Suspended versus bottom oyster culture in eastern Canada: Comparing stocking densities and clearance rates

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The objectives of this study were to compare the stocking density of suspended versus bottom oyster (Crassostrea virginica) culture in Atlantic Canada and to estimate the capacity of these oysters to clear particles from the water column. Surveys of multiple leases indicated that stocking densities for floating bag and floating cage culture techniques were on average 0.3 ± 0.1 and 0.5 ± 0.1 kg oysters m⁻², respectively. Bottom culture density was estimated at 1.0 ± 0.1 kg oysters m⁻², whereas natural reef density was assessed at 2.2 ± 1.1 kg oysters m⁻². In terms of grazing potential, suspended oysters had significantly lower gill areas per unit dry tissue weight than bottom oysters. This result was consistent with power functions relating clearance rate (CR, l h⁻¹) to dry tissue weight (DTW, g). CR increases relative to DTW were significantly lower in the suspended oyster category than in the bottom oyster category, as indicated by the exponent in the relationships CR = 6.35 ± 0.59 × DTW⁰.⁷⁸ ± ⁰.⁰⁸ (bottom) and CR = 4.34 ± 0.32 × DTW⁰.⁴¹ ± ⁰.⁰⁸ (suspended). Based on this information it was calculated that CR per unit area (CRArea) in the most heavily exploited leases was 66.5 ± 8.6 (floating bags), 86.5 ± 8.6 (floating cages), and 197.3 ± 144.4 (bottom culture) l h⁻¹ m⁻². The CRArea for suspended techniques was on average 10 to 14 times lower than the CRArea for healthy oyster reefs. A bay-scale assessment of an intensive culture site led to the conclusion that cultivated oysters do not exert a dominant top-down control on phytoplankton abundance.

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1. Introduction

The Eastern oyster, Crassostrea virginica (Gmelin 1791), has a remarkable latitudinal distribution range along the Northwest Atlantic seaboard. Native populations are found in the Gulf of Mexico (27°N) and northward into the Gulf of St. Lawrence (48°N), Canada (Carriker and Gaffney, 1996). In the two Canadian provinces of Prince Edward Island (PEI) and New Brunswick (NB), oyster farming was first started in 1865, when seed collected from natural reefs were transplanted to leased bottom areas for the purpose of rearing oysters to commercial size (Lavio, 1995; Mathieson, 1912). However, since the early 1990s, the traditional approach of relaying seed to bottom culture areas is being progressively replaced by suspended culture. Novel suspension techniques are being developed using various types of holding compartments. The most popular types are UV-resistant polymer mesh bags often referred to as Vexar™ bags. These bags can be equipped with individual floats (Fig. 1), or inserted into wire-mesh cage structures equipped with large floatation compartments. The most popular types are UV-resistant polymer mesh bags often referred to as Vexar™ bags. These bags can be equipped with individual floats (Fig. 1), or inserted into wire-mesh cage structures equipped with large floatation compartments (Fig. 2). Floating bags and cages are attached to longlines deployed in the subtidal zone where they can be flipped (180°) and temporarily exposed to the air to desiccate fouling organisms (Mallet et al., 2009). Prior to the onset of winter and the formation of a thick (~1 m) ice cover, entire longlines of bags or cages are lowered onto the bottom either by removing the floats, or flooding the flotation compartments.

From a farming perspective, there are several advantages to suspending oyster stocks in the upper water column. This strategy protects stocks from benthic predators and facilitates product grading and harvesting procedures. Also, the relatively warm and elevated food flux environment in the upper water column (Comeau et al., 2010) enhances growth (Bataller et al., 1999) and shortens the production cycle (Doiron, 2008). Oysters grown in suspension generally reach market-size within 3 to 4 years, which is much faster than the 5 to 8 years normally required when grown on the substrate. Finally, oysters grown in suspension are morphologically similar to those growing at low densities on firm bottoms. They have a tendency to develop round shells ornamented with radial ridges and foliated processes (Galtsoff, 1964). By contrast, oysters grown on soft, muddy bottoms tend to develop elongated and sparsely ornamented shells (Fig. 3).

