Auto-replenishing microbial lunch boxes: Animals with chemosynthetic symbionts (self-sufficient farmers and recyclers)

Why do we have to buy food at the shop?
Why can't we just grow all our own food at home?

View of City Farm, an urban farm in the city of Chicago, United States. Urban farming, rooftop gardening, and similar ideas are promoted as ways to educate city dwellers about where their food comes from, to use "wasted" spaces like rooftops for food production, and to reduce the distance that food has to travel to come to consumers. Photo by Linda N., 2008, CC-BY 2.0 (source: https://www.flickr.com/photos/22748341@N00/2737299930/)

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Animals with chemosynthetic symbionts

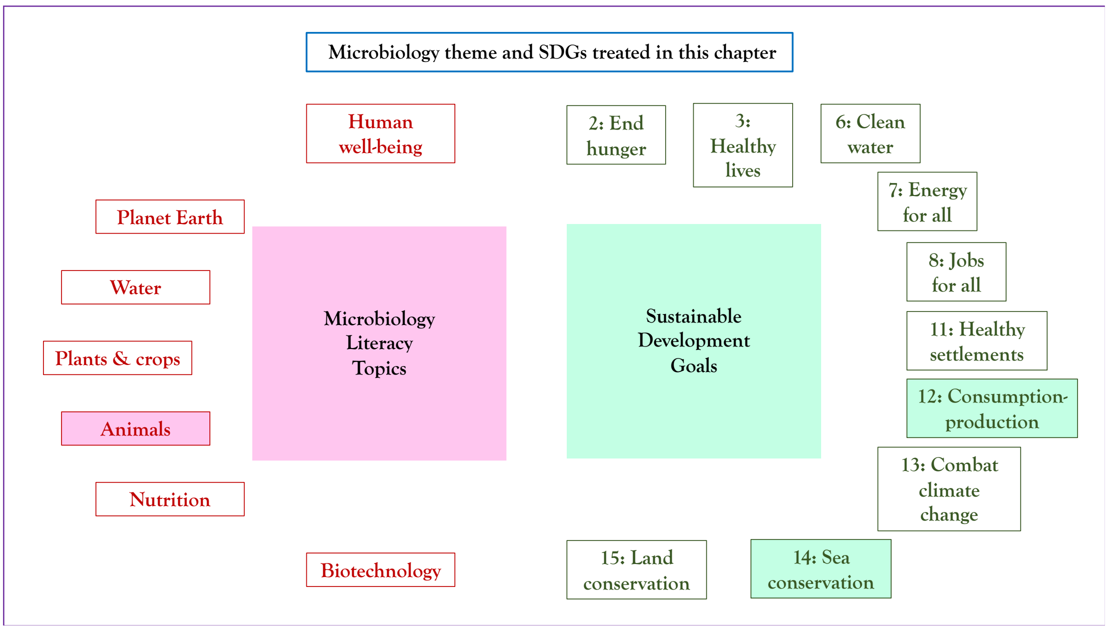
Storyline

Most animals feed on plants and other animals to sustain themselves. Humans are no exception, but in modern societies, most of us don't grow our own food; we depend on others to do so for us. How much land and resources does it take to feed a person? Why can't we just grow our own food at home or, even better, carry around a backpack filled with plants that we can simply harvest whenever we feel hungry? Some animals and animal-like single-celled organisms (protists) do in fact carry around such a "backpack" of food microbes with them. These microbes are able to use the energy in energy-rich chemical sources to convert carbon dioxide (CO_2) and small organic molecules into biomass, much like how plants use sunlight to power their growth through photosynthesis. The host animal/protist then eats the "harvest" produced by the microbes, at the same time keeping conditions favorable for their microbes to continue growing, just like how farmers would tend to their farms.

This seems like a great idea to ensure that you will never run out of food. If that is so, why don't more animals carry their farms around with them? One reason is that these organisms are limited to places where such chemical energy sources are available in sufficient quantity. Another reason is that most animals have much higher energy demands than can be met by what they can carry by themselves. For example, production of the food consumed by each human being on the planet requires on average about 0.7 ha of agricultural land, the almost exact size of one football (soccer) field. Imagine carrying that around with you all day! Thinking through what makes this symbiotic "food backpack" lifestyle possible therefore helps us understand our own status as food consumers sharing a planet with finite resources.

