



Meta-analysis of oyster impacts on coastal biogeochemistry

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Overfishing, nutrient-fuelled hypoxia and habitat destruction have reduced oyster populations to a fraction of their former abundance. Over the past two decades there has been a widespread effort to restore oyster reefs and develop oyster aquaculture. Yet it remains unclear how re-introduction of large oyster populations will change coastal biogeochemistry. Of particular interest is whether oysters may help offset excess nitrogen loading, which is responsible for widespread coastal water quality degradation, low oxygen conditions and biodiversity declines. Here we used a meta-analysis approach to assess how oysters alter inorganic nutrient cycling, with a focus on nitrogen removal. Additionally, we examined how oysters alter greenhouse gas emissions. We demonstrate that oysters enhance removal of excess nitrogen by stimulating denitrification, promote efficient nutrient recycling and may have a negligible greenhouse gas footprint. Further, oyster reefs and oyster aquaculture appear to have similar biogeochemical function, suggesting the potential for sustainable production of animal protein alongside environmental restoration.

Approximately 40% of the world's population lives within 100 km of the coast¹. These 2.4 billion people exert immense pressure on the ecology of coastal ecosystems, perhaps most dramatically by altering the availability of nitrogen (N)^{2–4}, phosphorus (P)^{5,6} and silica (Si)^{7,8}. Excess nutrient loading to coastal systems has led to a series of deleterious consequences (for example, eutrophication^{5,6}, low oxygen conditions⁹ and reduced productivity of valuable fisheries^{6,10}). The negative impacts of excess nutrients have been exacerbated by the decimation of coastal shellfish populations through overharvest¹¹, pollution¹² and disease¹³.

Historically, oysters were found in large populations in many coastal systems, and sustainably supported human populations for millennia¹⁴. Today, over 85% of reefs have been lost globally¹⁵, and less than 1% of wild populations remain in many locations¹⁶. Returning oysters to human-dominated coastal systems may help negate some deleterious anthropogenic impacts and achieve Sustainable Development Goal 14 of the United Nations, “To conserve and sustainably use the oceans, seas and marine resources for sustainable development”¹⁷. Specifically, rebuilding large and well-managed oyster populations can promote conservation and sustainable use of the seas by creating new habitat and maintaining productivity, cleaning water through removal of suspended particulates and excess nutrients^{18,19} and providing a source of animal protein for those living in coastal communities with limited access to livestock protein sources, at a low greenhouse gas (GHG) cost²⁰. Additionally, development of the oyster aquaculture industry provides economic benefits for small-scale fishers and coastal communities. Introduction or re-introduction of oysters to coastal systems may also be associated with negative ecological consequences (for example, competition for phytoplankton with other filter feeders, introduction of disease), particularly if a non-native species is used in restoration or aquaculture^{21–23}.

In this Analysis, we examine the role oysters play in regulating coastal biogeochemical cycling. In coastal ecosystems, N and P availability is controlled by external (for example, sewage discharge) and internal (for example, recycling of nutrients from the sediments

to the water column) sources²⁴. Oysters enhance recycling of nutrients by stimulating sediment decomposition processes following deposition of faeces and pseudofaeces (collectively ‘biodeposits’)¹⁸. Biodeposition can also reduce eutrophication by stimulating N loss through denitrification (the microbial conversion of biologically reactive N to non-reactive dinitrogen (N₂) gas)²⁵. Oysters themselves alter nutrient cycling by excreting N and P, and denitrification occurs in their digestive system²⁶.

Since the 1990s there have been large efforts to restore oyster habitat²⁷ and develop the oyster aquaculture industry for economic benefit and to regain lost ecosystem services. For example, New York City is working to return one billion oysters to its waters by 2035 (<https://billionoysterproject.org/>), and oyster aquaculture is practiced on every continent except Antarctica. In 2016, global harvest of oysters raised in aquaculture exceeded 5,438 million tonnes, an 8% increase since 2014²⁸, and there is still tremendous potential for expansion²⁹. So far, studies of the biogeochemical impact of oysters have focused on denitrification or nutrient regeneration at a single oyster farm or reef, making extrapolation to larger scales difficult. Here we used a meta-analysis approach to quantify the role oysters play in regulating coastal biogeochemical cycles at a global scale. Specifically, we focused on oyster-driven: regeneration of N, P and Si, N removal via denitrification and GHG emissions. We then compare the biogeochemical impact of different oyster habitats and species. Finally, we suggest future studies that will advance the field and clarify uncertainties identified in this meta-analysis.

Results and discussion

Our meta-analysis considered 1,012 studies and after screening included 45 (Supplementary Fig. 1). Included studies spanned 5 continents and 7 species of oyster, and most ($n=28$) were from the Atlantic coast of North America (Fig. 1). In total, 17 studies reported fluxes from oysters^{20,26,30–44}, with 626 individual flux measurements, and 31 studies (refs. ^{20,36,40,45–71}; and S. G. Ayvazian et al., manuscript in preparation) reported fluxes from sediments, providing 4,328 individual flux measurements. Below, all effect sizes for

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Fig. 1 | Location of studies used in this meta-analysis. Map created by Emily Moothart using ArcGIS software with data collected during the literature review.

sediment fluxes are reported as mean estimated Hedges's $g \pm 95\%$ confidence interval (CI) and a P value for significance. For context: small effect, $g = 0-0.2$; medium effect, $g = 0.2-0.5$; and strong effect, $g > 0.5$ (ref. ⁷²). For fluxes from oysters, we report the mean \pm s.e. ($\mu\text{mol ind}^{-1} \text{h}^{-1}$) for market size *Crassostrea virginica*. As oyster fluxes are not compared with a control, no g can be calculated.

