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Article

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Supporting information

Additional information on acronymns, abbreviations, databases, eutrophication assessment and oyster model methodological details, validation of models and detailed model production results referenced in text.

Abstract

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Land-based management has reduced nutrient discharges, however, many coastal waterbodies remain impaired. Oyster 'bioextraction' of nutrients and how oyster aquaculture might complement existing management measures in urban estuaries was examined in Long Island Sound, Connecticut. Eutrophication status, nutrient removal, and ecosystem service values were estimated using eutrophication, circulation, local- and ecosystem-scale models, and an avoided costs valuation. System-scale modeling estimated that 1.31% and 2.68% of incoming nutrients could be removed by current and expanded production, respectively. Up-scaled local-scale results were similar to system-scale results, suggesting this upscaling method could be useful in waterbodies without circulation models. The value of removed nitrogen was estimated using alternative management costs (e.g. wastewater treatement) as representative, showing ecosystem service values of \$8.5 and \$470 million per year for current and maximum expanded production, respectively. These estimates are conservative; removal by clams in Connecticut, oysters and clams in New York, and denitrification are not included. Optimistically, calculation of oysterassociated removal from all leases in both states (5% of bottom area) plus denitrification losses showed increases to 10% - 30% of annual inputs, which would be higher if clams were included. Results are specific to Long Island Sound but the approach is transferable to other urban estuaries.

Introduction

Eutrophication is among the most serious threats to the function and services supported by coastal ecosystems.^{1, 2} Waterbodies worldwide have experienced nutrient-related degradation^{3, 4} including excessive algal blooms, hypoxia⁵, and loss of seagrass habitat⁶ that can have cascading negative effects on fisheries.^{7, 8, 9} In the United States (U.S.; Table S1 for acronyms), 65% of estuaries and coastal bays are moderately to severely degraded by nutrients from agricultural and urban runoff, atmospheric deposition and wastewater treatment plant (WWTP) discharge.¹⁰ U.S. and European legislation aimed at mitigating eutrophication is focused mainly on reductions of land-based discharges.^{11,12} Practical limits on existing point and nonpoint source controls suggest that additional innovative nutrient management measures are needed.¹³

70	The use of shellfish cultivation for nutrient remediation, called 'bioextraction,' has been
71	proposed in the U.S. and Europe. 14, 15, 16, 17 Research investigating shellfish related nutrient
72	removal is consistent with U.S. policies promoting shellfish aquaculture and ecosystem service
73	valuation. 18, 19 Removal of phytoplankton and particulate organic matter (POM) from the water
74	column by shellfish filtration short-circuits organic degradation by bacteria and consequent
75	depletion of dissolved oxygen (DO) which can lead to death of fish and benthic organisms and
76	losses of fish habitat. Nutrients are sequestered into tissue and shell, and shellfish may enhance
77	$denitrification \ and \ burial.^{21,22,23,24} \ Local, \ state, \ and \ federal \ agencies \ have \ been \ exploring \ the \ use$
78	of shellfish aquaculture as a nutrient management measure in the Northeastern U.S. 15, 25, 26
79	Recent research has shown that the costs and removal efficiencies of nitrogen (N) through
80	shellfish cultivation compare favorably with approved Best Management Practices (BMPs). 13, 15
81	
82	Nutrient credit trading has been proposed, and in some states implemented, as a tool to achieve
83	water quality goals. $^{27, 28}$ These programs establish a market-based approach to provide economic
84	incentives for achieving nutrient load reductions to meet pollution reduction targets. They could
85	create new revenue opportunities for farmers, entrepreneurs, and others who are able to reduce
86	discharges below allocated levels at low cost and sell credits received to dischargers facing
87	higher-cost reduction options. A credit is the difference between the allowed nutrient discharge
88	and the measured nutrient discharge from a nutrient source (e.g. wastewater treatment plant).
89	Credits must be certified by a regulatory agency such as the Connecticut Department of Energy
90	and Environmental Protection before inclusion in a credit trading program such as the
91	Connecticut Nitrogen Credit Exchange. The Connecticut Nitrogen Credit Exchange (CT NCE)
92	was created in 2002 to improve nutrient-related hypoxia conditions in Long Island Sound (LIS),
93	providing an alternative compliance mechanism for 79 wastewater treatment plants (WWTPs)
94	throughout the state. During 2002-2009, $15.5 \times 10^6 \mathrm{N}$ credits were exchanged at a value of \$46
95	million, with estimated cost savings of \$300-400 million. ²⁹ The CT NCE trading between point
96	sources is active and successful but the program does not yet include non-point sources.
97	
98	The inclusion of shellfish bioextraction in non-point nutrient credit trading programs has been
99	proposed. 13, 15, 16 This study examined the role of shellfish bioextraction in the control of

eutrophication symptoms and the ecosystem service value of nutrient removal using an
integrated modeling framework at system- and farm-scales in CT waters of LIS, an urban
estuary. This study is an example of the potential use of shellfish aquaculture to supplement
nutrient management in urban estuaries, which often require additional nutrient reductions and
also support shellfish populations. LIS is a good representative of urban estuaries because the
high-level eutrophication impacts are well known and is among the 65% of U.S. estuaries with
Moderate to High level eutrophication. LIS has higher nitrogen (N) loads and chlorophyll a
(Chl), and lower dissolved oxygen (DO) concentrations than the median of U.S. estuaries (Table
S3). It is also representative of urban estuaries in the European Union, which have these same
characteristics. 30, 31 While results are specific to LIS, the approach is transferable and thus
relevant to other estuaries where nutrient reductions are required. The focus was nitrogen (N)
because it is typically the limiting nutrient in estuarine waterbodies. ³² While there are thriving
industries of both oysters (Crassostrea virginica) and clams (Mercenaria mercenaria) in LIS, the
focus of the study was oysters because they are the main shellfish being farmed in LIS. An
individual growth model was developed for oysters and was integrated into the local- and
ecosystem-scale models. While clams are also a productive cultivated species in LIS, it was not
possible to develop an individual growth model due to time and resource limitations and thus
only gross N removal by clams could be estimated. This was an additional reason that clam
results were not included in the analysis. Denitrification was also not included in the model
because the model focus is the oyster and denitrification is a downstream process, and
additionally because of the high variability among published rates. ^{24, 33} Project goals were to: (1)
determine the mass of N removed through oyster cultivation at current and expanded production;
(2) assess how significant oyster related N removal is in relation to total N loading under current
and expanded production scenarios; (3) estimate the economic value of this ecosystem service;
and (4) evaluate whether oyster related N removal may be significant enough to support a role
for shellfish growers in a nutrient credit trading program, taking into account the present
situation and potential expansion of aquaculture.

