



Refining the Farm Aquaculture Resource Management Model for Shellfish Nitrogen Removal at the Local Scale

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Abstract

Nutrient-related environmental degradation in coastal waters is a continuing global problem. Bivalve shellfish farms show nutrient removal capabilities similar to some traditional management strategies and in some places have been incorporated into nutrient management programs to help achieve water quality goals. Bioextractive nutrient removal varies by farmed species and is influenced by environment parameters; thus, data and information for both are needed to estimate nutrient mitigation potential of shellfish farms. The Farm Aquaculture Resource Management (FARM) model, calibrated for farmed species, uses local environmental and farming practice data to simulate interactions between the farmed population and the local environment and to optimize cultivation practices for economic gain. We calibrated the model to predict nitrogen removal by Eastern oyster (*Crassostrea virginica*) farms with specific field and experimental data on oysters, their local environment, and farm practices in Long Island Sound, CT, USA. Previous FARM applications were not validated for nitrogen removal with local data. In the harvest when ready (HWR) model scenario (oysters are harvested when they reach harvest size), the farm removed 159 kg N ha⁻¹ year⁻¹ while the non-HWR scenario (all oysters are harvested at one time) removed 274 kg N ha⁻¹ year⁻¹. These estimates are within the range of previously reported in-water bioextraction studies in the Northeastern USA. The robust outputs from this validated model can be reliably used in marine spatial planning efforts and by nutrient managers to predict the nitrogen removal benefits that could be achieved through new or expanded eastern oyster farms in eutrophic environments.

Keywords Nutrient bioextraction · Nutrient removal · Nitrogen budget · Oyster production model · Oyster aquaculture · Long Island Sound

Introduction

Nutrient-related degradation is a serious threat to coastal ecosystems around the world. Excess nutrients can cause the overgrowth of algae and seaweeds, nuisance and/or

toxic blooms, hypoxic conditions, and loss of seagrass habitats, a condition called eutrophication (Bricker et al. 2008; Breitburg et al. 2018). Nitrogen has been identified as the limiting nutrient for primary production in most coastal and estuarine ecosystems (Ryther and Dunstan 1971; Howarth and Marino 2006), and nitrogen source

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reduction efforts have been implemented in many countries in efforts to reverse the effects of eutrophication (Boesch 2019).

Nitrogen management programs have focused largely on reducing land-based sources, such as improving nitrogen removal efficiency of wastewater treatment plants, implementing best management practices to reduce diffuse agricultural and stormwater runoff, and regulating industrial emissions to reduce atmospheric deposition (Howarth et al. 2002). These efforts have led to some success, such as the recovery of seagrass habitats in Tampa Bay, FL, and the reduction of hypoxia in Long Island Sound (Whitney and Vlahos 2021). Hysteresis, however, is not uncommon, and coastal waterbodies may still fail to attain water quality standards after the successful implementation of a variety of nitrogen source controls (e.g., Duarte et al. 2009; Rabalais and Turner 2019; Ni et al. 2020).

The persistence of eutrophic conditions in coastal environments has led resource managers to seek out innovative solutions to achieve further nutrient reductions. Shellfish aquaculture has been identified as a potential additional tool for nitrogen control in coastal and estuarine environments (Lindahl et al. 2005; Rose et al. 2014). Shellfish are filter feeders that incorporate particulate nitrogen from seston into tissue and shell as they grow. When farmed shellfish are harvested, the nutrients in their tissues and shell are removed from the waterbody, a process that has been called nutrient bioextraction. Biodeposits from shellfish aquaculture have been shown to enhance sediment denitrification in some locations and may increase nitrogen burial rates (Beseres-Pollack et al. 2013; Ray and Fulweiler 2021). Nutrient bioextraction has been incorporated into nitrogen management programs at the municipal scale for hard clams and eastern oysters in Massachusetts, USA (Town of Mashpee Sewer Commission 2015), and at the regional scale for eastern oysters in Chesapeake Bay, USA (Cornwell et al. 2016).

There is growing interest in expanding shellfish aquaculture for nutrient management purposes, and predictive tools to aid in municipal and/or regional planning efforts are needed. Environmental models are commonly employed by nutrient management programs for a variety of purposes, such as determining the scale of nutrient reductions necessary to attain water quality standards and the effectiveness of nitrogen reductions associated with land-based nitrogen source controls. The Farm Aquaculture Resource Management model (FARM) was developed as a reduced-complexity model to inform site and species selection, optimize cultivation practices, and assess the potential for eutrophication reduction (Ferreira et al. 2007; www.farmscale.org). The model is well described and has been tested and applied in the USA, EU, China, and elsewhere (Ferreira et al. 2007, 2008, 2009, 2011, 2012; Nunes et al. 2011; Bricker et al. 2014, 2015, 2016,

2018, 2020; Parker and Bricker 2020; Saurel et al. 2014; Silva et al. 2011). The FARM model calibrated for Long Island Sound was used for this study.

FARM estimates nutrient removal attributable to assimilation into tissue and shell given particulate ingestion and known assimilation and excretion rates from previous allometric and physiological studies, but the nutrient balance is achieved using a net energy mass-balance approach. Currently, FARM does not model nitrogen dynamics directly, which limits its applicability as a nitrogen management planning tool. The incorporation of shellfish tissue, shell, and seston nitrogen content, as well as nitrogen absorption and excretion rates, would improve parameterization of nitrogen uptake and loss rates, including during pre-ingestive selection and processing in the gut. Improvements to simulation of nitrogen dynamics in the model enable FARM to better estimate both production and nitrogen removal at the farm scale.

In collaboration with two local community partners, Greenwich Shellfish Commission and Stella Mar Oysters, we collected data over a growing season to estimate farm-scale rates of nitrogen reduction through bioextraction for cultivated Eastern oysters grown in Greenwich Bay, Connecticut. These site-specific data include the following: (a) monthly environmental water samples, (b) monthly oyster samples from Stella Mar Oysters, (c) periodic field measurements of oyster filter feeding, including nitrogen absorption, and (d) oyster excretion measurements conducted at the NOAA Fisheries Lab in Milford, CT. The three objectives of these data collections were to (a) optimize the model for the Greenwich Bay area using one year of detailed field measurements and experimental data, (b) improve the quality of nitrogen data for both the individual-based AquaShell model and FARM population model (Ferreira et al. 2007), and (c) improve the nitrogen removal estimation produced by the FARM model.

Methods

Data Collection for FARM Model Calibration, Validation, and Simulation of Nitrogen Dynamics

Farming Practices

Information on cultivation practices was provided by industry partner Stella Mar Oysters. The farm operates in Greenwich, CT, USA on 6.31 acres, growing Eastern oysters (*Crassostrea virginica*) subtidally on bottom without gear. Growers typically plant 1–1.5-in. seed in late April at a stocking density of 75 oysters m^{-2} , totaling 1.90 million seeded individuals across the full lease. A 4.0-in., harvest-size, diploid oyster can be grown in 2–3 years, depending upon environmental conditions. Mortality over

the cultivation cycle is typically ~20%. Minimum harvest size in the State of Connecticut is 3 in.; this farm harvests at a larger size to maximize production profits. Seed costs were reported to be \$0.04 individual⁻¹ and farmgate sale price \$0.47 individual⁻¹. Table S1 shows the environmental drivers measured at the farm used for individual model runs and simulations at the farm scale.