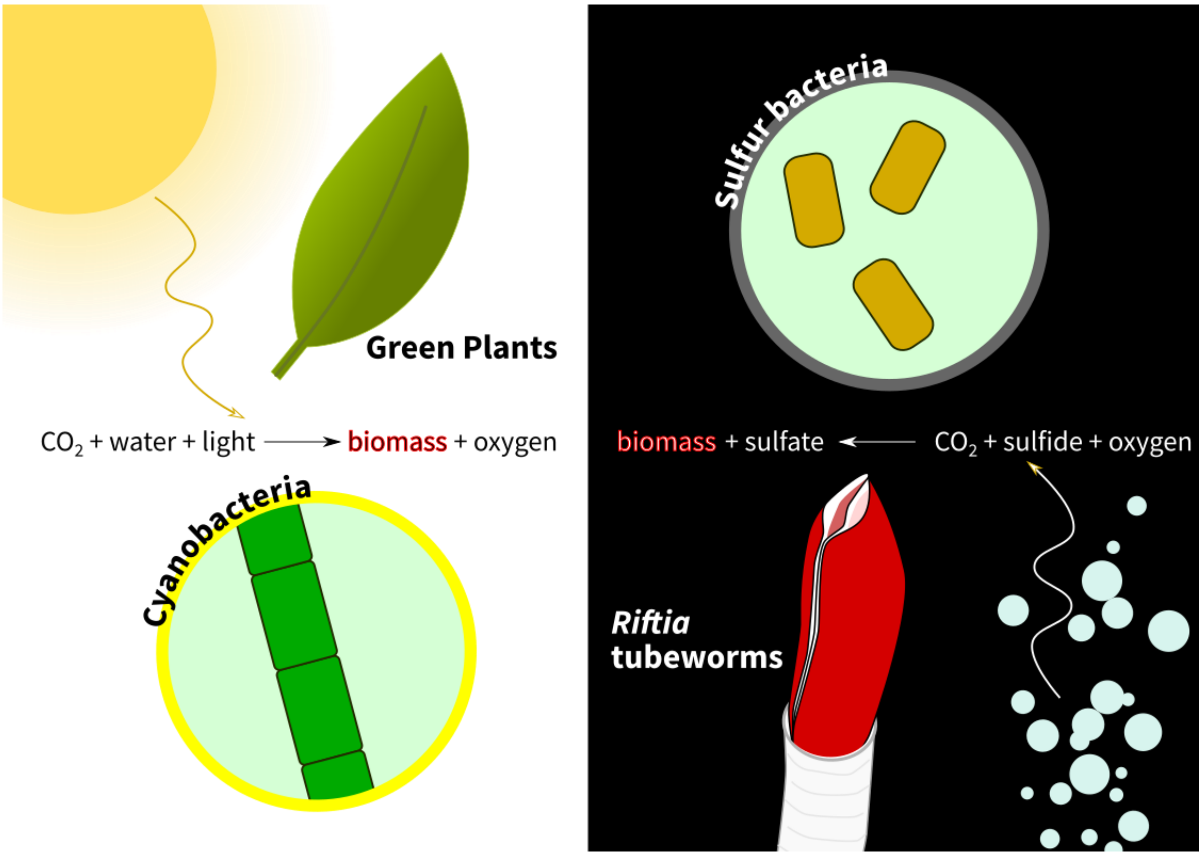
The Microbiology and Societal Context

The microbiology: marine animal:microbe symbioses; autotrophic-heterotrophic carbon and energy acquisition. *Sustainability*: responsible consumption-production; conserve the oceans.



Animals with chemosynthetic symbionts: The Microbiology

1. ***Many bacteria can make use of inorganic chemicals as energy sources to fuel biomass production*** *(chemosynthesis), analogous to how plants use light energy to grow by photosynthesis.* Growing involves the production of complex organic (carbon-based) biomolecules needed to create new cells, or biomass. The synthesis of biomolecules from simple building blocks – precursors – requires a lot of energy. Green plants and cyanobacteria harvest the energy of light to create cellular energy that is used to produce new biomass, by fixing carbon dioxide from the air, while splitting water, yielding oxygen gas as a by-product. Because photosynthetic organisms grow entirely on inorganic substrates, and gain energy from sunlight, they are said to be autotrophs, in contrast to organisms like us that need organic carbon substrates such as sugar and protein as sources of carbon and energy, and which are therefore called heterotrophs. However, some bacteria can use chemical energy in energy-rich ("reduced") compounds that is released in reactions, such as that between hydrogen sulfide (H_2S; "rotten egg" gas) and oxygen, or between hydrogen gas (H_2) and oxygen, to fuel the fixation of CO_2. Because of the parallel to photosynthesis, this type of autotrophic metabolism is called chemosynthesis.