Materials and Methods

Study site and cultivation practices
Long Island Sound (LIS; Figure 1) is a large estuary (3,259 km²) with an average depth of 20 m,
shared by the states of CT and New York (NY). The waterbody has historically received large
nutrient loads from its highly developed, intensely populated (8.93 x 10 ⁶ people in 2010)
watershed. The N load to LIS is estimated to be 50 x 10 ³ metric tons y ⁻¹ with point sources
accounting for 75% and the remaining 25% attributed to non-point sources. ³⁴ Summer thermal
stratification and a residence time of 2-3 months 10,35 combined with N loads have resulted in
notable water quality degradation including areas of regular summertime hypoxia ³⁶ and loss of
seagrass habitat. ³⁷ The Assessment of Estuarine Trophic Status (ASSETS) model was applied to
monitoring data (Table S2) to update the eutrophication status of LIS (Figures S1, S2). 10, 38, 39
Eutrophication condition improved from High to Moderate High since the early 1990s. ¹
Improvements resulted from increased bottom water DO concentrations reflecting load
reductions from 60.7×10^3 to 50.0×10^3 metric tons y^{-1} . However, Chl concentrations did not
change, receiving a rating of High in both timeframes. As nitrogen loads continue to decrease,
further improvements are expected, but may be counterbalanced by increasing population.
Hypoxia was used in the 2000 Total Maximum Daily Load analysis (TMDL) to guide
development of a plan for 58.5% N load reduction (by 2017) to fulfill water quality objectives
(NYSDEC and CTDEP, 2000). Implementation of the TMDL resulted in $>40\%$ reductions in N
loads by 2012, 83% of final reduction goals, primarily through WWTP upgrades to biological
nutrient removal. ³⁶ Atmospheric and agricultural loads also decreased. ³⁶ While water quality
improvements have been documented, they have been slow and masked by weather-driven
variability and continued population growth. ⁴¹ The TMDL analysis concluded that full
attainment of desired water quality standards would require additional reductions or increased
assimilative capacity. The updated eutrophication assessment results confirm this conclusion.
The TMDL identified alternative management methods, such as bioextraction, as potential
measures to help achieve DO standards. The well-established Eastern oyster (Crassostrea
virginica; hereafter 'oyster') industry makes LIS a compelling site to test the potential for N
removal through cultivation and harvest and a useful example for other urban estuaries that

support oyster growth. Recent CT shellfish harvests have provided over 300 jobs and \$30 million

158	in farmgate revenue (where farmgate price is the sale price of oysters that is received by the
159	grower) annually, with oyster harvest exceeding 40 x 10 ⁶ oysters. ⁴²
160	
161	Oyster cultivation practices in LIS typically involve collection of one- and two-inch oyster seed
162	from restricted areas and relay, or replanting, for on-bottom growout for one to two years in
163	approved areas. We have used seed of less than one inch in our model simulations to include
164	nutrient removal by early lifestages. Seed planting densities of 62 oysters $m^{\text{-}2}$ are reduced by an
165	estimated 55% mortality. Stocking area does not typically include the entire farm area, rather
166	planting occurs on a rotational basis on 1/3 of the farm annually within the three-year culture
167	cycle. ⁴³ Oyster seed planting takes place over 90 days beginning on May 1. Harvest occurs
168	throughout the year and a farmgate price of \$0.40 per oyster is used to calculate harvest value.
169	Growers have not reported harvest since 2008, so previous harvests were used to estimate
170	landings based on interviews with growers and managers. Growers did not specify what
171	proportion of the current > 61,200 acres of lease area is being used for cultivation. Thus, a
172	bracketing approach was used to capture the range of possible areas being cultivated within LIS
173	where the mid-range estimate (5,250 acres [21 km ²]) was used to represent current production
174	area and was used as the standard model scenario. The total potential area that could be
175	cultivated (11,116 acres [45 km²]) was determined as one half of all suitable area (e.g. all areas
176	that support oyster growth and are not classified as prohibited for legal or contaminant reasons)
177	within the 12 m (40 ft) bottom contour. The spatial distribution of production was estimated by
178	superimposing known harvests from different locations onto model grid boxes. Culture practices
179	and monthly monitoring data (temperature, salinity, total particulate matter [TPM], POM, Chl,
180	DO) from 17 stations in the LIS Water Quality Monitoring Program were used to support model
181	applications (Table S2, Figure S1). ⁴⁴ Five years of data (2008-2012) were used to provide a
182	robust dataset and to reduce bias due to anomalous weather years. Jonckheere-Terpstra (JT)
183	tests 45 were applied using a standard α - level of 0.05 indicating no trends in any variable at any
184	station. Other data (e.g. macroalgal abundance, occurrences of nuisance and toxic blooms) were
185	acquired from the LIS Study (LISS). 46 Additional methodological and analytical details are
186	available. ³⁹

