline solids – also called gas hydrates. When there is gas oversaturation, streams of gas escape from the seafloor into the ocean water. But why do these processes attract marine animals and what is the role of the microorganisms in this?

Methane, sulfide or hydrogen are reduced chemical compounds that, when consumed with oxygen can provide large amounts of energy. Animals (including humans) cannot harvest the energy stored in those compounds. They rely on the intake of complex organic molecules like sugars, proteins and fats, which they digest internally to drive their metabolism. In contrast, some microorganisms are metabolically much more versatile and can obtain energy directly from reduced gases in solution, like methane, sulfide and hydrogen that are transported with the seep and vent fluids. Humans also use hydrogen or methane gas to heat, cook, or drive a car. But, we have to burn the gas with oxygen in a flame, and then use the heat for generators. The gas-feeding microbes can use that energy directly, because they are equipped with specific enzymes that allow them to harvest the energy in cascades of chemical reactions. Some microbes do not even need oxygen to "respire" these compounds, but can use sulfate, part of the salt in seawater. The microorganisms use the energy gained by those reactions to produce biomass in a process called chemosynthesis. In this process, they fix CO_2 into sugars or other simple organic compounds, which they can then use to build cell materials, like lipids, proteins and nucleic acids. At seeps and vents there is so much energy to gain from gases, and there is also an endless supply of CO_2 dissolved in seawater, that thick mats of microbes can grow on the seafloor, forming visible white or yellow mats (Fig. 1). In the water column, they may grow in flocks, where they can serve as food source to filter feeding animals such as sponges and sea anemones.

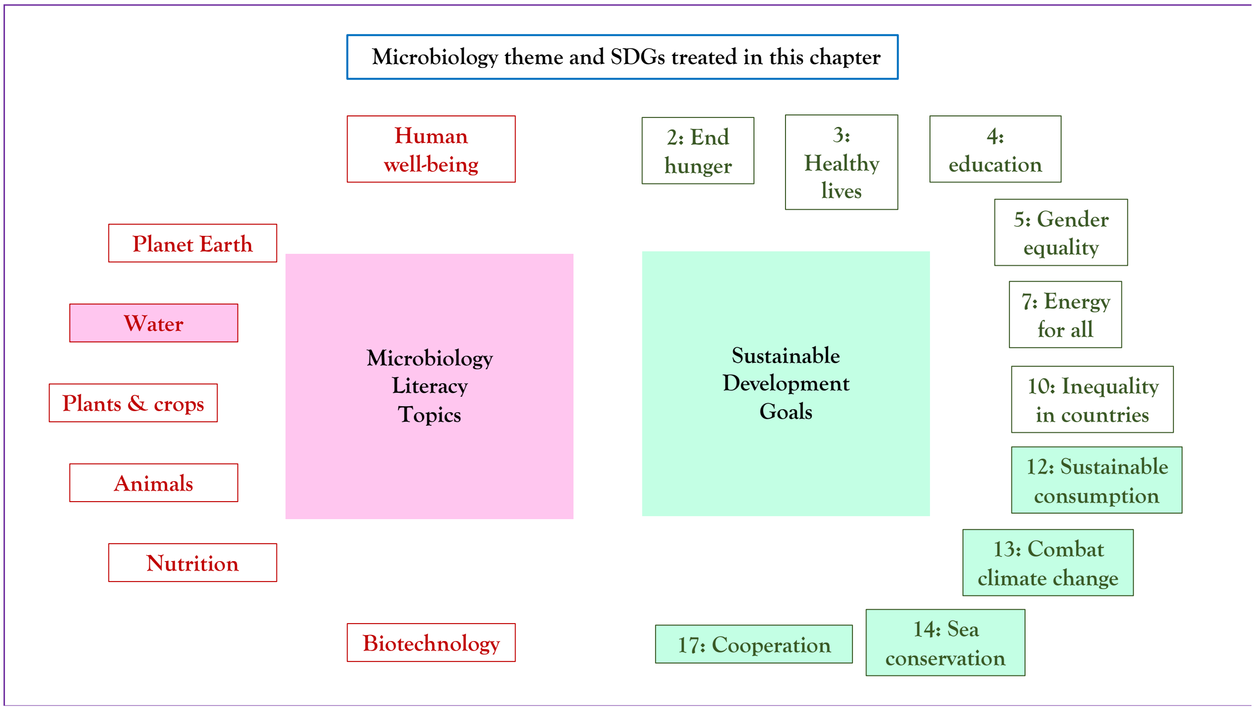
But the most interesting type of interaction between microbes and animals are the obligate symbioses at vents and seeps. This is a permanent partnership, with mutual benefits to both the microorganisms and the animals such as tube worms, mussels or shrimps. The animals provide a safe home for the microorganisms in specific cells and organs they build, like the trophosome in worms or on the back of shrimp. The animals provide transport of gases by their blood as in the worms or by pumping seawater as in the gills of bivalves in which the microbes live. In exchange, the chemosynthetic bacteria use the energy stored in those gases to produce food for the animals. These symbioses are highly successful in the deep sea – they form the densest biomasses and really giant forms of animals. Tube worms can get meters long and arm thick! We still know far too little about the role of cooperation between microbes and animals, and how it is organized. Like, how does the tube worms know how to select the perfect partner and not those that would harm them?