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Photosynthesis (left) in green plants and microbes like algae and cyanobacteria is a process that converts carbon dioxide gas into new biomass for growth, using energy from sunlight. Chemosynthesis (left) is a similar process that uses chemical energy, e.g. from sulfide gas, instead of sunlight. Chemosynthesis is performed by microbes, such as sulfur bacteria, some of which live symbiotically inside larger organisms like the *Riftia* tubeworms from the deep sea.

Habitats which can support chemosynthesis need a steady supply of such chemically-reduced substances. These include hydrothermal vents and seeps in the sea, where gases like hydrogen sulfide, hydrogen, and methane produced by geological processes escape into seawater. At the coast, reduced chemicals are also produced by the decay of organic material buried in the sediment. It is in such habitats that chemosynthetic microbes can thrive, sometimes forming dense microbial mats or forming close associations with animals that feed off the biomass that they produce.

2. ***Some animals and animal-like microbes ("protists") can form mutually beneficial relationships (symbioses) with such bacteria.*** Many types of invertebrate animals and protists[1] form symbioses with chemosynthetic bacteria.

Collage of symbiotic animals and protists that have symbiotic, chemosynthetic bacteria. Clockwise from top left: *Riftia pachyptila* tubeworms in the deep sea (up to 1 m long), *Kentrophoros* ciliates (ca. 0.5 mm long), *Paracatenula* flatworm (ca. 1-2 mm long), *Leptonemella* nematode (ca. 1-2 mm long), *Solemya velum* clam (shell 13 mm across).

They exploit the autotrophic primary production of these bacteria, much like how herbivores exploit the photosynthesis of plants for food. Their physical size ranges from the tubeworm *Riftia pachyptila* that can reach several meters in length, to microscopic flatworms *Paracatenula* spp. that are barely a millimeter long. Some carry the bacteria inside their bodies in specialized organs (e.g. modified gills in *Solemya* clams), or even inside their own cells (e.g. *Paracatenula*). Others let the bacteria "hitchhike" on their body surfaces, wearing them like a coat (e.g. nematode worm *Leptonemella*). The hosts are able to feed on the bacteria, either by digesting the cells or transferring nutrients directly into their bodies. In fact, many of these animals have lost their mouths and guts in the course of evolution, an unusual phenomenon that spurred scientists to take a closer look at them in the first place.

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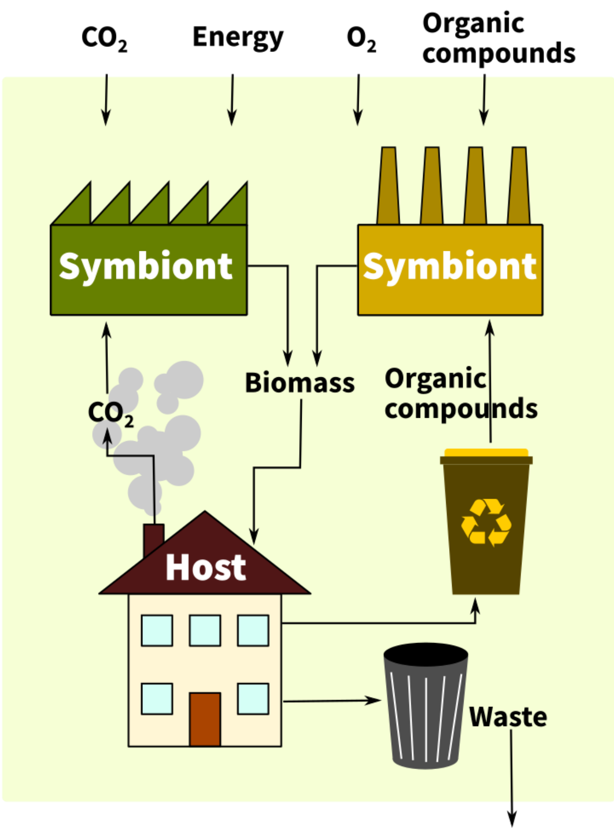
[1]The term "protist" is generally used to refer to any single-celled eukaryote, or more broadly to any eukaryote that is not an animal, plant, or fungus. The latter definition thus includes some large multicellular species like giant kelp (brown algae). It is preferred over the term "protozoan", which gives the misleading impression that they are a type of "primitive animals".

