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# Chemosynthesis in the deep-sea: life without the sun

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**BGD**

9, 17037–17052, 2012

## Chemosynthesis in the deep-sea: life without the sun

C. Smith

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Abstract

Chemosynthetic communities in the deep-sea can be found at hydrothermal vents, cold seeps, whale falls and wood falls. While these communities have been suggested to exist in isolation from solar energy, much of the life associated with them relies either directly or indirectly on photosynthesis in the surface waters of the oceans. The sun indirectly provides oxygen, a byproduct of photosynthesis, which aerobic chemosynthetic microorganisms require to synthesize organic carbon from CO<sub>2</sub>. Planktonic life stages of many vent and cold seep invertebrates also directly feed on photosynthetically produced organic matter as they disperse to new vent and seep systems. While a large portion of the life at deep-sea chemosynthetic habitats can be linked to the sun and so could not survive without it, a small portion of anaerobically chemosynthetic microorganisms can persist in its absence. These small and exotic organisms have developed a way of life in the deep-sea which involves the use of resources originating in their entirety from terrestrial sources.

## 1 Introduction

The Earth's surface is dominated by organisms which depend on energy captured from the sun through the process of photosynthesis, either as primary producers or heterotrophic consumers. Until the discovery of chemosynthesis in 1887 by Winogradsky, alternatives to light energy for the production of organic carbon remained unknown to science. Surprisingly, even after the process of chemosynthesis was observed, it was widely thought to be relatively insignificant as a mechanism of primary production (Van Dover, 2000). With the discovery of deep-sea hydrothermal vent systems in 1977 (Corliss et al., 1979), it became clear that chemosynthetic microorganisms were not only present in the deep sea where light energy from the sun is absent, but that they supported large communities and assemblages of higher organisms. Hydrothermal vent, whale fall, wood fall, and cold seep communities are able to make use of the

## Chemosynthesis in the deep-sea: life without the sun

C. Smith

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



chemical energy found in elements such as sulphide and methane because of symbiotic relationships with chemosynthetic microorganisms and are thus able to thrive in an environment which is normally characterized as having an extreme food limitation (Rex et al., 2006). Much of the energy provided by photosynthetic primary production in the surface waters, on which most other deep-water organisms depend, is exploited before it can make its way into the depths, leaving only about 1–20 % to sink past a depth of 1000 m where the last of the sun's light rays can still be detected. In a paper on the geomicrobiology of deep sea hydrothermal vents, Jannasch and Mottl (1985) suggest that it was this “dependence of entire ecosystems on geothermal (terrestrial) rather than solar energy” that made the discovery of the vent systems and other chemosynthetic communities in the deep sea so groundbreaking, prompting new theories into the origins of life (Wächtershäuser, 1988) and on the prospects of life on other planets in our own solar system (Van Dover, 2000). But is it true? Do chemosynthetic communities thousands of meters below the last rays of sunlight really exist in complete isolation from the influence of the sun? Could such communities persist if the sun were to be removed from the equation altogether? In answering these questions we must first examine the chemical processes involved in chemosynthesis as well as the structure of the organisms and communities which rely on it.

## 2 Discussions

First observed in the deep sea in the 1970s, chemosynthesis is the process by which microorganisms are able to use chemical energy to generate organic carbon from inorganic sources. Basic biochemistry tells us that all metabolic processes, including chemosynthesis and photosynthesis, are comprised of three fundamental elements: an energy source, an electron donor, and a carbon source (Van Dover, 2000). In the case of photosynthesis, light provides the energy while CO<sub>2</sub> and H<sub>2</sub>O provide the source of carbon and electrons respectively (see Fig. 1).

**BGD**

9, 17037–17052, 2012

### Chemosynthesis in the deep-sea: life without the sun

C. Smith

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Like photosynthetic metabolism, chemosynthesis involves the conversion of inorganic CO<sub>2</sub> into organic carbon compounds; the significant difference between the two is that in chemosynthesis, the reduction reactions are fueled by the potential energy found between different electron donors and acceptors. While a wide range of electron donors are suitable for use by chemosynthetic microorganisms (see Fig. 2), the most significant for deep-sea communities are sulphide and methane (Jannasch and Mottl, 1985).