The first objective of this study was to gain a better empirical understanding of the stocking density of suspended oyster culture in Atlantic Canada. Presently, information is lacking as to whether suspended leases are exploited to their full capacity. Based on their dimensions and mooring requirements, the floating bag technique allows a maximum deployment of 2000 bags ha⁻¹ (Doiron, 2008). Similarly, floating cage mooring guidelines dictate a maximum stocking density of approximately 1500 bags ha⁻¹. However, it remains unclear how

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these suspended culture densities compare with those found in bottom culture beds and natural reefs. Perhaps an impeding difficulty is that information on bottom oysters in eastern Canada is restricted to a grey literature that for the most part is difficult to trace.

The second objective of this study was to gauge the ability of cultivated oysters to clear particles from the water column. It could be postulated that suspended oysters have high clearance rates given that they grow relatively fast. Over the past century, pumping rates and clearance rates have been sporadically reported for wild *C. virginica* collected in the intertidal or subtidal zone (Galtsoff, 1926; Loosanoff, 1958; Palmer, 1980; Riisgard, 1988), with 10 l h$^{-1}$ g$^{-1}$ dry tissue weight documented as a maximum clearance rate (Eastern Oyster Biological Review Team, 2007). To my knowledge, the clearance rates of suspension-grown *C. virginica* were investigated in a single laboratory study which reported a maximum rate of 4 l h$^{-1}$ g$^{-1}$ dry tissue weight (Pernet et al., 2007).

2. Methods

2.1. Suspended oyster survey

A total of 133 suspended leases were surveyed across 20 embayments in NB and PEI in 2011–2012 (Fig. 4). All leases were surveyed by boat in early autumn, prior to the lowering of the gear onto the bottom to avoid winter ice. Floating bags, including those contained in floating cages, were counted in each lease. Bag content in terms of number and size of oysters was estimated based on standard husbandry practices (Doiron, 2008). Suspended leases typically hold four year classes distributed according to the proportions given in Table 1. Using this information it was calculated that a normalized bag contains 332 oysters, which weigh a total of 6.1 kg (see Table 1 caption for details). Lease-scale oyster density (OD) was calculated as follows:

$$OD = \frac{N_{bag} \times 6.1}{\text{Area}}$$

where OD represents oyster biomass (kg) m$^{-2}$, $N_{bag}$ is the number of bags counted within the lease, Area is the lease area (m$^2$), and 6.1 is the normalized oyster weight (kg) in each bag.

2.2. Bottom oyster survey

A total of 10 grey literature reports provided a detailed description of natural oyster reefs and leased bottom areas in eastern NB (Table 2). These surveys were conducted between 1974 and 2001, and the number of sites investigated ranged from 1 to 11. In all cases, live oysters within 0.12 to 1-m$^2$ quadrats were removed by hand, counted, and weighed (whole weight).
information was lacking in the report, it was calculated using the following allometry relationship (Landry et al., 2001):

\[
\text{whole weight in g} = 2.90 \log_{10}(\text{shell height in mm}) - 3.84 \quad (r^2 = 0.97, n = 152)
\]

Since no report was available for PEI, 26 quadrats were sampled across four bottom leases in Foxley River in July 2012. At each station, a 0.5-m² quadrat was thrown over the side of the boat and a SCUBA diver then collected all the live oysters within the quadrat. Oysters were counted and measured for whole weight, shell height, and dry tissue weight. Mean density in terms of oyster whole weight (kg m⁻²) was calculated for each bottom lease.

2.3. Clearance rates

Clearance rate (CR) is defined as the volume of water cleared of suspended particles per unit time. In this study, maximum CR was measured as part of a controlled comparison of bottom and suspended oysters fed a natural diet. On 28 September 2012, oysters of varying sizes were collected in Foxley River PEI and brought to a field laboratory in Georgetown PEI where they were held in a large tank (250 L) continuously supplied with natural seawater (temperature ~16 °C). After a one-week acclimation period, 10 oysters (5 bottom and 5 suspended) were transferred to individual acrylic chambers supplied with the same seawater as the holding tank. The chamber volume selected (190, 670 or 1100 ml) was dependent on the size of the oyster. Two additional chambers containing shells only served as controls to measure gravitational settling of particles. Particle mixing was promoted by fine bubble aeration, introduced in a manner that minimized the resuspension of feces. Each chamber was equipped with a fluorometer (CYCLOPS-7® submersible sensor, Turner Designs, Sunnyvale, CA) connected to a data acquisition controller with software (Microlink 751, Windmill Software Ltd, Manchester, UK) that provided a quasi-real time (5 s delay) graphical display of fluorescence. Following a 1-hour adaptation period, water flow was halted and the decline in fluorescence over time was monitored on the computer screen. Any oysters that expelled chlorophyll material into their chamber, creating major spikes in the fluorescence readings, were excluded from the experiment. Only chambers that showed a continuous exponential decrease in fluorescence over time were included in the final analysis. This standardization approach minimized the potential underestimation of CR. Particle depletion rates within the chambers were measured by counting suspended particles at the start of the static incubation and approximately 10 min later. Water samples (10 mL) were extracted from the chambers and aliquots (100 μL) were processed using a Beckman Coulter Counter Z1™ fitted with a 100-μm aperture tube. The instrument was set to measure particles in the size range of 5–19 μm, which