Oyster regulation of nutrient recycling. Both the magnitude and ratio of oyster-mediated nutrient regeneration are necessary considerations when discussing how oysters regulate coastal nutrient availability. Enhanced nutrient regeneration maintains a productive ecosystem, but changes in the availability of N relative to P and Si or ammonium (NH_4^+) relative to combined nitrate (NO_3^-) + nitrite (NO_2^-), NO_x , can lead to a phytoplankton community dominated by dinoflagellates and cyanobacteria^{9,73,74}, groups often associated with harmful algal blooms and less efficient transfer of energy across trophic levels.

Sediments beneath oysters return significantly more NH_4^+ to the water column than bare sediments ($g = 0.750 \pm 0.377$ ($P < 0.001$), $n = 25$; Fig. 2). In contrast, oysters have a highly variable effect on sediment NO_x fluxes, and one that is not significant across studies ($g = 0.406 \pm 1.577$ ($P = 0.583$), $n = 12$; Fig. 2). NO_3^- fluxes were also statistically unchanged in the presence of oysters ($g = 0.012 \pm 0.478$ ($P = 0.956$), $n = 9$). No conclusions could be drawn for oyster effect on NO_2^- release due to small sample size ($g = 0.784 \pm 0.927$ ($P = 0.059$), $n = 2$), but these limited data suggest that it may be enhanced in oyster habitats. Oysters also have a strong effect on sediment phosphate (PO_4^{3-}) regeneration ($g = 0.561 \pm 0.319$ ($P = 0.003$), $n = 12$; Fig. 2). Oysters may have a net positive effect on sediment Si flux ($g = 0.375 \pm 0.974$ ($P = 0.123$), $n = 2$), but again the data are too limited to draw a definitive conclusion.

We can consider the ratio of the calculated g values for two sediment nutrient fluxes to determine how oysters may change water column nutrient availability. For example, diatoms require an N:Si ratio ≤ 1 to dominate. A $g(\text{N}):g(\text{Si})$ ratio equal to 1 would indicate that oysters stimulate sediment regeneration of N and Si at the same rate, and do not change the ratio of sediment N and Si regeneration. If $g(\text{N}):g(\text{Si}) > 1$ then oysters drive greater N than Si regeneration relative to bare sediments, and if $g(\text{N}):g(\text{Si}) < 1$, then Si is regenerated more rapidly than N. Oysters only slightly change the ratio of sediment N and P regeneration ($g(\text{NH}_4^+ + \text{NO}_x):g(\text{PO}_4^{3-}) = 1.31$), and probably do not drive either nutrient to become limiting to production. However, oysters may drive greater regeneration of N relative to Si ($g(\text{NH}_4^+ + \text{NO}_x):g(\text{Si}) = 2.17$), though again only two

studies compared sediment Si fluxes between bare sediment and sediment beneath oysters. In areas with large oyster populations, sediments will probably regenerate at least twice as much NH_4^+ as NO_x ($g(\text{NH}_4^+):g(\text{NO}_x) = 2.38$). It appears oysters could potentially lead to shifts in phytoplankton community structure that preferentially use NH_4^+ to NO_x , such as dinoflagellates and cyanobacteria^{73,75}.

Both oyster reefs ($g = 0.684 \pm 0.428$ ($P = 0.002$), $n = 12$) and aquaculture ($g = 0.742 \pm 0.482$ ($P = 0.003$), $n = 11$) stimulate sediment NH_4^+ fluxes, with no statistical difference between the two habitat types ($P = 0.860$). Similarly, NO_x fluxes were statistically the same ($P = 0.706$) between reefs ($g = 0.673 \pm 3.043$ ($P = 0.665$), $n = 6$) and aquaculture ($g = 0.077 \pm 0.571$ ($P = 0.791$), $n = 4$). NO_3^- fluxes did not differ ($P = 0.063$) between habitat types, despite the appearance of NO_3^- uptake by sediments beneath aquaculture ($g = -0.307 \pm 0.616$ ($P = 0.328$), $n = 5$) and release from sediments adjacent to reefs ($g = 0.316 \pm 0.230$ ($P = 0.007$), $n = 4$). Too few studies reported NO_2^- fluxes to allow for statistical comparison. PO_4^{3-} fluxes were also no different ($P = 0.863$) from sediments beneath reefs ($g = 0.616 \pm 0.677$ ($P = 0.075$), $n = 4$) and aquaculture ($g = 0.550 \pm 0.314$ ($P < 0.001$), $n = 8$).

Oysters themselves recycle significant quantities of NH_4^+ ($5.73 \pm 0.91 \mu\text{mol individual (ind.)}^{-1} \text{h}^{-1}$) and PO_4^{3-} ($0.82 \pm 0.1 \mu\text{mol ind.}^{-1} \text{h}^{-1}$) to the water column. NO_x fluxes were much more variable ($2.64 \pm 5.74 \mu\text{mol ind.}^{-1} \text{h}^{-1}$), with one study reporting high NO_x emission⁴² and another reporting nearly equivalent NO_x consumption³⁸. NO_3^- fluxes were only reported in two studies that met our criteria but were slightly lower ($0.50 \pm 0.92 \mu\text{mol ind.}^{-1} \text{h}^{-1}$) than NO_x . Three studies reported NO_2^- fluxes, and they were lower ($0.11 \pm 0.02 \mu\text{mol ind.}^{-1} \text{h}^{-1}$) than the sum of NO_x and NO_3^- fluxes. We could not locate any studies that report oyster Si excretion. Other grazing organisms excrete Si^{2+} , so it is possible oysters may too. Unlike sediment nutrient regeneration, N and P excretion from oysters probably drives N to become limiting in the context of the Redfield ratio (16 N:1 P), with an N:P molar ratio of 6.99 $\text{NH}_4^+:\text{PO}_4^{3-}$.

