Review of the Literature on Oyster Bed Microbial Communities

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Introduction to the microbial world

Microorganisms are the unsung heroes of primary production in a narrative that usually centers around plants. Though they work on an invisible scale, their impacts are undeniable—half of the oxygen in each breath we take comes from oceanic microbes (Pomeroy et al., n.d.). Take a breath. (Thanks microbes!)

Let's start with the three domains of life: Bacteria, Archaea, and Eukarya. In biological classification (*i.e.*, domain, phylum, class, order, family, genus, and species), domain is the broadest level of distinction. Humans belong to Eukarya, along with plants, fungi, and many microbial species whose cells contain membrane-bound nuclei. In contrast, Bacteria and Archaea are exclusively microbial and prokaryotic. Prokaryotes are single-celled microbes with with free-floating genetic material in their cytoplasm. While they typically lack membrane-bound organelles, they have ribosomes (which all organisms have) and can have structures like flagella, which are extracellular hairlike-structures that enable movement. Think of a prokaryotic cells as DNA/RNA suspended in cytoplasm—like a molecular soup bound by a membrane.

The microbial world holds incredible biodiversity and functional diversity. Our genus (*Homo*) contains our species, *Homo sapiens*, and extinct relatives like *Homo erectus*. Compare this to the bacterial genus *Streptococcus*, which includes species that ferment milk into cheese and yogurt, live in soil, populate and help regulate human organ systems, and can cause infections like strep throat and scarlet fever–all within one one genera of bacteria.

Microbial Metabolism: Cross-Feeding and the Nitrogen Cycle

Unlike us, microbes do not typically complete metabolic pathways alone. In our digestive system, food follows a linear journey—from mouth to esophagus to stomach to small intestine—but microbes rely on **metabolic cross-feeding or handoffs** to accomplish comparable biological processes. A prime example microbial handoffs is denitrification (Figure 1), a key step in the nitrogen cycle, performed by microbial communities in marine sediments within oyster farms. In denitrification, nitrate (NO_3^-) is converted to nitrite (NO_2^-) which is converted to nitric oxide (NO) and then to nitrous oxide (N_2O) and finally to dinitrogen (N_2) (Figure 1).

Each microorganism in this pathway has a specific enzyme that catalyzes one step in the sequence, collectively resulting nitrogen removal from the system through the bubbling up of N_2 gas. Insert a sentence on why nitrogen is "removed" fom the system. Dr. Lawrence Pomeroy described this microbial community behavior as an "external digestive process" that benefits motile bacteria (Pomeroy et al., n.d.). Dr. Farooq Azam simplifies it even further, calling microbial communities the “ultimate swimming stomachs” (Pomeroy et al., n.d.).

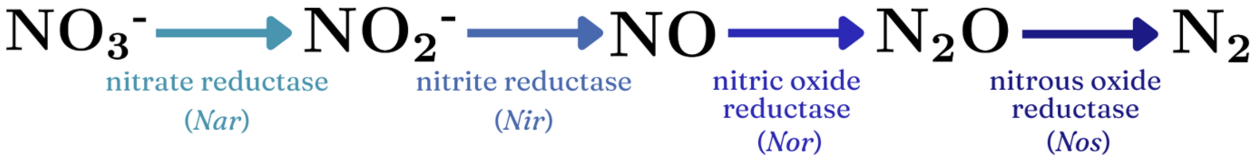

Figure 1: The microbial denitrification pathway. Below each nitrogen species is the enzyme that catalyzes the step (*e.g.* nitrate reductase) and the gene responsible for that enzyme (*e.g.* *Nar*) [@denitrif]. While denitrification appears linear here, it is just one microbially driven component of the broader, cyclical nitrogen cycle, which regulates ecosystems worldwide.

The Microbial Loop: Energy Flow in Ecosystems

Traditional food chains depict a pyramid: plants at the base with primary production, topped by secondary and tertiary consumers. However, much of the available energy in food webs is derived from microbes.

This microbial-driven energy flow is called the **microbial loop**. It begins with **primary production** performed by photosynthetic bacteria—either as **bacterioplankton**, which are bacteria and archaea that drift through the water column (Pomeroy et al., n.d.), or as **periphyton**, which attached to submerged surfaces like sediments and aquatic plants. These microbes convert sunlight (and sometimes heat energy—in a process known as **chemosynthesis**) into form organic compounds, just like terrestrial plants do (Pomeroy et al., n.d.).Their biomass then fuels the rest of the ecosystem. For example, bacterioplankton are consumed by microflagellates (<0.002 mm), which are in turn eaten by ciliates like *Paramecium* (~0.02-0.2 mm). These ciliates are then preyed upon by copepods (1-2 mm) and mid-size animal plankton called mesozooplankton (0.2-20 mm), before fish larvae enter the food web as predators, linking microbial production to larger organisms.

