Contents lists available at ScienceDirect







# Nitrogen removal potential of shellfish aquaculture harvests in eastern Canada: A comparison of culture methods



Aquaculture

Jeff C. Clements<sup>a,b,\*</sup>, Luc A. Comeau<sup>c</sup>

<sup>a</sup> Department of Biology, Norwegian University of Science and Technology, Høgskoleringen 5, 7491 Trondheim, Norway

<sup>b</sup> Department of Biological and Environmental Sciences, University of Gothenburg, Sven Lovén Centre for Marine Infrastructure, Kristineberg, Fiskebäckskil 45178, Sweden

<sup>c</sup> Fisheries and Oceans Canada, Gulf Fisheries Centre, 343 Université Ave., Moncton, NB, E1C 9B6, Canada

#### ARTICLE INFO

Keywords: Bioextraction Ecosystem services Molluscs Nutrient pollution Water quality

# ABSTRACT

Bivalve farming can contribute to nutrient removal in coastal and estuarine systems, as bivalves directly incorporate nutrients into their tissues and shells. We conducted a meta-analysis to compare the nitrogen removal potential (NRP; i.e., percentage of nitrogen in tissues and shells) of mussels, Mytilus edulis, and oysters, Crassostrea virginica. We then used species-specific NRPs to determine and compare the total and per-hectare NRPs for four shellfish aquaculture methods used in two Atlantic Canadian provinces - New Brunswick (NB) and Prince Edward Island (PEI) - based on current harvest biomasses. Finally, we determined the contribution of current shellfish farming to nitrogen load mitigation for a subset of bays in NB and PEI. Results revealed that on a per-weight basis, NRP was similar for the tissues of mussels and oysters, while mussel shells had a significantly higher percentage of nitrogen than oyster shells. Collectively, shellfish harvesting has the capacity to remove a mean annual total of 99088 kg and 204571 kg of nitrogen from NB and PEI, respectively. Given current harvesting practices for four culture methods employed in the region, suspended mussel culture provides the greatest NRP per hectare of farm area, followed in sequence by suspended mussel and oyster mixed culture, suspended oyster culture, and bottom oyster culture. Preliminary analysis suggested that harvests in the region typically remove < 10% of the total nitrogen load on the bay scale, with the exception of bays where nitrogen loads are low and farming intensity is high (where shellfish harvesting can remove higher percentages of nitrogen loads). Ultimately, harvests from shellfish farming in NB and PEI have the capacity to remove substantial amounts of nitrogen from local bays. Future studies assessing the influence of shellfish farming on full nutrient budgets across bays with varying physicochemical conditions will enhance our understanding the role of shellfish farms in nearshore nutrient dynamics, both regionally and globally.

# 1. Introduction

In nearshore coastal and estuarine systems, nutrients play significant biogeochemical roles (Burkholder et al., 2007; Hemminga and Duarte, 2000; Larkum et al., 2006). For example, nutrients in nearshore systems are important in controlling densities and toxicity of micro- and macro-algae and, along with temperature, can be significant drivers of toxic and non-toxic algal blooms (Anderson et al., 2002; Gilbert et al., 2018; Gobler et al., 2016). Although these algal blooms can be naturally occurring, human activities have substantially increased nutrient inputs to coastal and estuarine waters since the Industrial and Agriculture Revolutions (from increased use of chemical fertilizer; Boyer and Howarth, 2008; Howarth et al., 1995), resulting in nutrient pollution and a global increase in eutrophication (Nixon, 1995; Rabalais, 2002).

Eutrophication can have devastating effects on marine ecosystems,

as it is well documented to drive episodes of severe hypoxia, enhance the loss of critical habitat such as coral reefs and seagrass meadows, and increase the duration and severity of harmful algal blooms (HABs; Howarth et al., 2011). Indeed, increases in the area and number of oceanic "dead zones" devoid of oxygen have increased dramatically in recent years (Breitburg et al., 2018; Diaz and Rosenberg, 2008; Howarth et al., 2011). Increased incidences of eutrophication and its effects can ultimately affect species abundances and community composition (Coffin et al., 2018a, b), and can drive mass mortalities of even the most charismatic marine life (Fire et al., 2015; Scholin et al., 2000; Shumway et al., 2003). As such, ways of reducing nutrient input into coastal and estuarine systems are of significant benefit.

Although global in scope, nutrient loading and associated eutrophic conditions present local challenges in the Canadian Maritimes. Most estuaries on Prince Edward Island (PEI) are highly impacted by nutrient

\* Corresponding author.

E-mail address: jeff.clements@ntnu.no (J.C. Clements).

https://doi.org/10.1016/j.aqrep.2019.100183

Received 31 August 2018; Received in revised form 10 January 2019; Accepted 20 January 2019 Available online 04 February 2019

2352-5134/ Crown Copyright © 2019 Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/BY-NC-ND/4.0/).

loading due to a high degree of agricultural activity (Bugden et al., 2014; Coffin et al., 2018a, b; McIver et al., 2015; Meeuwig et al., 1998). Many New Brunswick (NB) estuaries have a lower risk of nutrient pollution and negative eutrophication effects compared to PEI and other highly-impacted locations; however, exceptions are apparent, such as Lamèque Bay in NB, which is highly impacted by nutrient loading (Coffin et al., 2018a, b; McIver et al., 2015; Schmidt et al., 2012). In local bays that experience higher degrees of eutrophication and, thus, lower oxygen conditions, species abundances and benthic community structure can be affected (Coffin et al., 2018a, b; Cullain, 2016). Consequently, eutrophication from nutrient loading presents an ecological and economic challenge to the Maritime provinces of Canada, both currently and in the future.

Given that nutrient loading has the capacity to negatively affect coastal bays and estuaries both globally and regionally, the exploration of mitigation tools to extract excess nutrients from these systems is warranted. One potential tool for nutrient extraction is through the farming of bivalves (Bricker et al., 2014; Grizzle et al., 2017; Higgins et al., 2011). Bivalves can remove nitrogen (N) from a given system by burying it in sediments and by enhancing the denitrification process through increased microbial activity in bivalve biodeposits (Kellogg et al., 2013). The harvesting of bivalve shells and tissues can also extract N, as bivalves directly incorporate N (i.e., from consumption of phytoplankton and detritus; not dissolved N in the water) into their tissues and shells (Carmichael et al., 2012; Grizzle et al., 2017; Newell, 2004; Reitsma et al., 2017; Rice, 2001; Rose et al., 2014, 2015; Sisson et al., 2011). With respect to aquaculture activities, studies suggest that bivalve aquaculture has the potential to stimulate rates of denitrification equal to that of wild oyster beds and that the impacts of biodeposition from aquaculture are minimal (Humphries et al., 2016; Testa et al., 2015; but see e.g. Cranford et al., 2007). Furthermore, bivalve aquaculture can provide a number of other ecosystem services alongside nutrient removal, including enhancing and increasing bottom habitat, as well as regulating other environmental parameters (e.g. sediment creation, nutrient cycling, carbon sequestration) (Van der Schatte Olivier et al., 2018). The presence of shellfish aquaculture (oysters) has also been reported to reduce disease transmission within natural bivalve populations (Ben-Horin et al., 2018).

The roles of bivalve harvesting in N removal can depend on localized biotic and abiotic conditions. Bivalve density is thought to impact nitrogen removal (Burkholder and Shumway, 2011). Localized hydrodynamics may also play a role in nutrient removal potential. For example, in some systems (e.g. high-energy with short residence times) phytoplankton can be exported out of the system hydrodynamically before it can sink to the bottom and be consumed by bacteria; in such systems, the removal of N via bivalve harvesting may be outweighed by the N input via biodeposits (although biodeposit accumulation may also be lower in such areas). In contrast, the filter-feeding roles of bivalves in lower-energy systems with longer residence times (e.g. systems with low to moderate flow conditions) where phytoplankton is retained may help to remove excess phytoplankton that would otherwise end up on the bottom and contribute to anoxic and hypoxic conditions (Petersen et al., 2014). In these lower-energy systems, biodeposits from bivalve aquaculture have the potential to suppress denitrification and increase sulfide accumulation (Cranford et al., 2007); however recent studies suggest that, even in low-energy systems, bivalve farming can stimulate denitrification at comparable rates to wild oyster beds (Humphries et al., 2016; Testa et al., 2015). Indeed, shellfish aquaculture typically occurs in calm, sheltered systems with relatively long residence times, most likely due to the protection from weather and ease of access that these systems provide (Gentry et al., 2017). As such, the 'bio-extraction' of N through the harvesting of bivalve shells and tissues may represent a significant ecological benefit in such systems. Moreover, in areas where natural shellfish beds are declining, bivalve aquaculture may serve to replace (at least partially) the lost ecosystem services due to natural shellfish bed loss.

Oyster (Crassostrea virginica) and mussel (Mytilus edulis) farming are common in eastern Canada. The majority of bivalve farming in the region is conducted in sheltered lagoon-type systems with relatively long residence times (Filgueira et al., 2015; Guyondet et al., 2013, 2015) where phytoplankton are not readily flushed out and, if not grazed, end up on the bottom and contribute to localized hypoxia and anoxia. Herein, different culture methods are used in NB and PEI, including suspended oysters (SO) and bottom oysters (BO) which are farmed in both NB and PEI, along with suspended mussels (SM) and mixed cultures of suspended oysters and mussels (SMO), which are farmed in PEI only. Harvesting practices associated with the different culture methods can drive the NRP of individual culture methods and. thus, regional bay-scale nitrogen removal. As such, it is important to understand the species-specific N removal potential (NRP) of farmed shellfish in Atlantic Canada to understand how different culture methods may contribute to nutrient mitigation.