<table>
<thead>
<tr>
<th>Year class</th>
<th>Shell height (mm)</th>
<th>Weight (g)</th>
<th>DTW (g)</th>
<th>Number per bag</th>
<th>Percent bags in lease</th>
</tr>
</thead>
<tbody>
<tr>
<td>Y1</td>
<td>&lt;31</td>
<td>1.77</td>
<td>0.04</td>
<td>1000</td>
<td>8</td>
</tr>
<tr>
<td>Y2</td>
<td>31–50</td>
<td>8.80</td>
<td>0.14</td>
<td>500</td>
<td>17</td>
</tr>
<tr>
<td>Y3</td>
<td>51–65</td>
<td>22.80</td>
<td>0.36</td>
<td>250</td>
<td>33</td>
</tr>
<tr>
<td>Y4</td>
<td>&gt;65</td>
<td>33.10</td>
<td>1.57</td>
<td>200</td>
<td>42</td>
</tr>
</tbody>
</table>

\[ a (1000 \times 0.08) + (500 \times 0.17) + (250 \times 0.33) + (200 \times 0.42). \]
\[ b ((1000 \times 0.08 \times 1.77) + (500 \times 0.17 \times 8.8) + (250 \times 0.33 \times 22.8) + (200 \times 0.42 \times 39.1))/1000. \]
are known to be completely retained by oysters (Risgard, 1988; Ward and Shumway, 2004). CR was calculated according to the formula:

\[ CR = \frac{V}{t} \times \frac{\ln C_0}{C_t} \]

where \( V \) is the volume of the chamber, \( t \) is time elapsed between measurements, and \( C_0 \) and \( C_t \) are particle concentrations at times 0 and \( t \), respectively (Risgard, 1988, 2001). At the end of the incubation period, oysters were removed from the chambers and replaced with new specimens taken from the holding tank. These trials were repeated until CR was successfully measured on 39 bottom oysters and 29 suspended oysters. Shell height, whole weight, and dry tissue weight (DTW) were determined for each individual.

Given that shell height and whole weight were poor predictors of CR, power equations describing CR as a function of DTW were established for bottom and suspended oysters. These equations were used to calculate a CR per unit surface area (\( CR_{\text{Area}} \)) for each of the culture categories under investigation. For suspended culture, CR was first scaled up to a normalized bag based on the number of oysters, the year-class proportions and the DTW values provided in Table 1. \( CR_{\text{Area}} \) was then calculated as follows:

\[ CR_{\text{Area}} = \frac{CR_{\text{Bag}} \times N_{\text{Bag}}}{\text{Area}} \times 0.686 \]

where \( CR_{\text{Area}} \) represents CR per unit leased area (1 h\(^{-1}\) m\(^{-2}\)), \( CR_{\text{Bag}} \) is the normalized bag CR (1 h\(^{-1}\)), \( N_{\text{Bag}} \) is the number of bags counted within the lease, Area is the lease area (m\(^2\)), and 0.686 represents the proportion of time (68.6%) oysters have their valves open when feeding on natural seston (Comeau et al., 2012). Similar calculations were made for assessing CR in bottom culture, and floating bag culture. In the model, \( C \) was declared a main effect (suspended, floating cage culture). In the model, \( C \) included four categories: natural reefs, bottom culture, floating bag culture, and floating cage culture. In the model, \( C \) was declared a main effect (suspended, bottom) was set as a fixed factor and the independent variable was identified as a covariate. Where the homogeneity of regressions was not rejected, an ANCOVA was performed to test whether oyster origin had a significant effect on the dependent variable.