However, the microbial loop can sometimes be short-circuited by **filter-feeders** like oysters and krill, which capture microoranisms en masse as they pump seawater through their gills. Some microbes also play a critical role in decomposition, a process known as **heterotrophy**, where they break down organic matter in the form of decaying organisms and detritus. This releases essential nutrients back into the water column, where they are reabsorbed by bacterioplankton, completing the cycle.

It’s a Microbial World

Microbes are diverse, abundant, and essential to life on Earth. Their community interactions cycle nutrients, regulate ecosystems, and sustain food webs. When we discuss the factors shaping ecological systems—whether its nutrient cycling, energy flow, or ecosystem stability—we must recognize that the true drivers of biological processes are microorganisms.

It’s a microbial world—we’re just living in it.

Introduction to oyster farming

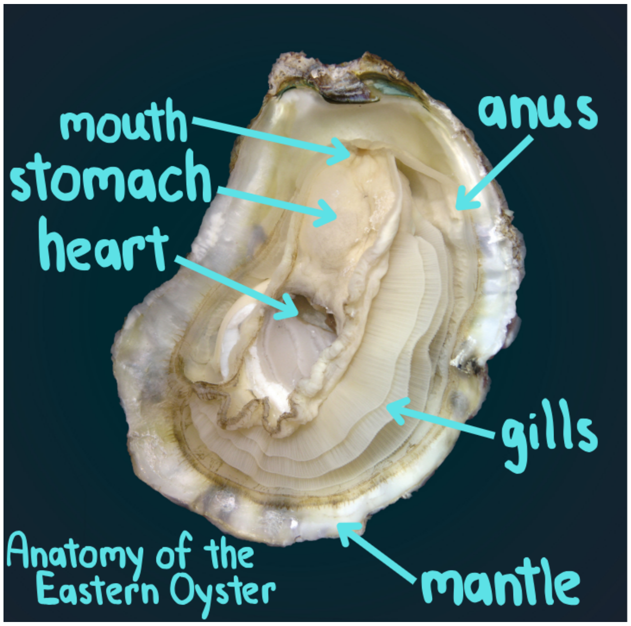

Figure 1: Selected Anatomy of an Eastern Oyster, *Crossastrea virginica*. (Source: https://www.mdsg.umd.edu/lesson-plans/eastern-oyster-education)

Insert few sentences that describe the history of oysters farming-see the beginning of Ray and Fulweiler meta-analysis.

As the ecological consequences of industrial and agricultural production become increasingly evident, oyster aquaculture has emerged as a potential solution for a more sustainable food system. Unlike traditional agriculture, oyster farming does not require land or freshwater resources and can provide ecological benefits to the marine environments where oysters naturally thrive. These benefits include improved water quality, habitat creation for marine species, and storm surge protection (Stevens et al. 2024).

Oysters are filter feeders, capable of filtering ~50 gallons of seawater per day. As water passes through their gills, they retain organic matter, consuming algae and large plankton while allowing smaller plankton and excess water to pass through. Retained material is either ingested and excreted as feces or rejected, encased in mucus, and deposited into the sediment as pseudofeces.

Theory #1: Oysters enhance the biodiversity and composition of microbial communities in the seafloor.

Oysters themselves filter water by taking in plankton while seawater passes through their gills, however, the perhaps greater source of denitrification in the relationship between oysters and their environment is the microbial communities in their biodeposits (poop). The abundance of urea and ammonia increases microbial growth. Most abundant in these samples were proteobacteria, firmicutes, bacteriodetes, and actinobacteria. Notably, these are all denitrifiers. Some studies showed underwhelming changes to the microbial community in the presence and absence of oyster farming. The one paper on different methods within the Mass Bay (I think it was the Northeastern paper?) found that hanging oysters (grown suspended in the water column) did not impact the soil communities as the oysters were not in contact with the ground. I think there was a study that said older oyster beds had different microbiomes compared to younger ones, measured at year 3, 5, and 7. One paper took into consideration the potential for pathogenic microbes to humans coming form oysters. This paper (#5) found that *Vibrio* species were found in the oyster sediments (*Vibrio* being associated with food-borne illnesses stemming from seafood). However, the *Vibrio* were not the pathogenic strains. The *Vibrio* present in the samples were determined to not be harmful to human health.

Oysters promote biodiverse microbial communities by providing the microbes in the marine sediments with diverse nutrients. Some bacteria species (some denitrifiers?) need trace metals to survive.

