

## Beyond Bioextraction: The Role of Oyster-Mediated Denitrification in Nutrient Management

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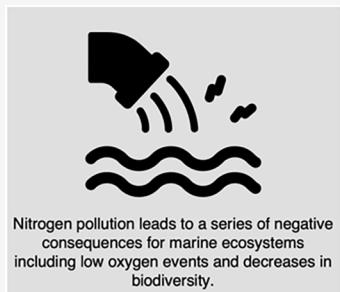


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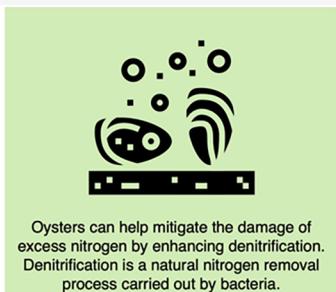
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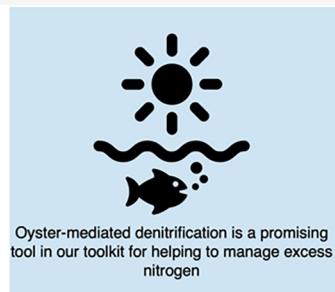
Article Recommendations



Nitrogen pollution leads to a series of negative consequences for marine ecosystems including low oxygen events and decreases in biodiversity.



Oysters can help mitigate the damage of excess nitrogen by enhancing denitrification. Denitrification is a natural nitrogen removal process carried out by bacteria.



Oyster-mediated denitrification is a promising tool in our toolkit for helping to manage excess nitrogen

**ABSTRACT:** Recently, interest has grown in using oyster-mediated denitrification resulting from aquaculture and restoration as mechanisms for reactive nitrogen (N) removal. To date, short-term N removal through bioextraction has received the most management interest, but there is a growing body of research that has shown oysters can also mediate the long-term removal of N through denitrification (the microbial conversion of reactive N to relatively inert dinitrogen ( $N_2$ ) gas). Oyster suspension feeding and ammonium release via waste and deposition of organic matter to the sediments can stimulate nitrification–denitrification near oyster reefs and aquaculture sites. Oysters also harbor a diverse microbial community in their tissue and shell promoting denitrification and thus enhanced N removal. Additionally, surface areas on oyster reefs provide a habitat for other filter-feeding macrofaunal communities that can further enhance denitrification. Denitrification is a complex biogeochemical process that can be difficult to convey to stakeholders. These complexities have limited consideration and inclusion of oyster-mediated denitrification within nutrient management. Although oyster-mediated denitrification will not be a standalone solution to excess N loading, it may provide an additional management tool that can leverage oyster aquaculture and habitat restoration as a N mitigation strategy. Here, we provide an overview of the biogeochemical processes involved in oyster-mediated denitrification and summarize how it could be incorporated into nutrient management efforts by various stakeholders.

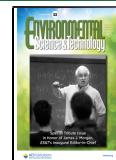
**KEYWORDS:** nitrogen cycle, eutrophication, shellfish, nitrogen mitigation, estuary, stakeholder engagement, best management practices

