

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, though the narrative usually centers on 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 exclusively prokaryotic.

The microbial world holds incredible biodiversity and functional diversity. As humans, 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 genus of bacteria.

Microbial Metabolism: Cross-Feeding and the Nitrogen Cycle

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 rely on each other to achieve comparable processes. These interactions in microbial communities are known as **handoffs** or **metabolic cross-feeding**. Cumulatively, they make up **intermediate microbial pathways**. A prime example of microbial handoffs is denitrification (*Figure 1*), a key step in the nitrogen cycle, and one that is performed by sediment microbial communities 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. 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.).

Denitrification results in the removal of nitrogen from the system, occurring when N_2 gas (a very stable, non-reactive form of nitrogen due to the triple bond between the two nitrogen molecules) bubbles up and is released into the atmosphere—where it naturally makes up nearly 80% of the air we breathe. In a world where greenhouse gas emissions resulting from human activity are knocking environmental equilibrium off balance, the storage of nitrogen as diatoms is especially vital now. When in more volatile forms (NO_x), nitrogen compounds have the potential to form nitrous oxide, a greenhouse gas three hundred times more potent than carbon dioxide.

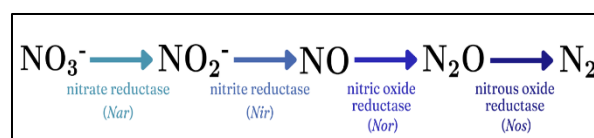


Figure 1: The microbial denitrification pathway. Below each nitrogen species is the enzyme that catalyzes the step (*e.g.* nitrate reductase) and the gene responsible for that enzyme (*e.g.* *Nar*) (Denitrifying Bacterium - an Overview | ScienceDirect Topics, n.d.). While denitrification appears linear 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 **bacterioplankton**, which are bacteria and archaea that drift through the water column, or **periphyton**, which are attached to submerged surfaces like sediments and aquatic plants (Pomeroy et al., n.d.). These microbes use sunlight energy (and sometimes heat energy—in a process known as **chemosynthesis**) to form organic compounds, just as terrestrial plants do (Pomeroy et al., n.d.). Bacterioplankton and periphyton's biomass—built by performing photosynthesis/chemosynthesis—then fuels the rest of the ecosystem. One food chain looks like this: 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). All of this occurs before fish larvae enter the food web as predators, linking microbial production to larger organisms.

However, the microbial loop can be short-circuited by **filter-feeders** like oysters and krill, which capture microorganisms en masse as they pump seawater through their gills. Regardless of whether or not the full microbial loop has occurred, it is closed by the microbes involved in decomposition, when they break down decaying organisms and detritus. This process releases essential nutrients into the water column, where they can be reabsorbed by bacterioplankton.

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. Therefore, when we discuss the factors shaping ecological systems—whether 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

Oyster aquaculture has been practiced globally since ancient times, when oysters were part of the Greek, Roman, and Chinese diets. (Botta et al., 2020). In the last two hundred years, overharvesting and coastal development activities (ex. dredging) have decimated reefs. More than “85% of oyster reefs have been lost globally, and less than 1% of wild populations remain in many locations” (Ray and Fulweiler, 2021).

Today, many coastal communities are trying to build back their oyster populations. As the ecological consequences of industrial and agricultural production become increasingly evident, responsible oyster aquaculture has emerged as part of a reimagined, more sustainable food system. Unlike traditional agriculture, oyster farming does not require land or freshwater resources—and can even provide ecological benefits. These benefits include improved water quality, habitat creation for marine species, and storm surge protection (Stevens et al., 2024).

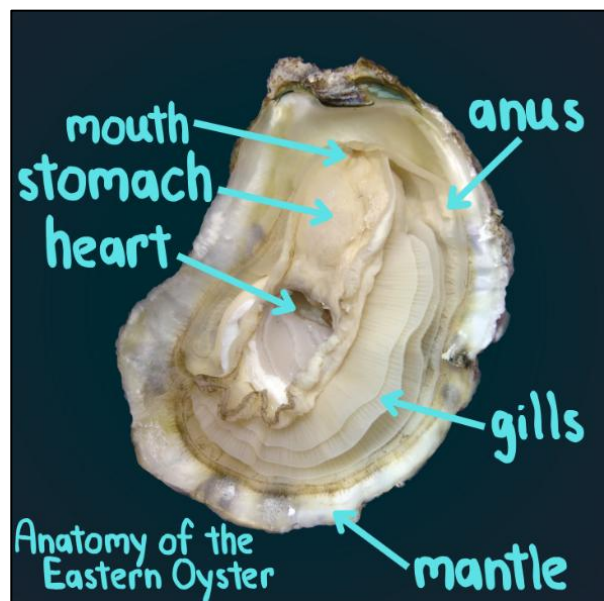


Figure 2: Selected Anatomy of an Eastern Oyster, *Crassostrea virginica*.