By their action, these microorganisms create unique ecosystems at the deep sea, which are independent of sunlight. They can provide so much energy that these environments are full of life: mussels, tube worms and other animals. These organisms also protect the planet from toxic or nasty compounds such as the smelly sulfide, which they convert into sulfate. The microorganisms also consume the methane, before it can reach the atmosphere. This is important, because methane is a strong greenhouse gas. Greenhouse gases are compounds that prevent the emission of infrared light from the Earth and this leads to global warming.

Microbiology and Societal Context

The microbiology: First life on Earth; life in extreme environments and on other planets; Archaea; Bacteria; extremophiles; chemoautotrophy; consumption of greenhouse gases; symbioses between microorganisms and invertebrates; inter-domain syntrophy; marine microbiomes; microbes as producers of fuels; microbial cycling of climate-active gases; electric microbes and element cycling; microbes as rock makers – inorganic carbon storage; metal cycles; origin and evolution of life;

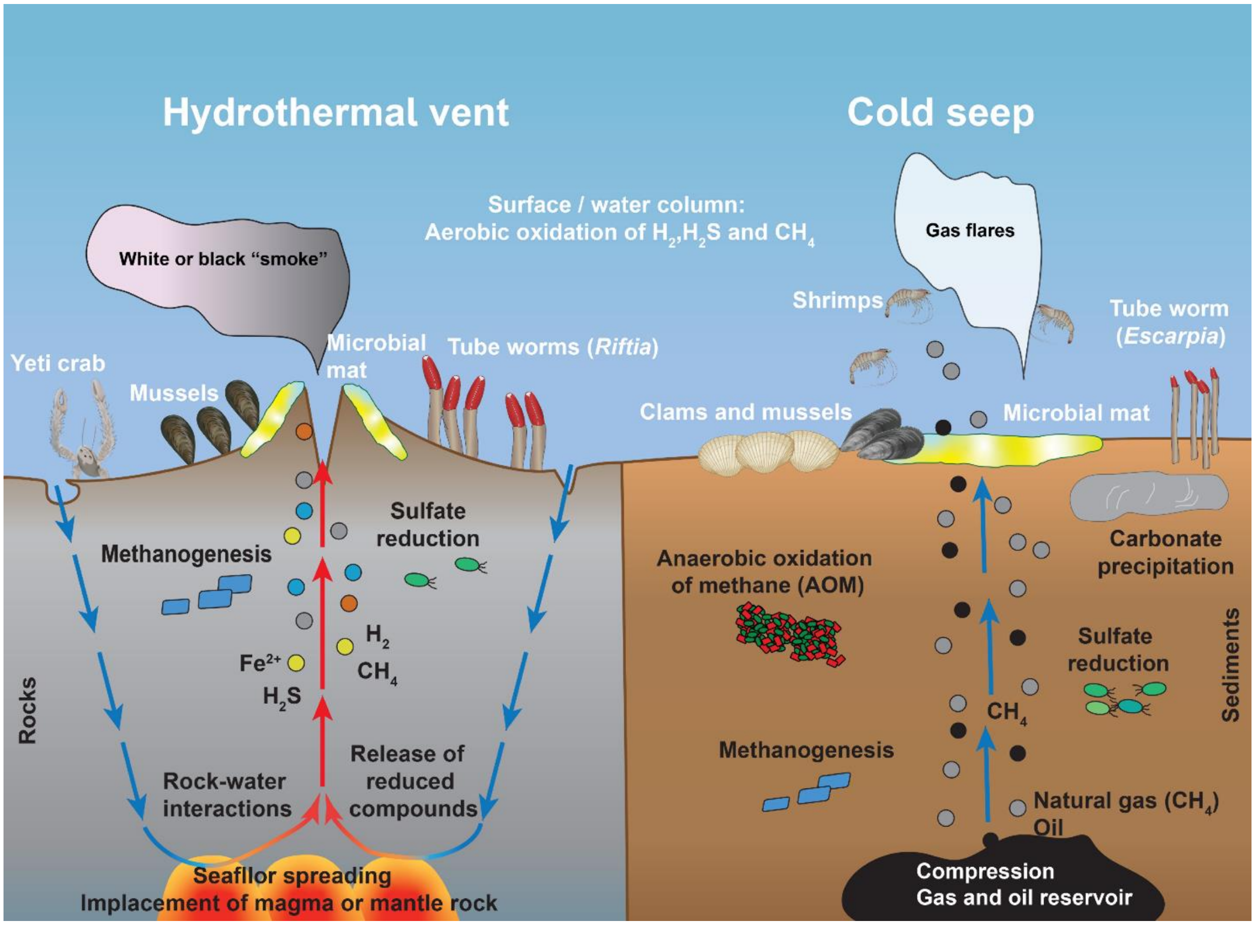
microbial mats; life driven by geological gas release; vhemoautotrophic primary production; oil spills; marine micronutrient cycles; carbon fixation; microbial greenhouse gas oxidation. *Sustainability issues:* sustainable production and consumption; climate change; sea conservation; biodiversity; cooperation.