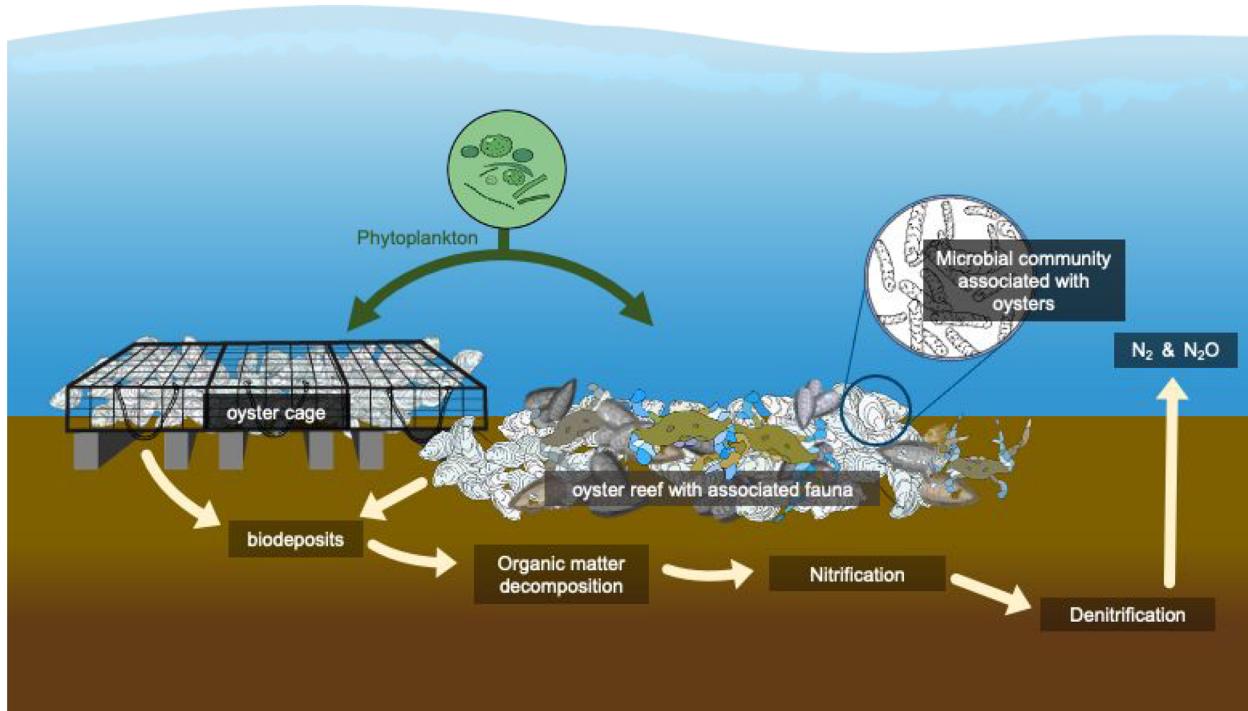
### INTRODUCTION

One of the most serious threats to coastal ecosystems globally is excess nitrogen (N) loading and subsequent eutrophication.<sup>1,2</sup> Local (e.g., runoff, sewage discharge), regional, and global (e.g., fertilizer use, fossil fuel burning) activities increase the amount of N discharged to coastal waters. While N is necessary for all life, too much of it leads to a range of negative ecological consequences such as shifts in primary producer (e.g., phytoplankton, macroalgae) composition and abundance, increased frequency and duration of low oxygen conditions,<sup>3</sup> and decreases in biodiversity.<sup>4,5</sup> These ecological consequences drive negative societal changes too, such as declines in economic prosperity when fisheries decline,<sup>6</sup> reduced property values,<sup>7</sup> degraded recreational experiences,<sup>8</sup> and loss of tourism revenue.<sup>9</sup>

In order to protect and restore our coastal systems, a variety of technologies, policy mandates, and management plans have been developed to reduce N inputs and mitigate impacts of excess N.<sup>10</sup> Traditional management and policy initiatives focused on intercepting and removing N from point (e.g., wastewater treatment plants) and nonpoint sources (e.g., agricultural fields) before it reaches coastal areas. Removal techniques include improved wastewater treatment infrastructure and using best management practices for fertilizer

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**Figure 1.** Nitrogen removal in oyster habitats. Oysters are efficient filter feeders and can increase organic matter deposition to the sediments via biodeposition. In turn, this organic matter is decomposed, releasing ammonium ( $\text{NH}_4^+$ ) to the environment. Ammonium can be used by phytoplankton and macroalgae, or it can be converted to nitrate ( $\text{NO}_3^-$ ) via nitrification. This nitrate can then fuel denitrification, the natural microbial process that converts biologically usable nitrogen to dinitrogen gas ( $\text{N}_2$ ) or nitrous oxide ( $\text{N}_2\text{O}$ ). These nitrogen cycling processes can take place in the sediments beneath aquaculture cages or surrounding oyster reefs as well as within the microbial community associated with the oyster themselves.

application.<sup>11</sup> Unfortunately, implementing such watershed-scale source control is costly and can take decades to be realized.<sup>12</sup> Given the logistical and economic challenges associated with successfully implementing N source control programs, additional tools that allow for removal of N directly from coastal systems are being explored.<sup>12</sup>