Environmental Data for Oyster Growth Curves — Monthly Sampling

Monthly measurements of local water conditions were made from May 2019 to March 2020 at the Stella Mar Greenwich oyster lease (41.011285° N, 73.590171° W). Water temperature, salinity, and dissolved oxygen were measured in situ using a handheld digital meter (Model ProODO, YSI Inc., Yellow Springs). Water samples for analysis of chlorophyll *a*, nutrients, and total particulate matter (TPM) from the seston were collected using a Niskin bottle at 1 m depth and transported on ice in a cooler back to the laboratory for filtration and analysis.

Chlorophyll *a* samples were filtered onto 25-mm GF/F filters, extracted at -20 °C in 90% acetone for 24 h, and then read on a Turner 10-AU digital fluorometer (Welschmeyer 1994). Samples for TPM content were filtered onto GF/C filters previously rinsed with Milli-Q water, dried, ashed at 450 °C for 4 h, and pre-weighed prior to collecting particulate content.

After filtration, seston samples were rinsed with isotonic ammonium formate. Seston filters were then dried to constant weight at 60 °C, weighed to calculate TPM, and ashed at 450 °C for 4 h and re-weighed to determine total inorganic matter (PIM). Particulate organic matter (POM) was calculated as the difference between TPM and PIM. Water samples for dissolved nitrate and nitrite were pre-filtered through 0.45-µm nylon syringe filters, frozen at -20 °C, and shipped to the MSI Analytical Laboratory (University of California, Santa Barbara) for analysis.

Water samples for ammonia were also pre-filtered through 0.45-µm nylon syringe filters and then analyzed immediately using a Hach Company ammonia test kit (detection limit 0.02 mg L⁻¹). The low-nutrient seawater reference standard (Sigma-Aldrich) was within ±0.01 mg L⁻¹ of the reported value. Water samples for CHN and particulate organic nitrogen (PON) analysis were filtered onto 25-mm GF/C filters that had been prepared and pre-weighed as described above for seston particulate content samples and were then frozen at -20 °C until analysis using a Costech ECS 4010 CHNS elemental analyzer (Valencia, CA). Samples for PON analysis were dried and acidified prior to elemental analysis (Martin 1993). During analysis, the standard reference material (SRM) 1547 (National Institute of Standards & Technology) was used to ensure nitrogen

accuracy and was 29,650 mg kg⁻¹ ± 540 (*n* = 140), which was within 0.22% of the reported value. During analysis, the SRM 8704 (National Institute of Standards & Technology) was used to ensure carbon accuracy and was 3.377 ± 0.003 (*n* = 145), which was within 0.77% of the reported value.

Average wind speeds were obtained on each sampling day from the Town of Greenwich (<https://www.greenwichct.gov/1081/Weather>). Current velocity at the shellfish farm was previously reported in Dvarskas et al. (2020).

Morphometrics and Nitrogen Composition — Monthly Oyster Sampling

Monthly samples of ~50 farmed oysters were obtained from Stella Mar from May 2019 to February 2020. Oysters were transported on ice to the laboratory and measured using calipers. Morphometric measurements included shell length (defined here as the longest distance between the hinge and the lip of the oyster, parallel to the long axis), shell width (defined here as the maximum distance between the anterior and the posterior margin measured parallel with the hinge axis), and shell depth (defined here as the greatest distance between the outsides of the closed valves measured at right angles to the place of shell commissure) (Galtsoff 1964). Individual, whole oysters were then weighed on an analytical balance to obtain total fresh weight, shucked using a shucking knife and scalpel; soft tissues and shells were separated and weighed again to determine tissue and shell wet weight. Tissue and shell samples were then dried to constant weight at 60 °C in a drying oven and weighed again to determine tissue and shell dry weight. After drying, whole tissue samples were ground to a powder with a McCrone ball mill grinder (Retsch GmbH, Haan, Germany). Shells were sampled for nitrogen analysis using a Dremel tool with a carbide burr on a drill press workstation. At least five locations on each shell were ground through, creating a fine powder that was captured in an aluminum weighing dish, and the powders from the individual sampled areas on each shell were combined to create a representative sample of the whole shell. The powder was sieved through a 1-mm sieve and stored in a whirl-pak® sampling bag. The Dremel tool and drill press were cleaned with a vacuum and with DI water in between each shell to prevent cross-contamination. Ground tissue and shell samples were stored in a desiccator until processing for CHN analysis on an elemental analyzer as described above.

Physiological Relationships — Filter Feeding Measurements

Filter-feeding experiments were conducted with Eastern oysters monthly from June to October 2019 at Elias Point, Greenwich (41.01137° N, 73.58809° W). Water temperature, salinity, and dissolved oxygen were measured during each

feeding experiment using a handheld digital meter (Model ProODO, YSI Inc., Yellow Springs). Filtration and related variables were quantified using the biodeposition method (Iglesias et al. 1998), as described in Galimany et al. (2011), and modifications to calculate nitrogen assimilation as described in Hoellein et al. (2014). Briefly, seawater was pumped from 1 m depth into a large reservoir tank and aerated to maintain suspension and even distribution of seston in the tank. Water flowed from the reservoir tank into 20 chambers, 18 of which contained an individual bivalve, and 2 control chambers that each contained an empty oyster shell. Flow rates to the individual chambers were maintained at 12 L h⁻¹, which was shown previously to result in homogeneous particle distribution, but minimal water recirculation or lateral flow between chambers. Oysters were obtained from a lease adjacent to Elias Point immediately prior to experiments, so were acclimated to local conditions. All individuals were allowed to recover in the flow-through chambers for several hours to minimize any handling stress.

Two sets of water samples (200–300 mL each) were collected from the inflow into the reservoir tank and the two control chambers every 15–20 min (six total samples per time point). Water samples were filtered onto GF/C filters that had been rinsed with Milli-Q water, dried, ashed at 450 °C for 4 h, and pre-weighed prior to conducting the experiments. One set of water samples was analyzed for particulate content. The second set was analyzed for seston nitrogen content (see below). Particulate samples were rinsed with ammonium formate during sample filtration to remove salts. Both sets of samples were transported to the laboratory on ice in coolers, dried to constant weight at 60 °C, and weighed to determine total particulate matter (TPM). Particulate samples were then ashed for 4 h at 450 °C and re-weighed to determine particulate inorganic matter to determine POM.

Gut transit time (GTT) was determined in the field and used to synchronize the seston within the water collection with the corresponding biodeposits produced by the individual bivalves (Hawkins et al. 1996). Five individuals were placed in beakers with a mixture of local seawater and cultured *Tetraselmis chui*. The time between an oyster opening and the production of green feces was considered to be the GTT. Water collection was initiated first, and subsequent collection of biodeposits from the experimental chambers of the flow-through system was delayed by the average duration of the GTT.

Immediately prior to biodeposit collection, individual chambers within the flow-through system were cleared of feces and pseudofeces produced during the recovery period. All feces and pseudofeces subsequently produced were then collected immediately using a pipette and stored separately. These biodeposits were filtered in the field onto GF/C filters that had been prepared and pre-weighed as described above.