It is clear oyster habitats drive substantial nutrient recycling, though they may increase $\text{NH}_4^+:\text{NO}_x$ with potentially negative consequences. There is a notable body of literature focused on top-down regulation of phytoplankton biomass and community by oysters, but less attention has been paid to how oysters may change phytoplankton community structure from the bottom up, despite evidence for stimulation of productivity using regenerated nutrients⁷⁷. Future research should address this so we can better understand how larger oyster populations may change the ecology of coastal ecosystems.

Removal of excess nitrogen by oysters via denitrification. Stimulation of sediment denitrification and denitrification in oysters can permanently remove excess N from coastal systems, reducing the impact of eutrophication. There are two commonly used methods for measuring rates of denitrification, the N_2/Ar (di-nitrogen gas/argon) technique⁷⁸ and the isotope pairing technique (IPT)⁷⁹. The N_2/Ar technique measures net exchange of N_2 between the sediment and the water column, and the resulting fluxes are either net positive (that is, denitrification) or net negative (that is, nitrogen fixation). The IPT requires the addition of a tracer and a series of methodological assumptions to calculate sediment denitrification, and IPT rates are generally lower than those measured with the N_2/Ar technique⁸⁰.

When we examined denitrification rates measured using the N_2/Ar technique, we found that oysters have a strong positive effect on sediment denitrification ($g = 0.682 \pm 0.276$ ($P < 0.001$), $n = 19$; Fig. 3). The effect of oysters on sediment denitrification is greater when measured using the N_2/Ar method ($g = 0.682 \pm 0.284$) relative to the IPT ($g = 0.239 \pm 0.745$ ($P = 0.463$), $n = 7$), probably due to under estimation of denitrification using the IPT⁸¹. While the

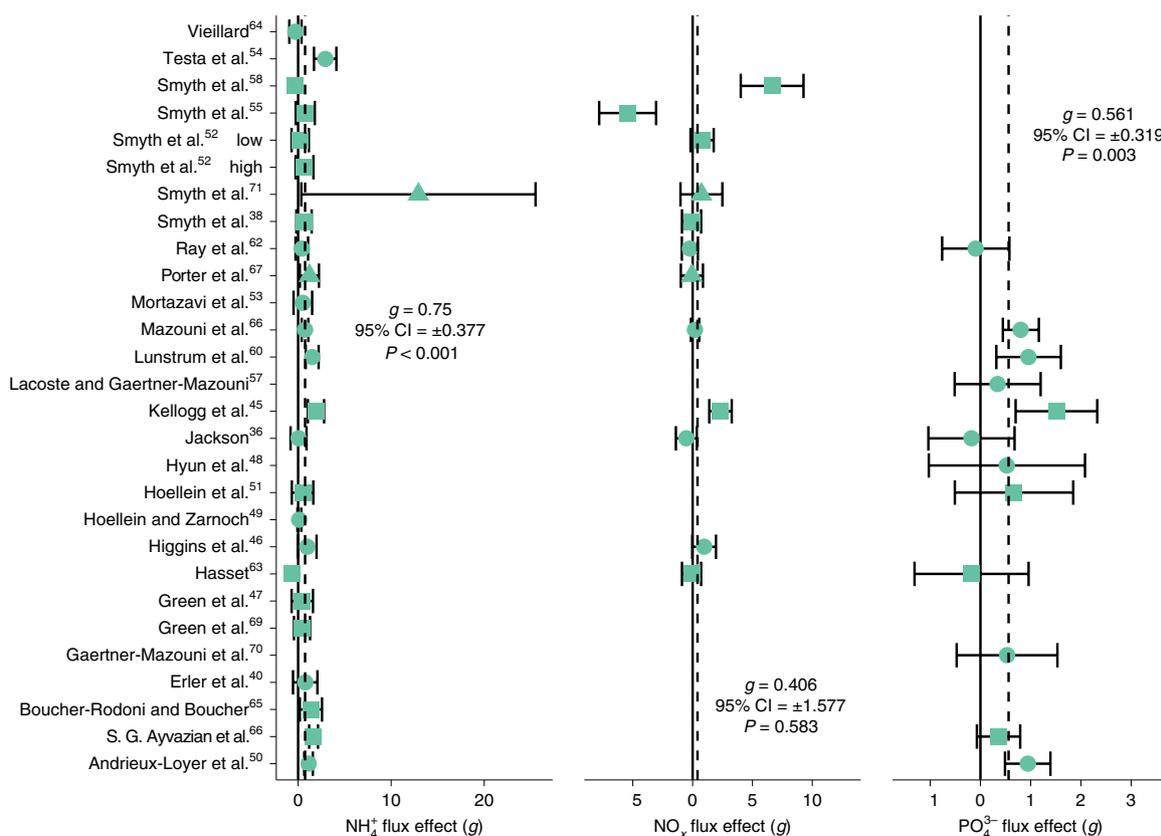


Fig. 2 | Effect size of oysters on nutrient fluxes. Effect size (Hedges's g , 95% CI, and random effect meta-analysis model P value) of oysters on rates of sediment regeneration of the nutrients NH_4^+ , NO_x and PO_4^{3-} from aquaculture studies (circles), reef studies (squares) and mesocosm studies (triangles). Each point represents the calculated Hedges's g for a given study and the error bars represent the 95% CI. Effect size describes the magnitude of increase ($g > 0$) or decrease ($g < 0$) of a flux beneath oysters relative to bare sediment. All points to the right of the solid line indicate a net positive effect, and points to the left of the solid line indicate a net negative effect. The dashed line indicates the mean effect size (g) of all studies together.

magnitude of the effect of oysters on net N_2 fluxes was higher in reef habitats ($g = 0.792 \pm 0.199$ ($P < 0.001$), $n = 11$) than aquaculture ($g = 0.514 \pm 0.220$ ($P < 0.001$), $n = 6$), there was no statistical difference between the two habitats ($P = 0.223$). A possible explanation for this discrepancy is that some studies that measured denitrification in reefs occasionally included the oysters in the incubation chamber. As oysters themselves produce N_2 (refs. ^{26,36,38,39,41,42}), this would probably increase the measured net N_2 flux.