Typically, *in situ* N reduction practices work by enhancing N removal by an ecological community or habitat within a system. Familiar examples include restoring a wetland plant community or installing floating islands of wetland plants to a coastal area. These practices are beginning to be used more widely<sup>13–15</sup> and are already included in some N management plans in the United States.<sup>16,17</sup> Another example would be restoring or installing communities of bivalves or macroalgae to support N removal via bioextraction.<sup>18</sup> In bioextraction, the N incorporated into the biomass of shellfish or seaweed is removed during harvest.<sup>19</sup> Total N mitigation via bioextraction is a relatively simple metric to quantify and is therefore increasingly used by managers seeking to reduce N pollution in coastal areas. A prominent example is bioextraction through oyster aquaculture, which is now being implemented or considered as a management tool for N mitigation throughout the United States<sup>20–25</sup> and internationally.<sup>26,27</sup> Bivalves can provide another mechanism of N removal via the enhancement of denitrification (the microbial conversion of reactive N to inert dinitrogen ( $\text{N}_2$ ) gas; Figure 1). Most research on bivalve N removal via denitrification enhancement has been conducted on oysters, and thus in this paper, we focus on them. It is worth noting, however, that there is a growing body of literature on the ability of other marine bivalves to enhance denitrification. Key examples include northern quahog (*Mercenaria mercen-*

*ria*) aquaculture,<sup>28</sup> blue mussel (*Mytilus edulis/trossulus*) aquaculture,<sup>29</sup> green-lipped mussel (*Perna canaliculus*) aquaculture<sup>30</sup> and restoration,<sup>31</sup> and ribbed mussel (*Geukensia demissa*) restoration.<sup>32,33</sup> In addition, there is emerging work on freshwater bivalves such as Unionid mussels,<sup>34,35</sup> Zebra mussels (*Dreissena polymorpha*),<sup>36,37</sup> and Asian clams (*Corbicula fluminea*).<sup>38</sup> Research on oyster-mediated denitrification likely inspired many of these studies on other bivalves. Likewise, an assessment of the N mitigation potential through oyster denitrification is applicable to other bivalves and may inspire similar research internationally and in freshwater ecosystems where links between shellfish culture and nutrient trading are being actively developed for nutrient reduction programs (e.g., in the EU<sup>22,39</sup> and China<sup>40,41</sup>). Here, we provide stakeholders and decision makers with an overview of oyster-mediated denitrification, examples of its use for potential incorporation into future N management programs, and areas of further study.

## ■ OYSTERS AND DENITRIFICATION

Not all N has the same impact on coastal ecosystems, and in fact, almost 80% of our atmosphere is dinitrogen ( $\text{N}_2$ ) gas. We refer to  $\text{N}_2$  gas as unreactive or biologically unavailable because most organisms cannot use it to grow. We refer to other forms of N such as nitrate or ammonium as reactive or biologically available because these nitrogen compounds support or are products of growth and cell metabolism.<sup>42</sup> Denitrification is a microbially driven process that converts reactive nitrogen (e.g., nitrate) to unreactive nitrogen (e.g.,  $\text{N}_2$  gas) and thus permanently removes the N from the waterbody. In many coastal ecosystems, denitrification is coupled to nitrification.

During nitrification, microbes convert ammonium to nitrate which subsequently fuels denitrification (Figure 1). Denitrification is regulated by a variety of environmental conditions including the availability of nitrate as well as the quality and quantity of available organic matter. Oysters can stimulate denitrification in at least three ways, by (1) enhancing denitrification through increasing organic matter deposition to the sediments, (2) hosting denitrifying bacteria on or within their bodies, and/or (3) providing habitat for other filter-feeding macrofaunal communities (Figure 1).