A mixed model analysis of variance (procedure GLM in SPSS) was developed to test the effect of oyster category (\( C \)) on oyster stocking densities (OD). \( C \) included four categories: natural reefs, bottom culture, floating bag culture, and floating cage culture. In the model, \( C \) was declared a main effect (\( C \lceil i = 1 \to 4 \rceil \)) and the data source (\( S \)) was set as a random effect (\( S \lceil j = 1 \to 10 \rceil \)). OD was rank-transformed to stabilize the variance (Levene’s test, \( P > 0.05 \)).

\[ OD_{ij} = \mu + C_i + S_j(C_i) + e_{ij} \]

A second mixed model was developed to test the effect of C on the \( CR_{\text{Area}} \). This analysis was restricted to leases that had the most oysters per unit area, and therefore that were exploited at, or near their full capacity. The same logic was applied to natural reefs by selecting the most densely populated examples. In keeping with this rationale, stocking density values above the 75th percentile for each category

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**Table 2**

Summary of the dataset that was built for the meta-analysis. n refers to the number of oyster leases or oyster reefs sampled.

<table>
<thead>
<tr>
<th>Lease type</th>
<th>Survey source</th>
<th>Survey year</th>
<th>n</th>
<th>Survey sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Suspended</td>
<td>This study</td>
<td>2011</td>
<td>111</td>
<td>19 bays, NB</td>
</tr>
<tr>
<td></td>
<td>Ferguson (1985)</td>
<td>1984</td>
<td>5</td>
<td>Caraquet, NB</td>
</tr>
<tr>
<td></td>
<td>McIver and Woo (1975)</td>
<td>1972</td>
<td>6</td>
<td>Bouctouche, NB</td>
</tr>
<tr>
<td></td>
<td>Doiron (1992)</td>
<td>1990</td>
<td>1</td>
<td>Spence Cove, NB</td>
</tr>
<tr>
<td></td>
<td>This study</td>
<td>2012</td>
<td>4</td>
<td>Foxley River, PEI</td>
</tr>
<tr>
<td></td>
<td>SENPaq (1990)</td>
<td>1990</td>
<td>2</td>
<td>Miramichi, NB</td>
</tr>
<tr>
<td></td>
<td>Landry et al. (2001)</td>
<td>1999</td>
<td>1</td>
<td>Caraquet, NB</td>
</tr>
<tr>
<td></td>
<td>Septon and Bryan (1988)</td>
<td>1987</td>
<td>1</td>
<td>Caraquet, NB</td>
</tr>
<tr>
<td></td>
<td>Lavoie and Robert (1981)</td>
<td>1979</td>
<td>1</td>
<td>Caraquet, NB</td>
</tr>
<tr>
<td></td>
<td>Lavoie (1977)</td>
<td>1974</td>
<td>1</td>
<td>Caraquet, NB</td>
</tr>
</tbody>
</table>

**2.4. Gill area**

In September 2012, bottom and suspended oysters were collected in Foxley River to investigate whether morphological differences existed between the two categories, specifically in regards to the size of their gills. Gills were excised from 24 bottom and 27 suspended oysters. Gill area (\( Gill_{A} \)) was assessed by digital image analysis following Honkoop et al. (2003). Once this analysis was completed, gills and other soft tissues were pooled to determine individual DTW. Shell height was also measured.

**2.5. Statistics**

All statistical analyses were conducted using SPSS v. 20 software (IBM SPSS, Armonk, NY, USA). Regression analysis was used to explore relationships between lease area (ha) and farming activity within leases, namely oyster biomass (tons) and oyster stocking density (kg m\(^{-2}\)). Serial independence of the error terms was graphically assessed and further tested using the Durbin-Watson test; residuals were screened for normality using expected normal probability plots and the Kolmogorov-Smirnov test. Residuals were both graphically and quantitatively (Levene test) assessed for homogeneity of variances. Data were sqrt-transformed or log-transformed where heteroscedasticity was detected. When data transformations failed to stabilize the variance, weighted-least square regression analysis was applied, in which case, weights were estimated by examining the relationship of the variance of the dependent variable to various powers of values of the independent variable.

Homogeneity of regression slopes was tested on log-transformed data using the SPSS GLM procedure. The oyster category (suspended, bottom) was set as a fixed factor and the independent variable was identified as a covariate. Where the homogeneity of regressions was not rejected, an ANCOVA was performed to test whether oyster origin had a significant effect on the dependent variable.