Depending on the nature of the electron acceptor in the reaction, chemosynthesis may either be aerobic or anaerobic (Van Dover, 2000). As the name suggests, aerobic chemosynthesis makes use of oxygen as the primary electron acceptor, while anaerobic chemosynthesis relies on a variety of acceptors such as nitrate, carbon dioxide, sulphur and sulphate. Reduction reactions involving oxygen tend to have a larger potential energy than those using alternative electron acceptors, and so aerobic chemosynthesis has the potential to produce more ATP and tends to dominate most deep-sea communities (Jannasch, 1985; McCollom and Shock, 1997). Like plants, microorganisms that make use of aerobic chemosynthesis couple their reduction reaction to the conversion of CO<sub>2</sub> into organic carbon compounds using the Calvin–Benson cycle (Van Dover, 2000). On the other hand, some microorganisms such as the Archaea that use anaerobic chemosynthesis have developed a more efficient pathway than the Calvin cycle for the generation of ATP. Termed the reductive acetyl-coenzyme A pathway or the Wood–Ljungdahl pathway, after its founders, it requires approximately one ATP to be used in the generation of pyruvate while the Calvin–Benson cycle requires seven (Berg et al., 2010). During the process, acetyl-CoA is formed from two molecules of CO<sub>2</sub> and then undergoes reductive carboxylation to generate the pyruvate used in the further synthesis of cellular material (Jannasch, 1985). While a more efficient means of CO<sub>2</sub> fixation, the reductive acetyl-CoA pathway is limited to anoxic environments, and indeed anaerobic chemosynthetic microorganisms seem to be limited in their distribution in deep-sea communities to locations that fit their anoxic needs, such as the hot

**BGD**

9, 17037–17052, 2012

## Chemosynthesis in the deep-sea: life without the sun

C. Smith

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



plumes of hydrothermal vents and the subsurface sediments of cold seeps (Jannasch, 1985).

To date, four distinct deep-sea habitats have been shown to provide the conditions and resources necessary to support significant chemosynthetic communities: hydrothermal vents, cold seeps, whale falls and wood falls. The chemosynthetic communities on whale and wood falls are opportunistic, capitalizing on the random appearance of large nutrient packages. Organic matter from the productive surface waters can occasionally find its way into the depths in the form of whale carcasses or sunken wood (Smith et al., 1989). Much of the easily accessible organic nutrients in these once in a lifetime feasts are quickly consumed by large scavenging fish, such as sleeper sharks (Collins et al., 2005). However, anaerobic breakdown of whale bone lipids (Demming et al., 1997) and wood (Duperron et al., 2008; Gaudron et al., 2010) has been shown to produce sulphide. The decomposition of such materials can last for decades, providing chemical energy for sulphide-reducing chemoautotrophs (Van Dover, 2000). While interesting, these chemosynthetic communities have a clear dependence on the sun, in that whales and trees directly make use of, or are themselves, photosynthetic primary producers. As such, the chemosynthetic communities which rely on the decomposition of whale carcasses and sunken wood in the deep sea would cease to exist without the sun.

In the case of hydrothermal vents and cold seeps, the search for life truly isolated from the sun becomes more interesting as geological phenomena linked to the movement of tectonic plates are responsible for the release of most of the necessary chemicals. Hydrothermal vents are areas where hot anoxic seawater, which can be rich in both volatile gases and metals, exits the seabed. These systems are the result of spreading centers and hotspots associated with mid-ocean ridges (Van Dover, 2000). New evidence published in 2008 by Tolstoy et al. suggests that vent water begins its journey by traveling down conduits in the ridge axis caused by tectonic fracturing. As the water penetrates the crust and gradually heats, it becomes slightly acidic and anoxic, able to leach various metals and sulphur from the surrounding rock (Tivey,