The video footage linked below under "Teaching aids" can help demonstrate this "bestiary" of symbiotic animals and protists to pupils.

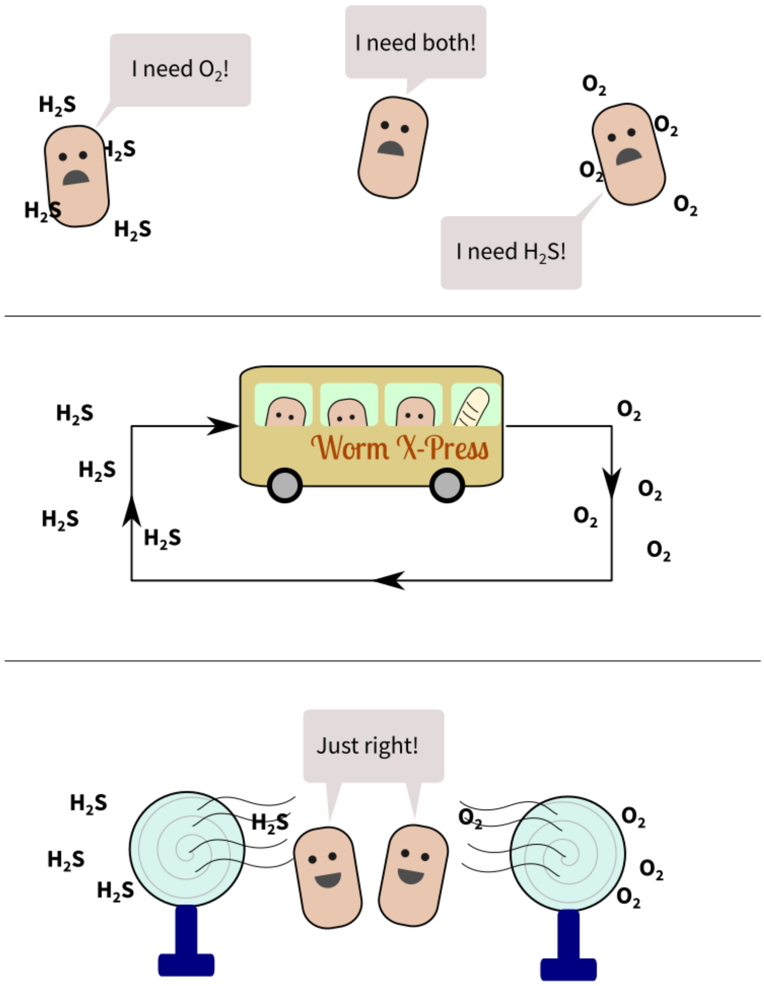
3. ***Many of these bacteria not only make new biomass from CO_2 like plants, but can also recycle waste products from other organisms.*** Much of the fascination with chemosynthetic symbiosis comes from the analogy to plants, and the fact that in dark, deep sea habitats, chemosynthetic bacteria take the place of green plants as the primary producers that support the ecosystem. However, it is increasingly recognized that many chemosynthetic bacteria not only produce "new" biomass from CO_2, but also recycle waste products such as acetate and propionate that come from fermentation by the host or by other organisms in the surrounding environment. Because these small molecules are also organic compounds, the bacteria are not strictly autotrophs but could be considered mixotrophs (able to switch between autotrophic and heterotrophic lifestyles). These waste compounds alone are poor energy sources, especially in low-oxygen environments, because they are highly oxidized. However, when the organism also has the ability to tap into other, non-carbon-based energy sources, as in the case of chemosynthetic bacteria, they become a feasible supplementary source of carbon to build new biomass, in addition to CO_2 fixation. After all, CO_2 is even more highly oxidized and requires yet more energy to convert into biomass.

It may even be possible to dispense with CO_2 fixation altogether, such as with the symbionts of a ciliate (single-celled eukaryote) called *Kentrophoros*, which lack the standard CO_2 fixation pathways, and appear to exclusively use such "low quality" organic compounds for growth, fueled by sulfide oxidation. This particular symbiosis therefore acts less like a green plant than a recycling plant for low-quality organic carbon.