Filters were rinsed with ammonium formate, transported on ice back to the laboratory, and dried to constant weight at 60 °C. Filters were re-weighed to determine dry weight, and ashed for 4 h at 450 °C and weighed again to determine ash weight. The physiological components of the absorptive balance (Table 1) were calculated according to Iglesias et al. (1998).

Nitrogen filtration, ingestion, rejection, and absorption rates were determined using a modification of the biodeposition method described in Hoellein et al. (2014). Biodeposits collected for each individual oyster were approximately divided in half and filtered separately. Both filters were dried to constant weight at 60 °C, weighed for determination of total particulate matter, and these weights were summed to calculate total TPM production per individual oyster. One filter was subsequently used for analysis of inorganic and organic content, as described above. The ratio of organic/inorganic content determined for this filter was applied to the total TPM produced per individual oyster. The second filter was analyzed for seston nitrogen content (%), and this percentage nitrogen was applied to the total TPM produced per individual oyster. Particulate nitrogen was analyzed using a Costech ECS 4010 CHNS elemental analyzer (Valencia, CA). During analysis, 1547 (National Institute of Standards & Technology) was used to ensure accuracy and was 29,650 mg kg⁻¹ ± 540 ($n = 140$), which was within 0.22% of the reported value.

At the end of each filtration measurement, oysters were transported to the laboratory on ice, shell length was measured using calipers, and, after shucking, soft tissue was dried to constant weight at 60 °C. Feeding variables were standardized to 1 g dried bivalve flesh (Y_w) using the following equation:

$$Y_w = Y_e \times (1/W_e)b$$

where Y_e is the experimentally determined filtration rate, W_e is the tissue dry weight for each individual, and b is the allometric coefficient which was set to 0.73 for oysters, as determined by Riisgard (1988).

Physiological Relationships — Excretion Rate Measurements

Oysters were maintained in 0.35- μ m-filtered seawater for depuration 24 h before measuring respiration (mg O₂ h⁻¹) and excretion (mg NH₃ L⁻¹ h⁻¹ g dry weight⁻¹) rates. Individual oysters were placed in closed chambers filled with 0.35- μ m-filtered seawater connected to a Loligo respirometry system (Viborg, Denmark) that records oxygen concentration depletion in eight chambers at the same time. In our system, we set up four large chambers (277–280 mL) and four small chambers (201–203 mL) to accommodate a range of oyster shell length sizes. One chamber was used as

a control using an empty shell, while the seven other ones were filled with live oysters.

A linear model was fitted to the oxygen concentration depletion data using the function “lm” from the core R software, which allowed calculation of respiration rate. Only data from oysters with active respiration behavior were used for calculating respiration rates, and background noise measured in the control chamber was subtracted from experimental chambers. Measurements lasted until 80% of oxygen saturation was reached in the experimental chambers. Thereafter, each chamber was opened carefully and a 5-mL seawater sample was collected to calculate excretion rate. Ammonia-N concentration was determined using salicylate-based ammonia HACH TNT kits (equivalent EPA 350.1, EPA 351.1, and EPA 351.2) with a detection limit of 0.015 mg L⁻¹. Reaction time was increased to 3.5 h to obtain a full color development.

Data from 17 different measurements that lasted 10–120 min were included to capture a range of oyster behaviors and excretion rates. Not all oysters opened/were active during the measurements; 55 oysters provided usable excretion rate data (Table S1). We repeated measurements at ambient seawater temperatures (11 to 22 °C) occurring on-site between September and December 2019. Longer trials were necessary at lower ambient temperatures to detect enough ammonia for measuring excretion rates. After each measurement, oysters were shucked and dried for dry weight required for calculating excretion rates.

Individual and Farm-Scale Modeling

The model framework consists of (i) the AquaShell individual growth model, used to simulate physiological processes determining growth, and the mass balance of substances of interest with respect to ecosystem services (i.e., nitrogen) for one oyster, and (ii) the Farm Aquaculture Resource Management (FARM) model (Ferreira et al. 2007), which combines an Individual-Based Model (IBM, see Ferreira et al. 2021), with an advection–diffusion model for transport of water properties, including settling of suspended particles. Both models use local water-quality data to simulate growth. FARM inputs also include water current speeds and farm operational details (i.e., farm size, length of the culture cycle, seeding densities, etc.) to simulate growth, nutrient removal, and changes in water quality at the farm level. Given some key assumptions (e.g., no depletion from neighboring farms, removal rates at all lease areas are the same), the local-scale FARM results can be upscaled to provide results at the waterbody scale.

These Eastern oyster models have been calibrated to Long Island Sound previously (Bricker et al. 2018). In the present work, modifications were made to the existing individual model to improve representation of growth and physiological rates observed in Greenwich oysters and to improve the

nitrogen mass-balance aspect of the model used for estimation of nutrient-removal ecosystem services. Additional details about model development are provided in Cubillo et al. (2021).

The AquaShell Individual Model

The AquaShell model simulates physiological processes of feeding and energy intake, metabolic expenditure and ammonia excretion rates, as well as reproductive behavior. The key equations used in this model are described in Table 1.

Simulation of Feeding and Energy Intake

The volume of water cleared of particles per unit time, clearance rate (CR , Eq. (1); Table 1), is modulated by environmental factors, including temperature (T), salinity (S), and seston concentration (TSS), with maximum clearance rate (CR_{max} , Eq. (2) dependent upon body size (Kobayashi et al. 1997).

Filtration rate (FR , Eq. (3) is then estimated as the product of CR and particulate organic matter concentration (POM).

The ingestion rate (IR , Eq. (4), food taken in per time, is limited in high seston environments by a pre-ingestive selection process that results in the production of pseudofeces (Bricelj and Malouf 1984; Prins et al. 1991). The production of pseudofeces (PF) is a function of TPM and a half-saturation constant for rejection (K_c), through a Michaelis–Menten formulation. The threshold for pseudofeces production ranged from 6 to 12 mg TPM L⁻¹ equivalent to 3 mg POM L⁻¹ (Barillé et al. 1997; Bayne and Worrall 1980; Deslous-Paoli et al. 1992).

Assimilation rate (AR , Eq. (5) or food absorption and thus the energy assimilated by oysters, and egestion rate (ER , Eq. (6) or discharge of waste, are both determined by the IR and the absorption efficiency of the feeding process (AE). The AE was set to 70% based upon mean results of feeding experiments, an average of 50% for algal POM and 90% for detrital POM.

Simulation of Metabolic Expenditure and Ammonia Excretion Rate

The energy lost as a result of anabolic processes (feeding catabolism) includes costs of capturing food, processing food (digestion, absorption), and utilization/incorporation of food materials. Losses are proportional to the energy intake and are represented as a fixed fraction of assimilated energy Eq. (7). The AquaShell model uses a coefficient of 0.6, meaning 60% of energy intake is lost in the feeding process.