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Modeling Framework

189	System-scale aquaculture model
190	The first step toward modeling aquaculture at the system-scale involved coupling of two models:
191	1) a high resolution 3-D coupled hydrodynamic-eutrophication-sediment nutrient flux model
192	(System Wide Eutrophication Model [SWEM]) that operates on the timescale of one year, and 2)
193	the broader scale EcoWin.NET (EWN) ⁴⁷ ecological model that operates on a decadal timescale.
194	The resulting model framework was used to simulate aquaculture practices and to support
195	economic analyses, both which require timescales greater than one year. SWEM was used to
196	describe the main features of annual water circulation and nutrient loading to LIS by means of
197	2300 grid cells divided into 10 vertical (σ) layers. The hydrodynamic model solves a system of
198	differential, predictive equations describing conservation of mass, momentum, heat and salt, but
199	does not include shellfish. SWEM was calibrated to data collected during 1994-95 and validated
200	for data collected in 1988-89. 48, 49, 50, 51, 52 The SWEM grid layout was superimposed on a two-
201	vertical-layer set of 21 larger boxes that were used for the EWN system-scale ecological
202	modeling. The EWN model includes oysters, simulated by a population model based on the
203	individual growth model developed for Crassostrea virginica which was integrated into the
204	ecosystem (and local scale) model (Figures S3 and S4). The larger EWN boxes, and the
205	simplified two-layer vertical formulation, were defined through consultation with the project
206	team and local stakeholders. The resulting EWN framework took into consideration state
207	boundaries, physical data and locations of aquaculture leases, and followed a well-established
208	methodology for merging the two types of models ⁵³ Water flows across the EWN model grid
209	box boundaries were calculated from SWEM to obtain as accurate a representation of the
210	circulation pattern as possible, using a four-stage process: (i) a Geographic Information System
211	(GIS) representation of EWN boxes was used to map these to the SWEM grid; (ii) SWEM flow
212	outputs for a one-year model run were integrated to provide hourly fluxes across the EWN box
213	boundaries (horizontal and vertical); (iii) external inputs at the land boundaries (rivers, WWTPs)
214	were added to the list of flows; (iv) the final data file was checked for volume conservation.

The use of an annual run from a detailed hydrodynamic model, which is the general approach for

upscaling hydrodynamics in EWN, captures all the relevant physical signals, i.e. the freshwater

217	component determined by the annual hydrological cycle, and the tidal current component,
218	including the high tide/low tide semi-diurnal cycle in LIS, and the spring-neap tide signal.
219	An annual cycle will never provide complete volume conservation, because the tidal state at the
220	end of the run will not be an exact match to that in the beginning, EWN makes a small volume
221	adjustment (in this case, the average per hourly timestep is 0.00016%), based on the deviation
222	from the closure condition, to allow mass balance conservation in multi-annual runs.
223	
224	The 42 box EWN model grid was used to simulate system-scale oyster production, and
225	associated drawdown of Chl, POM, and N using relevant transport, biogeochemistry, and
226	shellfish model components. The EWN oyster aquaculture model combined hydrodynamic
227	outputs from SWEM, as described above, with external nutrient loads that represented the level
228	of loads expected once the 2000 TMDL N and carbon load reductions had been fully
229	implemented. ^{54, 55} Note that these are model predicted future values for 2017, not measured
230	values. Oyster populations in EWN are modeled using standard population dynamics equations
231	driven by individual growth and mortality (Figure S4) ⁵³ , using 20 heterogeneous weight classes
232	spanning 0-100 g live weight. EWN explicitly simulates seeding and harvest, defined from
233	expert knowledge of local growers. Seeding takes place annually from Year 1, with first harvest
234	in Year 3. Harvest is regulated by the availability of market-sized animals and market demand.
235	EWN was calibrated and validated for a standard area of oyster farms within each of the six
236	boxes that contain aquaculture (Figure 1) using a standard stocking density. There were three
237	other scenarios simulated for sensitivity testing using the areas described above, but only the
238	standard (5,250 acre [21 $\rm km^2$]) and potential expanded aquaculture (11,116 acre [45 $\rm km^2$]) area
239	scenarios are discussed here due to space considerations.
240	
241	EWN model results for non-conservative water quality state variables (dissolved nutrients and
242	phytoplankton) were validated against SWEM results. In the version of SWEM used for
243	comparison, bivalves were included by considering a constant biomass of 2.8 g DW m ⁻² over all
244	of LIS. ⁵⁰ Note that the SWEM results are projected representations of full implementation of the
245	2000 TMDL with 1988 – 1989 hydrodynamic conditions without bioextractive technologies;
246	they are not measured data. The two models showed similar concentration ranges and annual

patterns for dissolved inorganic nitrogen (DIN) which was encouraging given that no model
coefficients (e.g. half-saturation constants or primary production rates) were shared between the
two models (Figure S5). The use of unique modeling coefficients was intentional, because the
two models are different in scale, formulations, and number of state variables. Comparisons
between both models for Chl concentrations also showed a match for ranges and spatial
distribution represented by model curves in the eastern part of LIS, but in central LIS the EWN
results did not reproduce the drop in concentration observed in SWEM for the latter part of the
year, and values in western LIS remained elevated in the EWN simulation for most of the year
(Figure S6). We accepted this deviation because the main nutrient loading is at the western end
of LIS, thus it seemed inconsistent to arrive at lower simulated concentrations of Chl in the
western Sound. Measured data confirm that Chl concentrations are higher in the western
Sound. ⁵⁶ Higher Chl concentrations might occur in eastern LIS if it was a fast-flushing system
that would transport phytoplankton blooms from the west to the east, but residence times of 2-3
months estimated by EWN and other studies 10,35 suggest that this is not the case. More likely, the
overestimate of Chl is the result of the absence of zooplankton grazers in the model which are
estimated to reduce primary production by up to 50% throughout the year. ⁴⁰

Local-scale aquaculture model

Local-scale oyster production and N removal was estimated by application of the Farm Aquaculture Resource Management (FARM) model which includes the oyster growth model developed for LIS and used in EWN. 57, 58, 59 Results were up-scaled to provide system-scale estimates to compare to EWN model results. FARM takes into account food conditions inside a farm, shellfish ecophysiological characteristics, and farming practices. Potential nutrient removal by the farms was estimated and compared to results from EWN simulations. The system scale EWN model differs from the local scale FARM model in that FARM does not have: a) harvesting, but harvestable biomass is estimated, b) overlapping shellfish year-class populations, c) multiple species of shellfish, or d) system-scale feedbacks. 53

A three-year culture cycle was simulated using data from one long-term monitoring station located within each of the four LIS zones (Figure S1), and the same inputs (e.g. seeding density,

mortality, etc.) as were used for the EWN simulations. Nutrient removal was determined for each simulated farm. Results were up-scaled in an approach developed previously for Potomac River⁶⁰ to evaluate total area-weighted current and potential removal using the same standard and expanded cultivation areas used by EWN. Additional assumptions were used for upscaling: i) there were no additional reasons that identified bottom area could not be cultivated, ii) all lease areas within a zone had the same oyster growth and N removal rates despite potential differences in water quality among farm locations, iii) and there was no interaction among adjacent farms, i.e., food depletion.