Relative to sediment denitrification measurements made using the N_2/Ar technique (403 individual measurements of net denitrification in sediment beneath oysters), there are only a few measurements of net N_2 from oysters themselves ($n = 37$). Regardless, it is clear that denitrification proceeds within oysters, with an average denitrification rate from oysters of $4.78 \pm 2.46 \mu\text{mol indiv.}^{-1} \text{h}^{-1}$. In dense populations, denitrification in oysters could be an important pathway for N removal from coastal ecosystems²⁶, perhaps more than doubling total removal of excess N.

Despite a large number of studies that quantified denitrification from sediments in oyster habitats, every study that used the N_2/Ar method was conducted on either the Atlantic or the Gulf coast of the United States, and used the oyster native to this region (*C. virginica*). The only study conducted elsewhere used the IPT method⁴⁰. While it is unlikely that other oyster species will have different effects from *C. virginica*, it is necessary to collect similar measurements in other locations and with other oyster species.

It is important to consider the simultaneous removal and recycling of N in oyster habitats in an ecosystem context. Greater N release from oyster habitats may at first seem to suggest that

oysters worsen water quality, but this may not be the case as any N oysters excrete or that is regenerated from sediments beneath oysters was previously held in phytoplankton and detritus processed by the oysters. Simply, oysters generally do not add new nutrients to the system, and recycled nutrients cannot support more phytoplankton than would be supported by external nutrient loading to the system¹⁸. Instead, oysters promote a second round of primary production and efficient re-use of nutrients already in the system, while removing some excess N (Fig. 4). Specifically, any increase in water column primary productivity probably increases deposition of organic matter to sediments. In turn, because sediment denitrification is positively correlated with organic matter, N removal is enhanced (Fig. 4)^{82–84}. Simultaneous promotion of N recycling and removal by oysters may not reduce the trophic status of a coastal system (and may in fact increase it through enhanced primary production and carbon fixation), but the presence of oysters in the system may help to reduce the effects associated with cultural eutrophication, such as high phytoplankton biomass, reductions in harvestable fish and shellfish and decreased water clarity.

GHG release from oyster habitats. Oyster biodeposition may promote release of carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) from sediments. Oysters can also release these gases during respiration, digestion and from the metabolism of the bio-film living on their shell. If oysters promote the production of these GHGs, it may offset benefits associated with nutrient recycling and denitrification.

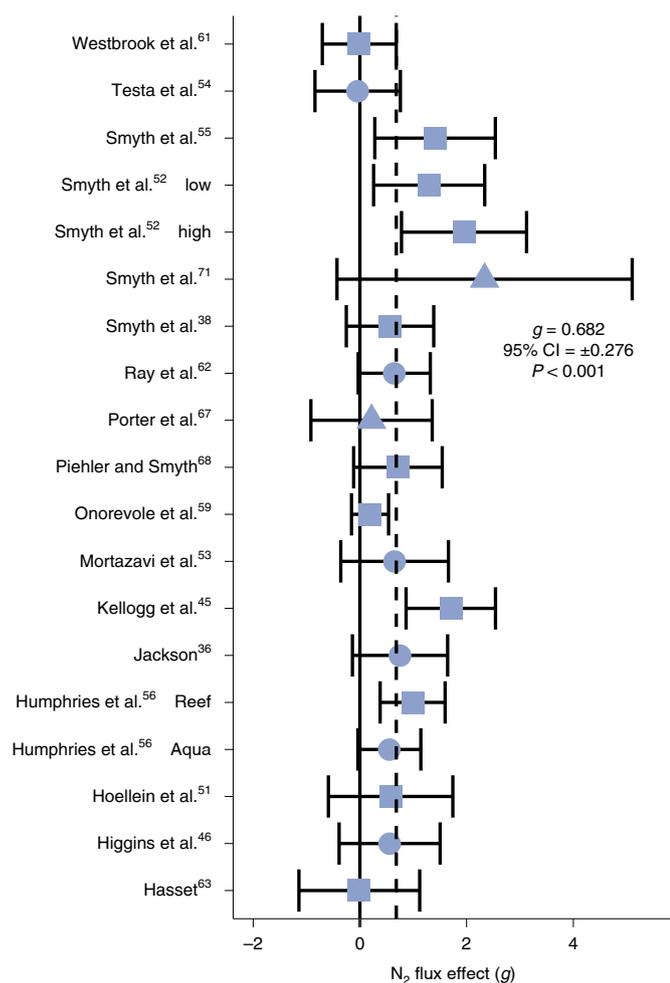


Fig. 3 | Effect size of oysters on N₂ flux. Effect size (Hedges's *g*, 95% CI and random effect meta-analysis model *P* value) of oysters on rates of sediment denitrification (N₂ flux) from aquaculture studies (circles), reef studies (squares) and mesocosm studies (triangles). Details as in Fig. 2.