To better understand the contribution of bivalve aquaculture to regional N removal in Atlantic Canada, we used a meta-analytical approach to: 1) quantitatively compare the NRP of mussels and oysters by comparing the N percentage of shells and tissues between the two species; 2) use species-specific shell and tissue N percentages (%N) to quantify and compare the NRP of shellfish harvesting for the four culture methods used in Atlantic Canada based on current harvest biomasses; and 3) quantify the contribution of shellfish farming to N load removal for a subset of bays in NB and PEI. In addition, we assessed the monetary value of shellfish farming N mitigation for each province. We hypothesized that %N would be similar between oysters and mussels and that the NRP of shellfish culture methods in Atlantic Canada would thus be largely driven by current harvesting biomasses.

# 2. Methods

#### 2.1. Data collection

# 2.1.1. Shellfish farming in NB and PEI

We obtained general information regarding shellfish culture activities in NB and PEI for the most current year 2018 from the New Brunswick Department of Agriculture, Aquaculture and Fisheries (NBDAAF) and the Prince Edward Island Aquaculture Leasing Division (DFO Charlottetown). The data included areal coverage of individual shellfish farming leases in both NB and PEI, organized by bay and shellfish culture method (i.e., BO, SO, SM, and SMO, as above). Estimated annual yields and associated dry weights (shell and tissue) for each culture method were also obtained from published and unpublished data (Table 1).

# 2.1.2. Species-specific nitrogen removal potential

We reviewed the literature to obtain published estimates of NRP for the two most common farmed shellfish species in eastern Canada: the eastern oysters (Crassostrea virginica) and the blue mussel (Mytilus edulis). An initial search using both Google Scholar (for peer-reviewed articles) and Google Web (for grey literature and unpublished reports) was conducted using keyword combinations as follows: (oyster and/or mussel and/or farming or aquaculture) + (nitrogen or nutrient) + (extraction or removal or assimilation or content); the keyword combinations above were searched with and without the terms shell and/or tissue. While Google searches can present biased search results based on user web activity for a given device, the background and online activity of the user conducting the literature search (JCC; aquaculture scientist) would have allowed for optimized search results. For each keyword search, we collected articles and reports from the first 15 search engine results pages (SERPs; 10 results page<sup>-1</sup>). The articles/reports were subsequently assessed for relevance, which was determined by whether or not a given article/report contained N content estimates for shells and/or tissues of C. virginca or M. edulis. The reference lists of each relevant article/report were subsequently checked to obtain additional

Annual yields, individual shell and tissue dry masses, and calculated shell and tissue dry masses harvested annually, for each shellfish culture method used in NRP calculations: bottom oysters (BO), suspended oysters (SO), suspended mussels (SM) and suspended mussels and oysters (SMO). Abbreviations: DM = dry mass, ind. = individual, ha = hectares.

			DM (g ind	1-1)	DM (kg ha <sup>-</sup>	<sup>1</sup> year <sup>-1</sup> )	
Culture method	Areal coverage (ha)	Annual yield (ind. $ha^{-1}$ )	Shell	Tissue	Shell	Tissue	References
BO SO SM SMO <sup>°</sup> Mussels	3676 3662 3678 877	13163 168000 987000	24.80 37.53 5.95	0.78 1.57 0.49	326.4 6305.0 5872.7	10.3 263.8 483.6 241.8	Doiron (1992); Comeau (2013) Comeau (2013) DFO (unpubl. data)
Oysters Total		84000 577500	37.53 -	1.57 -	3152.5 6088.8	131.9 373.7	conteau (2013), Dro (unpubl. data)

\* Direct estimates for SMO values are unavailable at present. We therefore divided the annual harvests for SO and SM each by two and added them to obtain annual harvest values and associated masses.

articles that may have been missed in the Google searches, which were then assessed for relevance as described above. Articles deemed relevant were then archived to later obtain N content estimates (recorded as percent nitrogen content of dry mass; hereafter referred to as %N) of shells and tissues for each species.

# 2.2. Estimation of nitrogen removal potential associated with regional shellfish harvests

Annual bay-scale NRP (measured as kg N bay<sup>-1</sup>) via shellfish harvesting in NB and PEI was calculated for each culture method. NRP was calculated for shells and tissue separately, and total NRP was derived by adding shell NRP and tissue NRP. For a given bay, NRP (kg year<sup>-1</sup>) for each culture method was calculated as:

$$NRP_{bay} = \left\{ \left[ (A \times I) \times (DM_{shell}) \right] \times \left( \frac{\% N_{shell}}{100} \right) \right\} + \left\{ \left[ (A \times I) \times (DM_{tissue}) \right] \times \left( \frac{\% N_{tissue}}{100} \right) \right\}$$
(1)

where, *A* is the areal coverage, in hectares (ha), of shellfish leases in a given bay, *I* is the number of individuals harvested ha<sup>-1</sup> for a given culture method (see column two in Table 1), *DM* is the individual dry mass of shell or tissue, in kilograms, for a given culture method (see columns three and four in Table 1), and %N is the percentage of nitrogen in shell or tissue for a given species (oyster or mussel). NRP was calculated separately for each %N estimate obtained in the literature search (see Table 2 for obtained estimates). For the SMO culture method, all combinations of mussel and oyster %N were used to calculate individual NRPs. Given that individual estimates of %N were fairly similar across studies for a given species and structure (i.e., shell or tissue; Table 2), we derived means and errors for statistical purposes; such an approach assumes that all collected %N estimates could potentially occur for oysters and mussels in NB and PEI.

## 2.3. Statistical analysis

Statistical tests were conducted based on *a priori* questions of interest, which were three-fold. We first wanted to determine if %N estimates in shell and tissue derived from the literature differed across species. Secondly, we wanted to explore whether or not NRP on a perhectare basis differed across culture methods. Finally, we sought to determine if the number of leases and/or areal coverage of shellfish farms were related to the total NRP of shellfish harvesting across individual bays.

To determine if %N in shells and tissues differed across species, we used linear mixed effects modeling (LME) to test for differences in %N between mussels and oysters; individual measurements were comprised of individual estimates obtained from the literature search (Table 2).

The model included species as a fixed factor (two levels: mussels and oysters), controlling for the random effect of %N estimate nested within each species-location combination, and the analysis was conducted separately for shell and tissue %N.

To determine if one or more culture methods were more effective than others in their NRP, LME was used to test for differences in NRP ha<sup>-1</sup> (in kg; calculated for each individual %N estimate obtained in the literature search) across the four culture methods. Total NRP ha<sup>-1</sup> was calculated adding the shell and tissue NRP ha<sup>-1</sup> as follows:

$$NRP \ ha.^{-1} = \left\{ DM_{shell} \times \left( \left( \frac{\%N_{shell}}{100} \right) \times I \right) \right\} \\ + \left\{ DM_{tissue} \times \left( \left( \frac{\%N_{tissue}}{100} \right) \times I \right) \right\}$$
(2)

where DM, %N, and I are as defined in Eq. 1. The model included culture method as a fixed factor (four levels: BO, SO, SM, SMO) controlling for the random effect of individual %N estimates nested within culture method. The analysis was conducted separately for shell, tissue, and total (shell + tissue) NRP.

Finally, we wanted to determine if the total NRP of shellfish harvesting across individual bays was related to the number of leases and total areal coverage of those leases. To do this, the relationship between total NRP bay<sup>-1</sup> and the number of leases bay<sup>-1</sup> was assessed using linear regression. The same analysis was conducted to explore the relationship between total NRP bay<sup>-1</sup> and the areal coverage of shellfish farms bay<sup>-1</sup>.

All statistical analyses were conducted in R version 3.5.1 (R Core Team, 2018) with a significance threshold of  $\alpha = 0.05$ . Annotated R-script and original raw data files for statistical analyses are available on Mendeley Data and can be accessed at https://doi.org/10.17632/wsf3n6j2w6.1. Linear mixed effects modeling (see below) was conducted using the *nlme* package (Pinheiro et al., 2018) and Tukey HSD *post hoc* tests were conducted using the *multcomp* package (Hothorn et al., 2008).

#### 3. Results

#### 3.1. An overview of shellfish farming in NB and PEI

Shellfish farming is common and widespread in both NB and PEI (Fig. 1); however, farming activities in PEI are almost double that of NB (Fig. 2). In 2018, a total of 1396 shellfish leases were granted across 55 bays in PEI (771 BO, 307 SO, 245 SM, and 73 SMO), resulting in a total farmed area of 7763 ha In comparison, NB granted 858 shellfish leases in 2018, spanning 22 bays (395 BO and 463 SO) and a total farmed area of 4129 ha Of the 4129 ha farmed in NB, 36% were BO and 64% were SO (Fig. 2). Of the 7763 ha farmed in PEI, 28% were BO, 13% were SO, 47% were SM, and 12% were SMO (Fig. 2).

Reported nitrogen percentages in the shells and tissues (% of dry mass) of oysters (*C. virginica*) and mussels (*M. edulis*) obtained in the literature review. Abbreviations: %N = percent nitrogen content.