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

Oysters are filter feeders, capable of filtering ~50 gallons of seawater per day. As water passes through their gills, they obtain algae and large plankton. This organic matter is either ingested and eventually excreted as feces—or rejected, encased in mucus, and deposited into the sediment as pseudofeces. Oyster biodeposition promotes a sediment environment that is rich in carbon (C), nitrogen (N), and phosphorous (P) and contains trace metals like iron (Fe), molybdenum (Mo) and copper (Cu). (Ray and Fulweiler, 2021).

Though carbon, nitrogen, and phosphorous naturally settle to the bottom of marine systems as **marine snow** (decaying organisms and water column detritus), the abundance of these elements is greatly increased by oyster biodeposition. Oysters excrete twice the concentration of carbon, nitrogen and phosphorous of marine snow particles (Mara et al., 2021). An environment rich with these nutrients can have altered biodiversity and community composition.

By adding trace metals to marine sediments, oysters promote biodiverse microbial communities (Feinman et al., 2018). Bacteria with the *Nar* gene might only be able to perform nitrate reduction in an environment with molybdenum, as “nitrate reductase requires a Molybdenum protein co-factor” (Stevens et al. 2024). Likewise for bacteria with the *Nos* gene: “nitrous oxide reductase requires Cu for reducing nitrous oxide (N₂O) to N₂” (Stevens et al. 2024).

Microbial communities found in oyster bed sediment

Based on sampling from Ninigret Pond, a coastal lagoon in Rhode Island, some of the most dominant bacterial phyla that showed a drastic increase in abundance from control to farmed sites were *Proteobacteria*, *Thermotogae*, and *Spirochaetes* (Stevens et al., 2024). Per the same study, 141 genera exhibited differential abundance between control and farmed site samples. 124 of those genera, including *Firmicutes*, *Deltaproteobacteria*, and *Epsilonproteobacteria*, were more abundant at the farmed sites (Stevens et al., 2024). Some genera were less abundant at the farmed sites—like *Alphaproteobacteria* and *Gammaproteobacteria* (Stevens et al., 2024). While the abundance of microbes was higher at farmed sites than control sites, the community composition did not appear drastically different in modelling by phyla. And, while there was some uniformity between the relative abundance of the various phyla from control sites, the farmed sites showed less agreement—particularly in the relative abundance of *Firmicutes* (Stevens et al., 2024). (See Figure 3).

One bacterial genus that increased in richness as a result of oyster farming was *Vibrio* (Feinman et al., 2018). Some species of *Vibrio* are associated with food-borne illnesses stemming from seafood ingestion (Feinman et al., 2018). However, Feinman et al. (2018) found that *Vibrio* present were not the pathogenic strains; there was insufficient evidence that the *Vibrio* richness increase from oyster farming was harmful to human health (Feinman et al., 2018).

Factors varying between oyster beds affect the influence oyster farming has on sediment microbial communities. The Feinman et al. study found that oyster stocking density (loosely versus tightly packed oyster farms) accounted for more of the variability in sediment microbial community composition between samples than did the location of the samples (intertidal versus subtidal range), though the paper did not find a direct connection (Feinman et al., 2018). Whether on-bottom methods or tray farming had been used—meaning the oyster colony was on a tray suspended in the water, instead of having contact with the sediments—impacted sediment microbial community composition, but less so than stocking density or location (Feinman et al., 2019).

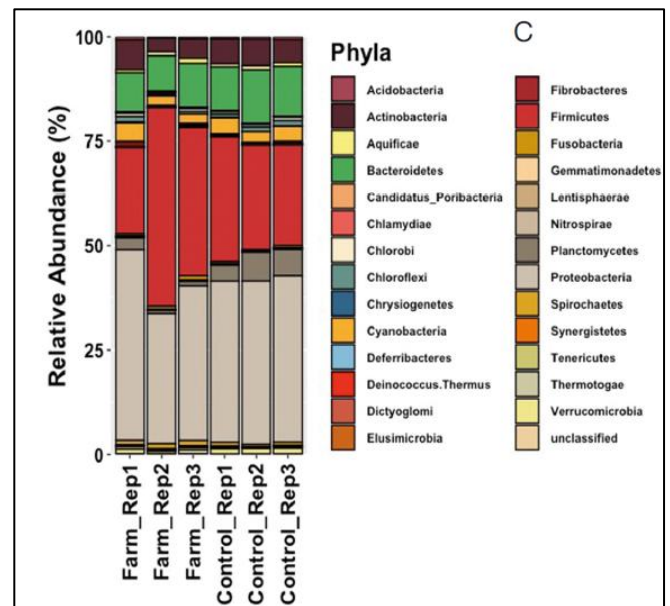


Figure 3: “The relative abundances of bacterial phyla in RefSeq-annotated RNA transcripts from control and 7 yr sites”. (Stevens et al., 2024).