In the first mechanism, oysters, which are efficient filter feeders and ingest large amounts of particulate matter from the water, release their waste products to the sediments as biodeposits (Figure 1). Biodeposits include feces or “pseudofeces”, which are rejected particles wrapped in mucus.<sup>43</sup> These organic-matter-rich biodeposits can help fuel denitrification. Oysters also directly excrete ammonium and stimulate sediment ammonium flux. In the presence of oxygen, this ammonium can promote coupled nitrification–denitrification. Demonstrating enhanced sediment denitrification from oyster biodeposition in a reef or aquaculture setting requires showing significantly higher rates compared to bare (i.e., no oysters) sediments. Past individual studies report varying effects of oysters on denitrification. Recently, however, a meta-analysis used a statistical approach to deal with interstudy variability and demonstrated that when examining all the studies together oysters—associated with restored reefs or aquaculture—significantly enhance sediment denitrification.<sup>44</sup>

In the second mechanism, oysters themselves both recycle and remove N through the diverse microbiome on their shells and in their digestive tracks<sup>45–48</sup> (Figure 1). Studies report high rates of denitrification<sup>46–49</sup> as well as high rates of nitrification<sup>46</sup> in the bodies of oysters and oyster shells. Ray et al.<sup>48</sup> synthesized these studies and found up to a four times difference in the rates of denitrification across studies for live oysters. Results from studies examining denitrification in oyster shells alone (i.e., dead oysters within a reef) have been mixed. Some studies found that shells had reduced denitrification<sup>46</sup> or no denitrification<sup>48</sup> compared to live oysters, while other studies have found similar rates of denitrification between live oysters and shells only.<sup>47</sup> As research progresses in this area, N removal rates may be applied to individual oysters in a similar way in which N content is applied in bioextraction efforts. This will facilitate scaling denitrification rates to aquaculture and reef restoration sites. Future studies should address the role of oyster size and environmental drivers (e.g., temperature, water chemistry, etc.) to better inform mitigation efforts.

In the third mechanism, oysters create a habitat for other filter-feeding organisms, such as mussels, tunicates, and barnacles.<sup>50,51</sup> These macrofaunal communities living on the surface area of oyster reefs may contribute additional opportunities for enhanced denitrification. Jackson et al. found that the biogeochemical measurements of intact oyster clumps from a restored reef that had undisturbed macrofaunal communities produced high rates of denitrification.<sup>51</sup> While this study did not directly assess the macrofaunal communities, it suggests that a measurement approach that incorporates the whole reef community (e.g., oysters, oyster-associated macrofauna, sediment microorganisms) likely produces estimates closer to the total N reduction from oyster-mediated denitrification. However, current methods to establish denitrification rates of whole reef communities are costly and more complex than sediment measurements alone.

Implementing oyster-mediated denitrification as a mitigation tool will require additional measurements of denitrification rates from oyster habitat and non-oyster habitat for comparison. Recently, an effort was undertaken to develop recommendations for managers on how best to measure denitrification and what environmental characteristics should simultaneously be collected to help inform future management goals.<sup>52</sup> Some of these recommendations include directly measuring denitrification with the N<sub>2</sub>/Ar technique (determines the net N<sub>2</sub> production as the difference between N<sub>2</sub> production by denitrification and N<sub>2</sub> consumption by N<sub>2</sub> fixation), collecting rate measurements seasonally, and reporting environmental parameters such as sediment oxygen demand and inorganic nutrient concentrations (i.e., ammonium and nitrate concentrations).<sup>52</sup> Additionally, there are efforts that are developing enhanced denitrification estimates using data where the sediments and the whole reef community are included in the N<sub>2</sub>–N flux measurements to determine the total N reduction from denitrification per reef acre.<sup>53</sup>

## ■ IMPLEMENTING OYSTER DENITRIFICATION INTO NITROGEN MANAGEMENT

Many coastal areas in the United States, Asia, Australia, and Europe are required to improve water quality using nutrient reduction targets for point (e.g., wastewater) and nonpoint (e.g., stormwater runoff, agricultural runoff) sources.<sup>10,54</sup> Although the specificity and enforceability of these targets vary according to region, many parts of the world have established concrete limitations to nutrient discharges to which nations and/or individual business owners (e.g., farmers and wastewater treatment plant operators) must comply.<sup>10</sup> In parts of Europe (i.e., surrounding the Baltic Sea), these targets are referred to as maximum allowable inputs (MAI), whereas in the United States, these targets are referred to as the total maximum daily load (TMDL). Historically, the establishment, expanded capacity, and treatment technologies of wastewater treatment facilities and sewerage have been implemented to address N reduction goals.<sup>10</sup> Currently, local or national governments faced with nutrient reduction targets are also seeking innovative and nontraditional solutions to their nonpoint water quality issues, including oyster-mediated denitrification.