Fasting catabolism Eq. (8) includes energy lost in standard metabolism, the processes necessary to survive, which are a function of body weight and seawater temperature. These include maintenance of concentration gradients across membranes, osmoregulation, the turnover of structural body proteins and other macromolecules, a level of muscle tension

Table 1 Equations for AquaShell individual model physiological processes

Physiological process	Equation	
Individual maximum clearance rate (CR , $L \text{ ind}^{-1} \text{ h}^{-1}$)	$CR_{\max} = aCR \times BW^{bCR}$ where $aCR = 2.51$ and $bCR = 0.28$	(Eq. 1)
Maximum clearance rate (CR_{\max} , $L \text{ ind}^{-1} \text{ h}^{-1}$)	$CR_{(T,S,TSS)} = CR_{\max} \times f(T) \times f(S) \times f(TSS)$	(Eq. 2)
Filtration rate (FR , $mg \text{ ind}^{-1} \text{ h}^{-1}$)	$FR = CR_{(T,S,TSS)} \times POM$	(Eq. 3)
Ingestion rate (IR , $mg \text{ ind}^{-1} \text{ h}^{-1}$)	$IR = FR \times (1 - PF)$	(Eq. 4)
Assimilation rate (AR , $J \text{ ind}^{-1} \text{ h}^{-1}$)	$AR = \mu_{POM} IR \times AE$ where μ_{POM} is energy content of organic seston, AE is absorption efficiency of feeding process (%) 50% for algal POM, 90% for detrital POM, mean experimental value = 70%	(Eq. 5)
Egestion rate (ER , $J \text{ ind}^{-1} \text{ h}^{-1}$)	$E = \mu_{POM} IR \times (1 - AE)$ where μ_{POM} is energy content of organic seston	(Eq. 6)
Feeding catabolism ($J \text{ ind}^{-1} \text{ h}^{-1}$)	$Feeding \text{ catabolism} = AR \times Coefficient$ AquaShell coefficient is 0.6	(Eq. 7)
Fasting catabolism ($J \text{ ind}^{-1} \text{ h}^{-1}$)	$Fasting \text{ catabolism} = f(T) \times f(W)$	(Eq. 8)
Oxygen consumption rate (OCR , $mg \text{ O}_2 \text{ ind}^{-1} \text{ h}^{-1}$)	$OCR = \frac{(AR \times coefficient) + (f(T) \times f(W))}{EO_2}$ (EO_2 is energy consumed by oxygen respiration)	(Eq. 9)
Ammonia excretion rate (AER , $mg \text{ NH}_3 \text{ ind}^{-1}$)	$AER = OCR \times Ar(N)$ $Ar(O) \times O:N$ ($O:N$ ratio is assumed to be 50) where $Ar(N)$ and $Ar(O)$ are the atomic weights of N and O respectively.	(Eq. 10)

and movement for shell closure, production of mucus, and repair of shell (Pouvreau et al. 2006). Also considered are costs to maintain a structurally and functionally sound digestive system, capable of rapid response to any improvement in food availability.

Oxygen consumption (OCR , Eq. (9)) and ammonia excretion rates (AER , Eq. (10)) are estimated from the energy lost in catabolic processes based upon the energy consumed by the respiration of oxygen (EO_2) and the O:N ratio (50:1 in molar mass). The heat dissipated in aerobic metabolism (the heat equivalent of oxygen consumption) is the product of oxygen consumption and the oxycaloric equivalent of the food. Although the oxycaloric equivalent varies with the proportions of fat, carbohydrate, and protein in the diet (Blaxter 1989), it is by convention given a standard value of 14.06 J mg^{-1} of oxygen consumed (Navarro et al. 1991; Hawkins et al. 2002), which is the value used here. The O:N ratio is set to 50.

Simulation of Reproductive Behavior

Temperature is the single most important factor governing spawning of Eastern oysters (Shumway 1996). Ripening and spawning begins at temperatures $> 15^\circ \text{C}$ (Loosanoff and Davis 1952; Loosanoff 1958) and is the threshold temperature used in the model. A minimum size threshold for reproduction is set to 0.2 g dry tissue weight ($\sim 35 \text{ mm}$), and positive Scope for Growth (SFG) or net energy gain is required. Spawning takes place when the gonadosomatic index (GSI, the ratio of gonad tissue weight to somatic tissue weight)

exceeds 20%, that is, when gonad weight accounts for 20% of total dry weight (Choi et al. 1993). Oysters are not trickle spawners; they lose all gonad content when spawning occurs. The fraction of energy allocated for gonadal growth was set to 50% of absorbed energy, which results in a weight loss of about 20–30% at each spawning event.

Due to the dependence on temperature for spawning, the Eastern oyster undergoes up to three spawning events within its distribution range (Gulf of St. Lawrence to Panama), typically from mid-June to mid-August (Thompson et al. 1996). Eastern oysters in Long Island Sound, our study system, have been observed to spawn during this same timeframe (Loosanoff 1942). Two variables were added to simulate multiple spawning events: (a) a variable that limits the maximum number of spawning events per year, three for diploids and zero for triploids, and (b) a counter for the number of spawning events that ranges from zero to three for diploids and is set to zero at the beginning of each simulated year.

The Farm Aquaculture Resource Management Model

Individual-Based Model (IBM) Population Approach The FARM model was updated to reflect changes to the individual model and now uses an Individual Based Model (IBM) population approach. The IBM framework allows a more realistic simulation of the cultivated bivalves, wherein

each individual in the population is ‘created’ and randomly assigned a number of attributes related to growth performance and environmental interactions (e.g., food eaten, particulate organic waste). Individuals may die during the culture cycle, and the mortality status is an intrinsic property of each. Traditional physiological models are deterministic, but the objective is to simulate typical variance of a cultivated population; thus, individuals in the cultivated population are stochastically assigned a fitness parameter in terms of assimilation efficiency, AE (± 0 –5% of the mean AE). This simulates genetic variation within the single cohort of organisms typically deployed at grow-out stage. Fitness is generated at runtime, so the probability of two model runs being identical is extremely small.

Estimation of Minimum Population Model simulation of large bivalve farm populations of millions is not time-efficient. Assuming normal distribution, a minimum population size was determined using an approach similar to Brigolin et al. (2009). This approach allows large populations to be simulated accurately and realistically with an acceptable model run time. The minimum population size of 10,000 individuals can be scaled to represent greater numbers of oysters (Ferreira et al. 2021).

Other Modifications A “harvest when ready” (HWR) option (Ferreira et al. 2021) is included in the IBM model such that when turned on, the model is configured to harvest oysters as soon as the threshold weight is reached (the minimum harvestable weight specified by the user). The HWR mode removes the oysters from the system, which translates to an overall lower net N removal for the culture cycle because the harvested oysters are no longer filtering seston through the entire culture cycle. The intent of the HWR option is to simulate optimal culture practice, but it additionally allows nutrient removal to be more accurately estimated. The non-HWR option is appropriate for estimation of nutrient removal in shellfish farms where harvesting takes place at the end of a culture cycle (e.g., Saurel et al 2014) or in natural reefs or restored reefs with little or no human intervention, i.e., where shellfish are not harvested.

FARM includes an option to use variable mortality for a more realistic description of natural mortality rates, linking mortality to oyster size to mimic natural mortality events during which smaller/bigger oysters suffer higher mortality rates. This can be done by changing the baseline and/or the slope of the mortality curve. This option also enables the setting of an annual, maximum size-dependent mortality rate.