Deep sea vents and seeps: the Microbiology

1. Hydrothermal vents and how they attract microorganisms. The Earth's solid crust is built from different plates that are moving on the Earth's mantle in a process called plate tectonics. Hydrothermal vents systems are especially abundant at active ocean plate borders, at mid-oceanic ridges, where melted rocks form new seafloor. The vents occur where the heat drives seawater circulation within the oceanic crust, and ultimately the heated fluids are expelled into the cold oceans, and precipitate their minerals (BOX 2, left panel).

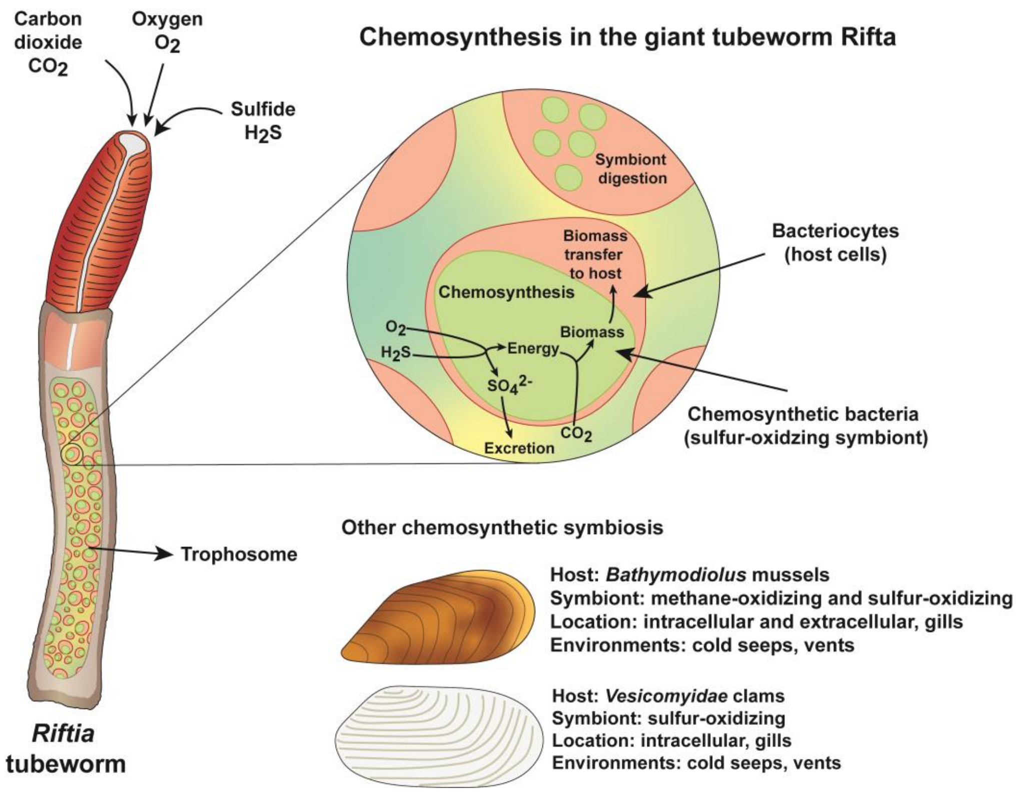
The heat transported from the inner Earth causes the intake of seawater into the newly formed seafloor. This water alters the fresh rocks and leaches large amounts of energy-rich reduced compounds. For instance, in the process called serpentinization, the weathering of Earth mantle rocks to clay by seawater intrusions, releases large amount of hydrogen gas (H_2). This gas might further react with carbon dioxide (CO_2) to form natural gas, mostly methane (CH_4). Also the volcanic rocks, called basalts, are leached by the intrusion of seawater. Here larger amounts of the toxic gas hydrogen sulfide (H_2S) are released. These reduced, energy-rich compounds are then transported and emitted into the ocean at the venting sites, where they mix with the oxygen-rich deep-sea waters. At this interface between reduced, energy-rich fluids and oxic water, the vent microorganisms thrive by consuming methane, hydrogen gas, sulfide or reduced iron. They gain energy by oxidizing these compounds with molecular oxygen (see BOX 3). These microorganisms can be found in or on the rocks, free-living in the vent plume, or as symbionts of invertebrates. The giant vent worms or bivalves have specific organs and cells, which offer a home to the microbes in which they are supplied with vent water and oxygen. Such a tight cooperation between animals and bacteria to utilize Earth's chemistry is unique for the ocean. The richness of life at vents attracts a large number of further organisms creating complex food webs and ecosystems.



BOX 2: Scheme of physiochemical and biological processes at vents and seeps. *Left panel: Hydrothermal Vents.* By the extrusion of hot magma new seafloor is formed. The heat causes porewater convection and leaches molecular hydrogen, methane and sulfide from the rocks. *Right panel: Cold seeps.* Sediment compaction mobilizes pore water enriched in natural gas (methane) and other hydrocarbons. In both environments, anaerobic microorganisms consume parts of the energy-rich compounds with sulfate as electron acceptor. In the surface sediments and the water column, sulfide and the remaining energy-rich compounds can be oxidized by aerobic bacteria with O_2. Many of those bacteria thrive as symbionts of vent macrofauna, such as tube worms, bivalves or other invertebrates. In the water column, residual compounds are oxidized by planktonic bacteria.