Oysters provide these to the sediment.

Although it may be easier to understand that oysters themselves are the big denitrifiers, one of the papers argue that the sediment microbes are doing more of the work. Similarly to how there is emphasis in agriculture on creating living soils, on soil as a community that pulls in CO2 from the atmosphere instead of just seeing plants as the main carbon sinks, the marine floor can be seen as a living sediment, where decaying matter is broken down by microbes for the nutrients to be sequestered or recycled.

Theory #2: Oysters stimulate increased denitrification by sediment microbiota.

Oyster sediment microbes boost the recycling, cycling, and sequestering of many nutrients in the water column, including nitrogen, phosphorous, and silicon. This can help to combat eutrophication and climate change. Industrial and agriculture production often releases excess nutrients, like the three mentioned above, into bodies of water in the form of fuel, fertilizer, and waste run-off. The papers contradict each other with how pronounced this impact is. Some did not even find the difference in eutrophication to be statistically significant. I am curious how they separate the impact of microbes living in and on oysters from those in the sediments. Just a thought. Sediment microbes, like actinobacteria and proteobacteria are part of the denitrification process.

Here's the pathway: nutrient loading on aquatic system - probably from anthropogenic activity. Then, this stimulates an increase in the abundance of many photosynthetic organisms, like cyanobacteria. All the time, decaying matter and detritus is falling through the water column in the form of marine snow. When oysters "catch" plankton and other microbes and algae, they are pulled out from the water column, boosting water clarity. The seafloor is, ideally covered in decay and also microbes. It is a place of regeneration, of recycling. When sediment microbes take in nitrogen paired with organic material (usually it will be in the form of ammonia or urea, although neither of those are organics?? But are they just with carbon anyway?) microbes break the bonds between nitrogen and hydrogen, returning hydrogen to the water column? At some points, our nitrogens in the process of denitrification are paired with oxygens but the oxygens are eventually returned to the water column. Close to the end of the process of denitrification, nitrous oxide is created. Nitrous oxide is a harmful greenhouse gas, however, the amounts released from sediment denitrification are very small. The Fulweiler meta-analysis suggests that the amount of nitrous oxide released is negligable. This would be a good place to put the Ray and Fulweiler nutrient flux diagram.

Oyster poop microbes remineralize unstable nitrogen compounds (urea, ammonia, nitrate, nitrite, nitric oxide, nitrous oxide), returning them to the water column as N_2. Diatom nitrogen makes up like 70% of our atmosphere and gas rises so a lot of the N_2 is recycled back into the air. Kind of cool that we are all breathing matter that had its energy spent and has been recycled billions of time. From death back unto life, or something like that.

So to sum it up, oyster sediment bacteria improves water quality and combat eutrophication. Now I am realizing that I need to learn more about how they actually combat eutrophication and mitigate global warming. I think I've mentioned sequestering, but do they really sequester? Maybe I'm getting carbon cycle and nitrogen cycle confused.

Summary of Ray & Fulweiler paper, "Meta-analysis of oyster impacts on coastal biogeochemistry"

Oyster aquaculture increases the cycling of nitrogen in marine systems by stimulating denitrifying bacteria and archaea.This improves water quality, with the trade-off of releasing a small amount of nitrous oxide (N_2o) into the atmosphere (Ray and Fulweiler 2021).

Testing another citation (Feinman et al. 2018).

Citations

Feinman, Sarah G., Yuna R. Farah, Jonathan M. Bauer, and Jennifer L. Bowen. 2018. "The Influence of Oyster Farming on Sediment Bacterial Communities." *Estuaries and Coasts* 41 (3): 800–814. https://doi.org/10.1007/s12237-017-0301-7.

Pomeroy, Lawrence R., Peter J. leB Williams, Farooq Azam, and John E. Hobbie. n.d. "The Microbial Loop | Oceanography." https://tos.org/oceanography/article/the-microbial-loop.

Ray, Nicholas E., and Robinson W. Fulweiler. 2021. "Meta-Analysis of Oyster Impacts on Coastal Biogeochemistry." *Nature Sustainability* 4 (3): 261–69. https://doi.org/10.1038/s41893-020-00644-9.

Stevens, Joshua T. E., Nicholas E. Ray, Alia N. Al-Haj, Robinson W. Fulweiler, and Priyanka Roy Chowdhury. 2024. "Oyster Aquaculture Enhances Sediment Microbial Diversity: Insights from a Multi-Omics Study." *Aquaculture Environment Interactions* 16 (December): 283–301. https://doi.org/10.3354/aei00484.