Ecosystem service valuation

An intriguing aspect of the bioextraction discussion is the potential economic value of the water filtering ecosystem service provided by oysters and whether growers should be paid for the oyster related N removal capacity within a nutrient credit trading program. We used the cost avoided, or replacement cost method, to estimate the value of N removal by oysters. ⁶¹ This method assumes that the costs of restoring a part of the ecosystem — in this case, clean water — through N removal by wastewater, agricultural and urban BMPs, provides a useful estimate of the value of the ecosystem service of N removal by oyster bioextraction. The use of the replacement cost method assumes that if oysters are no longer harvested, the N removal services they have been providing would need to be replaced. At present, WWTP upgrades, and agricultural and urban BMPs are the most likely candidates to replace the service that the oysters provide.

The value of shellfish aquaculture as a N removal device is estimated by taking the difference in minimum total costs for nitrogen reduction targets in the watershed with and without the inclusion of shellfish farms. ⁶² In this case, the value of shellfish aquaculture production is determined not only by its marginal cost in relation to other abatement measures (e.g., WWTPs), but also by its cleaning capacity. Marginal costs increase rapidly with higher N reduction levels due to the higher implementation costs of abatement measures required to meet reduction targets. In the case of LIS, where aquaculture operations already exist and the costs of production are a given (and are offset by oyster sales by the farmers), the value of the removed N is equal to the

307	minimum total cost without shellfish production (or the costs of WWTPs, agricultural and/or
308	urban BMPs that include wet ponds and submerged gravel wetlands).
309	
310	Costs used in this analysis were estimated for incremental upgrades of N reduction from current
311	was tewater effluent concentration levels to 8 mg $L^{1}\text{,}$ from 8 to 5 mg $L^{1}\text{,}$ and from 5 to 3 mg L^{1}
312	using an approach developed in Chesapeake Bay. 63, 64 Total capital costs, annual operating and
313	maintenance costs, and the combined annualized capital cost (20 year depreciation) associated
314	with plants of different sizes were used to determine average cost per kilogram (2.2 pound) of N
315	removed. These were adjusted to 2013 dollars with the Engineering News-Record Construction
316	Cost index (ENRCC) to account for inflation. ⁶⁴ Average annual costs of the N removal by the
317	three treatment levels were \$32.19 kg $^{\text{-}1}$ (\$14.63 lb $^{\text{-}1}$; 8 mg L $^{\text{-}1}$), \$37.00 kg $^{\text{-}1}$ (\$16.82 lb $^{\text{-}1}$; 5 mg L $^{\text{-}1}$
318	¹), and \$98.58 kg ⁻¹ (\$44.81 lb ⁻¹ ; 3 mg L ⁻¹ , Table 1).
319	
320	The estimated average annual cost for agricultural controls including riparian buffers and cover
321	crops, adjusted for inflation using the ENRCC Index, was \$38.92 acre-1. Use of such controls
322	was estimated to result in a maximum N load reduction of 0.59 x 10^6 kg yr $^{-1}$ (1.31 x 10^6 lb yr $^{-1}$)
323	for the entire CT River Basin and an estimated adjusted annual cost of $$7.68$$ million. 64 Given a
324	current estimated agricultural N load of 1.76 x 10^6 kg yr $^{-1}$ (3.89 x 10^6 lb yr $^{-1}$), the maximum
325	potential reduction would be 34.1% at a unit cost of about \$12.98 kg ⁻¹ yr ⁻¹ (\$5.90 lb ⁻¹ yr ⁻¹).
326	
327	The two most cost-effective urban BMPs are wet ponds and submerged gravel wetlands with
328	average construction costs of \$7,000 and \$11,000 acre-1 drained, respectively, resulting in N
329	removal of 55% and 85%, respectively. ⁶⁴ Total costs including construction costs and the cost of
330	land acquisition for full implementation within all of the sub-basins were estimated to be \$3,262
331	million in 2013 dollars. The total cost was divided by 20-year amortization period to derive an
332	estimated annual cost of \$163 million. The maximum N reduction that might be obtained in the
333	CT River Basin was estimated as $0.47 \times 10^6 \ kg \ yr^{-1} (1.04 \times 10^6 \ lb \ yr^{-1})$ with an annual per unit
334	cost of \$349 kg ⁻¹ yr ⁻¹ (\$159 lb ⁻¹ yr ⁻¹ , Table 1).
335	

Results and Discussion

337	System-scale oyster aquaculture bioextraction
338	Output for the 10-year standard (5,250 acres) EWN model simulation shows a spin-up period in
339	the first 4 years, followed by a stable cycle with alternating years of higher and lower harvest
340	(the fluctuations result from slight variations in water volumes in consecutive years; Figure S7).
341	The reason for the variability is that EWN uses water flux outputs from SWEM superimposed on
342	a 365-day cycle (see System-scale aquaculture model in the Methods section). These are due to
343	natural year-to-year fluctuations which this modeling scheme does not consider and which
344	cannot be forecast by any model due to limitations in predicting weather patterns.
345	
346	Year 9 of the EWN standard model run, after stabilization of the model, was chosen for a mass-
347	balance analysis of oyster cultivation and estimation of nutrient removal (Table 2; Figure S8).
348	The calculation of N removal and other eutrophication-related ecosystem services (e.g. Chl and
349	POM drawdown,) integrates physiological growth processes of the: (i) Year 3 cohort, much of
350	which will be physically removed (harvested) from the Sound; (ii) Year 2 cohort, which will be
351	harvestable only the following year; and (iii) Year 1 cohort, which will take an additional two
352	years to reach harvestable size. Nutrient removal is based on the filtration rate of the oysters
353	based on the outputs of the AquaShell individual growth model, calibrated and validated using
354	experimental data from this and other studies (Figure S3). EcoWin (and FARM) calculate the
355	total, or gross, phytoplankton and detrital carbon filtered by the oysters and then convert those
356	values to N. The net removal of N from the water is represented as the total N removed minus N
357	returned to the water as pseudofaeces, faeces, excretion, mortality, and spawning (Figure S8).
358	The model works internally in carbon units, and from those outputs other terms are calculated
359	(Table 2). The focus is N because carbon is not a limiting nutrient and thus poses no direct
360	concern for eutrophication.
361	
362	Overall, the standard model suggests that the combined volume of the boxes under cultivation is
363	filtered by oysters roughly once per year (0.95 y ⁻¹), though there is greater filtration in some
364	boxes (e.g. Box 25; Table 2). The total filtered volume of boxes that include aquaculture
365	corresponds to an annual clearance of 9 x 10 ⁹ m ³ of water (more than 300 x 10 ⁹ cubic feet). Note