		%N		
Species	Туре	Shell	Tissue	Reference
Crassostrea virginica	Wild	0.26	8.20	Reitsma et al. (2017)
	On-bottom	0.26	7.89	Reitsma et al. (2017)
	Off-bottom	0.21	7.95	Reitsma et al. (2017)
	Off-bottom triploids	0.32	8.50	Reitsma et al. (2017)
	Wild	0.30	7.00	Newell (2004)
	Off-bottom (submarket)	0.18	8.15	Higgins et al. (2011)
	Off-bottom (cocktail)	0.19	8.06	Higgins et al. (2011)
	Off-bottom (regular)	0.17	7.28	Higgins et al. (2011)
	Off-bottom (jumbo)	0.26	7.37	Higgins et al. (2011)
	Off-bottom	0.13	7.30	Grizzle et al. (2017)
	Off-bottom	0.20	7.65	Sebastiano et al. (2015)
	On-bottom	0.21	9.27	Kellog et al. (2013)
	Off-bottom (6 cm above bottom)	-	8.60	Carmichael et al. (2012)
	Off-bottom (10-20 cm above bottom)	0.26	11.80	Dalrymple (2013), unpbl. data [referenced in Kellog et al. (2013)]
Mytilus edulis	Off-bottom	0.68	9.93	Hedberg et al. (2018)
	Wild	-	7.79	Smaal and Vonck (1997)
	Off-bottom	0.90	-	Ek Henning and Åslund, 2012
	Off-bottom	0.56	-	Bucefalos (2015a)
	Off-bottom	0.56	-	Bucefalos (2015b)
	Off-bottom	0.97	6.50	Petersen et al. (2014)
	Off-bottom	1.13	10.64	Haamer (1996) with data from Lutz (1980)
	Wild	-	8.35	Rodhouse et al. (1984)
	Off-bottom	-	8.19	Rodhouse et al. (1984)

In 2018, the majority of bays in both NB and PEI were farmed with more than one culture method (i.e., BO, SO, SM, SMO) (Tables 3 and 4). In NB, where only BO and SO culture methods were conducted, 86% of bays were farmed using both culture methods, while only 14% of bays were farmed using a single type (one bay with BO only, and two bays with SO only). Similarly, in PEI, where all four culture methods are conducted, 87% of bays were farmed using more than one culture method; 44%, 27%, and 16% of bays were farmed with two, three, and four culture methods, respectively.

#### 3.2. Nitrogen content in C. virginica and M. edulis

The literature search resulted in multiple estimates of N content (measured as %N) for the shells and tissues of *C. virginica* and *M. edulis* that were highly consistent for each structure (i.e., shells and tissue) within species despite different sizes and culture methods (Table 2). For oysters, %N ranged from 0.13 - 0.32% ( $0.23 \pm 0.05\% \bar{x} \pm SD$ , n = 13) and 7.0–11.8 % ( $8.22 \pm 1.20$ , n = 14) in shells and tissues, respectively. In mussels, shell %N ranged from 0.56 to 1.13 % ( $0.80 \pm 0.24\%$ , n = 6), while tissue % ranged from 6.5 to 10.6 % ( $8.57 \pm 1.50\%$ , n = 6).



Fig. 1. Map of bay-scale bivalve farming activity in New Brunswick and Prince Edward Island. Data are for leases issued in 2018.



**Fig. 2.** Total areal coverage of each culture method in New Brunswick (NB) and Prince Edward Island (PEI). Abbreviations: BO = bottom oyster, SO = suspended oyster, SMO = suspended mussel and oyster, SM = suspended mussel.

Based on the %N values obtained in our literature search, oysters and mussels differed in the %N contained in their shells, but not in their tissues. On average, mussel shells had a significantly higher %N than oyster shells (LME:  $F_{1.17} = 73.2$ , p < 0.001). In contrast, %N in the tissues of mussels and oysters were similar (LME:  $F_{1.18} = 73.2$ , p =0.583). In general, tissues contained a higher %N than shells, regardless of species, as the %N in tissues was at least an order of magnitude higher than the %N in shells (Table 2). Within species, tissues generally had a higher %N than shells with tissues containing 8.22% and 8.57% N and shells containing 0.23% and 0.80% for oysters and mussels, respectively. Because the weight of shells at harvest is orders magnitude higher than that of tissues (Table 1), the total amount of N contained in shells and tissues at harvest was approximately equal. Shells of individual bottom oysters, suspended oysters, and suspended mussels, respectively, contained 60, 90, and 50 mg of N, which was comparable to 60, 120, and 40 mg N for tissues.

# 3.3. Nitrogen removal potential of shellfish culture methods in NB and PEI

Based on current harvesting methods and effort for each culture method, there were distinct differences in NRP between culture methods. LME revealed a significant effect of culture method on shell NRP ha<sup>-1</sup> ( $F_{3,11} = 118.6, p < 0.001$ ), tissue NRP ha<sup>-1</sup> ( $F_{3,11} = 250.0, p < 0.001$ ) p < 0.001), and total NRP ha<sup>-1</sup> (F<sub>3.10</sub> = 305.1, p < 0.001). In general, suspended mussel (SM) culture significantly outperformed all other culture methods, followed in sequence by suspended mussel and oyster (SMO), suspended oyster (SO), and bottom oyster (BO), with the exception of SMO tissue (SM and SMO tissue N were statistically similar; Fig. 3). Shell NRP ha<sup>-1</sup> of SM culture was  $63.5 \times$ ,  $3.1 \times$ , and  $1.5 \times$  higher than BO, SO, and SMO cultures, respectively, while SMO was 41.4× and 2.0× higher than BO and SO respectively, and SO was 20.7  $\times$  higher than BO. Similarly, tissue NRP ha  $^{\text{-1}}$  for SM was 37.0  $\times$ and  $1.3 \times$  higher than BO and SO respectively, while SM and SMO tissue NRP ha<sup>-1</sup> were similar. SMO tissue NRP ha<sup>-1</sup> was  $37.4 \times$  and  $1.4 \times$  higher than BO and SO respectively, and SO was  $27.6 \times$  higher than BO. In total, SM NRP ha<sup>-1</sup> was  $56.1 \times , 2.3 \times ,$  and  $1.3 \times$  higher than BO, SO, and SMO, while SMO was 42.4  $\times$  and 1.7  $\times$  higher than BO and SO respectively, and SO was  $24.3 \times$  higher than BO.

#### 3.4. Current nitrogen removal in NB and PEI

The harvesting process associated with shellfish farming has the potential to remove substantial amounts of N from farmed bays in NB and PEI. The average amount of N (average of NRP estimates from individual %N values in literature) removed from a given bay via harvesting was variable across bays and ranged from 11.9 to 13588.4 kg year<sup>-1</sup> in NB and 4.9–24782.9 kg year<sup>-1</sup> in PEI (Table 3). In total, harvesting cultured shellfish in 2018 removed an estimated average total of 99087.6 kg in NB, and 204571.3 kg in PEI (Table 3). Computationally (because NRP is calculated as a function of biomass at harvest), bay-scale total annual NRP is directly related to harvest biomass in a 1:1 fashion for bays in which only one species is harvested. Given that NB only farms oysters, total annual NRP is a direct function of harvested biomass ( $R^2 = 1$ ). Similarly, because many bays in PEI harvest a single species (Table 1), total annual NRP across bays is strongly influenced by total harvested shellfish biomass ( $R^2 = 0.85$ ). Bay-scale total annual NRP (pooled across culture methods) was also related to the areal coverage of shellfish farms ( $F_{1.75} = 148.7, p < 0.001$ , Adjusted  $R^2 = 0.66$ ), and weakly related to the number of leases  $(F_{1.75} = 12.2, p < 0.001, Adjusted R^2 = 0.13)$  (Fig. 4). When broken down by province, the relationship between the number of leases and NRP year<sup>-1</sup> was evident for NB (Adjusted  $R^2 = 0.59$ ) but not PEI (Adjusted  $R^2 = 0.03$ ) (Fig. 4). The relationship between farmed area and NRP year<sup>-1</sup> was apparent for both provinces, but was much stronger for PEI (Adjusted  $R^2 = 0,.76$  for PEI and 0.37 for NB) (Fig. 4; see Supplementary File 1 for statistical results of linear regressions).

# 4. Discussion

In this study, we quantified the potential of harvesting practices associated with shellfish aquaculture in NB and PEI to remove N from coastal and estuarine bays in the region, and to assess the efficacy of a socially-scrutinized farming method in removing N. Our results suggest that annual harvesting activities associated with shellfish farming in NB and PEI have the capacity to remove substantial amounts of N from nearshore coastal bays in the region. In total, harvesting mussels and oysters can remove 99088 kg (109 US tons) and 204571 kg (226 US tons) of N from bays in NB and PEI, respectively, and suspended mussel farming currently provides the best per ha NRP. While current mussel farming practices are regionally most effective, suspended oyster cultures can provide a high degree of N removal. Ultimately, shellfish harvesting activities can provide a substantial ecosystem services for nearshore bays in this region.

### 4.1. Nitrogen removal potential of shellfish aquaculture in eastern Canada

Our literature search revealed that, on a gram-by-gram basis, mussel shells contained a significantly higher %N content than oyster shells, while tissue %N of the two species was similar. This result suggests that individual mussels may be more efficient at removing N than individual oysters on a per-weight basis. At present, the biological explanation for the differences in shell %N are unknown. It is possible that the %N differences may be related to differences in the mineral composition of the shells between the two species, but such a mechanism has yet to be quantitatively described. Ultimately, the biological mechanism(s) responsible for differences in shell %N between these two species require future research.

While individual mussels have a higher NRP on a per weight basis (due to a higher shell %N; based on literature values) than oysters, this does not by default mean that mussel aquaculture activities will have a higher NRP than oyster aquaculture. Furthermore, simply harvesting a higher biomass of shellfish will not necessarily result in a higher NRP, as the species and size at harvest will also influence per hectare NRP. For Atlantic Canada, our results indicated that suspended mussel cultures outperformed all other culture methods with respect to NRP ha<sup>-1</sup>,

List of bays in Nev	v Brunswick (NB)	and Prince Edwa	d Island (PEI)	, and their associate	d shellfish cultu	re methods	(marked w	vith an X).	Abbreviations:	Abbr. =
abbreviation., BO =	= bottom oysters,	SO = suspended of	oysters, $SM = s$	suspended mussels, S	MO = suspende	d mussels a	nd oysters.			