**BGD**

9, 17037–17052, 2012

## Chemosynthesis in the deep-sea: life without the sun

C. Smith

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



2007). Once underground, the seawater flows over the hot magma chamber under-  
neath the ridge and heats up significantly. Depending on the pressure and temperature  
the water is exposed to, it may also undergo phase separation into vapor and brine (see  
Fig. 3). The exact chemical composition of the vent fluid can vary across different vent  
5 fields as the physical properties of the rock change from site to site and the various  
quantities of brine, vapor and hot water mix as they travel up towards the vent (Tivey,  
2007). These variations in chemical composition of the vent fluid affect the organisms  
and composition of the communities which surround the vent (Van Dover, 2000).

Cold seep communities have been observed on active and passive margins of the  
10 continental shelves and rely on the escape of methane or sulphide from the continental  
slope. Active margins are associated with tectonic activity caused by the subduction of  
one plate under the other, while at passive margins no subduction occurs. The sites  
of cold seeps tend to vary based on local conditions and the nature of the escaping  
elements that support them, for a full review of 24 distinctive sites see Sibuet and Olu  
15 (1998). In general there seems to be two basic geological processes that provide the  
right conditions for cold seep communities to form. They can be associated with mud  
volcanoes and active thrust faults, created by compression forces within sedimentary  
accretions forced off of tectonic plates during subduction or accretionary prisms. Or  
they can form as erosion or landslides removes sediment from previously inaccessible  
20 stores of methane (Sibuet and Olu, 1998). While some cold seeps actually release sul-  
phide from subterranean reservoirs (Paull et al., 1984), most sites acquire it through  
the action of anaerobic sulphate-reducing microorganisms working in the anoxic sedi-  
ments. The sulphide they release can then “seep” out of the sediment and be used by  
other aerobic chemosynthetic microorganisms as an energy source (Van Dover, 2000).  
25 The result of these processes is a deep- sea environment rich in elements suitable for  
a large amount of primary productivity through the action of chemosynthetic microor-  
ganisms.

To the casual observer, it is easy to be lured into the view that hydrothermal vent  
and cold seep communities could persist in the absence of the sun. After all, they

---

**Chemosynthesis in  
the deep-sea: life  
without the sun**

C. Smith

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



5 make use of the chemical energy obtained from compounds that are produced by geothermal processes far removed from the influence of direct solar radiation. However, the sun's influence on these deep-sea communities comes not as a provider of an energy "source", the role it plays in photosynthetic primary production, but as an indirect provider of a key element for the reduction reactions of aerobic chemosynthesis. As pointed out by Boyle et al. (1985), a critical piece of aerobic chemosynthesis is the presence of free oxygen as an electron acceptor. Free oxygen is only present on earth, both in the atmosphere and oceans, because it is released as a byproduct of the process of photosynthesis (Van Dover, 2000). Boyle et al. argue that because of this requirement, the notion that these deep sea chemosynthetic communities depend on "geothermal (terrestrial) rather than solar energy" (Jannasch and Mottl, 1985), is misleading. While one could argue about the technicalities of what is defined as the energy "source" in biochemical reactions, it is certainly true these deep-sea communities could not exist as they are now in the absence of free oxygen produced by photosynthesis (Boyle et al., 1985).

10 Further links to photosynthesis in deep-sea communities can be found in the life-history of many of the metazoan inhabitants of hydrothermal vents and cold seeps. These communities are able to flourish primarily because, in the deep, aerobic chemoautotrophic microorganisms have developed extremely productive symbiotic relationships with many invertebrate host species (Van Dover, 2000). By pairing up, microbial chemoautotrophs and their host invertebrates gain tremendous fitness advantages in habitats such as cold seeps and hydrothermal vents, where the spatial and temporal boundary between life and death can be quite narrow. As a free living aerobic chemoautotrophic microbe at a hydrothermal vent, life is a constant struggle to remain on the fine line between the anoxic vent fluid, providing sulphide or methane, and the oxygenated seawater, providing a vital electron acceptor. The task is exceptionally difficult given the fact that it is almost impossible for organisms of such small size to move quickly as this boundary changes with the currents. Invertebrate host species can more easily accomplish this task, either by being more motile as in the case of alvinocarid