366	that the clearance rate and mass balance outputs represent the role of all cultivated shellfish, as
367	opposed to only the harvested biomass. The N removal role of oysters is typically estimated by
368	applying a conversion factor (usually about 1%) ⁶⁵ to the harvested biomass.
369	
370	Current cultivation results in an estimated annual harvest of 31×10^3 metric tons of oysters and
371	removal of more than 650 metric tons of N (Table 2; Figure S8), the equivalent of 1.3% of total
372	annual inputs. This removal estimate represents an ecosystem service corresponding to about
373	200,000 Population Equivalents (PEQ) considering a per-person annual load of 3.3 kg N $\rm y^{-1}$. The
374	N removed, compared to total harvested biomass of oysters in the six model boxes that include
375	shellfish is 2-3.5%, with an aggregate value of 2.1% (Table 2). This is double the usual reported
376	value of 1% by weight that includes only harvested biomass, reflecting inclusion of the whole
377	population (see [17] for details). These results suggest some areas perform better than others in
378	terms of N removal per unit area, under identical conditions of seeding density. The area-
379	weighted average removal estimated by the model is 125 kg N acre-1 y-1 (275 lb N acre-1 y-1). By
380	comparison, a calculation based on final oyster stocking density at harvest of 30 individuals m ⁻² ,
381	an individual harvestable fresh weight oyster of 91 g, and an N content of 1% of total fresh
382	weight gives 110 kg N acre ⁻¹ (243 lb N acre ⁻¹), or 41.3 kg N acre ⁻¹ y ⁻¹ (91 lb N acre ⁻¹ y ⁻¹). The
383	higher value obtained by the EWN model is consistent with the alternative approach that
384	considers removal of N from the water column by all shellfish, not just those that are harvested.
385	
386	The EWN model outputs for standard (discussed above) and potential scenarios estimate that the
387	ratio of annual water clearance to aggregate volume increases from 0.95 to 2.08, meaning that
388	oysters filter the total volume of the cultivated boxes up to twice per year in the expanded
389	production scenario compared to less than one time per year in the standard scenario. The
390	percent reduction of Chl through filtration increases from an average of 1.3% to 2.1% from
391	current to expanded production, with Box 25 showing the greatest removals at 2.8% and 5.3% in
392	current and maximum production, respectively. The EWN model outputs for the potential
393	scenario estimate that harvest, and net N removal and PEQs would also double to 64 x 10 ³ y ⁻¹ ,
394	1,340 metric tons N y ⁻¹ , and over 400,000 PEQ, respectively (Table 2). The N removal represents
395	about 2.68% of total annual inputs. Nitrogen removal per acre, except in Box 41, decreases as the

396	stocked area increases, probably due to the shift in population distribution with more oysters in
397	the lower weight classes. There is only a small effect on food depletion at the higher density.
398	This smaller effect was reflected in the Average Physical Product (APP), the harvested biomass
399	divided by total seed weight, which decreases by 1.63 between the standard and potential
400	scenarios for the aggregate set of cultivated boxes (Table 2). The APP does not fall below 45 (i.e
401	$1\ kg$ of seed yields $45\ kg$ of product), which makes cultivation financially attractive even for the
402	largest stocking area scenario. These results suggest that even at potential expanded production
403	(11,116 acres in cultivation), ecological balance is maintained or improved—Chl is lower, but
404	oyster production appears to remain in the Stage I section of the carrying capacity curve, where
405	Marginal Physical Product (MPP) is greater than APP, suggesting capacity for additional seeding
406	density. ⁵⁷

Shellfish carrying capacity of Long Island Sound

There is great interest in expanding aquaculture for greater N removal and to increase domestic production of seafood. ^{18, 19, 20} An important consideration is whether there is capacity to increase production without causing detrimental impacts to the environment. We have used the EWN model to assess whether LIS is at carrying capacity following the overall definition ⁶⁶ and focusing on production and ecological categories. ⁶⁷ When evaluating the potential for increased bioextraction, the carrying capacity at a system perspective should be considered first and after that a local-scale model should be applied at selected sites. The reverse approach does not take into account the interactions among aquaculture farms in an expansion scenario, which are particularly important for organically extractive aquaculture. ⁶⁹ The EWN results explicitly account for those interactions. Executed at an ecosystem scale, the shellfish stock (per EWN box) is uniformly distributed in relatively large model cells, consequently results obtained here are less constrained (from a food depletion perspective) than those obtained with a farm-scale analysis for a particular box. ⁵³ On the other hand, EWN takes multiple culture cycles into account while the local-scale FARM model does not (see *Farmscale oyser aquaculture bioextraction*), which to some extent reduces the disparity between the approaches.

Overall, the standard EWN model suggests that the combined volume of boxes under cultivation is filtered by oysters about once a year (Table 2). At the scale of LIS, the shellfish simulated in

the standard model would take over 8 years to clear the total water volume (77.4 X 10⁹ m³). This estimate for water clearance is greater than the *overall* residence time for LIS estimated to be on the order of months ^{10, 35} and similar to the e-folding time of 2-3 months estimated in EWN by means of Lagrangian tracers. ³⁹ Even at the highest potential cultivation scenario, the system is below carrying capacity. Thus, from a food depletion perspective, there appears to be potential for expanded cultivation and increased oyster bioextraction, the challenge being more related to social license aspects and reduction of conflicts with competing water uses such as recreation. The modeling framework developed in this project is appropriate for testing different management strategies, however, results would be more complete if EWN included bioextractive nutrient removal by clams, and other authochtonous benthic filter-feeders that compete for the same food resource. ⁶⁸ As noted previously, it was not possible to develop a growth model for clams (or other filter feeders), thus we were unable to include estimates of their N removal capacity in the model.