The IBM FARM output includes both the number of individuals and total harvested biomass and also the proportion of harvested (oysters above minimum harvestable size), undersized and dead individuals at the end of the culture cycle. FARM displays three graphs in its output window,

showing the pattern for the condition index (given in % of wet tissue weight/live weight), harvestable biomass (in kg of fresh weight, FW), and individual weight (in g FW) throughout the culture cycle. Changes in Chl *a*, DO, and DIN concentrations in seawater from the start to the end of the culture cycle are also automatically calculated. The model provides the percentage of N removed in harvestable biomass and the percentage of N removed by the whole population (harvestable and under-sized oysters) after a typical cultivation cycle. The N removed by oysters that died during the culture cycle is returned to the environment.

The model allows the use of refractory detrital POM, which assumes detrital POM has less energy content than algal POM, attributable to lower availability of labile compounds (Enriquez et al. 1993). These authors report a median C:N mass ratio of 20.8:1 in phytodetritus POM, which includes macroalgae and seagrasses (range 12.6 to 51.1, $n=25$), which is substantially higher than the Redfield ratio (C:N in mass ratio of 45:7, or 6.4:1), which was used in algal POM. The median value from Enriquez et al. (1993) was used to parameterize AquaShell (which calculates the net energy balance) to determine both production (i.e., harvestable biomass) and environmental effects. This allows model simulations with or without refractory POM; thus, the model can be run under both conditions to understand what effect that has on nutrient removal.

Results

Data for Calibration and Validation

End-Point Growth and Growth Pattern

The typical culture period and average harvest size and weight were both used to validate the individual growth model. Simulation results show the modeled growth for a single oyster during the average 2.5-year (912 days) culture cycle using Greenwich growth drivers (Figure S1). The AquaShell mass balance (Fig. 1) shows that the Eastern oyster model was able to reproduce similar values to those reported by the farmer using the typical farming practice, providing an average shell height of 10.6 cm and 114 g live weight for a 2.5-year culture cycle.

Morphometric Relationships

The Eastern oyster individual growth model was calibrated to match experimental morphometric relationships in oysters farmed at the Stella Mar farm. Figure S2 shows the match between measured and simulated morphometric relationships. Drops in simulated weight represent spawning events.

Oyster Nitrogen Content

Sampled oyster soft tissues had a mean carbon content of 40.42% dry weight (range 30.4–47.18%), and shell carbon content was 11.78% dry weight (range 10.30–16.08%). Sampled oyster soft tissues had a mean nitrogen content of 7.51% dry weight (range 5.15–10.6%), and shell nitrogen content was 0.14% dry weight (range 0.10–0.30%).

Physiological Relationships

The individual growth model aims to reproduce the measured values obtained in the field and laboratory for the different physiological rates: clearance, filtration, rejection of pseudofeces, egestion (feces) (Table S2), oxygen consumption, and ammonia excretion (Table S3). Figures 2 and 3 show that AquaShell simulations provide a reasonable match with measured values for all the physiological rates analyzed.

Based on the biodeposition measurements conducted on natural seston (Fig. 4), 50% of the filtered nitrogen was absorbed, and the rest was eliminated (Table S2); the absorption efficiency used within the Eastern oyster individual model was also 50%.

The N content of filtered, ingested, and absorbed dry weight organic particulate matter (POM) was calculated based upon field measurements. The median N content of the filtered POM was 4.5% (interquartile range (IQR) 3.0–5.2), the median N content of ingested POM was 4.3% (IQR 2.8–5.0), and the median N content of absorbed POM was 4.1% (IQR 2.4–5.3).

Individual and Population Modeling

Individual Modeling — AquaShell Mass Balance

The simulation of oyster growth using Greenwich environmental drivers provides outputs on production and environmental effects, such as mass of phytoplankton or detritus removed from the environment, feces and pseudofeces produced, and ammonia excreted. The model also provides an integrated nitrogen mass balance over the culture cycle (Table 2). During the 912-day culture cycle, an Eastern oyster can clear on average 47.6 m³ of seawater, consume 38.0 g of oxygen, and remove over 0.88 g of nitrogen, i.e., 0.79% of the live weight produced (Fig. 1).

The individual effects were scaled to the oyster population of the farm by application of the FARM local-scale model, using the HWR mode, with a seeding density of 75 ind m⁻², harvest size oyster of 4 in., and 77 g FW for a 2.5-year culture cycle. FARM growth and production results compared well with reported data: Stella Mar reported a harvest of 1.5 million individuals in a typical year and 1.2 million in 2020, equivalent to about 136.1 t, and FARM simulated production was 125.1 t (Table 2). Model results in Table 2 are close to the reported range for both HWR and non-HWR, although harvest estimates are higher when using the non-HWR option.

Improvements to the FARM Model

FARM calculates the annualized C and N removed by the oyster population at the farm-scale through the filtration

Fig. 1 AquaShell mass balance results for an individual Eastern oyster m⁻³ over a 2.5-year growth cycle at the Stella Mar oyster farm using their typical culture practice and monthly environmental drivers for 2019. DW, dry weight; POM, particulate organic matter. Processes that result in losses are indicated by red arrows

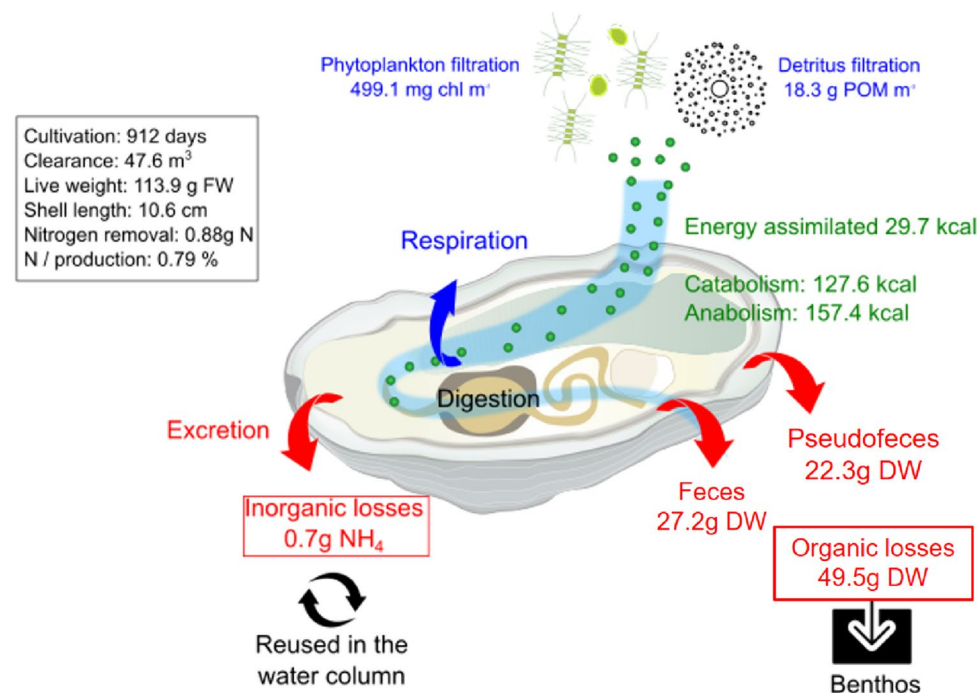


Fig. 2 Validation results of the Eastern oyster individual growth model showing the observed and the simulated physiological rates. In all plots, filled black squares indicate the model output and open orange circles are physiological rates collected in the field during this study. **A** Clearance rate, (open blue circles are data collected in the laboratory and reported in Kinsella (2019)), **B** filtration rate of the organic fraction of the seston, **C** rejection rate of the organic fraction of the seston, **D** egestion rate of the organic fraction of the seston