## Chemosynthesis in the deep-sea: life without the sun

C. Smith

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



shrimp or by simply having a long enough body to traverse the chemical gradient, as in the case of vestimentiferan tubeworms and vesicomid bivalves (Dubilier et al., 2008). In essence, host invertebrates are able to provide a stable environment with a steady stream of the necessary elements, such as carbon dioxide, sulphide, methane and oxygen, and in return receive organic carbon from their symbiotic chemoautotrophs (see Fig. 4). The relationship between chemoautotrophic microorganisms and invertebrates is so successful that it occurs in at least seven different animal phyla (Dubilier et al., 2008).

While the adult stages of many invertebrates at vents and cold seeps rely on chemosynthetic symbionts, the life history of some of these organisms involve planktonic larval stages which do not (Adams et al., 2012). Depending on the amount of maternal investment, larval stages can undergo direct, lecithotrophic or planktotrophic development. Both direct and lecithotrophic development are characterized by larval dependency on stored yolk for nutrition, while planktotrophic larvae are primarily free-swimming and must forage for food in the plankton. As the planktotrophic larvae of vent and seep invertebrates such as *Rimicaris exoculata* and *Bathymodiolus thermophilus* join the rest of the marine plankton they can only survive by consuming organic nutrients that derive directly from photosynthetic primary production in the surface waters (Van Dover, 2000). It is only once these larval stages locate and settle on a new vent or cold seep do they begin to acquire the chemosynthetic symbionts that will sustain them during their adult stages (Adams et al., 2012). Evidence also suggests that many of these invertebrates further rely on photosynthetically derived resources in the form of whale and wood falls which play a critical role as stepping stones for the colonization of newly formed vent and seep systems (Distel et al., 2000).

### 3 Conclusions

Given what we know about the community structure, biochemistry and geological processes involved in sustaining deep-sea chemosynthetic communities, is it correct to say

**BGD**

9, 17037–17052, 2012

## Chemosynthesis in the deep-sea: life without the sun

C. Smith

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





## Chemosynthesis in the deep-sea: life without the sun

C. Smith

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



they depend solely on geothermal rather than solar energy? While deep-sea communities have often been characterized in the literature as “life without the sun” (Tunnicliffe, 1992), the notion is only partially true and can be misleading. Almost all of the observable biomass associated with deep-sea communities such as hydrothermal vents, cold seeps, whale falls and wood falls depends on the action of aerobic chemosynthetic organisms which could not survive in complete isolation from the sun due to their oxygen requirement (Van Dover, 2000). Furthermore, invertebrates at deep-sea chemosynthetic sites vary in their direct reliance on photosynthesis, some require whale and wood falls either as direct providers of nutrients or as dispersal stepping stones, while others survive on the products of photosynthetic primary production as planktonic larvae (Adams et al., 2012). However, even though the vast majority of life in these communities would die out without the sun, I believe that the more significant result of the discovery of these communities remains intact. To focus on aerobic chemosynthesis in the deep-sea is predictable, given how dominant the process is, but ignores the fact it is not the only chemosynthetic lifestyle found at such sites. Anaerobic chemoautotrophs obtain both their electron acceptors and donors from geothermal processes, severing the last link to solar energy that their aerobic cousins could not (Boyle et al., 1985). What is truly significant about deep-sea chemosynthetic communities is not “how much” life lives in isolation from the sun, but the fact that any life at all accomplishes that feat. Although these small and seemingly insignificant microorganisms do not have the same impact in the deep as their aerobic counterparts, they serve a more fundamental purpose as reminders of the incredible adaptability of life. What could be more alien to us than organisms surviving in an anoxic environment thousands of meters below the surface of the ocean, living off energy obtained through geothermal and not solar processes.