We have extended the analysis and used the EWN model to perform a marginal analysis to indicate potential for increasing production by means of an optimization analysis. The analysis considers different stocking densities (S; here we use increased lease areas with the same stocking density) for various boxes (B), and would require S^B model runs. The number of required model runs rapidly reaches a limit in terms of computational time, thus the best way to optimize this analysis would be to produce a family of curves and use Monte Carlo methods for optimization. We have not conducted a Monte Carlo analysis due to lack of appropriate input from the management and grower communities, but have done a marginal analysis for one box (Box 25; Figure 1) to highlight what changes in seeding that box might do to harvest within the other boxes. Note that management decisions can be well informed by models of this type but policies that affect the livelihoods of shellfish farmers should be fully participative as there is a strong element of social choice that must be enacted.

The marginal analysis showed that changes in seeding of Box 25, which contains the majority of leases (Table 2), results in changes to harvest in all boxes (Figure S9, Table S5). The changes in harvest are a typical representation of the law of diminishing returns, such as presented for

FARM and EWN. 53, 57 The seeding density currently used in the standard model is low compared to other oyster cultivation operations throughout the world⁷¹, and the carrying capacity calculation above showed that stock could be increased. The marginal curve shows increased harvest (Total Physical Product [TPP] which is harvest) with increased seed but starts to flatten with an annual stocking in Box 25 of 20.0 x 10³ metric ton seed. The optimum profit point, considering $P_i = P_o$, is roughly at the maximum production level (where P_i is price of seed, P_o is harvest value). There are not enough data on industry costs or revenue to extend this analysis, however, note that that the more P_i is in excess of P_o , the greater will be the MPP for the optimum profit point. This will shift the stocking density for profit maximization to the left of the production curve. The simulated increase in stocking density in Box 25 caused decreased harvest in all other boxes. In all boxes except Box 23, directly west of Box 25, harvests decreased at all seeding levels. Harvest in Box 23 increased in early stages of increased stocking before decreasing, which is likely linked to additional subsidy of particulate organics from increased cultivation in Box 25 (Table S5). Maximum harvest reduction (32%) is seen in Box 27 directly east of Box 25. But even Box 41, on the eastern end of LIS, showed decreases in harvest with increased stocking in Box 25. Overall, the model suggests that stakeholders with aquaculture farms in other boxes would be affected by an overall decreased yield of 17%. This decrease in yield reinforces that decisions on expansion and redistribution of aquaculture among zones should reflect a social consensus, as well as appropriate environmental and production aspects.⁶⁹ This analysis also indicates that production could be increased, from a perspective of ecological sustainability. With respect to the use of this kind of tool, models should support decision-makers, rather than replace them.

Farmscale oyster aquaculture bioextraction

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The FARM model estimated N removal at Station 09 in western LIS (Figure S1) of 0.105 metric ton N acre⁻¹ y⁻¹, representing a population equivalent of 32 PEQ acre⁻¹ y⁻¹. Nitrogen removal and harvestable biomass in the farms simulated in the Narrows, Western and Central areas were 2 -3 times greater than in Eastern LIS. Results showed that Chl and DO concentrations changed only slightly (0.3% decrease in both) over the three-year culture cycle. The slight change suggests no negative effect on water quality from the aquaculture operation and that there may be a margin for increased stocking density. The local-scale simulations showed a range in N removal of 0.32

-0.021 metric ton acre⁻¹ yr⁻¹, decreasing from west to east, consistent with EWN results and within the range of removal rates estimated in other ecosystems.⁷¹

FARM model results provided an opportunity to compare local results to those from EWN. Results were up-scaled to represent potential system-scale impacts using acreages for current (5,250 acres) and potential (11,116 acres) production. Results from each station were used to represent conditions of the zone in which they reside for a system-wide area-weighted total N removal estimate of 549 metric tons N y^{-1} , or 1.10% of the total annual input at current cultivation and 1,160 metric tons N y^{-1} , 2.32% of inputs at expanded production. The removal estimate corresponds to land-based nutrient removal for 167,000 and 353,000 PEQ for current and potential production, respectively. These results are within 16% of EWN results for oyster related N removal and PEQs. In locations with no system-scale circulation model upscaling farm level results may provide reasonable estimates for bioextraction capabilities, provided overall system stocking remains low enough that farms do not significantly interact with respect to food depletion.

Ecosystem service valuation

Annualized cost estimates for removal of one kilogram (2.2 pound) of N via WWTPs and agricultural and urban BMPs were applied to the estimates of current and potential N removal estimated by EWN. The annual cost to replace the removal of N through bioextraction is estimated to range from \$8.5 million y⁻¹ to \$230.3 million y⁻¹ (depending on the abatement technology considered) under the standard acreage scenario (Table 3). Under the potential production scenario, avoided costs range from \$17.4 million to \$469 million y⁻¹. Note that these costs are a proxy for the value of N removal through bioextraction. These values could be considered as potential payment in a nutrient credit trading program for ecosystem services provided by the oyster aquaculture production. A weighted average value per acre per year is calculated for each scenario and N removal method where the lowest is for agricultural BMPs at current (\$1,630 acre⁻¹ yr⁻¹) and potential production (\$1,570 acre⁻¹ yr⁻¹) and the greatest is for urban BMPs at current (\$43,900 acre⁻¹ yr⁻¹) and potential expanded production (\$42,200 acre⁻¹ yr⁻¹). As the number of acres increases, the average value for each effluent N level decreases; in the standard scenario at the 8 mg L⁻¹ level, an average value per acre per year is \$4,030 while at

516	the potential scenario under the same 8 mg ⁻¹ level, the value per acre decreases to \$3,880 (Table
517	3).
518	
519	Could oyster aquaculture bioextraction help nutrient management in urban
520	estuaries?
521	Oyster aquaculture is a promising complement to land-based nutrient management measures in
522	LIS, an urban estuary. Model results of N removal at current and potential oyster production
523	seem small compared to total inputs (1.31% -2.68% of total input) but per-acre removal is
524	relatively large and represents an ecosystem service that would need to be replaced by source
525	load reductions such as WWTP upgrades and enhancement of agricultural and urban BMPs.
526	Note that this model approach includes bioextractive N removal by all oysters, not just those that
527	are harvested resulting in estimates that are about double what is typically estimated, which
528	could be a useful approach for estimation of N removal by restored reefs. Per-acre bioextractive
529	removal (0.13 metric tons acre-1 y-1) is comparable to approved BMPs and may be more cost
530	effective than some abatement alternatives. 13, 71, 72 Based on these results it would take
531	cultivation of $> 60\%$ of the bottom area to remove the total N input to LIS, though it is unlikely
532	that such a large area would be approved for cultivation due to suitability and use conflicts.
533	However, these results show that LIS is not at carrying capacity and bioextraction could play a
534	more prominent role in N reduction strategies if cultivation area or seeding densities were
535	expanded. Consistency between the local- and system-scale model results suggests that the local-
536	scale approach could provide a reasonable estimate of bioextractive services in waterbodies that
537	lack a circulation model.
538	
539	The ecosystem value of oyster mediated N removal in LIS is estimated to range from \$8.5 to
540	\$230 million y ⁻¹ under current production and up to \$469 million y ⁻¹ if production is increased.
541	The values are significant compared to CT NCE activity between 2002 and 2009 where 15.5 x
542	10^6 credits were traded representing \$45.9 million in economic activity. Currently, only WWTPs
543	participate in the CT NCE, which allows WWTPs around the State to share in the costs and
544	benefits of removing N from wastewater.