Very few studies have reported the impact of oysters on GHG fluxes. These limited data demonstrate high variability between studies, and no conclusions could be made for the effect of oysters on sediment CO₂ ($g = 0.620 \pm 1.194$ ($P = 0.155$), $n = 3$; Fig. 5), CH₄ ($g = 0.432 \pm 1.592$ ($P = 0.364$), $n = 3$) or N₂O fluxes ($g = -0.771 \pm 2.969$ ($P = 0.469$), $n = 4$). There was not enough data to compare whether oyster reefs or aquaculture have a greater impact on sediment GHG fluxes. Quantifying how oysters may change sediment GHG production is an important step as aquaculture continues to expand and restoration projects are planned and completed.

Only three studies reported CO₂ and CH₄ fluxes from sediments beneath oysters and a control site, and those studies were conducted in two locations. Two were conducted at the same location in Ireland^{47,69} and the other on the Atlantic coast of North America²⁰. The two studies in Ireland were conducted by building oyster reefs then destructively sampling them a few months later, effectively creating a perturbation experiment. Ray et al.²⁰ measured sediment GHG fluxes at an oyster farm along a 7yr chronosequence and demonstrated an initial stimulation in sediment CO₂ and CH₄ release after the installation of oyster aquaculture, followed by a return to baseline conditions. Together, these results suggest that oysters may stimulate sediment GHG release, but for only a brief period.

Oysters themselves release N₂O ($0.00027 \pm 0.00054 \mu\text{mol indiv.}^{-1}\text{h}^{-1}$) and CH₄ ($0.0057 \pm 0.00085 \mu\text{mol indiv.}^{-1}\text{h}^{-1}$). Oyster N₂O release is dictated by the availability of dissolved N in the water column, with higher rates of production when dissolved inorganic nitrogen (nitrate + nitrite + ammonium; DIN) concentrations are high and N₂O consumption in the absence of DIN⁴³. There are at least two, not mutually exclusive, possibilities as to how N₂O production associated with large oyster populations will interact with enhanced nutrient recycling and denitrification. Enhanced regeneration of dissolved NH₄⁺ from sediments followed by transformation to NO_x via water column nitrification may lead to N₂O release. Alternatively, as DIN loading to coastal systems is reduced or removed via denitrification, there will be less N₂O production by oysters. Two of four studies reported enhanced uptake of N₂O in sediments beneath oyster aquaculture, which generally occurs in estuarine sediments when nitrate is limiting to denitrification. If site-specific conditions influence how oysters alter sediment N₂O fluxes, smart installation of oyster restoration and aquaculture could be an important strategy to help reduce estuarine N₂O emissions, particularly in systems anthropogenically enriched with N. It is unclear what controls oyster CH₄ production and consumption. Oyster respiration of CO₂ varies by size, water temperature and food availability, though when estimating the GHG footprint of animals in food production systems CO₂ release is typically ignored as it is a return of photosynthetically fixed carbon to the atmosphere^{85,86}. Oysters also release some CO₂ to the atmosphere during precipitation of calcium carbonate in shell formation^{87,88}.

Jackson et al.⁴² showed a 1:1 relationship between dissolved inorganic carbon (DIC) fluxes in oyster-only incubations relative to oyster and sediment incubations, indicating that the majority of CO₂ release in oyster reefs comes from the oysters themselves. Oysters may also influence the carbon (C) budget over space and time. Primary production and CO₂ sequestration may be higher downstream of oyster habitats than upstream, driven by enhanced light and nutrient availability⁸⁹ that could offset oyster associated CO₂ release. As oyster reefs accrete over time, they switch from a net source of C to the atmosphere, driven by respiration and shell formation, to a net sink as organic material accumulates in the reef habitat and is buried⁸⁷. It is necessary to consider these spatial and temporal factors alongside direct measurements of CO₂ flux from oyster habitats.

Comparison between oyster species. In some regions, native oyster species are used in restoration and aquaculture (for example, *C. virginica* on the Atlantic coast of the United States), and the biogeochemical changes associated with expanding this population may be considered beneficial. In other areas, non-native oysters have either invaded or been introduced. For example, *Crassostrea gigas* has largely replaced *Ostrea edulis* populations in Europe, both in natural habitats and in oyster farms⁹⁰. *O. edulis* also threatens *Saccostrea glomerata* populations in Australia⁹¹. Non-native introductions have been associated with negative consequences, such as reduced ecosystem carrying capacity and alteration of food web structure^{90,92}. It is less clear how non-native oysters may alter biogeochemical function relative to the native species because of a paucity of data. Here we were able to compare the biogeochemical impacts of *C. gigas* with *C. virginica* on only sediment NH₄⁺ and PO₄³⁻ fluxes as there were not enough studies that met our criteria for other fluxes or species. Nevertheless, this preliminary analysis affords some insight. We found that sediment NH₄⁺ fluxes were higher ($P = 0.749$) under both *C. gigas* ($g = 0.836 \pm 0.295$ ($P < 0.001$), $n = 5$) and *C. virginica* habitats ($g = 0.742 \pm 0.497$ ($P = 0.003$), $n = 19$). *C. gigas* appears to enhance sediment PO₄³⁻ fluxes ($g = 0.847 \pm 0.124$ ($P < 0.001$), $n = 3$) more than *C. virginica* ($g = 0.451 \pm 0.473$ ($P = 0.062$), $n = 7$), though the two species were not significantly different in regard to their effect on sediment PO₄³⁻ release ($P = 0.113$).