Chemosynthetic symbionts produce new biomass that feeds their hosts, but they can also recycle some of the waste products from the host, like small organic compounds and carbon dioxide.

4. ***The animals that have these symbionts have adaptations to supply them with oxygen and chemical substrates they need for growth.*** The host animals and protists do not simply benefit without paying any costs. They have to maintain suitable growth conditions for their symbiotic bacteria. Some do this by moving back and forth between sources of the chemical fuels and of oxygen, e.g. the nematode worms that live in coastal sediments and move up through the sediments to access oxygen in surface layers and down to access reduced compounds in deeper layers. Others maintain a continuous flow of new oxygen- and substrate-rich seawater through their bodies, so that they and their bacteria have enough of these substances for growth, e.g. deep sea mussels whose symbionts live in their gills. When actively producing biomass, these bacteria can consume oxygen at a high rate, and this oxygen demand sets a limit on the host's own metabolism rate. It is not a surprise, then, that the host animals are often sessile (attached to a physical substratum), like the deep sea tube worms, because not moving around reduces the energy use and hence the amount of oxygen the host needs for itself. Alternatively, if the host animal is small, like the nematodes that are only a millimeter or two long, oxygen can diffuse faster into the animal's body than it can into a larger organism, so they can still support a population of bacterial symbionts on top of their own oxygen needs. The bacteria can take up a significant percentage of the organism's volume, e.g. ~5% in the *Riftia* tubeworms, to ~30-50% in *Paracatenula* flatworms and *Kentrophoros* ciliates.



How hosts help symbionts find the right conditions for growth. Chemosynthetic bacteria need both oxygen and chemicals like sulfide for growth, but bacteria are not able to move large distances quickly (top). Some hosts, like worms, are able to carry the bacteria and shuttle them back and forth between sources of the different raw materials they need for growth (middle). Other hosts, like clams, are able to pump and mix water containing these substances, and bring them within reach of their symbionts (bottom).

5. ***Why can't we carry around all the plants that are needed to feed ourselves, like these symbiotic animals do?*** Compared to them, our metabolic needs are much higher because we are warm-blooded, larger sized, and much more active. The ratio of our metabolic rate to the plants' growth rate sets a lower limit on how much plant matter we would need to feed ourselves. This is in addition to the soil, fertilizer, and water that would be needed to nurture the plants themselves. A rough way to picture this is to calculate how much agricultural land is available per person on Earth. As of 2013, there was about 0.7 ha per person globally, but the value varies widely from region to region, ranging from about 0.18 ha in South Asia to 1.52 ha in South America, where much more land is used for livestock pasture. Improvements to agricultural technology and breeding (or genetic modification) of crops have improved yields over time, but this is offset by the growing global population and consumption per person.

6. ***Metabolic strategies of the chemosynthetic bacteria have analogies in applied and industrial microbiology.*** Many chemosynthetic symbionts can store carbon or energy sources inside their cells as a "buffer" against future scarcity or fluctuating conditions. This is actually a common strategy among microbes in general, and is not limited to symbiotic species. The storage typically takes the form of globules or granules inside the cell, made of polymers such as polyhydroxyalkanoates (PHA), glycogen, or polyphosphates. Polymers like PHA are called "bioplastics", because they can have plastic-like properties and, moreover, be produced by microbes from renewable sources, and are themselves also biodegradable. Industrial microbiologists use free-living bacteria to transform fermentation waste products from wastewater into PHA; the metabolic pathways involved are related to those found in the symbiotic chemosynthetic bacteria.