Bay	Bay abbr.	BO	SO	SM	SMO
Aldouane River	AldR	Х	Х		
Bay du Vin	BDV	Х	Х		
Bouctouche Bay	BoucB	Х	Х		
Caraquet Bay	CaraB	Х	Х		
Cocagne Bay	CocB	Х	Х		
Inkerman	Ink		Х		
Lameque Bay	LamB	Х	Х		
Little Shemogue Harbour	LSH	Х	Х		
Miramichi Bay	MiraB	Х	Х		
Miscou Harbour	MiscH	Х	Х		
Neguac Bay	NegB	Х	Х		
Peacock Cove	PeaC	Х			
Petit-Barchois Bay	PBB		Х		
Petite-Lameque Bay	PLB	Х	Х		
Richibucto Harbour	RichH	Х	Х		
Shediac Bay	ShedB	Х	Х		
Shippagan Bay	ShipB	Х	Х		
Shippagan Harbour	ShipH	Х	Х		
Spence Cove	SpenceC	Х	Х		
St-Simon Bay	SSB	Х	Х		
Tabusintac Bay	TabB	Х	Х		
Tracadie Bay	TracB_NB	Х	Х		

PEI					
Bay	Bay abbr.	BO	SO	SM	SMO
Bentick Cove	BenC	Х	Х	Х	Х
Bideford River	BideR	Х	Х	Х	
Boughton River	BoughR	Х	Х	Х	Х
Brackley Bay	BrackB	Х	Х		
Brudenell River	BrudR	Х		Х	Х
Cardigan Bay	CardB			Х	Х
Cardigan River	CardR	Х	Х	Х	
Cascumpec Bay	CascB	Х	Х		
Chichester Cove	ChicC	Х	Х	Х	
Conway Narrows	ConN	Х	Х		
Covehead Bay	CoveB	Х			Х
Darnley Basin	DarnBa	Х	Х	Х	Х
Dock River	DockR	Х	Х		
East River	EastR	Х	Х		
Egmont Bay	EgmB	Х	Х		
Enmore River	EnmR	Х	Х		
Fortune Bay	FortB	х			
Foxley River	FoxR	Х	Х		
Gascoigne Cove	GasC	х			
Grand River	GrandR	х	Х		
Haldimond	Hald	х			
Hillsborough Bay	HillsB	х	х	х	х
Hope River	HopeR	x	x		
Howe Bay	HowB	x			
Hunter River	HuntR	x	х	х	х
Kildare River	KildR	x	x		
ennox Channel	LenncovCh	x	x		
Malpeque Bay	MalpB	x	x	v	
Marchwater	March	v	v	v	
Mill Divor	MillD	v v	л V	л	v
Montagua Biyor	MontD	л	Λ	v	л
Murroy Divor	MurrD	v	v	A V	v
Muildy River	NUD	A V	л	A V	л
New London Bay	INLD	л		А	v
	NL OD	v	v	v	A V
Jrwell Bay	OrwB	X	X	Х	Х
Percival River	PercR	X	Х		
Pinette River	PINK	X			
Pownal Bay	PownB	X	Х		
Rustico Bay	RustB	X		Х	Х
Salutation Cove	SalC	X	X		-
Savage Harbour	SavH	Х	Х	Х	Х
Souris River	SourR	Х	Х		Х
South Lake	SL	Х	Х		Х
Southwest River	SWR	Х	Х	Х	
Spry Cove	SpryC	Х	Х		
St. Marys Bay	SMB	Х	Х	Х	
St. Peter's Bay	SPB		Х	Х	х
Stanley River	StanR	Х		Х	х
Sunbury Cove	SunbC	Х	Х		
Гracadie Bay	TracB_PE	х	Х	Х	х
Vernon River	VernR	Х	Х		
Victoria	Vic	х	Х		
West River	WestR	Х	Х		
Winter Bay	WintB	х		Х	х
Wolfe Inlet	WolfeI	х	Х		

despite the per ha harvested biomass of suspended mussel culture being lower than (but close to) other culture methods (i.e., suspended oyster and suspended mussel and oyster). This finding was driven by mussels having a higher %N in their shells than oysters, coupled with the fact that per ha harvested biomass of suspended mussel culture, while lower than other culture methods, was close to the other culture methods (see Table 1; the latter being driven by a large number of individuals being harvested rather than the size at which individuals are harvested). However, if individual oysters were harvested at an even greater biomass than mussels, then the per ha NRP of oysters could potentially exceed that of mussels. Thus, for other regions comparing the NRP of different shellfish culture methods with different species, it is critical to consider the respective biomass at which individuals are harvested, and the number of individuals harvested per ha. Furthermore, while not considered in our analysis, the turnover rate of individuals via harvesting can also influence NRP. For example, while larger individuals contain more nitrogen than smaller individuals, harvesting smaller individuals more frequently may ultimately lead to a higher NRP than harvesting larger individuals less frequently. It is thus important to collectively consider species, individual biomass at harvest, the number of individuals harvested, and the frequency of harvesting when computing the per ha NRP of shellfish aquaculture activities in other regions.

Given current harvesting practices, suspended oyster farming would have to approximately double its biomass yield to provide comparable per ha NRP to that of suspended mussel farming. Nonetheless, oyster

4	
e	
Б	
a]	
Ĥ	

Annual NRP via shelffish harvesting for bays in New Brunswick (NB; 22 bays) and Prince Edward Island (PEI; 55 bays). Values are averages of individual %N estimates in shells and tissues (dry mass) of mussels and oysters obtained in our literature search (see Table 1). Data are sums of bay-scale averages (calculated from individual estimates of %N for each species). Abbreviations: NRP = nitrogen removal potential, BO = bottom oysters, SO = suspended oysters, SM = suspended mussels, SMO = suspended mussels and oysters, Prov. = province, No. = number, Tiss. = tissue, Tot. = total, kg = kilograms. Full names for bays can be found in Table 3.

Table O																	
				Average	annual NF	tP via harve	esting (kg)										
				0g			20			SM			SMO			Grand tot.	
Prov.	Bay	No. leases	Area farmed (ha)	Shell	Tiss.	Tot.	Shell	Tiss.	Tot.	Shell	Tiss.	Tot.	Shell	Tiss.	Tot.	kg	Prov. tot. (kg)
NB	AldR	33	97.8	22.2	25.3	47.4	901.7	1470.7	2262.4	I	I	I	I	I	I	2309.8	9087.6
	BDV	19	86.9	17.3	19.7	36.8	845.4	1379.0	2121.3	ı	I	I	I	I	ı	2158.1	
	BoucB	38	268.6	44.9	51.1	95.9	2763.2	4507.0	6933.3	I	I	I	I	I	I	7029.2	
	CaraB	79	39.1	68.8	78.3	146.9 22.2	4068.1	6635.4	10207.3	ı	I	I	I	I	ı	10354.2	
	CocB	57	262.0	38.9	44.3	83.0	2/83.1	4539.5	6983.2 400.0	ı	I	I	I	I	I	7066.2	
	Ink	n ü	0.61	1		1 00	198.9	324.4	499.U	I	I	I	I	I	I	499.U	
	Lamb	30	1/1.3	62.1	/.0/	132.6	1162.0	1895.2	2915.5	I	I	I	I	I	I	3048.1	
	LSH	ы.	25.6	9.5	10.8	20.2	170.5	278.1	427.9	I	I	I	I	I	I	448.0	
	MiraB	42	299.0	189.6	215.9	404.7	571.5	932.2	1434.1	I	I	I	I	I	I	1838.8	
	MiscH	57	319.3	124.7	142.0	266.1	2006.4	3272.5	5034.2	I	I	I	ļ	ı	I	5300.3	
	NegB	118	351.1	93.9	106.9	200.3	2981.9	4863.7	7481.9	ı	I	I	I	I	I	7682.3	
	PeaC	1	7.5	5.6	6.3	11.9	I	I	I	I	I	I	I	I	I	11.9	
	PBB	1	2.0	I	I	I	3350.3	5464.6	8406.3	I	I	I	I	I	I	8406.3	
	PLB	18	46.6	21.8	24.8	46.5	228.3	372.5	573.0	I	I	I	I	I	I	619.4	
	RichH	39	209.4	34.0	38.7	72.5	2172.9	3544.1	5452.0	I	I	I	I	I	I	5524.6	
	ShedB	15	103.7	47.9	54.6	102.3	518.9	846.3	1301.9	I	I	I	I	ı	I	1404.2	
	ShipB	35	319.9	70.5	80.3	150.5	2986.0	4870.4	7492.3	I	I	I	I	ı	I	7642.8	
	ShipH	13	54.4	20.1	22.9	42.9	362.3	590.9	0.606	I	I	I	I	ı	I	952.0	
	SpenceC	9	42.1	23.1	26.3	49.4	144.8	236.1	363.3	I	I	I	I	ı	I	412.6	
	SSB	156	597.2	147.5	167.9	314.8	5290.2	8628.6	13273.6	I	I	I	I	I	I	13,588.4	
	TabB	68	273.2	41.3	47.0	88.1	2889.1	4712.4	7249.2	I	I	I	I	I	I	7337.3	
	TracB_NB	25	17.2	10.5	12.0	22.5	2164.8	3530.9	5431.7	I	I	I	I	I	I	5454.2	
PEI	BenC	17	107.8	23.4	26.7	50.0	309.1	504.2	775.6	1330.1	879.7	1254.6	320.6	330.6	701.3	2781.4	204571.3
	BideR	53	138.9	46.8	53.3	100.0	911.4	1486.5	2286.7	223.5	147.8	210.8	I	I	I	2597.5	
	BoughR	21	249.1	24.3	27.7	52.0	605.4	987.5	1519.1	4848.2	3206.6	4573.0	487.5	502.7	1066.4	7210.5	
	BrackB	з	7.8	4.4	5.0	9.4	24.1	39.4	60.6	I	I	I	I	I	I	70.0	
	BrudR	15	130.2	0.2	0.2	0.4	I	I	I	3849.9	2546.3	3631.4	215.7	222.4	471.8	4103.6	
	CardB	12	116.6	I	I	I	I	I	I	3466.8	2292.9	3270.0	180.3	185.9	394.4	3664.4	
	CardR	16	166.8	1.5	1.7	3.2	32.1	52.4	80.5	5084.9	3363.1	4796.2	I	ı	I	4880.0	
	CascB	11	27.5	15.8	18.0	33.8	80.9	132.0	203.0	I	I	I	I	I	I	236.8	
	ChicC	13	100.9	30.8	35.0	65.6	667.1	1088.0	1673.7	286.6	189.5	270.3	I	I	I	2009.7	
	ConN	129	471.0	279.4	318.1	596.4	1247.2	2034.2	3129.3	I	I	I	1	1	1	3725.7	
	CoveB	80 0	46.0	6.6	7.5	14.0		1	1 1	1	1 0		1137.8	1173.4	2489.0	2503.0	
	Darnba	38	230.8	10.9	09.3 01.0	1.29.9	0.207	/ 38.1	C.CE11	3.12 cU S	2018.7	28/8.9	8.626	540.2	9.6411	5290.2 1535 0	
	DUCKR	7 7	09.90	10.0	7.12	1.90	0.0%C	212.2	0.021	I	I	I	I	I	I	2.0001	
	EastK	4/	C.421	91.0	103./	194.3 95.1	0 1 0 3	33.U	0.00	ı	I	I	I	I	I	248.2	
	EnmD	11	9.701 1.77 Q	165	1.01	25.1	0.7001	7.000	2510.2	I	I	I	I	I	I	2551 2	
	Eort D	00	10 5	0.01 0 7	0.01	1.00 166	1402.0	1.1022	7.6100	I	I	I	I	I	I	3334.3 16.6	
	FOLLD	170	C.UI	0./	0.7	0.01	-		1	I	I	I	I	ı	I	10.0 F 1001	
	LOXK	4/1 م	290.9	1.16	0.011	C./U2	4.6222	0.0000	1.6666	I	I	I	I	I	I	1.1000	
	DandD	4	30.0	141	16.0	1.05	1577	- 757 7	305.7							7.304	
	Hald		12.4	00	11 3	1.00		4:104	1.000		1		II	1	II	21 1 21 1	
	riillep	- 00	10:1 10:1	1.00	2110	1.12	0.09	1 22 0	0 606	1 707 1	- 2166	4616 A	11214	11505	7150 7	7775 0	
	HoneR	) C C	2.022 24.3	1.22	C.C.2	0.74 15.4	00.7 0110	360.4	754 5	1.10/1	7.0010	1.0101	1.1211		1.60+2	560 Q	
	Howe	9	28.1	26.7	30.4	1.01	0.122	t.000			1 1				1 1	57.0	
	HuntR	14	54.9		6.1	11.4	13.6	22.2	34.1	486.0	321.4	458.4	953.7	983.4	2086.1	2590.0	
	KildR	32	49.1	22.8	26.0	48.7	243.2	396.6	610.2	1		-				658.9	
																(contin	ed on next page)