A mixed model analysis of variance (procedure GLM in SPSS) was developed to test the effect of oyster category (\( C \)) on oyster stocking densities (OD). \( C \) included four categories: natural reefs, bottom culture, floating bag culture, and floating cage culture. In the model, \( C \) was declared a main effect (\( C \lceil i = 1 \to 4 \rceil \)) and the data source (\( S \)) was set as a random effect (\( S \lceil j = 1 \to 10 \rceil \)). OD was rank-transformed to stabilize the variance (Levene’s test, \( P > 0.05 \)).

\[ OD_{ij} = \mu + C_i + S_j(C_i) + e_{ij} \]

A second mixed model was developed to test the effect of \( C \) on the \( CR_{\text{Area}} \). This analysis was restricted to leases that had the most oysters per unit area, and therefore that were exploited at, or near their full capacity. The same logic was applied to natural reefs by selecting the most densely populated examples. In keeping with this rationale, stocking density values above the 75th percentile for each category
were selected for analysis. In the model, C was declared a main effect (C \( i = 1 \) to 4) and the data source (S) was set as a random effect (S \( j = 1 \) to 10). \( \text{CRArea} \) was rank-transformed to stabilize the variance (Levene's test, \( P > 0.05 \)).

\[
\text{CRArea}_{ij} = \mu + C_i + S_j(C_i) + \epsilon_{ij}
\]

When the main effect, C, was significant, Tukey's HSD post hoc tests were performed to determine homogeneous groups. In this paper, all measures of variability reported along with the mean values represent 1 standard error of the mean (mean ± 1 SEM).

3. Results

3.1. Oyster densities

Of the 133 suspended leases surveyed, 123 were classified as being active, i.e., containing oysters that were suspended in the water column by some means. While a small proportion of these oysters were suspended using strings, tables, racks or other means, the bulk (95.4%) of the surveyed stock was contained in floating bags or floating cages.

Further analyses were conducted on leases containing exclusively floating bags (n = 48 leases) or floating cages (n = 39 leases). It was first examined whether allocated lease area, a metric which is readily available from licensing departments, is a good indicator of the farming activity level within the lease, either in terms of total biomass or stocking density. No significant correlations were found between lease area and farming activity metrics for leases containing floating bags. However, for leases populated with floating cages, lease area was a weak but significant predictor of total biomass (Fig. 5a, \( r^2 = 0.28, P < 0.01 \), weighted least squares) and stocking density (Fig. 5b, \( r^2 = 0.38, P < 0.01 \), ordinary least squares). In general, smaller leases tended to be more densely stocked than larger leases.

Stocking densities for floating bag and floating cage techniques were respectively 0.3 ± 0.1 and 0.5 ± 0.1 kg oysters m\(^{-2}\) (Fig. 6); the difference in stocking density between gear types was significant. It is also noteworthy that both average densities were below prescribed mooring deployment guidelines for suspended culture. In relative terms, floating bag and floating cage densities were 77.2 ± 3.7% and 47.6 ± 6.1% below the recommended level, respectively.

Based on the NB grey literature and the Foxley River data, bottom culture density was estimated at 1.0 ± 0.1 kg oysters m\(^{-2}\). This estimate is significantly higher than those for suspended techniques. Bottom culture densities were statistically similar to those found in natural reefs, which averaged 2.2 ± 1.1 kg oysters m\(^{-2}\). The elevated variance in the latter category is mainly attributable to two highly aggregated reefs (8.4 and 14.3 kg oysters m\(^{-2}\)).

3.2. Clearance rate (per unit body weight)

Power functions relating CR (l h\(^{-1}\)) to DTW (g) were calculated for bottom (CR = 6.35 ± 0.59 \( \times \) DTW\(^{0.78 ± 0.06}\), \( r = 0.85, P < 0.001 \)) and suspended (CR = 4.34 ± 0.32 \( \times \) DTW\(^{0.41 ± 0.08}\), \( r = 0.71, P < 0.001 \)) oysters (Fig. 7a). The exponent describes how fast CR increases relative to body weight. The hypothesis of equal slopes (exponent) between the two oyster categories was rejected (\( P = 0.002 \)). CR increases relative to body size were significantly lower in the suspended category than in the bottom category, starting at a dry tissue weight of approximately 0.25 g. The equations predict that a 1 g DTW bottom oyster has a CR of 6.3 l h\(^{-1}\) whereas a suspended oyster of comparable DTW has a CR of 4.3 l h\(^{-1}\).