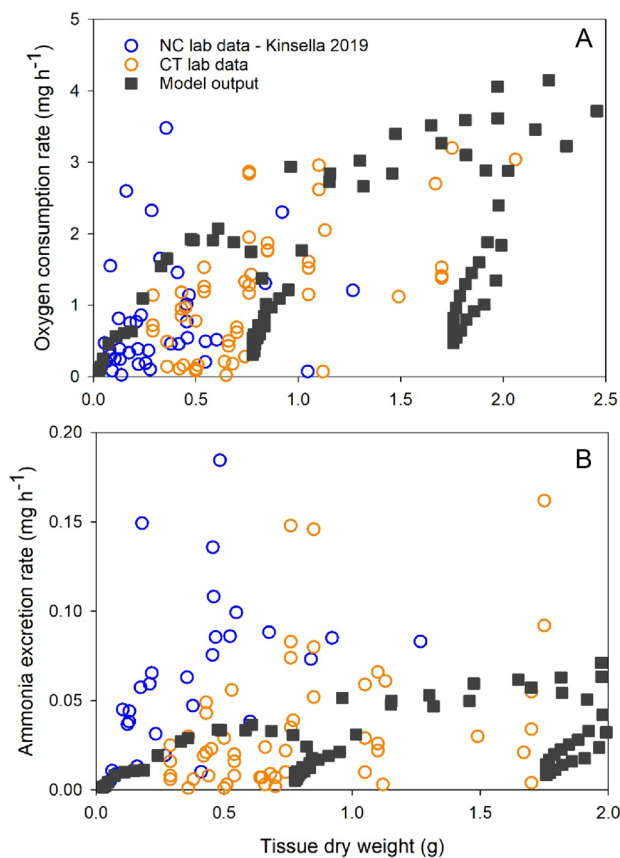
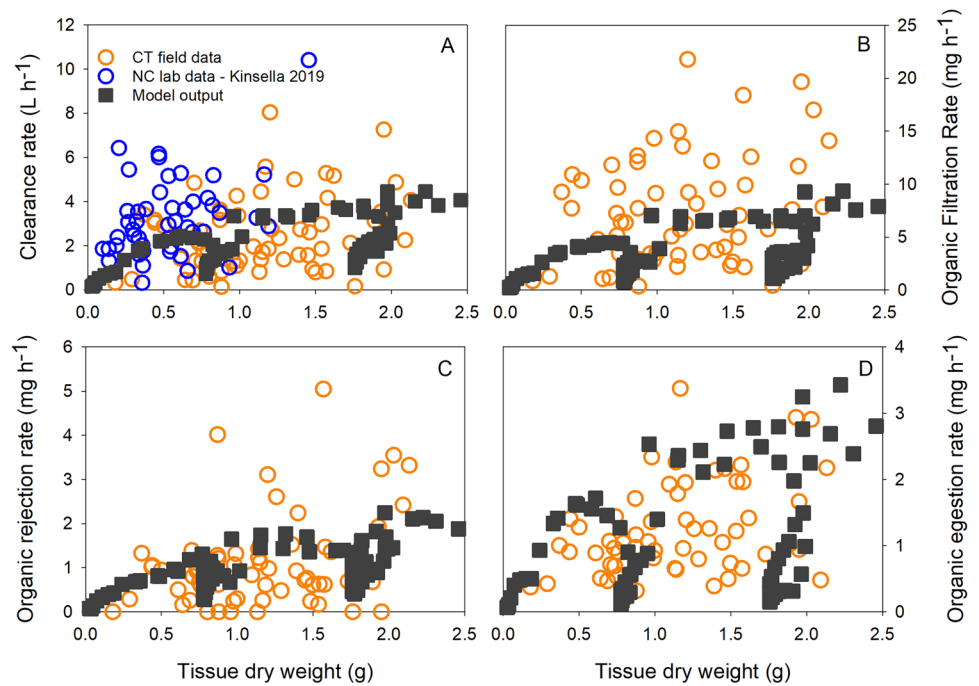


Fig. 3 Validation results of the Eastern oyster individual growth model showing the observed and the simulated physiological rates. In all plots, filled black squares indicate the model output, open orange circles are physiological rates collected in the laboratory during this study, and open blue circles represent data collected in the laboratory and reported in Kinsella (2019). **A** Oxygen consumption rate, **B** ammonia excretion rate

of algae and detritus. It also estimates the amount of N excreted by the oysters, the N egested in the form of pseudofeces and feces, and the N returned to the system through mortality. This allows the nitrogen mass balance for the farm to be calculated, and the determination of net N removal from the farm. On the 6.31-acre lease in Greenwich, CT, 400 kg of N per year using the HWR option and 691 kg of N per year with the non-HWR option were removed (Fig. 5).

Table 2 shows the production outputs integrated over one culture cycle and the potential nitrogen removed by the oysters farmed by the Stella Mar Oyster Company. The model was run in both HWR and non-HWR modes.

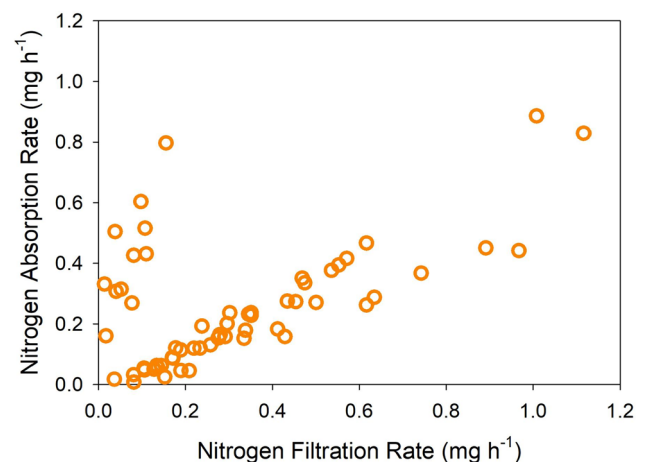


Fig. 4 Relationship between the nitrogen filtration rate and the nitrogen absorption rate in Eastern oysters, from field measurements with natural seston

The N removal in harvestable and non-harvestable biomass was greater using the non-HWR mode because the oysters remain in the water longer, often beyond the time they reach harvest size. Comparison of results from the HWR and non-HWR options shows that non-HWR harvested oysters are larger (117.5 g FW) than harvested oysters of the HWR simulation (77.0 g FW). Likewise, N removed by non-HWR oysters was greater (1727 kg N cycle⁻¹) than the N removed by a cultivation cycle in the FARM model HWR mode (999 kg N cycle⁻¹). Per oyster N is estimated to be 0.62 g for the HWR oyster and 1.15 g for the non-HWR oyster (Table 2). The nitrogen removal without refractory POM was 1.23 g ind⁻¹ versus 0.88 ind⁻¹ with the refractory POM option.