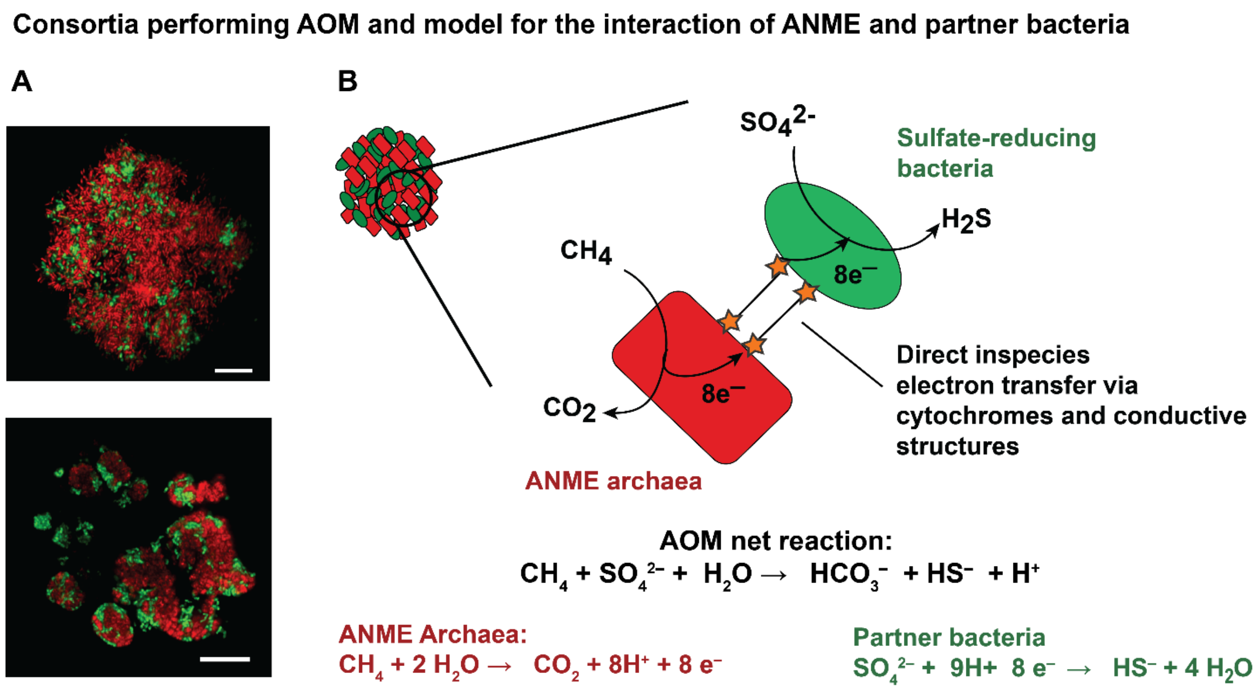
2. Cold seeps and their microbial communities. Cold seeps emit natural gas (mostly methane) and sometimes volatile oils from deep subsurface sediments. Most cold seeps are found along continental margins, concretely at the continental shelf and slope. Methane gas can be produced by specific types of microorganisms, the methanogenic archaea, as final product of the biotic degradation of organic matter. In addition, gas and oil is produced by the heat-induced, thermal degradation of fossil organic matter deposited in the seafloor over geological times. As methane and oil are lighter than sediment and water, they tend to migrate from these deep sediments into the water column. These toxic and climate-relevant compounds reach surface sediments, and would be finally released into the water column at cold seeps (BOX 2, right panel).

However, large parts of the natural gas, particularly the methane, is already consumed by microbes in anoxic sediment layers. This process has long been enigmatic, but today we know that methane can be oxidized with sulfate or nitrate instead of oxygen. This metabolic process called the anaerobic oxidation of methane (AOM) is mediated by microbial consortia consisting of two microorganisms: anaerobic methane-oxidizing archaea (ANME) and sulfate-reducing partner bacteria (see BOX 4). These microorganisms form a symbiosis called syntrophy: the ANME completely oxidize the methane to carbonate (or carbon dioxide), and the partner bacteria use the reducing power (electrons) released during AOM for sulfate reduction producing sulfide as final metabolic product. Together both organisms are able to thrive on the miniscule energy released during AOM.