The discovery of chemosynthetic communities in the deep sea, starting with hydrothermal vents in 1977 (Corliss et al., 1979), is possibly one of the most significant biological discoveries of the late 20th century. It had the effect of restructuring the general view on the importance of the sun and has been an area of significant research

activity for the last 30 yr (Van Dover, 2000). Invertebrate hosts and chemosynthetic microorganisms form tight symbiotic relationships in the deep and have highlighted the ability for non-photosynthetic primary production to support large communities (Dubilier et al., 2000). While often characterized as communities in isolation from the sun, much of the life on hydrothermal vents, cold seeps, whale and wood falls could not and would not exist in its absence. The underlying point however, that there exists life which does not require the sun at these sites, remains true. A small portion of organisms in the deep sea make use of anaerobic chemosynthesis which does not have the same free oxygen requirements as the aerobic version. Even as the majority of life on earth would vanish without the sun, there exists the continued potential for a small group of lonely microorganisms to persist deep down in the perpetual darkness of our deepest seas.

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## Chemosynthesis in the deep-sea: life without the sun

C. Smith

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



---

**Chemosynthesis in  
the deep-sea: life  
without the sun**C. Smith

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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**BGD**

9, 17037–17052, 2012

## **Chemosynthesis in the deep-sea: life without the sun**

C. Smith

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

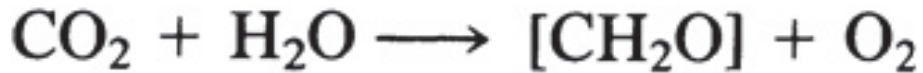
Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





**Fig. 1.** Simplified equation for photosynthesis.

**Chemosynthesis in  
the deep-sea: life  
without the sun**

C. Smith

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Chemosynthesis in the deep-sea: life without the sun