The concept of using oysters and other filter feeding shellfish for nutrient removal directly from
the water is gaining momentum. The Chesapeake Bay Program is evaluating the science
supporting the assignment of nutrient credits to cultivated oysters and restored oyster reefs and
recently approved the use of harvested oyster tissue as a nutrient reduction BMP. ²⁶ The town of
Mashpee, MA has already begun to use oysters for nutrient reduction to address TMDL N
reduction requirements, targeting cultivation and harvest of 500,000 oysters to remove 50% of
the 5000 kg N per year required by the TMDL. ⁷³ The Mashpee, MA management plan includes
additional clam harvest areas for the same use. Bioextraction appears to be a promising
management strategy in impacted waterbodies of all sizes – LIS is 3,259 km², the Mashpee River
complex is <5 km ² , the Chesapeake Bay region is >11,000 m ² .
Note that our calculations for LIS underestimate the total N removal capability and thus the
economic value of shellfish bioextraction because the model was unable to include N removal by
clams in CT and by clam and oyster aquaculture in >400,000 acres of shellfish lease area in NY.
Denitrification, which could be a significant N loss based on the range of previous estimates (648
lb acre ⁻¹ yr ⁻¹ , [295 kg acre ⁻¹ yr ⁻¹] ²³ , 2.16 lb acre ⁻¹ yr ⁻¹ , [0.98 kg acre ⁻¹ yr ⁻¹] ³³) was also not
included in the analysis. Using the same ratio of lease (400,000 acres) to current cultivated acres
in NY as for CT, we estimate that an additional 34,300 acres of cultivated oysters could be
removing N from LIS. Assuming the same per acre N removal rate by NY oyster aquaculture as
was determined for CT oyster farms, we estimate an additional 4,460 metric tons of N could be
removed by oysters in NY for a total removal of 5,110 metric tons per year, 10% of total annual
inputs to LIS. Based on the range of published areal denitrification rates and the total oyster
aquaculture acreage in CT and NY, denitrification losses of N could be between 38.7 and 11,700
metric tons N yr ⁻¹ . Thus, oyster sequestration into tissue and shell plus denitrification losses
could potentially remove as much as 16,800 metric tons N yr ⁻¹ , or about one third of the total N
input to LIS by cultivation of 5% of the bottom area of LIS. The total could be greater if N
removal by clams was also included.
While these optimistic results are specific to LIS, physical and biogeochemical process equations
and shellfish growth models used in this study are transferable, although typically the growth

576	models require recalibration to local oyster growth conditions. The physics of a system-scale
577	model must also be calculated on a case-by-case basis, since circulation is different in each
578	system, but an up-scaled local-scale model can be used in waterbodies that lack a circulation
579	model. Shellfish culture practices (including species, use of triploids, etc) also vary across
580	different systems, so transferability is not direct but the EWN and FARM models accommodate
581	most of these differences. Despite expected differences in results in different systems, even in
582	adjacent boxes in LIS there are differences, the overall result shows that bioextraction provides
583	net removal of N and is thus relevant as a potential management strategy in impacted estuaries.
584	
585	The potential use of bioextraction as a nutrient management measure can complement existing
586	measures - a positive externality of commercial shellfish production shown in this study and in
587	previous work in the U.S. ^{23, 24, 25, 60, 65, 73, 74} , in Europe ^{14, 53, 58} , and in China. ^{43, 75} While it is not
588	possible to compare the percent of incoming N removed by cultivated shellfish in these studies,
589	farm-scale modeled N removal at 14 locations in 9 countries across 4 continents and from
590	several different species of bivalves ranged from 105 - 1356 lbs acre 1 yr 1 (12 $-$ 152 g m 2 yr 1)
591	with mean N removal of 520 lbs acre $^{-1}$ yr $^{-1}$ (58 g m $^{-2}$ yr $^{-1}$). 71 By comparison, the average areal
592	removal of N by oyster aquaculture in LIS is 275 lb N $acre^{-1}$ yr^{-1} (31 g m^{-2} yr^{-1} ; Table 2); within
593	in the range but on the lower side of reported removal rates. The ecosystem service value
594	associated with oyster related nutrient removal is also highlighted 73,74. The use of bioextraction
595	as a water quality management tool is gaining support in the U.S. and elsewhere, though
596	inclusion of growers in economic nutrient credit trading programs requires further study.
597	Regardless of whether shellfish farmers become eligible for payment, they are already
598	contributing to required nutrient reductions in several U.S. jurisdictions. ^{26, 73, 74} and thus could be
599	used elsewhere. The valuation of ecosystem services associated with shellfish cultivation has the
600	benefit of enhancing public awareness of water quality issues and could help shift attitudes to
601	allow increased opportunities for shellfish aquaculture, jobs creation and reduction of U.S.
602	dependency on imported shellfish aquaculture products in addition to improving water quality.