Discussion

The goal of our study was to improve the FARM model's ability to directly model nitrogen dynamics by incorporating data on nitrogen content of seston, Eastern oyster tissue, and shell, together with nitrogen absorption and excretion rates. We (a) improved the nitrogen uptake and loss rates in the individual based model for the Eastern oyster (Fig. 1) and (b) estimated nitrogen removal for the Stella Mar Oyster farm, optimizing the model for Long Island Sound (Fig. 5).

Individual Model

The mean oyster tissue and shell nitrogen content observed in this study (tissue = 7.51% DW; shell = 0.14% DW) was consistent with previous studies of *C. virginica* across the northeastern USA. Cornwell et al. (2016) reviewed published and unpublished literature for Eastern oyster tissue nitrogen content from oysters collected from Virginia to New Hampshire and reported mean 8.2% DW (range 7.3–9.3%). Clements and Comeau (2019) reviewed published literature for Eastern oyster shell nitrogen content from the northeastern USA and reported mean 0.23% DW (range 0.13–0.32%).

Direct measurements of nitrogen absorption by eastern oysters feeding on natural seston are rare in the published literature. Hoellein et al. (2014) used the biodeposition method to measure nitrogen absorption by wild oysters feeding on natural seston at two locations in New Hampshire, USA. This study reported mean nitrogen absorption rates of 0.05 and 0.17 mg N g DW⁻¹ h⁻¹, which was similar to our observations in the present study (mean 0.16 mg N g DW⁻¹ h⁻¹; range 0.04–0.34).

We surveyed the existing literature for ammonia excretion rates of Eastern oysters and identified only three relevant studies (Sma and Baggaley 1976; Hammen et al. 1966, Pietros and Rice 2003) to provide context to our observations and those of Kinsella (2019). The rates

Table 2 Production outputs and potential nitrogen removal based on FARM model simulations of an Eastern oyster farm in Greenwich (Connecticut) for a whole culture cycle, using typical cultivation practice based on Stella Mar Farm data for both harvest when ready (HWR) and non-harvest when ready (Non-HWR) options. FW, fresh weight

	Units	HWR	Non-HWR
Cultivation period	days	912	912
Seeded biomass	ton FW ha ⁻¹ year ⁻¹	1.15	1.15
Harvested biomass	ton FW ha ⁻¹ year ⁻¹	20.0	28.0
Harvested biomass	ton cycle ⁻¹	125.1	176.2
Harvested animals	million ind	1.62	1.50
Non-harvestable biomass	ton cycle ⁻¹	0.0	0.0
Undersized animals	million ind	0.0	0.0
Dead biomass	ton cycle ⁻¹	8.8	20.2
Mean harvest weight	g FW	77.0	117.5
Dead animals	%	13.4	20.0
Dead biomass	%	6.6	10.3
Harvestable biomass	%	93.4	89.7
N content in harvest	%	0.8	0.98
N content in farmed biomass	%	0.8	0.98
N removal	kg N ha ⁻¹ year ⁻¹	159	274
N removal	kg N cycle ⁻¹	999	1727
N/B ratio	kg N ton ⁻¹ harvestable oyster	8.0	9.8
N removal	g N oyster ⁻¹	0.62	1.15

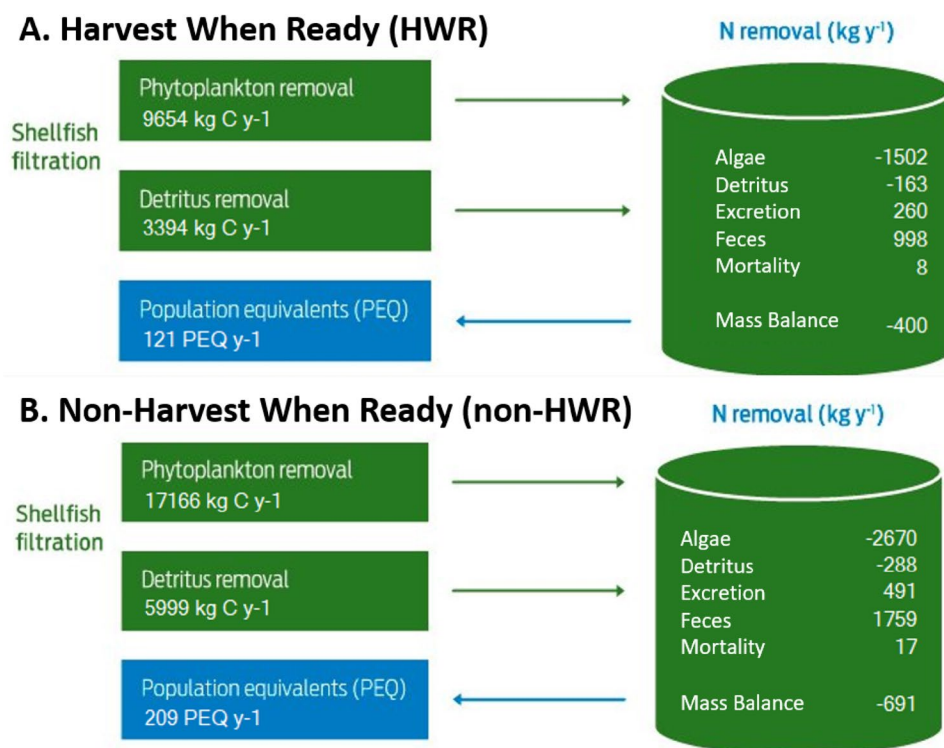


Fig. 5 FARM model annualized mass balance for the Eastern oyster farm in Greenwich, CT, with cultivation density 75 individuals m⁻² and cultivation period 912 days for the **A** HWR and **B** non-HWR options. The two green boxes on the left show the mass of detritus and phytoplankton carbon that shellfish (oysters) filter annually, resulting in a mass balance of kg N removed per year (using the Redfield ratio and the refractory POM ratio) in the green cylinder on the

right indicating consumed nitrogen categories (algae, detritus) and nitrogen produced (excretion, feces, mortality). The negative values indicate N removed from the local environment and positive values is N added by oysters. The number of population equivalents (PEQ; assumed to be 3.3 kg N per person) is then reported in the left blue box for the total nitrogen removed per year

reported herein and in Kinsella (2019) were similar to the existing literature for Eastern oysters (Table S4) and have the added value of measurements on individual oysters (Hammen et al. 1966 measured excretion rates of a group of oysters) and across multiple temperatures (Pietros and Rice 2003 made measurements at a single temperature). The addition of our measurements of ammonia excretion rates across a range of temperatures, in combination with the Kinsella (2019) data likely, represents the most improved aspect of the nitrogen parameterization.