C. Smith

Type of metabolism	Electron donor	Electron acceptor	Redox reaction
Methanotrophy	CH <sub>4</sub>	O <sub>2</sub>	CH <sub>4</sub> + 2O <sub>2</sub> = CO <sub>2</sub> + 2H <sub>2</sub> O
Methanotrophy	CH <sub>4</sub>	SO <sub>4</sub> <sup>2-</sup>	CH <sub>4</sub> + SO <sub>4</sub> <sup>2-</sup> = HCO <sub>3</sub> <sup>-</sup> + HS <sup>-</sup> + H <sub>2</sub> O
Methanogenesis	H <sub>2</sub>	CO <sub>2</sub>	H <sub>2</sub> + 1/4CO <sub>2</sub> = 1/4CH <sub>4</sub> + 1/2H <sub>2</sub> O
S reduction (sulfate reduction)	H <sub>2</sub>	SO <sub>4</sub> <sup>2-</sup>	H <sub>2</sub> + 1/4SO <sub>4</sub> <sup>2-</sup> + 1/2H <sup>+</sup> = 1/4H <sub>2</sub> S + H <sub>2</sub> O
S reduction (sulfur reduction)	H <sub>2</sub>	S <sup>0</sup>	H <sub>2</sub> + S <sup>0</sup> = H <sub>2</sub> S
S oxidation	H <sub>2</sub> S	O <sub>2</sub>	H <sub>2</sub> S + 2O <sub>2</sub> = SO <sub>4</sub> <sup>2-</sup> + 2H <sup>+</sup>
S oxidation	S <sup>0</sup>	O <sub>2</sub>	S <sup>0</sup> + H <sub>2</sub> O + 31/5O <sub>2</sub> = SO <sub>4</sub> <sup>2-</sup> + 2H <sup>+</sup>
S oxidation	S <sub>2</sub> O <sub>3</sub> <sup>2-</sup>	O <sub>2</sub>	S <sub>2</sub> O <sub>3</sub> <sup>2-</sup> + 10OH <sup>-</sup> + O <sub>2</sub> + 4H <sup>+</sup> = 2SO <sub>4</sub> <sup>2-</sup> + 7H <sub>2</sub> O
S oxidation/denitrification	S <sub>2</sub> O <sub>3</sub> <sup>2-</sup>	NO <sub>3</sub> <sup>-</sup>	S <sub>2</sub> O <sub>3</sub> <sup>2-</sup> + 6OH <sup>-</sup> + 4/5NO <sub>3</sub> <sup>-</sup> + 4/5H <sup>+</sup> = 2SO <sub>4</sub> <sup>2-</sup> + 17/5H <sub>2</sub> O + 2/5N <sub>2</sub>
S oxidation/denitrification	S <sup>0</sup>	NO <sub>3</sub> <sup>-</sup>	S <sup>0</sup> + 32/5H <sub>2</sub> O + 6/5NO <sub>3</sub> <sup>-</sup> = SO <sub>4</sub> <sup>2-</sup> + 34/5H <sup>+</sup> + 3/5N <sub>2</sub> + 6OH <sup>-</sup>
S oxidation/denitrification	H <sub>2</sub> S	NO <sub>3</sub> <sup>-</sup>	H <sub>2</sub> S + 36/5H <sub>2</sub> O + 16/5NO <sub>3</sub> <sup>-</sup> = 2SO <sub>4</sub> <sup>2-</sup> + 84/5H <sup>+</sup> + 8/5N <sub>2</sub> + 16OH <sup>-</sup>
H <sub>2</sub> oxidation	H <sub>2</sub>	O <sub>2</sub>	H <sub>2</sub> + 1/2O <sub>2</sub> = H <sub>2</sub> O
Fe reduction	H <sub>2</sub>	Fe(III)	H <sub>2</sub> + 2Fe <sup>3+</sup> = 2Fe <sup>2+</sup> + 2H <sup>+</sup>
Fe oxidation	Fe(II)	O <sub>2</sub>	Fe <sup>2+</sup> + 1/4O <sub>2</sub> + H <sup>+</sup> = Fe <sup>3+</sup> + 1/2H <sub>2</sub> O
Fe oxidation/denitrification	Fe(II)	NO <sub>3</sub> <sup>-</sup>	Fe <sup>2+</sup> + 1/5NO <sub>3</sub> <sup>-</sup> + 2/5H <sub>2</sub> O + 1/5H <sup>+</sup> = 1/10N <sub>2</sub> + Fe <sup>3+</sup> + OH <sup>-</sup>
Mn reduction	H <sub>2</sub>	MnO <sub>2</sub>	H <sub>2</sub> + MnO <sub>2</sub> + 2H <sup>+</sup> = Mn <sup>2+</sup> + 2H <sub>2</sub> O
Nitrification	NO <sub>2</sub> <sup>-</sup>	O <sub>2</sub>	NO <sub>2</sub> <sup>-</sup> + 1/2O <sub>2</sub> + 2OH <sup>-</sup> + 2H <sup>+</sup> = NO <sub>3</sub> <sup>-</sup> + 2H <sub>2</sub> O
Nitrification	NH <sub>3</sub>	O <sub>2</sub>	NH <sub>3</sub> + 3OH <sup>-</sup> + 4O <sub>2</sub> = 3NO <sub>3</sub> <sup>-</sup> + 2H <sub>2</sub> O
Denitrification	H <sub>2</sub>	NO <sub>3</sub> <sup>-</sup>	H <sub>2</sub> + 2/5NO <sub>3</sub> <sup>-</sup> + 2/5H <sub>2</sub> O = 1/5N <sub>2</sub> + 8/5H <sup>+</sup> + 2OH <sup>-</sup>

**Fig. 2.** List of potential electron donors and acceptors for chemosynthesis in the deep sea. Adapted from Takai et al. (2006).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