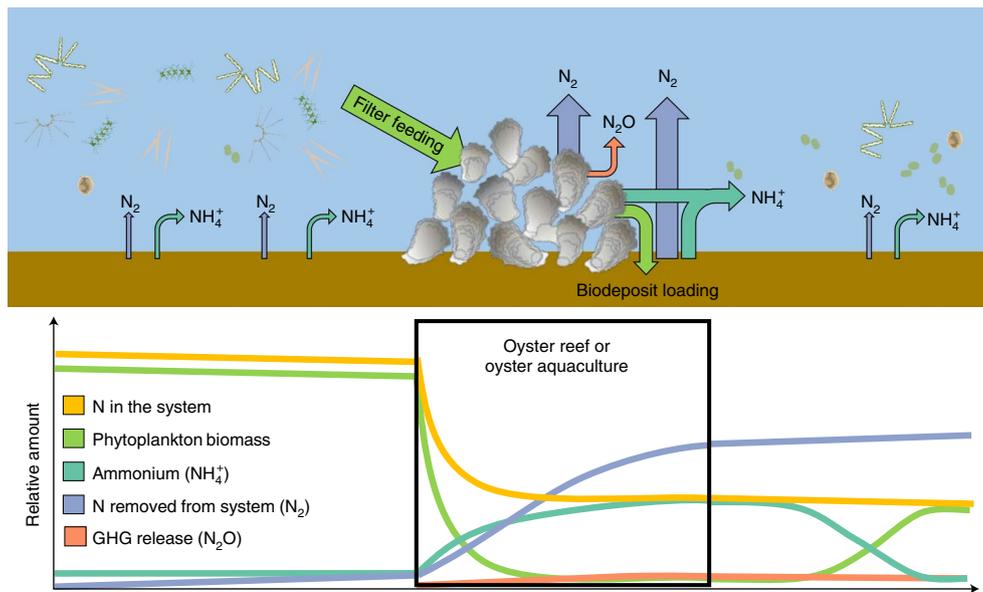


Fig. 4 | Transport of nitrogen through coastal ecosystems with oyster habitats. Oysters consume phytoplankton and move biodeposits containing N to the sediments. Oysters excrete NH_4^+ and drive NH_4^+ regeneration from sediments, supporting water column primary production. Oysters also enhance N removal from the system through denitrification (N_2 production) in their digestive system and by stimulating sediment denitrification. A very small amount of N_2O is released from the oyster digestive system, probably due to inefficient denitrification. Larger arrows indicate greater rates. Oyster and phytoplankton symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols).

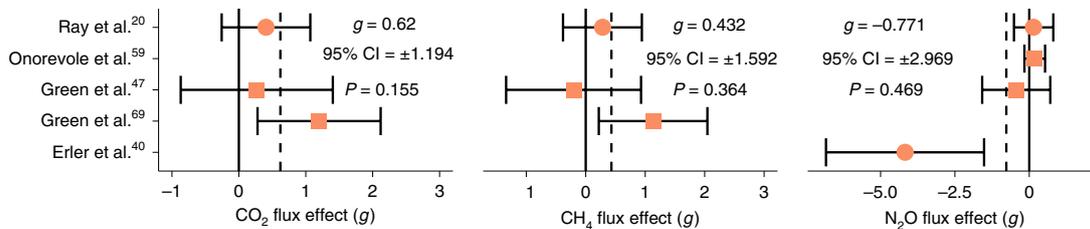


Fig. 5 | Effect size of oysters on GHG fluxes. Effect size (Hedges's g , 95% CI and random effect meta-analysis model P value) of oysters on rates of sediment production of the GHGs CO_2 , CH_4 and N_2O from aquaculture studies (circles) and reef studies (squares). Details as in Fig. 2.

There is also limited information on direct fluxes from oysters apart from *C. virginica* (Table 1). For this reason, we could not conduct statistical comparisons, though qualitatively it appears that most fluxes were of a similar range across species. There is a clear need for more studies of the impact of oysters on sediment biogeochemical fluxes as well as direct fluxes from oyster species besides *C. virginica*. With the limited evidence available, we cautiously suggest similar effects of oysters on coastal biogeochemistry across species, consistent with a recent study that reported no significant difference in GHG production by native (*C. virginica*) and non-native (*O. edulis*) species in the northeastern United States⁴⁴.

Similar biogeochemistry in oyster reefs and aquaculture. Oyster reefs and aquaculture had similar effects on sediment NH_4^+ and PO_4^{3-} recycling, as well as denitrification. Here we show that, while not identical, oyster aquaculture may have similar value in recovering ecosystem services associated with biogeochemical cycling to oyster reefs. Additionally, oyster reefs and aquaculture provide similar quality habitat^{93–95} and both may help to protect shorelines from storm surge^{96,97}. Considering these benefits, we cautiously suggest that financial investment in native oyster aquaculture may provide similar benefits to oyster reefs, while also expanding production

of a sustainable food resource and enhancing local economies^{28,98}. A recent study suggests oceans can be restored by 2050²⁷ and includes oyster reef restoration as a major step in that effort. Several roadblocks to oyster reef restoration were noted, including poor management of fisheries on remaining reefs and the economic cost of restoration. We propose that promoting oyster aquaculture may allow for these two roadblocks to be side stepped while still achieving similar restoration goals and benefits.

Human demand for animal protein is increasing^{99,100}. Oyster aquaculture provides a viable alternative source of animal protein with the added benefit of promoting coastal productivity and does not require the additional exploitation of limited resources. Additionally, like other bivalves, oysters have adapted to live in estuarine systems where they experience diurnal, seasonal and annual patterns of temperature, salinity, pH and oxygen fluctuations, potentially making adult oysters more resilient to the impacts of a changing climate. Further, oysters are a low GHG emitting protein source and even a small change in their consumption could lead to a significant reduction in GHG emissions²⁰.

