

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. They work on a scale we cannot see, but the effects of their cumulative efforts are impossible to miss; half of the oxygen in each breath we take has been produced by 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 free-floating genetic material in their cytoplasm. While they typically lack membrane-bound organelles, prokaryotes 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.

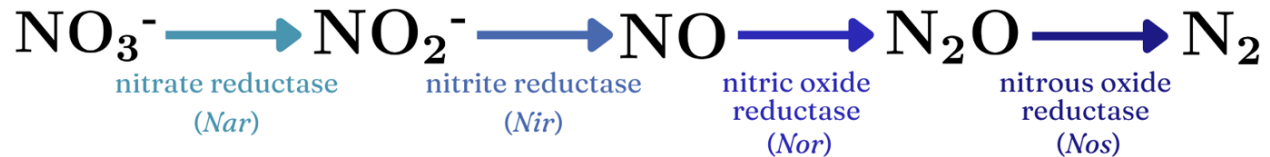
The microbial world holds incredible biodiversity and functional diversity. Our genus (*Homo*) contains our species, *Homo sapiens*, and extinct relatives like *Homo erectus*. Compare this to the bacterial genus *Streptococcus*, which includes species that ferment milk into cheese and yogurt, live in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

Microbial Metabolism: Cross-Feeding and the Nitrogen Cycle

Unlike us. "Instead of performing metabolic pathways from start to finish, like the way our digestive systems pass food from mouth to esophagus to stomach to small intestine, etc., microorganisms are reliant on each other to achieve comparable biological processes.", 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 in nitrogen removal from the system through the bubbling up of N_2 gas. **Insert a sentence on why nitrogen is "removed" from 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 simplified it even further, calling microbial communities the “ultimate swimming stomachs” (Pomeroy et al., n.d.).

^^^“intermediate microbial pathways”



****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

While the traditional depiction of the food chain is a pyramid with plants at the base, topped by primary, secondary, and tertiary consumers—much of the available energy in our food webs derives 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**) to 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 microorganisms 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

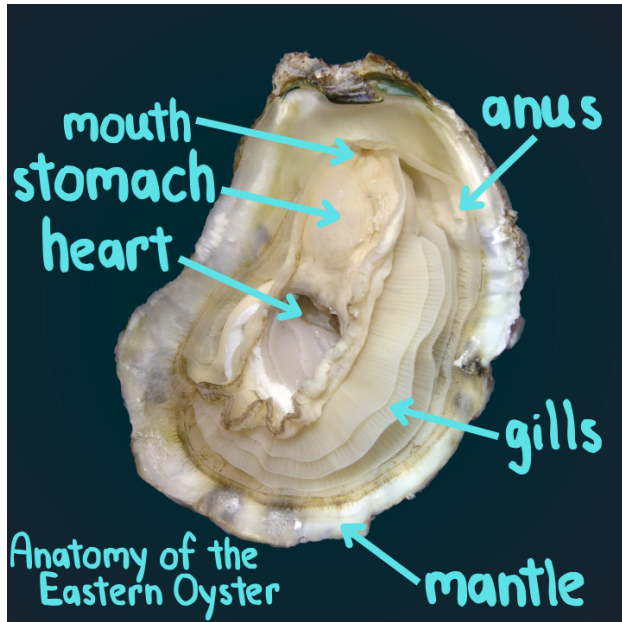


Figure 1: Selected Anatomy of an Eastern Oyster, *Crossostrea virginica*. (Source: <https://www.mdsg.umd.edu/lesson-plans/eastern-oyster-education>)

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

Oyster aquaculture has been practiced globally since ancient civilizations—the likes of Greece, Rome, and the Han Dynasty (Botta et al. 2020). [quote about oyster abundance in the Hudson Bay in the 1800s?] While we face the deleterious ecological impacts of current industrial and agricultural production methods, oyster farming has been proposed as part of a reimagined, more sustainable food system. Not only does oyster cultivation bypass certain agricultural issues like land scarcity; common scientific thought has it that farming oysters can provide benefits to the health of the ecosystem. These potential benefits include enhanced water quality, habitat provision to other marine species, and storm surge protection (Stevens et al. 2024).