CR results are consistent with gill measurements taken on a sample of large oysters (Fig. 7b). The relationship between gill area (cm\(^2\)) and DTW (g) was best described as Gill\(_{a} = 12.27 \times \text{DTW}^{0.59 ± 0.06}\) (\( r = 0.90, P < 0.001 \)) and Gill\(_{b} = 9.93 \times \text{DTW}^{0.61 ± 0.05}\) (\( r = 0.92,
Pb 0.001) for bottom and suspended oysters, respectively. The hypothesis of equal slopes was not rejected (P = 0.77). However, suspended and bottom oysters had significantly different gill areas per unit body weight (ANCOVA, Pb 0.001). Gill area standardized to an oyster of 1 g DTW was 12.3 cm² for the bottom category and 9.9 cm² for the suspended category.

Suspended oysters were in good physiological condition, i.e., they had elevated DTW values. This observation became evident after plotting DTW against shell height, a size indicator commonly used by field observers. The plot shows large suspended oysters (>60 mm) having higher DTW values than bottom oysters of comparable shell height (Fig. 8). The hypothesis of equal slopes (exponent) between the two oyster categories was rejected (Pb 0.001): DTW increases relative to shell height were significantly higher in the suspended category than in the bottom category.

3.3. Clearance rate (per unit area)

Fig. 9 shows CRₐrea for the most densely populated (>75th percentile) leases and natural reefs contained in the dataset. CRₐrea for the floating-bag leases was 66.5 ± 8.5 l h⁻¹ m⁻², or approximately 42% below the CRₐrea expected for this technique assuming full exploitation (based on mooring guidelines). CRₐrea for floating-cage leases was 86.5 ± 8.6 l h⁻¹ m⁻², consistent with a full exploitation of this technique (84.5 l h⁻¹ m⁻²). The CRₐrea calculated for suspended techniques was on average 10 to 14 times lower than the CRₐrea for natural oyster reefs.

The range of possible CRₐrea values for suspended culture was calculated by assuming all bags contain one of four year classes (Table 3). It was found that CRₐrea ranges from 41.3 ± 5.2 l h⁻¹ m⁻² where all floating bags contain small (< 31 mm) oysters, to 108.5 ± 10.8 l h⁻¹ m⁻² where all floating cages contain large (>65 mm) oysters.

4. Discussion

4.1. Oyster stocking densities

Oyster tables in France’s Normandy area support approximately 6 kg oysters m⁻² (Crassostrea gigas), assuming a restrained deployment of
5000 bags ha\(^{-1}\) × 12 kg oysters bag\(^{-1}\) (Kopp et al., 2001). Here it is reported that densities for floating bag and floating cage culture techniques in eastern Canada were on average ≤ 0.5 kg oysters m\(^{-2}\). Interestingly, the recent transition to suspended culture resulted in an actual reduction in stocking density compared to traditional bottom culture operations. Densities of 0.3 ± 0.1 and 0.5 ± 0.1 kg oysters m\(^{-2}\) were recorded for floating bags and floating cages, compared to 1.0 ± 0.1 kg oysters m\(^{-2}\) for the more traditional bottom culture. Suspended culture densities were generally well below technical guidelines prescribed by gear developers, suggesting that leases were underexploited and that the industry was still undergoing a developmental phase. Only a fully exploited suspended lease, one containing floating gear moored according to guidelines throughout its entire area, would compare with a bottom lease in terms of stocking density.

The reported densities for suspended culture are comparable to natural populations identified as being in a precarious state, which are presently being targeted for repletion and restoration. In Chesapeake Bay, for example, median values for live oyster abundance were 0.3 (Southworth et al., 2010) and 0.7 (Mann et al., 2009) kg m\(^{-2}\) from 1993 to 2009. Maximal abundance was approximately 8 kg m\(^{-2}\) for the 30 reefs surveyed in these two papers and 14.3 kg m\(^{-2}\) for the dozen reefs reported in the present study. Unfortunately, absolute oyster densities prior to the degradation of natural reefs by destructive fishing practices, siltation, diseases and other habitat disturbances are poorly quantified. At the turn of the 20th century, when a number of oyster reefs were already considered depleted over the continental margin of North America (Kirby, 2004; Morse, 1971), Bastien-Daigle et al. (2007) estimated that there would have been a standing stock in the order of 35,912 t in NB. In 2005, the standing stock of cultured oysters in this province was evaluated at 1,249 t (Bastien-Daigle et al., 2007) based on year class proportions indicated in Table 1.