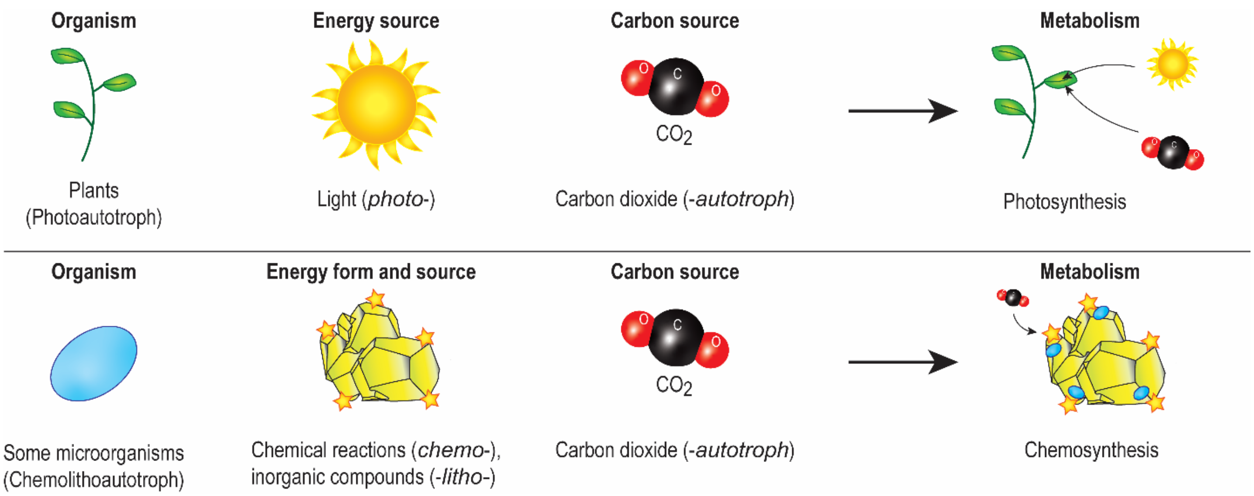
BOX 3: Concept of chemosynthesis and symbiosis in the giant tube worm *Riftia* (see also Fig. 1). *Riftia* inhabits sulfide-rich vent areas, where it takes up oxygen and sulfide from the environment. Its tube is filled with the trophosome, an organ containing numerous bacteriocytes. These bacteriocytes are specialized worm cells that host sulfide-oxidizing bacteria. These bacteria produce energy from the oxidation of sulfide. This energy is used to fix CO_2 from the environment, in a process called chemosynthesis. The host obtains energy from the bacteria: either through a direct transfer of organic products or by the digestion of parts of the bacterial symbionts. Similar symbioses exist in mussels, clams and many other invertebrates.

Both carbonate and sulfide diffuse upwards through the sediment. Carbonate is the main constituent of limestone. Hence, in the upper sediments carbonates and calcite from the water column precipitate as carbonate rocks. Sometimes these carbonate rocks remain for millions of years and are witnesses for the importance of AOM throughout Earth' history. Sulfide, the other product, is a very toxic compound that is transported towards the sediment surface. There, sulfide can be an energy source for other free-living and symbiotic microorganisms that consume the sulfide with oxygen from seawater.



BOX 4: Micrographs of AOM consortia and concept of their obligate syntrophic lifestyle. (A) ANME archaea (red) and sulfate-reducing partner bacteria (green) form either well-mixed (upper panel) or structured (lower panel) consortia; scale bars depict 10 µm **(B)** Current knowledge on the metabolic interaction. The ANME archaea completely oxidize methane to CO_2. This process liberates reducing equivalents (here depicted as electrons, e^-) that are transferred to the partner bacteria. It is not fully clear how the electrons are transferred, yet this transfer likely involves redox-active proteins (cytochromes) and potentially conductive nanowires. The bacteria use these electrons to reduce sulfate to sulfide. Both organisms in the aggregates completely depend on each other: they are obligate syntrophs. Chemically those separated processes can be seen as half reactions performed by the ANME (red) and the partner bacteria (green), that together add up to the net AOM reaction. AOM consumes 90% of the methane produced in marine sediments. Hence it is a key element of the global carbon cycle and important for Earth' climate.

3. Microorganisms form biomass with energy from the oxidation of gases and with CO_2 from seawater. Primary producers are organisms that convert inorganic carbon (CO_2) into organic compounds that can be used by themselves or by other organisms of the ecosystem. On land, plants are the main primary producers. They use the energy of light to fix CO_2 from the atmosphere and form biomass. In seeps and vents, there is no light. Therefore, the primary producers are microorganisms called chemolithoautotrophs (BOX 5). These microorganisms gain energy through chemical reactions (*chemo*), by oxidizing inorganic chemical compounds (*litho*). They use this energy to fix inorganic carbon (*auto*). In contrast, plants are called photoautotrophs (they use the sun light energy and fix carbon dioxide). Interestingly, plants and most chemolithoautotrophic microorganisms use the same metabolic pathway to fix CO_2, the Calvin cycle, with the key enzyme RuBisCo (Ribulose-1,5-bisphosphate carboxylase). In chemolithoautrophic microorganisms present in vents and seeps, the energy for carbon fixation is often generated by the oxidation of the inorganic compounds hydrogen and sulfide. With their action these microorganisms convert chemical compounds into biomass. Whereas most life forms won't be able to survive the high pressure and temperatures, and the toxic gases at hydrothermal vents and seeps, specific chemolithoautotrophic bacteria and also some invertebrates bloom under these conditions, reaching enormous densities. Here, these microorganisms may form dense mats, which serve as food source for grazing invertebrates such as snails, sea cucumbers, polychaetes and other annelids. Some invertebrates, such as the giant vent tube worm *Riftia*, the smaller tube worms of the genus *Lamellibrachia*, and the mussel *Bathymodiolus*, host symbiotic chemoautotrophic bacteria in their bodies (see point 7 for more information). Other chemoautotrophic microorganisms are freely living in the water column, where they are grazed by protozoans. Such chemoautotrophs are the base of light-independent food webs with a complex fauna.



BOX 5: Comparison between chemolithoautotrophic and photoautotrophic metabolism. Primary producers are organisms that convert inorganic carbon (carbon dioxide, CO_2) into organic molecules. Plants including algae are the most important primary products on Earth. Plants use the energy of the sun (*photo-*) to fix carbon dioxide (*-autotroph*). The process is called photosynthesis. In dark environments such as deep-sea vents and seeps, microorganisms are the main primary producers. They use the energy obtained in chemical reactions (*chemo-*) of inorganic compounds (*-litho-*), such as pyrite minerals that are composed of energy-rich iron and sulfur species or dissolved gases such as hydrogen, to fix carbon dioxide (*-autotroph*) and produce organic molecules. This process is called chemosynthesis.