A good example of such an oyster-driven nutrient reduction program is The Chesapeake Bay Program Partnership, which has implemented one of the most comprehensive nutrient-reduction programs in the world, and its efforts are resulting in improvements of water quality.<sup>55</sup> The program uses a suite of best management practices (BMPs) that are recommended by expert panels. The Chesapeake Bay Program Partnership are now in the process of evaluating BMPs involving oyster-mediated denitrification through oyster reef restoration. Specifically, they have given interim approval to BMPs for N reduction through enhanced denitrification<sup>20</sup> from oyster reef restoration practices using hatchery-produced oysters and/or reef substrates. The enhanced denitrification protocol for the interim oyster restoration BMPs was developed from efforts in Harris Creek, Maryland, using methods that assessed the whole reef community.<sup>20</sup> As part of this effort, they have described how to scale denitrification rates to estimate N removed in units that match TMDLs. Briefly, to obtain the net denitrification enhancement, they subtract the oyster habitat denitrification rate from a non-oyster habitat reference rates. The difference is then scaled by time as well as the density of

**Table 1. Common Stakeholder Groups and Their Roles in Oyster-Mediated Denitrification Best Management Practices<sup>a</sup>**

stakeholder group	example roles in oyster-mediated denitrification BMPs
national, regional, and local decision makers	<ul style="list-style-type: none"> <li>-deliver messages to other groups (stakeholder communication)</li> <li>-develop program and management options for oyster-mediated denitrification, including reporting mechanism and monitoring</li> <li>-secure funding to support program</li> <li>-serve as a clearing house for concerns and issues</li> <li>-coordinate and convene management efforts</li> <li>-consider alternatives financially and in practice</li> <li>-support as an option to contribute to meeting their nutrient reduction needs</li> <li>-implement program for denitrification (monitoring)</li> </ul>
WWTP operators and public works	<ul style="list-style-type: none"> <li>-understand need for abatement of excess nitrogen and oyster-mediated denitrification concepts</li> <li>-support nitrogen abatement actions</li> </ul>
community residents/general public	<ul style="list-style-type: none"> <li>-identify and avoid shellfish farms or reefs</li> <li>-refrain from harvesting shellfish from nondesignated (i.e., closed) areas</li> <li>-limit activities that could harm farms or reefs, including discharge of waste</li> <li>-collect data as part of citizen science monitoring efforts</li> </ul>
water recreationists (boaters, anglers, shellfish harvesters)	<ul style="list-style-type: none"> <li>-understand their potential role in creating excess nitrogen, need for nitrogen abatement, and potential actions they can take to support reduction</li> <li>-support the role of oyster-mediated denitrification in nitrogen loading and abatement actions</li> <li>-implement oyster restoration</li> <li>-conduct monitoring of restoration sites and water quality</li> <li>-stakeholder communication</li> <li>-secure or provide funding to support programs for restoring oyster reefs or increasing oyster aquaculture production</li> <li>-grow oysters</li> </ul>
shoreline property owners	<ul style="list-style-type: none"> <li>-monitor oyster "growth" to support denitrification calculations</li> <li>-provide education through tours and other public outreach opportunities on their farms and practices</li> <li>-collaborate with researchers to collect data at their farm sites</li> <li>-stakeholder communication</li> <li>-participation in BMP review stakeholder panels</li> </ul>
environmental and civic organizations	<ul style="list-style-type: none"> <li>-consider role in nitrogen loading and consider abatement actions</li> <li>-consider opportunities for oyster growing</li> <li>-consider role in nitrogen loading and consider abatement actions</li> <li>-may develop/implement a management plan to help meet TMDL</li> </ul>
aquaculture industry	<ul style="list-style-type: none"> <li>-consider role in nitrogen loading and consider abatement actions</li> <li>-consider opportunities for oyster growing</li> <li>-consider role in nitrogen loading and consider abatement actions</li> <li>-may develop/implement a management plan to help meet TMDL</li> </ul>
ports/working waterfront	<ul style="list-style-type: none"> <li>-consider role in nitrogen loading and consider abatement actions</li> <li>-consider opportunities for oyster growing</li> <li>-consider role in nitrogen loading and consider abatement actions</li> <li>-may develop/implement a management plan to help meet TMDL</li> </ul>
community industries/polluters	<ul style="list-style-type: none"> <li>-consider role in nitrogen loading and consider abatement actions</li> <li>-may develop/implement a management plan to help meet TMDL</li> </ul>