### Table 3

<table>
<thead>
<tr>
<th>Year class</th>
<th>Shell height (mm)</th>
<th>Number oysters per bag</th>
<th>CR(_{bag}) (l h(^{-1}))</th>
<th>Floating bag CR(_{area}) (l h(^{-1}) m(^{-2}))</th>
<th>Floating cage CR(_{area}) (l h(^{-1}) m(^{-2}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Y1</td>
<td>&lt;31</td>
<td>1000</td>
<td>515.6</td>
<td>41.3 ± 5.2</td>
<td>53.7 ± 5.3</td>
</tr>
<tr>
<td>Y2</td>
<td>31–50</td>
<td>500</td>
<td>685.3</td>
<td>54.8 ± 7.0</td>
<td>71.3 ± 7.1</td>
</tr>
<tr>
<td>Y3</td>
<td>51–65</td>
<td>250</td>
<td>714.2</td>
<td>57.2 ± 7.3</td>
<td>74.3 ± 7.4</td>
</tr>
<tr>
<td>Y4</td>
<td>&gt;65</td>
<td>200</td>
<td>1042.9</td>
<td>83.5 ± 10.6</td>
<td>108.5 ± 10.8</td>
</tr>
<tr>
<td>Y1–Y4</td>
<td>various</td>
<td>332</td>
<td>831.4</td>
<td>66.5 ± 8.5</td>
<td>86.5 ± 8.6</td>
</tr>
</tbody>
</table>

CR\(_{Area}\) (mean ± SEM) for the most densely populated (>75th percentile) suspended leases. Results show scenarios where all bags in leases contain a single year class (Y1, Y2, Y3 or Y4), and also the average scenario (Y1–Y4) based on year class proportions indicated in Table 1.

### 4.2. Clearance rate (per unit body weight)

Clearance rate (per unit body weight) for C. virginica were summarized in Grizzle et al. (2008). CR standardized to an oyster of 1 g DTW was reportedly 6.79 L h\(^{-1}\) (Riisgard, 1988), 6.40 L h\(^{-1}\) (Newell and Koch, 2004), and 7.46 to 9.62 l h\(^{-1}\) (FDA, 1968). These values were derived from wild oysters primarily feeding on laboratory diets under optimal conditions (20–29 °C). CR for bottom-cultivated oysters acclimated to 16 °C and grazing on natural seston were consistent with this literature. A 1 g DTW bottom-cultivated oyster had a CR of 6.3 l h\(^{-1}\). The CR equation developed for bottom-cultivated oysters (CR = 6.35 ± 0.59 × DTW\(^{0.78} ± 0.08\)) was very similar to the one reported by Riisgard (1988): CR = 6.79 ± 1.41 × DTW\(^{0.73} ± 0.22\).

For suspended oysters, a low exponent in the equation CR = 4.34 ± 0.32 × DTW\(^{0.41} ± 0.08\) indicated that CR increases relative to body size were lower than in bottom cultured oysters. Filgueira et al. (2008) reported that low exponents in CR power functions are expected when the condition index increases with body size. In keeping with this information, a significant and linear correlation between CI and DTW was found for the suspended category only (r = 0.81, P < 0.001, not shown in results). The low exponent is also consistent with the observation that gill size per unit DTW was relatively low in large suspended oysters. Gills in oysters not only serve in respiration; they contain cilia that create complex water flow patterns to capture food particles and transport them to the mouth (Newell and Langdon, 1996). It seems that suspended oysters direct most of their dietary supplement, derived from the high food flux environment in which they reside (Comeau et al., 2010), towards the buildup of energy stores and somatic growth, without proportional investments in gill development. My results predict that a 1 g DTW suspended oyster has a CR of 4.3 l h\(^{-1}\). This rate is very similar to the 4.0 l h\(^{-1}\) g\(^{-1}\) reported by Pernet et al. (2007). Oysters in their laboratory investigation also originated from suspension culture.