4. Deep-sea animals cooperating with microbes in obligate symbioses. Most deep-sea vents and seeps host dense communities of worms, bivalves and crabs that can only be found at those places. The most prominent species belong to the bivalves such as mussels from the genus *Bathymodiolus* or clams of the genus *Vesicomya*. Vents located in the Pacific Ocean are often populated by the giant tube worms *Riftia* (see BOX 3), but also many other annelids. These animals can get enormously large and can form denser biomasses than found in coastal seas, because they contain bacteria in specific organs and tissues, where the bacteria grow and multiply. These bacteria obtain energy from gas delivered to them by the animals in different ways. For instance, the tube worms use their blood and circulatory system to deliver all the chemicals required by the bacteria. The animals and the bacteria establish a mutually beneficial relationship called symbiosis. The animal is the host and the bacteria are the symbionts.

What are the benefits for the bacteria to thrive on and in animals? The animals provide the bacteria safe place to live and supply them with oxygen and their food (gases and other energetic compounds that the animal cannot use). Tube worms, for instance, use hemoglobin to supply oxygen to their bacteria –as humans do to their cells – and, at the same time, the worms dig deep into the sediment to access sulfide as food for their symbionts. *Bathymodiolus* has a variety of symbionts that thrive on the oxidation of sulfur compounds, hydrogen, methane and reduced nitrogen species usually located in their gills. The circulation of seawater in the gills provide the symbionts all the required food and oxygen

What are the benefits for the host provided by the bacteria? In exchange, the bacteria provide food to the host, either with sugars and other organic compounds produced via chemosynthesis, or they are grazed upon by animals such as vent crabs that grow bacteria on their carapaces. The bacteria are so productive, that the host can exclusively live on the nutrients provided by the symbionts. Actually, this process is capable of sustaining complex local food webs.

5. ***Hydrothermal vents and deep-sea mining.*** The hot fluids rising in hydrothermal vents are rich in rare metals including gold, copper, zinc and nickel that are precipitating at and around the vent sites. Such metals are indispensable for the production of high-tech devices such as mobile phones and cars. The demand for them is increasing because terrestrial resources are sometimes limited. Pioneering missions started to explore mining around deep sea vents in the Pacific. However, deep-sea mining is highly debated. The mining may destroy unique ecosystems and endangers endemic species. Hence pioneering deep-sea mining attempts should be accompanied by biomonitoring approaches and, if possible, sites should be protected.

6. ***Use of thermophilic microorganisms in biotechnology.*** Microorganisms, in particular from hot vents, have characteristics and produce compounds that are highly interesting for biotechnological applications. For instance, such microorganisms withstand enormous pressures and temperatures, high metal concentrations or extreme pH values. One example is enzymes that are highly efficient in capturing carbon dioxide. Another example is thermostable DNA polymerases from hyperthermophilic (heat loving) microorganisms. DNA polymerases catalyze the replication of DNA in all living organisms. DNA polymerases from those heat-loving organisms work at temperatures of 100°C. One enzyme produced by a microbe from a hot spring in Yellowstone National Park (USA), was key to the development of modern gene amplification and DNA sequencing technologies, based on the famous Polymerase Chain Reaction (PCR) that has many applications in medicine, biology and forensics. Many new enzymes from such environments have potential for biotechnological applications.

Relevance for Sustainable Development Goals and Grand Challenges

- **Goal 12: Responsible production and consumption.** Habitats at hydrothermal vents and cold seeps are endangered by trawler fishing, climate change and changing water conditions. A responsible use of Earth' resources will also ensure the survival of unique hydrothermal vent ecosystems.

- **Goal 13: Combat climate change.** The microorganisms at hydrothermal vents and cold seeps service the planet in consuming the greenhouse gas methane before it gets to the atmosphere. Reducing climate gas emissions is the only way to avoid heat waves in the ocean that could thaw methane permafrost.
- **Goal 14: Life under water.** Chemoautotrophic microorganisms require time to establish on sites. They are important biomass-rich sites in the deep subsurface. These sites often host endemic fish and invertebrates such as specific bivalves, octopus, echinoderms and more. Vents and seeps should be protected until we know more about their origin, fate and biodiversity.
- **Goal 17: Cooperation and international science.** Access to science, technology and innovation and enhancement of knowledge sharing on mutually agreed terms is essential for human development and a sustainable future. This encompasses ocean and microbial literacy. The exploration, understanding and protection of these unique environments requires the cooperation of countries including sufficient funds, capacities, technologies