<sup>a</sup>This list provides some common roles but is not a comprehensive representation of all potential roles.

oysters. Based on this value they conservatively estimate that 10.5 kg N ha<sup>-1</sup> y<sup>-1</sup> are removed annually.<sup>20</sup> Additionally, modeling efforts are developing estimates for total N removed through bioextraction and denitrification related to oyster aquaculture and reef restoration.<sup>25</sup> Generally, bioextraction appears to remove more N than denitrification, but there are critical differences between the two that confounds such a comparison. For example, if the oysters are consumed after removal a portion of that N will be returned to coastal ecosystems through wastewater. Oyster shells can also be returned, for example, to help provide substrate for larval recruitment. In contrast, denitrification results in turning the reactive N into a gaseous form which would have been "fixed" (naturally by bacteria or through industrial fertilizer production) before being usable again.

The Chesapeake Bay Program is the most advanced in its consideration of oyster-mediated denitrification as a management tool. Other regions such as Cape Cod, Massachusetts, are also considering this practice. There are several towns experimenting with the use of oysters as an in-water mitigation tool for their coastal nutrient pollution challenges.<sup>56–60</sup> Currently, all mitigation projects involving shellfish that have been accepted by the state for meeting the TMDLs require the removal of oysters (i.e., bioextraction<sup>56</sup>). In addition, some municipalities have explored getting credits for denitrification from oysters. Howes and Eichner<sup>59</sup> determined N removal

potential of oyster bioextraction and oyster-mediated sediment denitrification for Linnie's Pond, a subestuary of Pleasant Bay; however, to date, Massachusetts regulators have not approved the use of oyster-mediated sediment denitrification values to meet individual waterbody TMDLs.

## ■ STAKEHOLDER ENGAGEMENT AND COMMUNICATION IN OYSTER-MEDIATED DENITRIFICATION BMPs

Meeting N reduction goals necessitates behavior change by residents and governments as well as public support for localized and regional mitigation efforts.<sup>61</sup> Stakeholder engagement is a critical piece in the implementation of all nutrient BMPs because it broadens the ideas and creativity of management efforts<sup>62</sup> and increases acceptance from local communities and decision makers.<sup>63</sup> For example, engaging diverse perspectives in environmental management can increase the perception of fairness as well as the trust of those who may affect or be affected by the management efforts.<sup>64</sup> Thus, for oyster-mediated denitrification to work as a part of nutrient management strategies, stakeholders must be included. Denitrification is a complicated topic and requires varied communication approaches specific for individual stakeholder groups. For example, what a wastewater treatment plant (WWTP) operator needs to know to meet their local nitrogen management goals is different from what the wider

public needs to understand. Different approaches and discussion points may be needed when communicating the potential of oyster-mediated denitrification. Applying key principles of effective public engagement, it is important to consider:

- Who are the stakeholders?
- What are their roles in nutrient management?
- How do they best receive AND provide information?
- What challenges may exist that may impede the ability to communicate and ultimately achieve “support” for the effort?

There is a contingent of common stakeholders that may need to be engaged in a nutrient management process that is considering the use of oyster-mediated denitrification BMPs (Table 1). Stakeholder engagement and communication needs to include both formal and informal methods.<sup>65</sup> Some suggested mechanisms for engagement and communication include the development of simplified infographics, guest lectures from respected scientists, site visits to restoration or aquaculture sites, citizen science water quality monitoring programs, technical reports, newspaper and other general news media, community meetings, workshops, webinars, and direct one-on-one meetings.