7

Table 4 (continued)

				Average BO	e annual NI	RP via harv	esting (kg) SO			SM			SMO			Grand tot.	
Prov.	Bay	No. leases	Area farmed (ha)	Shell	Tiss.	Tot.	Shell	Tiss.	Tot.	Shell	Tiss.	Tot.	Shell	Tiss.	Tot.	kg	Prov. tot. (kg)
	LenncoxCh	17	119.1	37.0	42.1	79.0	919.1	1499.1	2306.0	I	T	I	I	I	-	2385.0	
	MalpB	45	199.3	62.8	71.5	134.1	62.6	102.2	157.2	3439.0	2274.5	3243.8	I	I	I	3535.0	
	March	33	518.4	22.9	26.0	48.8	162.4	264.9	407.5	14886.6	9846.0	14041.6	I	I	I	14497.9	
	MillR	28	46.1	16.6	18.9	35.4	119.0	194.2	298.7	I	I	I	450.5	464.6	985.6	1319.7	
	MontR	12	67.9	ı	I	ı	I	ı	I	2126.6	1406.5	2005.9	I	I	I	2005.9	
	MurrR	44	402.8	18.5	21.0	39.4	88.9	145.0	223.0	10002.0	6615.3	9434.3	1589.7	1639.4	3477.5	13174.2	
	NLB	22	327.7	48.6	55.3	103.7	I	I	I	8210.7	5430.5	7744.6	I	I	I	7848.3	
	NL	3	20.3	ı	ı	ı	ı	I	I	I	I	I	623.4	642.9	1363.7	1363.7	
	OrwB	26	233.0	60.3	68.6	128.7	201.9	329.3	506.6	4089.0	2704.4	3856.9	181.1	186.7	396.1	4888.2	
	PercR	41	114.2	62.2	70.8	132.8	402.2	656.0	1009.2	I	I	I	I	I	I	1142.0	
	PinR	14	37,3	27.6	31.4	58.9	ı	I	I	I	I	I	I	I	I	58.9	
	PownB	22	50.8	31.9	36.3	68.1	103.1	168.2	258.7	I	I	I	I	I	I	326.8	
	RustB	21	225.6	15.2	17.3	32.4	I	I	I	468.6	309.9	442.0	5826.4	6008.3	12745.2	13219.6	
	SalC	5	6.0	44.2	50.4	94.4	70.4	114.9	176.7	I	I	I	I	I	I	271.1	
	SavH	28	192.9	28.2	32.2	60.3	28.8	46.9	72.2	1219.3	806.5	1150.1	3483.4	3592.2	7619.9	8902.5	
	SourR	6	35.0	8.9	10.1	19.0	89.6	146.1	224.7	I	I	I	498.2	513.7	1089.7	1333.4	
	SL	13	61.2	16.3	18.6	34.8	49.2	80.3	123.6	I	I	I	1087.8	1121.8	2379.7	2538.1	
	SWR	40	87.8	37.8	43.0	80.6	187.4	305.6	470.1	709.6	469.3	669.3	I	I	I	1220.0	
	SpryC	з	2.7	1.2	1.3	2.5	15.3	24.9	38.3	I	I	I	I	I	I	40.8	
	SMB	27	315.0	20.4	23.2	43.5	22.0	36.0	55.3	4820.3	3188.2	4546.7	I	I	I	4645.5	
	SPB	28	635.7	I	I	I	107.5	175.4	269.8	16607.8	10984.3	15665.1	4044.8	4171.1	8848.0	24,782.9	
	StanR	7	16.3	6.8	7.7	14.5	I	I	I	221.7	146.6	209.1	2984.5	3077.7	6528.6	6752.2	
	SunbC	12	67.5	44.5	50.6	94.9	99.4	162.1	249.4	I	I	I	I	I	I	344.4	
	TracB_PE	45	662.2	36.4	41.4	77.6	103.6	169.0	260.0	18647.5	12333.4	17588.9	305.9	315.5	669.2	18595.8	
	VernR	45	103.2	53.3	60.7	113.8	414.3	675.7	1039.4	I	I	I	I	I	I	1153.2	
	Vic	10	41.7	24.9	28.4	53.2	107.7	175.7	270.3	I	I	I	I	I	I	323.5	
	WestR	23	41.3	23.5	26.7	50.1	127.7	208.3	320.4	I	I	I	I	I	I	370.5	
	WintB	17	104.7	1.7	2.0	3.7	I	I	I	2342.5	1549.3	2209.5	844.5	870.9	1847.4	4060.6	
	WolfeI	7	44.0	29.6	33.7	63.1	53.6	87.4	134.5	I	I	I	I	I	I	197.6	



Culture type



**Fig. 4.** Average NRP year<sup>-1</sup> as a function of the number of shellfish leases (left panels) and the total areal coverage of shellfish farms (right panels) for PEI (blue plots; bottom panels), NB (yellow plots; middle panels), and NB and PEI combined (red plots; top panels). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

farming can provide substantial NRP regionally. Based on our calculations of current harvesting rates in NB and PEI, suspended oyster

Fig. 3. Shell, tissue, and total (shell + tissue) NRP ha<sup>-1</sup> of the four different culture methods employed regionally (i.e., in NB and PEI). Data are means ± standard deviation. Letters above boxes indicate significant differences (from Tukey HSD post hoc tests; see Supplementary File 1). Values were obtained by multiplying annual harvest of individuals per hectare by published measurements of nitrogen percentage for shell and tissue, thus variation reflects the range of nitrogen content reported in the literature. Abbreviations: BO = bottom oyster, SO = suspended oyster, SM = suspended mussel, SMO = suspended mussel and ovster, NRP = nitrogen removal potential, kg = kilograms, ha = hectares.

Table 5

SO

SMO

SM

Total

d

Percentage of total N loading removed via shellfish harvesting (all culture methods combined) under current farming densities for six bays in New Brunswick. Total N load values were obtained from Table 3 in McIver et al. (2015) for NB, and from Table 1 in Coffin et al. (2018) for PEI.