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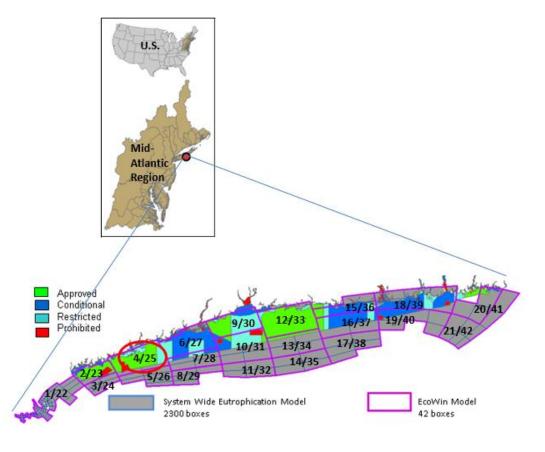


Figure 1: Location map of Long Island Sound with inset U.S. and North Atlantic region maps. High resolution System Wide Eutrophication Model (SWEM) grid box boundaries shown in blue, and broader scale EcoWin (EWN) ecological model boxes shown in purple. Shellfish classification areas in EWN model boxes that included oysters also shown (see key at left). Surface and bottom boxes are enumerated where 1/22 indicates surface box 1 and bottom box 22. Oyster production uses bottom boxes only to simulate bottom culture with no gear, the typical cultivation practice in LIS where boxes 23, 25, 27, 30, 33, and 41 are the only boxes that include oyster aquaculture. Box 25 which includes the largest lease area and is the box used for marginal analysis is denoted with a red circle.

Table 1: Incremental costs and reductions from point source controls at three levels of effluent nutrient concentration, and costs of implementation of agricultural and full urban best management practices (from Evans, 2008). Results are reported in 2013 U.S. dollars

Alternative nutrient	Capital	O&M	Annualized cost	Nitrogen removed	Average cost
reduction measure	costs	(\$ million)	(\$ million)	10^3lb yr^{-1}	\$ lb ⁻¹ yr ⁻¹
	(\$ million)			10^3kg yr^{-1}	\$ kg ⁻¹ yr ⁻¹
WWTP 8 mg L ⁻¹	433	8.67	30.4	2,070	14.63
				941	32.19
WWTP 5 mg L ⁻¹	143	4.22	11.4	677	16.82
				308	37.00
WWTP 3 mg L ⁻¹	316	12.6	28.4	634	44.81
				288	98.58
Agricultural BMP			7.68	1,310	5.90
				595	12.98
Full Urban BMP			163	1,040	159
				473	349

Table 2: EcoWin model outputs for Standard model scenario, and specific results for Potential scenario (bold font), for oyster aquaculture impacts on water clearance and nutrient removal in Long Island Sound, Connecticut determined from model simulations for Year 9. Note: i) the whole acreage is used, rather than the annual seeded acreage, because bioextraction is evaluated as a contribution of all year classes, ii) Total POM uptake includes both phytoplankton and detrital organic material, phytoplankton uptake is also shown separately. Total N inputs are 50 x 10³ metric tons y⁻¹.

Year 9	Box 23	Box 25	Box 27	Box 30	Box 33	Box 41	Total for Standard Scenario	Total for Potential Scenario
Acres (Standard scenario)	105	4,040	53	788	53	210	5,250	11,100
Oyster Harvest (ton y ⁻¹)	630	24,300	306	4,490	303	1,220	31,300	63,900
Clearance volume (%total volume y ⁻¹)	20.8	370	7.00	145	5.00	19.6	95.0	208
Total phytoplankton uptake (kg N y-1)	15,000	490,000	5,990	87,000	5,700	22,300	626,000	
Total POM uptake (includes phytoplankton) (kg N y ⁻¹)	24,500	846,000	11,320	183,200	14,500	83,000	1,160,000	
Total DIN excretion (kg N y ⁻¹)	2,270	80,800	1,040	15,700	1,080	4,680	106,000	
Total feces (kg N y ⁻¹)	7,770	276,000	3,860	65,500	5,540	34,800	394,000	
Total mortality (kg N y ⁻¹)	136	5,590	76.0	1.17	78.9	326	7,370	
Total N uptake (kg N y ⁻¹)	24,500	846,000	11,300	183,200	14,500	823,000	1,160,000	
Total N release (kg N y-1)	10,200	363,000	4,980	82,300	6,690	39,800	507,000	
Net N removal (kg N y-1)	14,400	484,000	6,340	101,000	7,800	43,200	656,000	1,340,000
N removal as % biomass	2.28	1.99	2.07	2.25	2.57	3.53	2.10	
Net N removal (lb N acre ⁻¹ y ⁻¹) (kg N acre ⁻¹ y ⁻¹)	301 137	264 120	266 121	282 128	327 149	453 206	275 ¹ 125 ¹	265 ¹ 120 ¹
Average Physical Product (APP)* (harvest / seed)	47.9	48.0	46.5	45.4	46.0	46.4	47.5 ²	45.9 ²
Population-equivalents (PEQ y ⁻¹)	4,350	147,000	1,920	30,600	2,360	13,100	199,000	405,000
% reduction in percentile 90 Chl concentration (from phytoplankton loss)	1.40	2.80	1.50	1.40	0.800	0.100	0.100 - 2.80	0.500 - 5.30

¹Net N removal for total is an average of all boxes; ²APP for total is aggregate value

^{*}When APP is >1 this means that there is more than one kg of product that is harvested from one kg of seed where the profit margin will depend on the cost of the seed and the value of the harvested product. The breakeven point is dependent on the relative costs of seed and product, technically the threshold is the point where APP is equal to Pi/Po (price of input/price output).

	Level	1000 U.S. \$						Total	Weighted
Scenario		Box 23	Box 25	Box 27	Box 30	Box 33	Box 41	Value (10 ³ U.S. \$ y ⁻¹)	Average (10 ³ US \$ acre ⁻¹ yr ⁻¹)
	8mg/l	462	15,600	204	3,250	251	1,390	21,100	4.03
Standard	5mg/l	532	17,900	235	3,740	289	1,600	24,300	4.63
(5,250	3mg/l	1,420	47,800	626	9,950	770	4,260	64,800	12.30
acres)	Agricultural BMP	187	6,300	82	1,310	101	561	8,540	1.63
	Urban BMP	5,040	170,000	2,230	35,400	2,740	15,100	230,000	43.90
	8mg/l	935	31,600	421	6,720	528	2,950	43,100	3.88
Potential	5mg/l	1,080	36,300	484	7,720	607	3,390	49,600	4.46
(11,116	3mg/l	2,860	96,700	1,290	20,600	1,620	9,020	132,000	11.90
acres)	Agricultural BMP	377	12,700	170	2,710	213	1,190	17,400	1.57
	Urban BMP	10,200	344,000	4,580	73,100	5,750	32,100	469,000	42.20