An important next step in understanding the effect of oysters on coastal biogeochemistry is the development of predictive models that use local environmental characteristics, such as temperature,

Table 1 | Mean (\pm s.e.) flux of dissolved nutrients and gases from various oyster species

Species	N ₂ flux	NH ₄ ⁺ flux	NO _x flux	NO ₃ ⁻ flux	NO ₂ ⁻ flux	PO ₄ ³⁻ flux	N ₂ O flux	CH ₄ flux
<i>Crassostrea gigas</i>	ND	2.81 \pm 0.42	0.20 \pm 0.05	ND	0.08 \pm 0.01	0.87 \pm 0.09	ND	ND
<i>Crassostrea virginica</i>	4.78 \pm 2.46	9.44 \pm 2.56	2.89 \pm 6.33	0.80 \pm 1.46	0.11 \pm 0.03	1.33 \pm 0.67	0.11 \pm 0.76	2.93 \pm 1.23
<i>Ostrea chilensis</i>	ND	0.89 \pm 0.20	ND	ND	ND	ND	ND	ND
<i>Ostrea edulis</i>	ND	ND	ND	ND	ND	ND	0.47 \pm 0.04	0.21 \pm 0.97
<i>Saccostrea glomerata</i>	ND	5.65 \pm 0.10	ND	-0.03 \pm 0.01	ND	0.38 \pm 0.06	67.66 \pm 16.46	ND
All species	4.78 \pm 2.46	5.73 \pm 0.91	2.64 \pm 5.74	0.50 \pm 0.92	0.11 \pm 0.02	0.82 \pm 0.10	0.27 \pm 0.54	1.84 \pm 0.85

All values reported in $\mu\text{mol ind}^{-1}\text{h}^{-1}$ except N₂O and CH₄ fluxes which are in $\text{nmol ind}^{-1}\text{h}^{-1}$. N₂ fluxes only report values measured using the N₂/Ar method. All rates were collected from previous studies and are available in the published dataset accompanying this manuscript. ND indicates no published rates met our study selection criteria.

salinity, water column dissolved nutrient concentrations and/or sediment physical and chemical properties. To do this, future studies must thoroughly report environmental data associated with flux measurements and publish full datasets alongside manuscripts and theses.

Methods

Literature search. We aggregated studies measuring oyster fluxes and fluxes from sediments beneath oysters and a control site from peer-reviewed studies and non-reviewed literature. Peer-reviewed study identification was finalized on 23 September 2019 using Web of Science (webofknowledge.com) and the following searches and terms: search (1) (oyster) AND (sediment) AND (nitrogen OR denitrification OR phosphorus OR silica OR methane OR nitrous oxide OR carbon dioxide); search (2) (oyster) AND (nitrogen OR denitrification OR phosphorus OR silica OR methane OR nitrous oxide OR carbon dioxide). Together, these searches yielded 998 results (Supplementary Fig. 1). In addition to the initial literature search, we added published journal articles, dissertations, theses and journal articles in review that we were aware of ($n=14$) that did not appear in the Web of Science search, for a total of 1,012 studies.

Study selection criteria. We applied two screening steps to select studies for inclusion in our analysis. In the first step, we read the abstract of each study. If the abstract did not include a flux measurement from oysters or sediment beneath oysters, or indicate that such a measurement might be found in the manuscript, the study was rejected for further analysis. Next, we read all studies that passed the first screening step. If the study did not measure a net flux from adult oysters, report fluxes from both control sediment and sediment beneath or directly adjacent to oysters or report sample sizes, standard deviation or standard error, we excluded it. Studies that manually added organic material or biodeposits to sediments were excluded. If the same dataset was reported in multiple studies, only one version of that dataset was included (the earliest paper that reported the data). We also excluded published abstracts for conference talks, and studies not published in English.

In some cases, studies reported sample size but mean values and standard deviation or error had to be estimated from figures in the paper. These studies were included in the analysis, and the missing values were estimated by extracting them from plots and images embedded in the manuscript using WebPlotDigitizer Version 3.9 software. When the error bar did not pass the edge of the bar (or did not exist), error was calculated as 0, but an s.d. value of 1 was used to calculate g values in the meta-analysis. When sample size was reported as a range, we used the median possible sample size (that is, if the study reported $n=3-4$, we assigned n a value of 3.5). Following the second extraction step, 45 studies met our criteria for inclusion in the analysis.

Sediment flux data analysis. When studies reported s.e. for sediment fluxes, we converted it to s.d., as s.d. is needed for calculating Hedges's g (equation (1)). We converted all flux rates to either $\mu\text{mol g dry tissue weight}^{-1}\text{h}^{-1}$ (oysters) or $\mu\text{mol m}^{-2}\text{h}^{-1}$ (sediments). If rates were reported seasonally or monthly but no study mean was reported, we manually calculated a pooled study mean (X_{pooled} ; equation (2)) and variance ($\text{s.d.}_{\text{pooled}}$; equation (3)), where a and b represent rates reported different seasons or months. In studies that compared two habitat types with one control site, we used the same control site for both habitat types. Two studies reported the sample size as " $n=3$ or 4 " for each sampling month. In this case, we assigned an n value of 3.5, and used that while combining monthly mean and error. In all cases, we considered each sediment flux as an independent sample.