Bay	Total N load (kg TDN year <sup>-1</sup> )*	Total NRP (kg year <sup>-1</sup> )	%N removed year <sup>-1</sup>
NB			
Bouctouche	188324	7029.2	3.7
Cocagne	94562	7066.2	7.5
Lamèque	67223	3048.1	4.5
Richibucto	265027	5524.6	2.1
St. Simon	15772	13588.4	86.2
Tabusintac	130624	7337.3	5.6
PEI			
Bideford	41688	2597.5	6.2
Enmore	219600	3554.3	1.6
Kildare	90132	658.9	0.7
Mill	1097569	1319.7	0.1
Montague	3516786	2005.9	0.1
Souris	158632	1333.4	0.8
Stanley	196784	6752.2	3.4
West	374880	370.5	0.1

culture alone accounts for the removal of 108667 kg N vear<sup>-1</sup> in the region, accounting for 35.8% of the NRP of shellfish harvesting in NB and PEI. Furthermore, suspended oyster operations alone have the potential to remove exceptional amounts of N in a given bay. For example, while current oyster harvesting activities in NB typically have the potential to remove < 10% of the total N load of a given bay, upwards of 86% of the total N load can be removed via oyster harvesting in some bays where nutrient loads are relatively low and bivalve farming is relatively intense (e.g. St.-Simon; Table 5). It is thus clear that while suspended mussel farming can optimize N removal (under current farming practices), suspended oysters can significantly contribute to bay-scale N removal in some areas if strategically placed. This finding is locally critical, especially for PEI, given the susceptibility of mussels to marine climate change (Clements et al., 2018) and the ongoing shift from mussel to oyster cultures in that province (The Guardian, 2014).

Despite clear differences in NRP ha<sup>-1</sup> across culture methods, there was a strong relationship between bay-scale areal coverage of shellfish farming and annual total N removal. This suggests that a higher areal coverage of shellfish farming in the region, regardless of culture method, can increase total annual NRP. Thus, at present, a bay in NB or PEI with a high density of shellfish cages is likely to have a higher rate of N removal (via harvesting) than less-densely farmed bays.

While not a focus of this study, N removal via shellfish harvesting can be economically valued as well. Rose et al. (2015) synthesized the

Approximate cost ranges (in Canadian (C\$) millions; conversion rate of US\$ 1.00 = C\$ 1.33) of N removal for oyster and mussel farming in NB and PEI. Values are based on total harvest (in kg) of each species for each province and the maximum and minimum costs reported in Supplement 3 in Rose et al. (2015).

Province	Mussels	Oysters	Total shellfish
NB	-	0.00 - 8.88	0.00 - 8.88
PEI	0.46 - 2.97	0.00 - 5.96	0.46 - 8.93
Regional total	0.46 - 2.97	0.00 - 14.84	0.46 - 17.82

financial costs of using shellfish as a nitrogen removal strategy, reporting variable monetary costs that were dependent on location and approach. Using those values, we calculated ranges of total annual cost of using shellfish aquaculture as a nitrogen mitigation tool for NB and PEI, showing costs (in Canadian dollars, C\$) ranging from C\$ 0 to more than C\$ 17 million for the region (Table 6). These associated costs could potentially be considered in a nutrient credit system. Herein, a limit on nutrient discharge can be set and dischargers who reduce nutrients below the set limit can sell their nutrient offset to other dischargers in the same system (Ferreira and Bricker, 2015). Additionally, if nutrient discharge can be reduced at low cost, credits can be sold to other dischargers who need to implement higher-cost reduction measures (Ferreira and Bricker, 2015). Such a system has the potential to allow a wide variety of dischargers to meet pollution targets and can serve as a financial boost for local shellfish farmers (and other industries that can reduce pollution at low costs). Nutrient credit systems have been successfully implemented in areas of the United States (see Ferreira and Bricker, 2015 for an overview) and are thus viable for implementation in Canada. More research is needed regionally, however, before such a system can be implemented, as the cost, feasibility, and impact of nonpoint source alternatives must be considered (Stephenson et al., 2010).

The results of this study also have implications for resource management. Herein, resource managers could potentially use NRP calculations in marine spatial planning activities to optimize the expansion of shellfish aquaculture activities to provide maximum ecosystem services. This approach is not only regionally applicable, but it can be applied in other areas of Canada where shellfish aquaculture is common (e.g. Nova Scotia and British Columbia). In general, our results suggest that bays where N loading is relatively low and shellfish farm densities are relatively high are likely to benefit most from shellfish farming nutrient removal (i.e., farming in St. Simon Bay removed far higher percentage of bay-scale N load compared to other regional bays; Table 5). As such, this information could be used in marine spatial planning activities for shellfish aquaculture to optimize coastal nutrient management in Canada. Field experiments coupled with numerical modeling would also serve well in understanding and predicting shellfish harvesting NRP for individual bays to further inform marine spatial planning for nutrient management.

# 4.2. Study limitations

Our study has a number of limitations. Most notably, we did not employ a full N-budget approach. Indeed, there are a number of additional processes that should be considered when determining the NRP of shellfish aquaculture. For example, while harvesting may remove N that has accumulated in tissues and shells, biodeposition under shellfish farms can result in N retention in a system. Consequently, the efficacy of processes such as denitrification and N burial (in sediments) beneath a given shellfish farm may dictate the net N budget of the farm. While not incorporated here, studies suggest that processes such as denitrification and N burial underneath shellfish farms is comparable to that of wild shellfish beds, suggesting that a net N removal of shellfish farms is likely (Humphries et al., 2016). Furthermore, it has been reported that the vast majority of biodeposits beneath shellfish farms in shallow

nearshore systems is resuspended and transported away from the site of the farm, resulting in a minimal environmental impact (Testa et al., 2015). In contrast, however, other studies suggest a net N retention to some systems with intensive aquaculture (Cranford et al., 2007; Luo et al., 2018; Stadmark and Conley, 2011). Such contrasting N budget results are likely driven by various model parameters including (but not necessarily limited to) farm density and localized hydrodynamics (e.g. residence time, currents, and water velocity). Furthermore, a number of technical issues with studies reporting negative effects of aquaculture on nutrient budgets have been highlighted (Petersen et al., 2012; Rose et al., 2012). Unfortunately, residence times and detailed hydrodynamic data for regional bays in NB and PEI are not readily available and fall outside the scope of our analysis. Bay-scale estimates of freshwater input and water volume would aid in estimating residence times and, coupled with estimates of biodeposition rates, would be useful striving toward a more holistic understanding of source-sink nutrient dynamics associated with bivalve aquaculture on regional bays in Atlantic Canada. Ultimately, future studies assessing complete N budgets for individual bays with varying physicochemical properties are needed to understand the full role of shellfish aquaculture in localized nearshore nutrient budgets.

We quantified the percentage of estimated N loads that could potentially be removed from nearshore systems in NB and PEI via shellfish harvesting; however, our analysis was not able to account for the percentage of the total N loading removed by shellfish harvesting for all bays where NRP was calculated. Nonetheless, we were able to assess this aspect for a subset of bays in NB and PEI, which suggested that current shellfish harvesting typically removes < 10% of the total N load (Table 5). As such, current shellfish aquaculture activities are not sufficient for reducing eutrophication by themselves, and other nutrient mitigation techniques need to be considered, However, in bays where nutrient loading is relatively low and bivalve farming is relatively intense, shellfish harvesting can remove substantial proportions of N loading. For example, in one bay, shellfish harvesting was estimated to remove > 86% of the total N load (St. Simon; Table 5), even though only oysters are harvested in that bay. It is thus apparent that shellfish harvesting has the potential to remove substantial percentages of bayscale N loading where loads are relatively low; however, in most bays, harvests of farmed shellfish remove only a small percentage of total N loads. An important consideration for such systems, however, is whether or not such extensive grazing might promote the proliferation of harmful algal blooms (HABs), as selective grazing may promote the proliferation of HABs. Future studies measuring the total N load of a swath of bays regionally would serve well to understand how much shellfish aquaculture may contribute to nutrient mitigation in these bays relative to the total nutrient input. Furthermore, reginal studies assessing the potential impact of extensive grazing of farmed bivalves on HABs is warranted.

Our analysis considered the %N in tissues and shells of mussels and oysters in our calculations of NRP. Nitrogen accumulation, however, is not necessarily restricted to these structural components of the animals. This is particularly apparent for mussels, as it is documented that the byssal threads can also accumulate nitrogen, although the amount may be limited (Hedberg et al., 2018). Consequently, our calculations of mussel NRP may be underestimated. It is also important to note that nitrogen is not the only nutrient that can accumulate in nearshore systems and bivalves. Although nitrogen is considered the primary nutrient involved in coastal and estuarine eutrophication (Gobler et al., 2016), phosphorous can also accumulate in these systems (Howarth et al., 1995). As such, future studies would benefit from understanding the phosphorus removal potential of shellfish aquaculture in the region.

#### 5. Conclusions

The results of this study suggest that mussel and oyster farming have the potential to remove substantial amounts of N in nearshore coastal and estuarine bays. It is apparent that harvesting activities associated with shellfish aquaculture have the capacity to substantially contribute to nearshore nutrient removal. Shellfish aquaculture will not solve eutrophication issues alone, however, and it is likely best to tackle eutrophication at the source (i.e., reducing agricultural discharge and coastal runoff). Nonetheless, the culturing and harvesting of shellfish-when implemented efficiently-may help to partially tackle eutrophication issues where they exist. Such an ability highlights the likely-important role of shellfish aquaculture in tackling issues related to anthropogenic pressure and global climate change in eastern Canada and abroad.

#### Data accessibility

Annotated R-script and original raw data files are available through Mendeley Data at https://doi.org/10.17632/wsf3n6j2w6.1.

### **Conflict of interest**

We declare no conflict of interest.

#### Acknowledgements

We wish to acknowledge Leon Lanteigne and Thomas Landry for insightful discussions regarding the ecosystem services of shellfish aquaculture which lead to this project. We thank Chris Mills at Fisheries and Oceans Canada for providing data on shellfish leases. We also thank Dr. Thomas Guyondet and Mike Coffin at the Gulf Fisheries Centre for constructive feedback on an earlier version of this manuscript. The project was funded through in-kind support from Fisheries and Oceans Canada.