While engagement, collaboration, and communication in BMP development is important, it can also be challenging.<sup>66</sup> Stakeholder groups have different incentives to participate, and anticipating these differences by examining localized elections or funding initiatives will help frame productive stakeholder conversations. In some cases, a lack of interest may inhibit stakeholder engagement. For example, members of the general public may be antagonistic toward increased aquaculture or reef restorations out of concerns for impacts on the aesthetics or available uses of local waters. This was highlighted in a recent study that found support for aquaculture was not a clear-cut for/against attitude. Instead, support depended upon the waterbody, the acreage of the farm, and farming methods.<sup>67</sup>

Implementation will also be heavily dependent upon the ability to permit the reef restorations or increases in oyster production as well as funding for restoration, monitoring, and maintenance. Integrating oyster aquaculture and restoration activities into BMPs can become complicated because of the private industry, public institutions, and other stakeholders who may be involved. Allocation and acquisition of funding can be contentious, and many of these projects can be quite expensive. For example, one study estimated a median restoration cost for oyster reefs at \$189,665 (2010 USD\$) per hectare.<sup>68</sup> Clearly, articulating a cost–benefit analysis, including comparing the costs of oyster-mediated denitrification with other N removal strategies (e.g., advanced treatment septic systems or permeable reactive barriers) will be key. One such study used an avoided cost analysis, with wastewater treatment as the alternative management measure, to calculate the maximum potential value of N removal from Great Bay, New Hampshire.<sup>25</sup> Estimation of the annual value of N removal via assimilation from aquaculture and restored reef oysters and denitrification from reef oysters is \$461,000 and \$760,000 for current (10.3 ha) and expanded (39.7 ha) leased aquaculture areas, respectively, in the Great Bay Piscataqua Estuary.

Perceptions from different stakeholders may come down to not understanding the complex processes involved in oyster-mediated denitrification. This is something that can be

overcome by developing a communication approach that clearly emphasizes the potential importance of oyster-mediated denitrification to each type of stakeholder. For example, building off the insights from Dalton and Jin<sup>67</sup> that support for aquaculture varies depending on the place and type of farming could allow for more targeted communication to coastal homeowners or zoning officials about the potential co-benefits of denitrification within their specific waterbodies. This communication is particularly challenging as eutrophication and denitrification are highly technical and can be difficult to explain, thus it is critical to communicate select key messages with stakeholders (for a general set of key messages, see Figure 2). These messages include the need for basic public

Oyster-mediated denitrification provides promise for expanding nitrogen management efforts.

Too many nutrient inputs harm many marine waterbodies & their aquatic life which are valued by communities & visitors. These water quality issues are caused by excess nitrogen and phosphorus (nutrients) from agriculture, wastewater, air pollution, & more.

Denitrification can remove some excess nitrogen.

Denitrification may occur at an enhanced rate on or near oyster reefs & aquaculture sites due to the biological activity of the oysters.

Oyster-mediated denitrification as a nutrient management practice requires significant stakeholder engagement & communication.

More research & management frameworks are needed to support widespread implementation of oyster-mediated denitrification in nitrogen management.

Oyster-mediated denitrification cannot meet the entire TMDL requirements but is an in-water option that could contribute to reducing excess nutrients.

**Figure 2.** Examples of key messages for communicating oyster-mediated denitrification to many of the stakeholders identified in Table 1. Images in the example factsheet are from The Noun Project ([thenounproject.com](http://thenounproject.com)): Eucalyp, “oyster”; Yu Luck, “water pollution”; Smalllike, “oyster”; and Olena Panasovska, “Communication”).

information about the impacts of nutrients on coastal waters which may include simplified explanations of the nitrogen cycle or nutrient impacts. It is essential that all stakeholders understand that oyster-mediated denitrification will not meet the entire TMDL requirements but can be a useful component of a larger multifaceted approach.

## ■ NEXT STEPS

**Implementation Needs.** To date, oyster-mediated denitrification has not been formally included in a watershed management plan for N reduction. As a step toward integrating this approach into nutrient management plans, the Chesapeake Bay Partnership has initiated strategies for developing spatially

explicit verifiable metrics for including oyster-mediated denitrification rates of the whole reef community to apply toward meeting TMDL N loading targets. To gain widespread acceptance for inclusion of oyster-mediated denitrification in N management plans local or national governments will have to pioneer proposed approaches through to implementation, and that may prove challenging. Implementation will depend on creating BMP guidelines for standardized procedures to verify denitrification rates, followed by monitoring protocols, and maintenance for either a restoration site or an aquaculture operation. Once an oyster aquaculture operation is expanded or a restoration effort is implemented, crediting these approaches can take any number of forms, all of which require agreements among diverse stakeholders and agencies. The existing strategy for bioextraction in the Chesapeake Bay can serve as a model for other programs and countries to build upon for future management implementation of oyster-mediated denitrification as monitoring standards are developed and management implications are better understood.