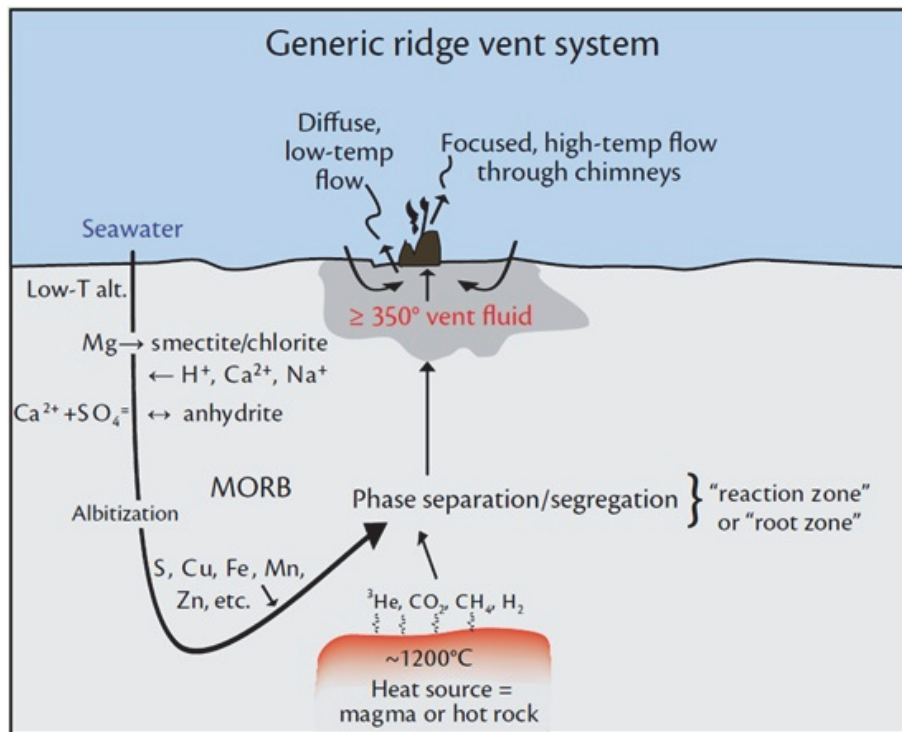
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Full Screen / Esc

Printer-friendly Version

Interactive Discussion





**Fig. 3.** Schematic drawing of a generic ridge vent system, showing the path seawater takes and the chemical processes involved in modifying the composition of vent fluid. Adapted from Tivey (2007).

**Chemosynthesis in the deep-sea: life without the sun**

C. Smith

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

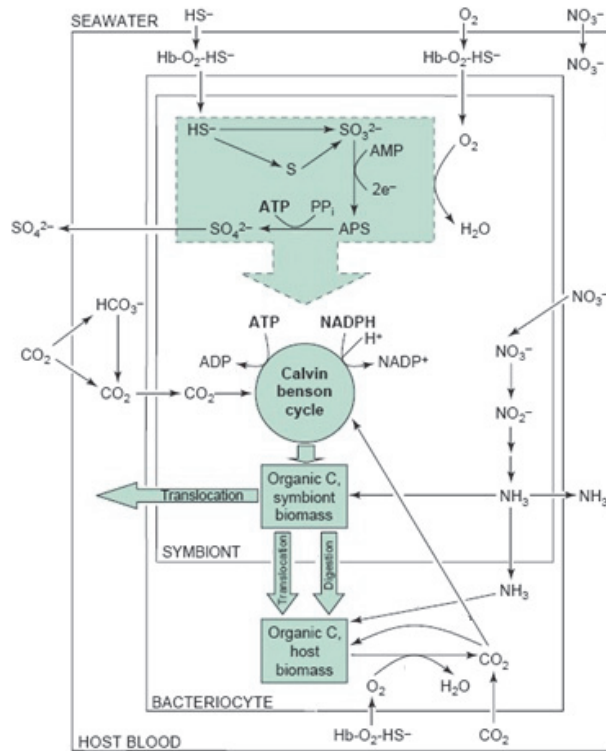
Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





**Fig. 4.** Schematic diagram of chemosynthetic symbiosis inside *Riftia pachyptila*. The host provides a special tissue of the trophosome for the chemoautotrophic microorganisms and transports sulfide,  $O_2$  and  $CO_2$  to it via the blood. In return the symbiont generates organic carbon through aerobic chemosynthesis coupled to the Calvin–Benson cycle. Adapted from Rogers (2012).

Chemosynthesis in the deep-sea: life without the sun

C. Smith

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