Next we calculated Hedges's g effect size (equation (4)) and variance (equations (2) and (3)); same method as for pooling means and variance within a study, but in this case the mean of sediments beneath oysters (X_E) and control sediments (X_C) for whole studies were pooled, as were all variances) using a fixed-effects model approach in the metafor package¹⁰¹ in R statistical software version 3.6.0, following similar methods to Harrer et al.¹⁰² and Anton et al.¹⁰³

The J value in equation (4) controls bias associated with different sample sizes between studies, and J is calculated in equation (5), where N_E and N_C are the experimental and control sample sizes, respectively. When interpreting g , the value reflects the effect size of the experimental treatment (in this case, presence or absence of oysters on sediment net N₂ flux) in terms of number and direction of standard deviations the experimental treatment is from the control. A g value between 0–0.2 is typically considered a small effect, 0.2–0.5 a medium effect, and >0.5 is considered a strong effect⁷².

$$\text{s.d.} = \text{s.e.} \times \sqrt{n} \quad (1)$$

$$X_{\text{pooled}} = ((X_a \times n_a) + (X_b \times n_b)) / (n_a + n_b) \quad (2)$$

$$\text{s.d.}_{\text{pooled}} = \sqrt{((n_a - 1) \times (\text{s.d.}_a)^2 + (n_b - 1) \times (\text{s.d.}_b)^2) / (n_a + n_b - 2)} \quad (3)$$

$$g = ((X_E - X_C) \times J) / \text{s.d.}_{\text{pooled}} \quad (4)$$

$$J = 1 - (3 / (4 \times (N_E + N_C - 2) - 1)) \quad (5)$$

To compare the influence of oysters on sediment fluxes between oyster reefs and oyster aquaculture, we used a random-effects meta-analysis model via the dmetar package¹⁰⁴. In this model, we used the Sidik–Jonkman method for determining τ^2 (the variance of the distribution of the true study effects) and the Hartung–Knapp adjustment¹⁰². We repeated this approach to compare sediment fluxes in oyster habitats with *C. gigas* and *C. virginica*.

Regarding denitrification, we excluded all studies that used acetylene techniques as acetylene is known to alter sediment microbial community function and provide inaccurate measurements^{105,106}. While only net N₂ fluxes from sediments and oysters matter in an ecosystem context, we also accepted studies that used the isotope pairing technique (IPT)⁷⁹ to compare this direct measurement with a measurement of the net N₂ flux (N₂/Ar technique)⁷⁸. Studies using the IPT were not included in the total estimate of oyster effects on sediment denitrification or comparison between habitat types.

Sediment flux publication bias. We followed the same methods used by Anton et al.¹⁰³ to test for publication bias among sediment flux studies that may distort the results of the meta-analysis. We evaluated bias using Egger's test, which estimates a regression using standard error of study specific effect sizes and is considered significant when the model intercept is statistically different from zero¹⁰². Additionally, we identified outlier studies that may exert substantial influence on the direction of the meta-analysis as those where the upper bound of the study 95% CI was lower than the lower bound of the pooled 95% CI (that is, an extremely small effect), or the lower bound of the study 95% CI was higher than the upper bound of the pooled 95% CI (that is, an extremely large effect)¹⁰². Both tests are available in the dmetar package¹⁰⁴. When Egger's test indicated significant publication bias ($P \leq 0.05$) for models that included possible outlier studies in the meta-analysis, we removed them and reported results from the newer, outlier-free test. We also excluded significant outliers from our habitat comparison. We had to remove only one outlier from the N₂/Ar meta-analysis (Supplementary Table 12), indicating a generally robust dataset free of publication bias.

Oyster data analysis. Oyster fluxes were reported in various units. We elected to convert all fluxes to $\mu\text{mol indiv.}^{-1}\text{h}^{-1}$, as some studies reported this rate without information about oyster tissue mass. For studies that reported flux as $\mu\text{mol g}^{-1}\text{h}^{-1}$, we assigned a value of 2.93 g indiv.⁻¹ to convert the rates, as this is the dry tissue mass of commercial size oysters where most of the measurements included in this meta-analysis were made (Atlantic coast of the United States). We opted to report rates in units of $\mu\text{mol indiv.}^{-1}\text{h}^{-1}$ so that we could maximize the amount of

data included in this study and because reporting on a spatial scale (for example, $\mu\text{mol m}^{-2} \text{h}^{-1}$) is less descriptive than reporting on an individual basis for several reasons. For example, there is and can be high variance in oyster stocking density in reefs and aquaculture dependent on habitat, oyster size, food availability, farm management practices and so on. Additionally, the vertical structure of the reef or oyster aquaculture gear (for example, cages in deep water that are several metres high can hold several bags of oysters) will have a different oyster density (and flux m^{-2}) from gear in shallow water with only one bag of oysters. However, this choice also probably introduces some bias as oyster weight and life stage vary across reef and aquaculture communities. To help reduce this bias we specifically excluded juvenile and larval oysters from this meta-analysis. After converting flux rates to $\mu\text{mol indiv}^{-1} \text{h}^{-1}$, we calculated pooled means and variance across studies using equations (2) and (3). We report all oyster flux values as mean \pm s.e. We did not perform publication bias analyses on fluxes from oysters alone, as these studies only report rates and do not compare oyster fluxes with anything.

Data availability

All data used in this study is available in the Figshare repository under the access number <https://doi.org/10.6084/m9.figshare.12488753>.

Code availability

The R script used in this meta-analysis is available in the GitHub community repository (<https://github.com/nray17/Meta-analysis-oyster-impacts-on-biogeochemistry>).

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Author contributions

N.E.R. and R.W.F. conceived and designed the study. N.E.R. constructed the dataset and performed statistical analyses. Both authors interpreted the results. N.E.R. wrote the manuscript with significant contribution from R.W.F. N.E.R. and R.W.F. edited the manuscript. Both authors take full responsibility for the contents of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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