Pupil Participation

1. **Class discussion on food webs at seeps and vents**
    a. What are the energy sources that sustain life at seeps and vents?
    b. How are these energy sources produced?
    c. What are the main invertebrates at vents and what do they eat?
    d. What do chemosynthetic bacteria thrive at vents?
    e. What are the similarities and differences between vent bacteria and plants?
    f. Who produces the biomass at the vents and has the role of plants?
    g. Describe the principles of symbioses at vents
    h. Which are the benefits for the animal host in a symbiosis with chemosynthetic bacteria?
2. **Class experiments (select appropriate experiment from the Class Experiment list)**
    a. Winogradsky column: Establishing a microbial community with chemoautotrophic members from mud. The preparation of a Winogradsky column can be found here: Anderson, Delia Castro, and Rosalina V. Hairston. "The Winogradsky column & biofilms: models for teaching nutrient cycling & succession in an ecosystem." *The American Biology Teacher* 61, no. 6 (1999): 453-459.
    b. Volta experiment in lakes. Collecting methane with a funnel or something similar from a eutrophic lake and light this gas. Show that ow microorganisms make methane, and how much energy can be gained from the oxidation of methane.
    c. Demonstrate the energy stored in gases, i.e. methane and hydrogen and compare principles of batteries with those of syntrophic microorganisms.
    d. Cultivation of methanotrophic bacteria with methane / oven gas / or methanol or cultivation or Knallgas bacteria that eat hydrogen. Visualize those bacteria by microscopy.

The Evidence Base, Further Reading and Teaching Aids

Teaching aids / there are plenty of good lectures

- https://www.pac.dfo-mpo.gc.ca/education/lessonplans-lecons/endeavour-eng.html
- https://oceanexplorer.noaa.gov/okeanos/explorations/ex1103/background/edu/media/ex1103_htadvent.pdf
- https://www.thirteen.org/edonline/ntti/resources/lessons/s_dive/index.html
- https://schmidtocean.org/wp-content/uploads/Virtual-Vents-Lesson-Plan.pdf

A great resource is also the World Ocean Review https://worldoceanreview.com/en/

Literature

Books about seep and vent life

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Hoagland, P., Beaulieu, S., Tivey, M.A., Eggert, R.G., German, C., Glowka, L., Lin, J. 2010. Deep-sea mining of seafloor massive sulfides. *Marine Policy*, **34**(3), 728-732.

Interesting websites on deep-sea mining:

- https://www.theverge.com/2017/10/3/16398518/deep-sea-mining-hydrothermal-vents-japan-precious-metals-rare-species
- https://www.lifegate.com/people/news/hydrothermal-vent-mining-japan
- https://www.bbc.com/future/article/20181221-japans-grand-plans-to-mine-deap-sea-vents

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Glossary

Aerobic	In reference to an organism, it refers to the ability to survive in an oxygenated environment. An obligate aerobic organism requires oxygen to grow and obtain energy. Animals, plants and some microorganisms are aerobes.
Anaerobic	In reference to an organism, it refers to those organisms that do not require oxygen for growth. Many of the anaerobic organisms are obligate anaerobes and cannot grow in the presence of oxygen, for instance, methanogens.

ANME	Acronym of ANaerobic MEthane-oxidizing archaea. These microorganisms are archaea living in syntrophic consortia with sulfate-reducing bacteria and together they performed the anaerobic oxidation of methane (AOM). With their action ANME archaea reduce methane emissions from the marine sediments into the water column.
Anoxic	State of environments devoid of molecular oxygen
AOM	Acronym of Anaerobic Oxidation of Methane. This process occurs in marine sediments and is coupled to sulfate reduction. It is performed by consortia of anaerobic methane-oxidizing archaea (ANME) and sulfate-reducing bacteria.
Archaea	Group of microorganisms that form one of the three domains of life, the other two are bacteria and eukaryotes, the latter includes animal and plants. Similar to bacteria archaea are single-celled microorganisms. Archaea are the only microorganisms that are able to thrive on the production of methane.
Autotrophs	Organisms that build their biomass using inorganic carbon that is carbon dioxide (CO_2). Autotrophic organisms are the plants and some bacteria. They are also called primary producers.
Bacteria	Group of microorganisms that form one of the three domains of life. They are single-celled organisms, present a wide diverse of metabolisms and can be found in really different ecosystems.
Bathymodiolus	A genus of deep-sea mussels, marine bivalves of the family Mytilidae. Many of them contain intracellular chemoautotrophic bacterial symbionts.
Carbon dioxide	Gaseous compound, also known by the chemical formula CO_2. It contains carbon in its most oxidized redox state. It is a form of inorganic carbon that can be produced as an end product by different organisms. Autotrophic organisms use CO_2 to form biomass.
Carbon fixation	Process defining the biological transformation of inorganic carbon (CO_2) into organic compounds. The process is performed by autotrophic organisms such as plants but also many bacteria.
Chemosynthesis	Defines the use of energy released by chemical reactions to produce biomass. Chemosynthesis is the basis of deep-sea communities, sustaining life in absolute darkness, where sunlight does not penetrate.
Chemolithoautotrophy	Literally means inorganic chemical self-nourishment. Chemolithoautotrophs gain energy with chemical reactions (*chemo*). They oxidize inorganic molecules (*litho*) like hydrogen sulfide, reduced iron or