As the ecological consequences of industrial and agricultural production become increasingly ev-

ident, 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.

- nitrogen loading responsible for biodiversity declines (Ray and Fulweiler 2021) pg 1

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

1. how oysters impact biodiversity (through poop)
2. what is in oyster poop
3. what microbes are there (on/in the seafloor) (**compare to control**)
4. why this matters

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, bacterioidetes, 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 from 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 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.

- “nitrate reductase requires a Molybdenum protein co-factor for reducing nitrate to nitrite” (Stevens et al. 2024)
- “nitrous oxide reductase requires Cu for reducing nitrous oxide (N₂O) to N₂” (Stevens et al. 2024)
- concentration of iron has sig. role in how microbes cycle P (Stevens et al. 2024) makes me need to go back to biogeochem paper to learn about P cycling

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 negligible. 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 improve 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.

- 17/45 studies report fluxes from oysters, 31/45 report fluxes from sediments (Ray and Fulweiler 2021), pg 1
- "sediments beneath oysters return significantly more NH_4^+ to the water column than bare sediments" (Ray and Fulweiler 2021), pg. 2, 1st col, oysters have highly-variable effect on NO_x fluxes between studies, in contrast
- "oysters also have a strong effect on sediment phosphate regeneration" (Ray and Fulweiler 2021), si unclear
- "Stimulation of sediment denitrification and denitrification in oysters can permanently remove excess N from coastal systems, reducing the impact of eutrophication." (Ray and Fulweiler 2021), pg 2'
- check pg 3z - effect on primary production. promote nitrogen recycling, but add back to system? How does this combat denitrification?
- Seems that oysters do not have a net positive ability related to sequestering carbon. Installing oyster aquaculture initially increases sediment CO_2 and CH_4 release, before returning to baseline. This is good compared to more typical forms of raising protein because for example, cow corn monoculture releases hella GHGs from soils. But there are limited studies on the impact of oyster aquaculture on GHG emissions. I am left wondering about the strength of the one study discussed in the Ray paper. Also, do oysters themselves release GHGs?*

Are there other pieces of oyster aquaculture that release GHGs? Restoration projects are underway; should they be?

- *Omg. Discussed in next paragraph. pg 4 column 2 of ray and fulweiler

Trade-offs

I attended a Cornell presentation session with my dad on the NYC campus many years ago. One of the presentation discussed the planning of coastal cities, with a focus on Hudson Bay oysters. I knew from this experience that oysters were once prevalent in the Hudson, but populations were decimated in the nineteenth and early twentieth centuries. I heard about projects to build up the oyster populations for storm surge protection (coral reefs work similarly and it is the same concept as keeping a ground cover on cropland to prevent erosion (and dust bowls!). Barnacle life slows the advance of oncoming waves.) and to improve water quality through their filtration properties. This sounded like a wonderful solution and something that should be widely implemented. However, the studies I have read (not even my actual research project, just learning about other people's work) has made me wary of trade-offs to "sustainable" solutions. For example, the denitrification by sediment microbes is an intermediate, and therefore leaky process. Before nitrates and nitrites (NO_x groups) are fully reduced to N₂, they become nitrous oxide molecules (a potent greenhouse gas), some of which escape into the atmosphere. This happens on a much smaller scale than anthropogenic greenhouse gas emission, but it is still happening. The paper that

increasing dinoflagellate growth

Conclusion

Citations

- Botta, Robert, Frank Asche, J. Scott Borsum, and Edward V. Camp. 2020. "A Review of Global Oyster Aquaculture Production and Consumption." *Marine Policy* 117: 103952. <https://doi.org/https://doi.org/10.1016/j.marpol.2020.103952>.
- 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>.