#### References

- Anderson, D.M., Gilbert, P.M., Burkholder, J.M., 2002. Harmful algal blooms and eutrophication nutrient sources, composition, and consequences. Estuaries 25, 704–728. https://doi.org/10.1007/BF02804901.
- Ben-Horin, T., Burge, C.A., Bushek, D., Groner, M.L., Proestou, D.A., Huey, L.I., Bidegain, G., Carnagie, R.B., 2018. Ntensive oyster aquaculture can reduce disease impacts on sympatric wild oysters. Aquacult. Environ. Interac. 10, 557–567. https://doi.org/10. 3354/aei00290.
- Boyer, E.W., Howarth, R.W., 2008. Nitrogen fluxes from rivers to the coastal oceans. In: Capone, D., Bronk, D.A., Mulholland, M.R., Carpenter, E.J. (Eds.), Nitrogen in the Marine Environment, 2nd ed. Elsevier, Amsterdam, the Netherlands.
- Breitburg, D., Levin, L.A., Oschiles, A., Grégoire, M., Chavez, F.P., Conley, D.J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K., Jacinto, G.S., Limburg, K.E., Montes, I., Naqvi, S.W.A., Pitcher, G.C., Rabalais, N.N., Roman, M.R., Rose, K.A., Seibel, B.A., Telszwski, M., Yasuhara, M., Zhang, J., 2018. Declining oxygen in the global ocean and coastal waters. Science 359https://doi.org/10.1126/science.aam7240. eaam7240.
- Bricker, S.B., Rice, K.C., Bricker, O.P., 2014. From headwaters to coast: influence of human activities on water quality of the Potomac River estuary. Aquat. Geochem. 20, 29–323. https://doi.org/10.1007/s10498-014-9226-y.
  Bucefalos, 2015b. Skörd av musslor från fasta föremål Öresundsbron (2015). Report
- Bucefalos, 2015b. Skörd av musslor från fasta föremål Oresundsbron (2015). Report from the Bucefalos project. BUCEFALOS/LIFE11/ENV/SE/839.
- Bucefalos, 2015a. Design of Full Scale Blue Mussel Cultivation Site in Öresund (2015). Report from the Bucefalos Project. BUCEFALOS/LIFE11/ENV/SE/839.
- Bugden, G., Jiang, Y., van den Heuvel, M.R., Vandermeulen, H., MacQuarrie, K.T.B., Crane, C.J., Raymond, B.G., 2014. Nitrogen loading criteria for estuaries in prince edward island. Can. Tech. Rep. Fish. Aquat. Sci 3066.
- Burkholder, J.M., Shumway, S.E., 2011. Bivalve shellfish aquaculture and eutrophication. In: Shumway, S.E. (Ed.), Shellfish Aquaculture and the Environment. John Wiley & Sons, West Sussex, UK.
- Burkholder, J.M., Tomasko, D.A., Touchette, B.W., 2007. Seagrasses and eutrophication. J. Exp. Mar. Biol. Ecol. 350, 46–72. https://doi.org/10.1016/j.jembe.2007.06.024.
- Carmichael, R.H., Walton, W., Clark, H., 2012. Bivalve-enhanced nitrogen removal from coastal estuaries. Can. J. Fish. Aquat. Sci. 69, 1131–1149. https://doi.org/10.1139/ F2012-057.
- Clements, J.C., Hicks, C., Tremblay, R., Comeau, L.A., 2018. Elevated seawater temperature, not pCO<sub>2</sub>, negatively affects post-spawning adult mussels (*Mytilus edulis*) under food limitation. Cons. Phys. 6https://doi.org/10.1093/conphys/cox078. cox078.
- Coffin, M.R.S., Courtenay, S.C., Knysh, K.M., Pater, C.C., van den Heuvel, M.R., 2018a. Impacts of hypoxia on estuarine macroinvertebrate assemblages across a regional nutrient gradient. FACETS 3, 23–44. https://doi.org/10.1139/facets-2017-0044.

- Coffin, M.R.S., Courtenay, S.C., Pater, C.C., van den Heuvel, M.R., 2018b. An empirical model using dissolved oxygen as an indicator for eutrophication at a regional scale. Mar. Poll. Bull. 133, 261–270. https://doi.org/10.1016/j.marpolbul.2018.05.041.
- Comeau, L.A., 2013. Suspended versus bottom oyster culture in eastern Canada: comparing stocking densities and clearance rates. Aquaculture 410-411, 57–65. https:// doi.org/10.1016/j.aquaculture.2013.06.017.
- Cranford, P.J., Strain, P.M., Dowd, M., Hargrave, B.T., Grant, J., Archambault, M.C., 2007. Influence of mussel aquaculture on nitrogen dynamics in a nutrient enriched coastal embayment. Mar. Ecol. Prog. Ser. 347, 61–78. https://doi.org/10.3354/ meps06997.
- Cullain, N., 2016. Macroinfaunal Communities in Seagrass Beds in Atlantic Canada: Regional Variation and the Effects of Eutrophication and Finfish Aquaculture. MSc thesis. Halifax, Dalhousie University.
- Dalrymple, D.J., 2013. Effects of Ontogeny on Nitrogen Sequestration and Removal Capacity of Oysters. M.S. thesis. University of South Alabama, Mobile, AL.
- Diaz, R.J., Rosenberg, R., 2008. Spreading dead zones and consequences for marine ecosystems. Science 321, 926–929. https://doi.org/10.1126/science.1156401.
- Doiron, S., 1992. Évaluation des huîtres de semence d'une batture privée de l'AnseSpence. Ministère des pêches et de l'aquaculture, services techniques, Shippagan, Nouveau-Brunswick 19 pp.
- Ek Henning, H., Åslund, M., 2012. Pilotmusselodlingar i Östergötlands Skärgård -Kunskapsunderlag för Storskaliga Musselodlingar Länsstyrelsen Östergötland, rapport 2012. 8.
- Ferreira, J.G., Bricker, S.B., 2015. Goods and services of extensive aquaculture: shellfish culture and nutrient trading. Aquac. Int. 24, 803–825. https://doi.org/10.1007/ s10499-015-9949-9.
- Filgueira, R., Guyondet, T., Bacher, C., Comeau, L.A., 2015. Informing Marine Spatial Planning (MSP) with numerical modelling: a case-study on shellfish aquaculture in Malpeque Bay (Eastern Canada). Mar. Poll. Bull. 100, 200–216. https://doi.org/10. 1016/j.marpolbul.2015.08.048.
- Fire, S.E., Flewelling, L.J., Stolen, M., Durden, W.N., de Wit, M., Spellman, A.C., Wang, Z., 2015. Brevetoxin-associated mass mortality event of bottlenose dolphins and manatees along the east coast of Florida. USA. Mar. Ecol. Prog. Ser. 526, 241–251. https:// doi.org/10.3354/meps11225.
- Gentry, R.R., Lester, S.E., Kappel, K.V., White, C., Bell, T.W., Stevens, J., Gaines, S.D., 2017. Offshore aquaculture: spatial planning principles for sustainable development. Ecol. Evol. 7, 733–743. https://doi.org/10.1002/ece3.2637.
- Gilbert, P.M., Heil, C.A., Wilkerson, F.P., Dugdale, R.C., 2018. Nutrients and harmful algal blooms: dynamic kinetics and flexible nutrition. In: Glibert, P., Berdalet, E., Burford, M., Pitcher, G., Zhou, M. (Eds.), Global Ecology and Oceanography of Harmful Algal Blooms. Ecological Studies (Analysis and Synthesis). Springer Nature., Cham, Switzerland.
- Gobler, C.J., Burkholder, J.M., Davis, T.W., Harke, M.J., Johengen, T., Stow, C.A., Van de Waal, D.B., 2016. The dual role of nitrogen supply in controlling the growth and toxicity of cyanobacterial blooms. Harmful Algae 54, 87–97. https://doi.org/10. 1016/j.hal.2016.01.010.
- Grizzle, R.E., Ward, K.M., Peter, C.R., Cantwell, M., Katz, D., Sullivan, J., 2017. Growth, morphometrics and nutrient content of farmed eastern oysters, *Crassostrea virginica*, in New Hampshire, USA. Aquat. Res. 48, 1525–1537. https://doi.org/10.1111/are. 12988.
- The Guardian, 2014. Oysters Versus Mussels. Accessed online from, on August 24, 2018. http://www.theguardian.pe.ca/opinion/editorials/oysters-versus-mussels-110996/.
- Guyondet, T., Sonier, R., Comeau, L.A., 2013. Spatially explicit seston depletion index to optimize shellfish culture. Aquacult. Environ. Interact. 4, 175–186. https://doi.org/ 10.3354/aei00083.
- Guyondet, T., Comeau, L.A., Bacher, C., Grant, J., Rosland, R., Sonier, R., Filgueira, R., 2015. Climate change influences carrying capacity in a coastal embayment dedicated to shellfish aquaculture. Estuar. Coast. 38, 1593–1618. https://doi.org/10.1007/ s12237-014-9899-x.
- Haamer, J., 1996. Improving water quality in a eutrophied fjord system with mussel farming. Ambio 25, 356–362.
- Hedberg, N., Kautsky, N., Kumblad, L., Wikström, S.A., 2018. Nutrient Removal Capacity and Potential Ecological Consequences of Blue Mussel Farms for Nutrient Abatement in the Baltic Sea. Baltic Eye Report. Accessed online from, on August 24, 2018. https://balticeye.org/globalassets/fokusomraden/overgodning/musselfarming/ nutrient-removal-capacity-and-potential-ecological-consequences-of-blue-musselfarms-for-nutrient-abatement-in-the-baltic-sea.pdf.
- Hemminga, M.A., Duarte, C.M., 2000. Seagrass Ecology. Cambridge University Press, Cambridge, UK.
- Higgins, C.B., Stephenson, K., Brown, B.L., 2011. Nutrient bioassimilation capacity of aquacultured oysters, quantification of an ecosystem service. J. Environ. Qual. 40, 271–277.
- Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biom. J. 50, 346–363. https://doi.org/10.1002/bimj.200810425.
- Howarth, R.W., Jensen, H., Marino, R., Postma, H., 1995. Transport to and processing of phosphorus in near-shore and oceanic waters. In: Tiessen, H. (Ed.), Phosphorus in the Global Environment: Transfers, Cycles, and Management. John Wiley and Sons, Chichester, UK.
- Howarth, R., Chan, F., Conley, D.J., Garnier, J., Doney, S.C., Mariano, R., Billen, G., 2011. Coupled biogeochemical cycles: eutrophication and hypoxia in temperate estuaries and coastal marine ecosystems. Front. Ecol. Environ. 9, 18–26. https://doi.org/10. 1890/100008.
- Humphries, A.T., Ayvazian, S.G., Carey, J.C., Hancock, B.T., Grabbert, S., Cobb, D., Strobel, C.J., Fulweiler, R.W., 2016. Directly measured denitrification reveals oyster aquaculture and restored oyster reefs remove nitrogen at comparable high rates. Front. Mar. Sci. 3, 74. https://doi.org/10.3389/fmars.2016.00074.