	hydrogen gas. They use the energy for fixation of carbon dioxide into organic molecules (*auto*).
Clathrates (gas hydrates)	In the marine environments, clathrates refer to condensates of water molecules and methane gas. They occur naturally in methane-rich sediment and trap large amounts of methane in the ocean floor.
Cold seeps	Seafloor structures that emit fluids (water). In most cases these fluids are produced deep in the seafloor by sediment compaction and are often enriched in natural gas produced by methanogenic archaea or thermocatalytic decay of organic matter
Conservation	Defines preserving and carefully managing natural resources so that they can be used by present and future generations.
Consortia	Plural of consortium. In microbiology, it refers to the association of two or more microorganisms that live symbiotically. One example are anaerobic methane-oxidizing archaea (ANME) living with sulfate-reducing bacteria. Together they are able to degrade methane and produce sulfide.
Continental margins	Submerged area next to a continent comprising the continental shelf, the continental slope and deposits at the base of the continental slope.
Continental shelf	Portion of a continent (and therefore formed by continental crust) that is submerged under the ocean. It has a gentle slope and shallow depth. It extends until there is an increase in the slope angle (shelf break) and then the continental slope starts.
Continental slope	A relatively steep slope occurring after the continental shelf that ends in the continental rise or the abyssal plain.
Crust	The uppermost outer layer of Earth's structure. It can be divided in oceanic (consisting of basaltic minerals) or continental (granitic rocks).
Deep sea	Layers of the ocean where light does not penetrate. There is no clear definition of the extent of the deep sea, but often it refers to oceans from 200 m depth down to the seafloor. The deep-sea also characterizes by high pressure, low temperatures and many exotic and unknown life forms.
Ecosystem	A community and the interactions of living and nonliving things in an area. Different areas of the ocean can be classified as different types of marine ecosystems.

Endemic	Referred to an organism, indicates that this organism is exclusively found on one place or habitat type on earth.
Food web	Natural relation of food chains in an ecosystem community. It includes primary producers like photoautotrophs or chemolithoautotrophs; grazers and predating organisms.
Habitat	A place where something lives is its habitat. It is a place where it can find food, shelter, space, and protection.
Hydrogen gas	H_2, a highly reactive gas that can be produced by geochemical process like serpentinization. Hydrogen gas can also be produced and consumed by microorganisms
Hydrogen sulfide	H_2S. Toxic, water-soluble gas that represents the most reduced form of sulfur, and in combination with metals such as iron it forms minerals such as pyrite
Hydrothermal vents	Hydrothermal (of or related to hot water) vents are the areas where ocean water is heated up by the molten magma under the earth's crust and recirculated back to the ocean forming vent-like structures. This water carries numerous compounds like energy-rich molecules such methane, hydrogen gas or sulfide.
Lithosphere	The uppermost solid earth mantle and crust, which is of solid state, but mobile
Methane	CH_4. Smallest hydrocarbon gas compound, produced either chemically by mineral reactions, or by microorganisms in a process called methanogenesis.
Mantle	The intermediate Earth's layer. It is located between the crust and the most inside layer, the core. The upper part of the mantle consists of molten magma.
Metabolism	Combination of all chemical reactions in a cell or organism
Methanogenesis	Biological metabolic process performed by some archaea that are called methanogens. These organisms thrive on the reduction of simple carbon molecules to methane. They are abundant in many anoxic habitats such as animal guts, swamps but also anoxic layers of the ocean sediment.
Natural gas	Mixture of short-chain alkanes (methane, ethane, propane and butane) that are gaseous under standard conditions (room temperature and atmospheric pressures). These gases are produced in anoxic sediments or rocks. The largest amount of natural gas is produced by methanogenic microorganisms. This gas is exclusively methane. The thermocatalytic (heat-induced) decay of

	organic matter and the abiogenic chemical reaction of hydrogen and CO_2 at vents produce natural gas that is mostly methane but contains up to 20% of the other gaseous alkanes (ethane, propane, butane).
Oxic	State of environments that contains molecular oxygen
Photosynthesis	Process that occurs in plants and some bacteria, wherever there is sufficient sunlight – on land, in shallow water, even inside and below clear ice. Photosynthetic organisms use solar energy to turn carbon dioxide and water into sugar and oxygen. Therefore, light energy is converted into chemical energy.
Primary producers	Organisms that synthetize new organic matter from CO_2. They are also called autotrophs. Plants and some chemosynthetic bacteria are primary producers.
Serpentinization	Chemical process in which earth mantle rocks are transformed to clay minerals. This process releases heat and molecular hydrogen
Sulfate reduction	Metabolic process performed by some microorganisms in which sulfate is “respired” to produce energy. Sulfide is produced as metabolic product produced. This process occurs under anoxic conditions in deep ocean sediments. Sulfate-reducing organisms thrive on simple organic compounds including hydrocarbons. Some sulfate-reducing bacteria establish syntrophic relationships with anaerobic methane-oxidizing archaea (ANME).
Symbiosis	Defines a close and often long-term interaction between two different biological species, usually to the benefit of both.
Syntrophy	Specific kind of symbiosis in which two organisms cooperate to degrade compounds that cannot be degraded alone. Usually implies an interdependency, one organism lives of the products of another species. One example are the syntrophic consortia formed by methane-oxidizing archaea (ANME) and sulfate-reducing bacteria.
Plate tectonics	Describes the motion of continental and oceanic crust segments in geological time scales, caused by convections in the Earth mantle; responsible for mountain formation, earth quakes and the formation of hot vents
Tube worms	Sessile annelid animals that host sulfide-oxidizing symbionts, the species *Riftia* can grow up to several meters in length within a few weeks