**Research Needs.** One of the most salient scientific needs is the demand for consistent, rapid, and cost-effective methodologies and metrics for quantifying denitrification, including enhanced sediment denitrification, individual-oyster based denitrification through shell and gut microbial activity, and whole reef community denitrification measurements. Successful use of oyster-mediated sediment denitrification includes calculating N budgets for both restoration and aquaculture efforts that include both bioextraction and denitrification values, identifying N burial potential, determining legacy impacts on sediments from oyster aquaculture, calculating estuary-specific oyster growth potential, tracking fate of oyster biodeposits, and identifying adequate larval recruitment to ensure reef sustainability. For oyster microbial communities, if individual oyster denitrification values can be calculated and replicated, it may be possible to implement denitrification credits for individual oysters and incorporate into a BMP for nutrient credit schemes. Whole reef community denitrification requires more research from different habitat types (e.g., intertidal, subtidal), differing levels of disturbance (e.g., water flow, harvesting method, harvesting schedules), and varying water quality/nutrient gradients to better understand factors affecting denitrification rates leading to improved estimates for N reduction crediting. Urgent future research will need to determine how multiple biological and chemical-physical drivers (e.g., oyster size, density, reef age, cultured vs reef oysters, water column N, temperature, salinity, dissolved oxygen, seasonal variation) may affect denitrification rates. Identifying the environmental conditions that enhance N removal in oyster habitats would enable better use in N management. In building these research efforts, deliberate and informative engagement with a range of stakeholders may also identify additional research needs that will better facilitate the use of oyster-mediated denitrification in nutrient management.

**Limitations.** Although oyster-mediated denitrification offers considerable promise for contributing to N reduction in coastal waters, it will not replace extensive source control efforts. In particular, there are concerns that focusing on *in situ* remediation will lead to less efforts preventing N from entering the system. There are limits to both ecological and social carrying capacity in coastal systems for oyster aquaculture and restoration.<sup>69,70</sup> Ecological constraints could include food availability, appropriate habitat, and water quality.<sup>71</sup> Social acceptance has been identified as a primary deterrent to the

use of BMPs such as oyster aquaculture.<sup>67,69,72</sup> Social constraints may include conflicts in use of the space by recreational users or aesthetic impacts on coastal homeowners and visitors.<sup>67,69</sup>

**Moving Forward.** Tackling N pollution remains a great environmental challenge in coastal systems across our nation and the world. Oyster-mediated denitrification has the potential to make important contributions to N reduction and management planning in conjunction with more traditional point source control and other BMPs. Broader incorporation into management necessitates a better understanding of how denitrification works and what limitations exist in the implementation of oyster-mediated denitrification by managers and practitioners. Careful engagement with a range of stakeholders to identify information and research needs, facilitate adoption, and incorporate limitations is critical for increasing the use of oyster-mediated denitrification for nitrogen reduction. With advancements in research and engagement, there is considerable opportunity for the incorporation of oyster-mediated denitrification into nutrient mitigation policies in coastal areas.

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**Notes**

The authors declare no competing financial interest.

**Biography**

Robinson W. (“Wally”) Fulweiler is a professor in the Department of Earth and Environment and the Department of Biology at Boston University. She is an ecosystems ecologist and biogeochemist. She is especially interested in how anthropogenic changes affect the ecology and elemental cycling of ecosystems on a variety of scales (i.e., local nutrient loading; regional/global climate change). Current research is centered on the transformations of elements across the land–ocean continuum, the ultimate fate of nitrogen in the marine environment, the impact of climate change on benthic–pelagic coupling, and the role of coastal systems in greenhouse gas budgets. Her work on oysters focuses on understanding how they mediate biogeochemical cycles, with an emphasis on quantifying the ecosystem services they provide. She enjoys working with stakeholders interested in environmental processes. This manuscript was developed during a two day workshop that engaged a range of representative stakeholders. She is especially proud of it because of this stakeholder engagement and because of the hard work of co-authors during the workshop and beyond, including during the COVID pandemic. She is thankful for everyone’s effort.

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