Relevance for Sustainable Development Goals and Grand Challenges

- **Goal 12. Responsible consumption and production.** Chemosynthetic bacteria both produce new biomass from CO_2 (primary production) and recycle organic compounds that are waste products from their hosts or other organisms in the environment. The recycling of waste back into biomass by these microbes is analogous to the use of waste materials from agriculture or food production to make new products, a process that is called "waste valorization" in industry. An example of waste valorization from the food industry is the use of orange peel waste after juice has been extracted from the oranges. Peel waste is conventionally processed into animal feed or simply incinerated. However, it is rich in substances like essential oils and pectin that can be extracted and used for consumer products. There is also evidence that raw peel waste can be a fertilizer to restore degraded forest lands over a period of several years. The other side of the coin is to reduce the amount of food wasted in the chain from producer to retailer to consumer. It was estimated in 2011 that up to one third of all food production globally is wasted, or about 1.3 billion tons a year. In developed countries, up to 40% of the waste happens with the retailer or consumer, i.e. at the shops and at home, rather than at the production stage. This is where individual actions and habits can have a sizable impact.
- **Goal 14. Conserve the oceans.** These symbiotic organisms live in habitats like deep sea hydrothermal vents and coastal mangrove forests. They are directly threatened by human activities such as deep sea mining, which specifically targets mineral deposits at hydrothermal vents, minerals that are used for steel making and electronics, and sand mining on coasts and rivers that is used in making concrete for construction. This is in addition to global changes caused by a warming climate. Sessile clams and microscopic worms may be less visible or visually appealing to the public than "charismatic species" like colorful octopuses or large mammals.

Nonetheless, they underpin the biogeochemical cycles in their respective habitats, and are inherently interesting to scientists for what they can teach us about how living systems work.

Potential Implications for Decisions

1. ***Individual***
    a. Appreciate the quantities of resources required for primary production to support animal life, whether from green plants or microbial sources.
    b. Reconsider personal habits regarding food preparation, storage, and consumption, to minimize food waste.
    c. Reconsider commonly held beliefs that habitats like marshes and mangroves are "stinky" and unhygienic.

2. ***Community***
    a. Motivate community efforts to reduce food waste, e.g. donation to food banks, redistribution of unwanted food items.

3. ***National***
    a. Inform policies on development or resource exploitation from coastal and deep sea ecosystems, and be accountable for the impact on "unseen" biodiversity and ecology.

Pupil participation

1. ***Class discussion about who should have the responsibility for reducing food waste: producers, retailers, or consumers?***

Pupils can take the following points into consideration:
a. Where in the chain of production/consumption does most waste occur?
b. How do consumers' individual choices influence the decisions that are made by retailers and producers? (e.g. discarding deformed vegetables)
c. Where does your food come from? How do producers ensure that it survives the journey?

2. ***Pupil stakeholder awareness. Personal resource audit: what are the resources required to produce the food that I eat every week?***

This can be measured in terms of farmland, energy consumption, CO_2 emissions, water, and/or time to harvest. This exercise also aims to build numeracy skills, in making estimates and working with order-of-magnitude approximations.
a. Invite pupils to make an educated guess after providing some examples of the resources required to produce common food items.
b. Then ask them to perform a personal audit, with guidance on what are reliable resources for statistics on resource consumption.
c. Compare the initial guesses with their final estimates after working through the exercise. Are they higher or lower than they expected?

3. ***Exercises***
    a. Define primary production and autotrophy as the biological production of new organic carbon from inorganic carbon sources, primarily carbon dioxide.

b. Compare and contrast autotrophy with heterotrophy, giving examples of organisms belonging to both categories.
c. Define chemosynthesis as the use of chemical energy sources (reducing agents) for autotrophic growth.
d. Compare and contrast chemosynthesis with photosynthesis.
e. Give examples of organisms that have a chemosynthetic metabolism, and where they live.
f. Propose reasons, based on ecological conditions and the metabolic abilities of organisms, why chemosynthesis is limited to specific habitats and would not adequately support the nutritional needs of animals like humans.
g. Explain how one would estimate the resources required for agriculture in personal context, i.e. how much land and resources are required to support one's own consumption.
h. Design your own symbiotic animal. You've seen pictures of these ciliates, worms, mussels, and clams that have symbiotic bacteria. Now is your chance to design your own symbiotic animal with its own special abilities. Make sure to answer the following questions - (i) Where do the bacteria live in/on the animal, and how many of them are there? (ii) How do the bacteria make biomass, and how does the animal make sure that the bacteria get enough oxygen and chemical resources to do so? (iii) How do the nutrients get transferred from the bacteria to the animal? Teachers could use images and diagrams of invertebrate animal phyla to help get this exercise started.

The Evidence Base, Further Reading, and Teaching Aids

Evidence base

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Treuer, T.L.H., Choi, J.J., Janzen, D.H., Hallwachs, W., Peréz-Aviles, D., Dobson, A.P., et al. (2017) Low-cost agricultural waste accelerates tropical forest regeneration. *Restor. Ecol.* **26**: 275–283.