Theme #2: Oysters stimulate increased denitrification by sediment microbiota

Oyster sediment microbes boost the cycling and recycling of nitrogen, phosphorous, and silicon in the water column (Ray and Fulweiler, 2021). As agricultural and industrial production load freshwater and marine systems with these nutrients in the form of fuel, fertilizer, and waste run-off, nutrient cycling is critical to mitigating eutrophication. While an overabundance of nitrogen and phosphorous causes phytoplankton overgrowth and

harmful algal blooms, the long-term result is anoxia—conditions in which very few organisms from the original, oxygenic ecosystem can survive. This is where oyster bed microbes come into play: “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).

Oyster bed sediment microbiota could be net greenhouse gas emitter

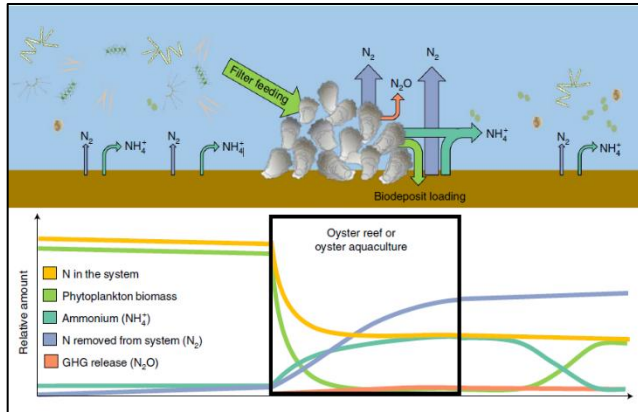


Figure 4: “Transport of nitrogen through coastal ecosystems with oyster habitats.” (Ray & Fulweiler, 2021).

While oysters themselves have denitrifying microbes in their microbiomes, a 2021 meta-analysis by Ray & Fulweiler suggested that sediment microbes may have a greater impact on nitrogen cycling. While 17/45 studies in the meta-analysis reported N fluxes from oysters, 31/45 reported N fluxes from sediments (Ray and Fulweiler, 2021). However, denitrification is an intermediate and therefore leaky process.

Filippini et al. (2023) found that the ratio of *Nir* genes to *Nos* genes in oyster reef sediments was greater than 1, indicating that early stages of denitrification could be occurring at higher rates than later stages—which increases the likelihood of nitrous oxide build-up (Filippini et al., 2023). In contrast, the study found that biofilms on the oysters themselves had a *Nir* : *Nos* ratio ≤ 1 (Filippini et al., 2023). Therefore, it is unclear what the net impact of oyster aquaculture is, with regard to climate change. The few studies on greenhouse gas emissions from oyster aquaculture have produced mixed results (Filippini et al., 2023).

Ray & Fulweiler (2021) and Filippini et al. (2023) concluded that more research is needed on greenhouse gas emissions from oyster beds, especially as the oyster aquaculture industry is on the rise (Ray and Fulweiler, 2021; Filippini et al., 2023). Figure 4 shows the impact of oysters on ecosystem nutrient cycling; note the small N_2O emission in the instance of oyster reef or aquaculture introduction (Ray and Fulweiler 2021).

Conclusion - next steps

From my review of the literature on oyster sediment microbial communities, I have formed the following thoughts to guide my own research:

1. Is there a significant difference in the biodiversity of microbial communities in control versus oyster sediments based on my dataset?
2. How pronounced is the impact of denitrifying microbes in these communities? With the trade-off of nitrous oxide emission to consider, it is important to weigh the value of the nutrient cycling performed by oyster sediment microbes.

Sediment microbial community changes are one factor to be considered in an evaluation of oysters' impact on the environment. The introduction of oyster aquaculture to non-native environments and the introduction of non-native oyster species carries the potential to throw off balance in the ecosystem. A careful review of the conditions prior to growing oysters could prevent adverse effects to the surrounding area.

With previously stated considerations in mind (*i.e.* greenhouse gas emission, non-native oyster planting), the growth of oyster aquaculture demonstrates a shift in the way we view our relationship with nature. As we emit greenhouse gases and burn through natural resources at an unsustainable rate, it is important to think creatively about transitions to practices that promote harmony with nature—as is it critical to recognize that we are not indomitable, though many of us do not yet feel the dangerous implications of the climate crisis. Oyster aquaculture and reef restoration could be both a remedy to anthropogenic environmental harm and a small-footprint protein source.

Citations

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