FARM Model

The FARM model estimated a nitrogen removal of 159 kg N ha⁻¹ year⁻¹ (HWR) and 274 kg N ha⁻¹ year⁻¹ (non-HWR) on a 6.31-acre, subtidal, bottom lease. This areal nitrogen removal rate is consistent with existing literature for nitrogen removal by bottom and water-column shellfish farms. Barrett et al. (2022) reviewed the aquaculture-related, nitrogen-removal literature and reported a mean of 538 kg N ha⁻¹ year⁻¹ (range 59–1436 kg N ha⁻¹ year⁻¹) for Eastern oysters across nine studies, which included both

direct measurements and model approaches. A review of the original FARM model reported a nitrogen removal range of 120–1,520 kg N ha⁻¹ year⁻¹, although this range included model outputs from oysters, clams, and mussels of a variety of species and cultivation practices (Rose et al. 2015).

The eastern oyster FARM model for Chesapeake Bay estimated nitrogen removal at a bottom oyster farm with no gear in the Potomac River, USA, to be 570 kg N ha⁻¹ year⁻¹ (Bricker et al. 2014) which is much higher than our estimates in this study (HWR 159 kg N ha⁻¹ year⁻¹, non-HWR 274 kg N ha⁻¹ year⁻¹; Table 2). A model in Harris Creek, Chesapeake Bay, estimated removal of 72.4 kg N ha⁻¹ year⁻¹ by restored reefs in the waterbody (Kellogg et al. 2018) which is less than half of our model's lower values. A study of nitrogen content in aquacultured oysters in Great Bay, New Hampshire, estimated that a typical annual harvest would result in removal of 140 kg N ha⁻¹ year⁻¹ (Grizzle et al. 2016) which is closer to our HWR estimate. Very similar estimates were obtained in a multi-year study of bioextraction in Lonnie Pond on Cape Cod, MA. Labrie et al. (2023) estimated removal rates of 164.5, 203.8, and 133.2 kg N ha⁻¹ year⁻¹ for the years 2016, 2017, and 2018 by floating

aquaculture operations. An earlier study showed removal by harvest of $12.0 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (Pollack et al. 2013) in Mission Aransas, TX, which is much lower than our model estimates. It is likely that the variation in estimates could result from methods of nitrogen estimation, variation in seasons, climate, and geography.

In the last two decades, there has been growing interest in the potential for shellfish aquaculture to contribute to ongoing nitrogen management programs in eutrophic coastal waters (Lindhahl et al. 2005; Rose et al. 2014; Petersen et al. 2014). One important limitation to incorporation of shellfish farms into nitrogen reduction planning efforts by states and towns has been local environmental and species-specific nitrogen data. The approach taken in this study, and the expanded parameterization of the FARM model, improves the utility of the model as a planning tool that can be used to run scenarios based upon local water-quality data to decide on locations where Eastern oyster farms may be most effective at reducing nitrogen in the environment.

Models can optimize site selection with local data (e.g., Bricker et al. 2016) and evaluate the performance of different culture practices (e.g., bottom, floating cage; Ferreira et al. 2009). An added benefit of using this model is to provide insights about the suitability of potential lease locations without the need to implement an actual farm or farms for one cultivation cycle (~2–3 years). Scenarios using water-quality data from potentially suitable locations can be used to determine how best to maximize nutrient removal (and production) by more densely seeding an existing farm area or by expanding the cultivation area while leaving seeding densities the same (e.g., Filgueira et al. 2016; Bricker et al. 2018). The improved model results will allow farmers and resource managers to determine carrying capacity limits to maintain or improve ecological balance, whereby nutrients are removed but biodeposits and over-population of bivalve farms do not create other water quality issues (Gibbs 2007).

Policy and Management Implications

The improvements to the FARM model increase its relevance to managers and farmers, particularly with respect to lease-siting policies and incorporation of aquaculture into nutrient management programs. For example, model simulations could be used to determine how effective a farm would be in reducing nutrients, thereby helping to reach water quality standards. Likewise, model scenarios could be used to help determine the culture practices that would result in the greatest nutrient removal. For example, the model scenarios could be used to determine the total number of oysters that would be required to remove part or all of the excess nutrient load to a waterbody, helping to make a comprehensive nutrient management plan successful from near the beginning of implementation.

The FARM model has been parameterized in this study for Eastern oysters, but the approach taken here could be used to parameterize the model for other cultivated shellfish species and other locations around the world. In the USA, hard clam aquaculture has been approved for nutrient mitigation in the Northeast (Reitsma et al. 2017; Town of Mashpee Sewer Commission 2015). In Europe, the cultivation of blue mussels for nitrogen management has been proposed (Petersen et al. 2014; Taylor et al. 2019). The cultivation of species can be for water quality purposes alone, as with the ribbed mussel, *Geukensia demissa*, which is not commercially harvested for human consumption and can thrive in urban waters that have been highly degraded by human activities (Galimany et al. 2017). Shellfish restoration programs have long been highlighted as a way to reduce excess nutrients in eutrophic coastal waters (e.g. Officer et al. 1982; Newell et al. 1988), and recent efforts to connect shellfish farms with restoration programs represent an additional way for shellfish aquaculture to contribute to nitrogen management (Pew Charitable Trusts 2023). Beyond shellfish aquaculture, the FARM model has also been adapted to seaweed species such as kelp, which have been proposed as additional nitrogen management tools (Kim et al. 2014; Racine et al. 2021) and may absorb nitrogen at different rates between species (i.e., Umanzor and Stephens 2023). The FARM model results for filter feeders (reducing particulate nitrogen forms) and/or seaweeds (reducing dissolved nitrogen forms) could be integrated into ecosystem-based modeling approaches to evaluate nutrient cycling within integrated multi-trophic aquaculture (IMTA) operations.

The FARM model can be useful as a tool for siting, as shown in Greenwich, CT (Bricker et al. 2016), by showing which of a number of potential lease locations would be the most successful. A good example is shown by the study of Reitsma et al. (2017) that showed a harvest of 500,000 oysters from the Mashpee River System would remove 2500 kg N per year, equal to 50% of the legally required nutrient reduction.

These types of estimates can also contribute to discussions about shellfish aquaculture in coastal communities around the world that support bivalve populations and struggle with eutrophication impacts. The quantification of environmental benefits provided by shellfish aquaculture, including nitrogen removal, may increase social license in communities where aquaculture is new and/or expanding (e.g., Whitmore et al. 2022). The recognition of water quality benefits provided by shellfish aquaculture in the permitting processes depends on robust science. This caliber of research gives resource managers confidence in the quantity of nitrogen removed by farms and the variation in this service provided across farm practices and variable environmental conditions.

We have successfully parameterized the FARM model for Eastern oysters with respect to nitrogen uptake and

deposition for a local Long Island Sound farm. This model approach can be transferred to other locations that support Eastern oyster farms with an appropriate calibration of the FARM model for local conditions of oyster growth, farm culture practices, and environmental data. Using appropriate species-specific physiological data, the model can also be calibrated and parameterized for other bivalve species (e.g., clams, mussels). With the outputs at the population scale, nitrogen crediting and trading policies can be implemented at the local and state levels to benefit both local water quality and environmental health, as well as the shellfish industry.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12237-024-01354-7>.

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Data Availability Statement Data collected for the model optimization in this study is available in the supplementary materials. Additional data requests can be sent to the first author of the manuscript.

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