- Kellogg, M.L., Smyth, A.R., Lukenbach, M.W., Carmichael, R.H., Brown, B.L., Cornwell, J.C., Piehler, M.F., Owens, M.S., Dalrymply, D.J., Higgins, C.B., 2013. Use of oysters to mitigate eutrophication in coastal waters. Estuar. Coast. Shelf Sci. 151, 156–168. https://doi.org/10.1016/j.ecss.2014.09.025.
- Larkum, A.W.D., Orth, R.J., Duarte, C.M., 2006. Seagrasses: Biology, Ecology, and Conservation, 1<sup>st</sup> ed. Springer, Dordrecht, the Netherlands.
- Luo, Z., Hu, S., Chen, D., 2018. The trends of aquacultural nitrogen budget and its environmental implications in China. Sci. Rep. 8https://doi.org/10.1038/s41598-018 29214-y. 10877.
- Lutz, R., 1980. Mussel Culture and Harvest: A North American Perspective. Elsevier, New York, USA.
- McIver, R., Milewski, I., Lotze, H.K., 2015. Land use and nitrogen loading in seven estuaries along the southern Gulf of St. Lawrence, Canada. Estuar. Coast. Shelf Sci. 165 (137), 148. https://doi.org/10.1016/j.ecss.2015.08.011.
- Meeuwig, J.J., Rasmussen, J.B., Peters, R.H., 1998. Turbid waters and clarifying mussels: their moderation of empirical chl:nutrient relations in estuaries in Prince Edward Island, Canada. Mar. Ecol. Prog. Ser. 171, 139–150. https://doi.org/10.3354/ meps171139.
- Newell, R.I.E., 2004. Ecosystem influences of natural and cultivated populations of suspension- feeding bivalve molluscs: a review. J. Shellfish Res. 23, 51–61.
- Nixon, S.W., 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. Ophelia 41, 199–219. https://doi.org/10.1080/00785236.1995.10422044.
- Petersen, J.K., Timmermann, K., Carlsson, M., Holmer, M., Maar, M., Lindahl, O., 2012. Mussel farming can be used as a mitigation tool - a reply. Mar. Poll. Bull. 64, 452–454. https://doi.org/10.1016/j.marpolbul.2011.11.027.
- Petersen, J.K., Hasler, B., Timmermann, K., Nielsen, P., Tørring, D.B., Larsen, M.M., Holmer, M., 2014. Mussels as a tool for mitigation of nutrients in the marine environment. Mar. Poll. Bull. 82, 137–143. https://doi.org/10.1016/j.marpolbul.2014. 03.006.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2018. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3. 1-131.1. https://CRAN.Rproject.org/package=nlme.
- R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rabalais, N.N., 2002. Nitrogen in aquatic ecosystems. Ambio 31, 102–112. https://doi. org/10.1579/0044. 7447-7431. 2.102.
- Reitsma, J., Murphy, D.C., Archer, A.F., York, R.H., 2017. Nitrogen extraction potential of wild and cultured bivalves harvested from nearshore waters of Cape Cod, USA. Mar. Pollut. Bull. 116, 175–181. https://doi.org/10.1016/j.marpolbul.2016.12.072.
- Rice, M.A., 2001. Environmental impacts of shellfish aquaculture: filter feeding to control eutrophication. In: Tlusty, M., Bengtson, D., Hlavorson, H.O., Oktay, S., Pearce, J., Rheault, R.B. (Eds.), Marine Aquaculture and the Environment: A Meeting for Stakeholders in the Northeast. Cape Cod Printing., Maine, USA.
- Rodhouse, P.G., Roden, C.M., Hensey, M.P., Ryan, T.H., 1984. Resource allocation in *Mytilus edulis* on the shore and in suspended culture. Mar. Biol. 84, 27–34. https:// doi.org/10.1007/BF00394523.
- Rose, J.M., Ferreira, J.G., Stephenson, K., Bricker, S.B., Tedesco, M., Wikfors, G.H., 2012.

Comment on Stadmark and Conley (2011) "Mussel farming as a nutrient reduction measure in the Baltic Sea: consideration of nutrient biogeochemical cycles. Mar. Poll. Bull. 64, 449–451. https://doi.org/10.1016/j.marpolbul.2011.11.024.

- Rose, J.M., Bricker, S.B., Tedesco, M.A., Wikfors, G.H., 2014. A role for shellfish aquaculture in coastal nitrogen management. Environ. Sci. Technol. 48, 2519–2525. https://doi.org/10.1021/es4041336.
- Rose, J.M., Bricker, S.B., Ferreira, J.G., 2015. Comparative analysis of modeled nitrogen removal by shellfish farms. Mar. Poll. Bull. 91, 185–190. https://doi.org/10.1016/j. marpolbul.2014.12.006.
- Schmidt, A.L., Wysmyk, J.K.C., Craig, S.E., Lotze, H.K., 2012. Regional-scale effects of eutrophication on ecosystem structure and services of seagrass beds. Limnol. Oceanogr. 57, 1389–1402. https://doi.org/10.4319/lo.2012.57.5.1389.
- Scholin, C.A., Gulland, F., Doucette, G.J., Benson, S., Busman, M., Chavez, F.P., Cordaro, J., DeLong, R., De Vogelaere, A., Harvey, J., Haulena, M., Lefebvre, K., Lipscomb, T., Loscutoff, S., Lowenstein, L.J., Marin III., R., Miller, P.E., McLellan, W.A., Moeller, P.D.R., Powell, C.L., Rowles, T., Silvagni, P., Silvery, M., Spraker, T., Trainer, V., Van Dolah, F.M., 2000. Mortality of sea lions along the central California coast linked to a toxic diatom bloom. Nature 403, 80–84. https://doi.org/10.1038/47481.
- Sebastiano, D., Levinton, J.S., Doall, M., Kamath, S., 2015. Using a shellfish harvest strategy to extract high nitrogen inputs in urban and suburban coastal bays: practical and economic implications. J. Shellfish Res. 34, 573–583. https://doi.org/10.2983/ 035.034.0242.
- Shumway, S.E., Allen, S.M., Boersma, P.D., 2003. Marine birds and harmful algal blooms: sporadic victims or under-reported events? Harmful Algae 2, 1–17. https://doi.org/ 10.1016/S1568 9883(03)00002-7.
- Sisson, M., Kellogg, M., Luckenbach, M., Lipcius, R., Colden, A., Cornwell, J., Owens, M., 2011. Assessment of Oyster Reefs in Lynnhaven River as a Chesapeake Bay TMDL Best Management Practice. Final Report to the U.S. Army Corps of Engineers, Norfolk District and the City of Virginia beach. Virginia institute of Marine Science (Special Report No. 429 in Applied Marine Science and Ocean Engineering).
- Smaal, A.C., Vonck, A.P.M.A., 1997. Seasonal variation in C, N and P budgets and tissue composition of the mussel *Mytilus edulis*. Mar. Ecol. Prog. Ser. 153, 167–179. https:// doi.org/10.3354/meps153167.
- Stadmark, J., Conley, D., 2011. Mussel farming as a nutrient reduction measure in the Baltic Sea: consideration of nutrient biogeochemical cycles. Mar. Pollut. Bull. 62https://doi.org/10.1016/j.marpolbul.2011.05.001, 13851388.
- Stephenson, K., Aultman, S., Metcalfe, T., Miller, A., 2010. An evaluation of nutrient nonpoint offset trading in Virginia: a role for agricultural nonpoint sources? Water Resour. Res. 46https://doi.org/10.1029/2009WR008228. W04519.
- Testa, J.M., Brady, D.C., Cornwell, J.C., Owens, M.S., Sanford, L.P., Newell, C.R., Suttles, S.E., Newell, R.I.E., 2015. Modeling the impact of floating oyster (*Crassostrea virginica*) aquaculture on sediment-water nutrient and oxygen fluxes. Aquacult. Environ. Interact. 7, 205–222. https://doi.org/10.3354/aei00151.
  Van der Schatte Olivier, A., Jones, L., Le Vay, L., Christie, M., Wilson, J., Malham, S.K.,
- Van der Schatte Olivier, A., Jones, L., Le Vay, L., Christie, M., Wilson, J., Malham, S.K., 2018. A global review of the ecosystem services provided by bivalve aquaculture. Rev. Aquacult. https://doi.org/10.1111/raq.12301.