Further reading

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Teaching aids – Videos

Shallow water symbioses
Kentrophoros : Life with Sand and Sulfur https://vimeo.com/446257781
Kentrophoros : A Symbiotic Dance https://vimeo.com/89605962
Paracatenula sp. https://vimeo.com/290672261
Various symbiotic animals from coastal sediment https://vimeo.com/479952519
Dissection of *Kuphus polythalamia*, supplementary information to Distel et al. 2017 https://www.pnas.org/content/suppl/2017/04/14/1620470114.DCSupplemental
Deep sea symbioses
"How giant tube worms survive at hydrothermal vents | I Contain Multitudes", presented by Ed Yong https://youtu.be/8W_ywzhkR90
"Hydrothermal vents in the deep sea", by marumTV https://youtu.be/rTR6gGDWcJk
"40 Years of Hydrothermal Vent Exploration | Nautilus Live", by EVNautilus https://youtu.be/UVzBjY8oLkk

Image sources for the collage

- *Solemya velum*

  - https://commons.wikimedia.org/wiki/File:Solemya_velum_(I1271)_(29011292636).jpg
  - Smithsonian Environmental Research Center, CC BY 2.0 <https://creativecommons.org/licenses/by/2.0>, via Wikimedia Commons
- *Paracatenula*
  - https://commons.wikimedia.org/wiki/File:Paracatenula_sediment_OJ_2015.tif
  - Oliver Jäckle, CC BY-SA 4.0 <https://creativecommons.org/licenses/by-sa/4.0>, via Wikimedia Commons
- *Riftia pachyptila*
  - https://commons.wikimedia.org/wiki/File:Riftia_tube_worm_colony_Galapagos_2011.jpg
  - NOAA Okeanos Explorer Program, Galapagos Rift Expedition 2011, Public domain, via Wikimedia Commons
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  - https://commons.wikimedia.org/wiki/File:Kentrophoros_from_Isola_D%27Elba.jpg
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Glossary

Carbon dioxide – An inorganic carbon compound (chemical formula CO_2) that is a component of the atmosphere and also aquatic environments (e.g. seawater, lake water) in its dissolved form. Carbon dioxide is produced as a waste product by aerobic respiration, and is used by autotrophic organisms (see "Autotrophy") like plants to produce new biomass. It is therefore an important part of the carbon cycle on Earth.

Chemosynthesis – The use of energy from inorganic chemical reactions, e.g. the oxidation of hydrogen gas by oxygen, as the main energy source to power the production of biomass by an organism.

Photosynthesis – The use of light by an organism as the main energy source to power the production of biomass.

Autotrophy – Production of new biomass by an orgnaism that uses only inorganic compounds (carbon dioxide, methane) as carbon sources. Plants, cyanobacteria, and sulfur-oxidizing bacteria are examples of autotrophs.

Heterotrophy – Production of new biomass by an organism using primarily organic compounds, e.g. sugars, proteins, fatty acids, as carbon sources. Humans and enterobacteria like *E. coli* are examples of heterotrophs.

Mixotrophy – Production of new biomass by an organism using a mixture of autotrophic (see "Autotrophy") and heterotrophic (see "Heterotrophy") pathways. Many eukaryotic algae (e.g. *Euglena*) and sulfur-oxidizing bacteria (e.g. *Beggiatoa*) are mixotrophs.

Primary production – In ecology, this refers to new biomass (organic compounds) produced from carbon dioxide by autotrophic organisms (see Autotrophy). This term is more commonly applied at the systems level (e.g. the net primary production of an ecosystem) rather than to single organisms.

Fermentation – Use of organic compounds, especially carbohydrates, an energy source without involving respiration.

Polymer – A chemical compound that is made of repeating units, forming long chains that may sometimes also be branched. These can be of natural origin (e.g. starch, cellulose in plant cells) or synthetic (e.g. polyester, nylon).
Hydrothermal vent – A type of geological feature on the seafloor where water heated by geothermal processes is released. This vent fluid contains dissolved chemicals that come from rock and sediment in the crust. Some of these chemicals can be used by chemosynthetic organisms to support their growth (see "Chemosynthesis").
Waste valorization – The recycling of waste, e.g. from agriculture or industrial processes, to be reused as raw materials for producing economically useful products.