### 4.3. Clearance rate (per unit area)

The dataset was sufficiently detailed to conduct a bay-scale impact assessment in Foxley River, an intensive culture site where leases cover 22% of the bay area (1354 ha). An index of seston depletion (I\(_0\) = CT/RT) was calculated following Dame (1996). I\(_0\) provides an indication of how important seston uptake may be in relation to estuarine volume and tidal flushing. Clearance time (CT), the number of days required for the combined bottom and suspended stocks to filter the total estuarine volume (22.24 × 10\(^6\) m\(^3\)), was estimated at 9.8 days. This estimate takes into account a total standing stock of 1095 t distributed among 32 suspended (100 ha) and 98 bottom (196 ha) leases. The estimate assumes that oysters were feeding 68.6% of the time (Comeau et al., 2012). Residence time (RT) is the number of days required for tidal action to replace the total estuarine volume. The deployment of a tidal gauge in 2012 and calculation of the tidal prism indicated an RT of 2.1 and 4.6 days during spring and neap tides, respectively (Thomas Guarydett, DFO, pers. comm., 2013). In keeping with these values, the I\(_0\) (CT/RT) estimate for Foxley River ranges between 2.13 (neap tide) and 4.65 (spring tide), meaning that the bay-scale food renewal rate by tidal action is on average 3.39 times faster than the filtration rate by cultivated oysters. Converting all bottom leases into suspended leases would increase the I\(_0\) to 4.94, consequently reducing the grazing pressure in the system. All of these I\(_0\) estimates fall in the upper range of I\(_0\) values reported for 11 other aquaculture bays (Dame and Prins, 1997). In intensive culture areas, it was found that grazing pressure has exceeded water renewal rates (I\(_0\) = 1). Such is the case for oyster table culture (I\(_0\) = 0.38) in Marennes-Oléron France (Dame and Prins, 1997), mussel raft culture (I\(_0\) = 0.54) in the Ría de Arosa Spain (Dame and Prins, 1997), and longline mussel culture (I\(_0\) = 0.34) in Tracadie Bay, PEI (Comeau et al., 2008). There is also evidence that bivalves naturally exerted a dominant effect in some coastal systems prior to the development of aquaculture. Historical (c. 1880–1910) baselines for North American oyster reefs suggest I\(_0\) values ≤ 1 for
six of eight estuaries in the Gulf of Mexico (Ermgassen et al., 2013). In Foxley River, raising the suspended lease coverage from 22 to 100% of the bay area would reduce the IO from its present 3.9 value to 1.17. Although these calculations do not take into account natural reefs, which are poorly documented, they suggest that cultivated oysters do not exert a dominant top-down control on phytoplankton abundance in the Foxley River system.

Finally, as the industry embraces suspended culture, coastal residents and recreational boaters tend to oppose the technique on the basis of visual or leisure amenity values. Others oppose suspended culture on the basis of perceived negative environmental impacts. At first glance, multiple floating structures distributed over large estuarine areas seem disruptive to ecological health. Yet, often overlooked are the positive ecological effects of suspended oyster culture. By making available a 3-dimensional substrate, suspended structures provide habitat for native fish and invertebrate species (DeAlteris et al., 2004; Marenghi and Ozbay, 2010; O’Beirn et al., 2004; Tallman and Forrester, 2007). Moreover, floating bags or cages in Atlantic Canada contain native oysters that were historically thriving in pre-colonial times (Kirby, 2004; Kirby and Miller, 2005), but have since been decimated by disease, overfishing, and deteriorating bottom habitats. There is compelling evidence that oysters improve estuarine water quality by filtering suspended particulate matter from the water column (Forrest et al., 2009); they may also improve estuarine water quality by rating bottom habitats. There is compelling evidence that oysters improve estuarine water quality by filtering suspended particulate matter from the water column (Forrest et al., 2009); they may also serve as a top-down control of phytoplankton blooms in eutrophic systems. Such positive services are vital to the ecological integrity of estuaries and provide the impetus for oyster restoration projects worldwide.

5. Conclusion

This investigation provides one of the first numerical assessments of suspended oyster culture in eastern Canada. It was found that the present transition from bottom to suspended culture results in an actual reduction in oyster stocking density. Moreover, it was reported that suspended oysters have a weak grazing potential per unit body weight when compared to bottom oysters. A bay-scale assessment of an intensive culture site led to the conclusion that cultivated oysters do not exert a dominant top-down control on phytoplankton abundance.

Acknowledgments

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