



Revisiting ecological carrying capacity indices for bivalve culture

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ABSTRACT

Ecological carrying capacity (ECC) indices for bivalve culture rely on key ecosystem turnover rates: 1. clearance time (CT), the time needed for the cultured bivalves to filter the entire bay volume; 2. renewal time (RT), the time required to replace the entire bay volume with external water; and 3. production time (PT), the time needed for phytoplankton biomass renewal via local primary production. These turnover rates are conceptually straightforward but lack measurement standardizations in the context of ECC assessments. This study compares simple turnover rate methods with more complex approaches designed to address key assumptions and improve accuracy. Method comparisons were performed across multiple embayments (systems) in Prince Edward Island, Canada. When crop aggregation and system-scale refiltration effects were considered, CT increased by a factor of 14 to 22 depending on the system and species under cultivation. Seasonal temperature considerations further impacted CT by a factor of 38 to 142. Regarding RT, validated hydrodynamic models and tidal prism models produced remarkably different outcomes; the tidal prism approach underestimated RT by 77–94% across the studied systems. Conversely, PT was unaffected by contrasting phytoplankton parameterization; pre-aquaculture (1969–1970) and contemporary (2011–2012) datasets led to similar PT outcomes. However, other metrics revealed a contemporary shift towards low phytoplankton biomass and smaller phytoplankton cells (picophytoplankton); these observations suggest that PT provides insufficient granularity regarding microalgae biomass replacement. Overall, the study rejects a common assumption that the bay-scale turnover rates serving the conventional CT/RT and CT/PT indices can be easily and accurately parameterized; these indices should be used cautiously in assessing the sustainability of farming activities.

1. Introduction

The concept of carrying capacity first emerged in the 1870s (Chapman and Byron, 2018) as a quantity that could be carried or supported by the environment, specifically regarding rangeland productivity and cattle grazing on grasslands (Thomson, 1887). Aquaculture carrying capacity has been studied since the 1960s, often for determining farm-area production limits (Weitzman and Filgueira, 2020). Within this dedicated literature, production carrying capacity is generally recognized as the maximum biomass or marketable cohort at a given location (Filgueira et al., 2015a), and this focus on maximizing production is coherent with the primary goal of growing animals for food. More recently, the rise of sustainable aquaculture has motivated

consideration of an alternative metric; ecological carrying capacity (ECC) is the production capacity that meets acceptable standards regarding impacts on ecological processes, species, populations, and communities in the environment (Byron and Costa-Pierce, 2013; McKindsey, 2012). An “unacceptable” threshold implies that ECC is intricately linked to social carrying capacity; this is the level of aquaculture beyond which environmental and social impacts exceed acceptable levels (Dalton et al., 2017). The ecological sciences attempt to describe such interactions between aquaculture and natural ecosystems to identify the limits of aquaculture that preserve ecosystem function or services (Filgueira et al., 2015a; Kluger et al., 2017). The present study focuses exclusively on the ecological aspects relating to ECC; societal values and acceptability aspects are not considered here.

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Ecological models can contribute to ECC assessment by providing quantitative information on energy fluxes, trophic interactions, and ecosystem services (Filgueira et al., 2015a). Although the modeling of food web dynamics in bivalve aquaculture is still immature, it holds promise for understanding effects on lower/higher trophic levels. Most of this research has focused on the pelagic environment and the coupling of biogeochemical processes (nutrient-phytoplankton-grazers) to hydrodynamic domains at scales ranging from individual farms to entire embayments. These efforts have led to powerful planning tools for predicting the effects of cultured bivalves on phytoplankton (Filgueira et al., 2015b), which are the primary step in marine food webs and critical to ecosystem-based management efforts and ECC assessments (Crowder and Norse, 2008). However, these spatially-explicit models require specialized modeling expertise and huge datasets for model calibration and validation (Kremer et al., 2010).

A simpler ECC assessment method uses key ecosystem turnover rates: the renewal time (RT) is the time required for the bay volume to be replaced with external water; the production time (PT) is the time needed for phytoplankton biomass renewal via local primary production; and clearance time (CT) is the time needed for cultured bivalves to filter the entire bay volume. These turnover rates can be combined to provide a coarse comparison of bivalve filtration capacity with food renewal through water advection (CT/RT) and with food renewal through phytoplankton production (CT/PT). Such indices lack spatial and temporal resolution and reduce the geographic and hydrodynamic complexity of a bay to a homogenous and dimensionless system. Nonetheless, this simplicity has motivated their application at several bivalve aquaculture sites across the world (Dame and Prins, 1998). Worldwide usage levels of ECC indices are unknown, but these metrics are undeniably appealing for coastal planning and eco-certification purposes because they require few turnover rates. Therein lies the importance of producing robust turnover rates.

In this paper, we examine the influence of methodology on key turnover rate calculations in Prince Edward Island (PEI), where eastern oysters (*Crassostrea virginica*) and blue mussels (*Mytilus edulis*) are cultivated in 39 embayment and estuary systems (Fig. 1, Annex I). First, we focus on CT and the possibility that crop aggregation leads to refiltration that may increase CT up to the system scale. Similarly, we assess the effects of seasonal temperature on CT. We then compare RT values generated from a common tidal prism method against those produced by a more realistic spatial hydrodynamic model. Regarding food production, we compare PT results calculated from historical (pre-aquaculture) and contemporary datasets and question whether PT is sensitive to depleted phytoplankton biomass and shifting phytoplankton community structure. Finally, we rank the 39 systems by grazing intensity (CT/PT) and then elaborate on the utility and limitations of such ranking scores. Overall, this study provides new insights into the balance between phytoplankton clearance and renewal capacities in a cultured bivalve ecosystem.

2. Methods

2.1. Turnover rates

2.1.1. Bivalve clearance time (CT)

CT represents the time needed for the cultured bivalves to filter the entire system volume once. As a first step in this calculation, the lease (farm) surface area (L_{Area} , m^2) was determined for each culture system. L_{Area} was categorized in four groups according to lease licensing conditions (Clements and Comeau, 2019): bottom oysters (BO), suspended oysters (SO), suspended mussels (SM), and mixed cultures of suspended oysters and mussels (SMO, assumed 50% oysters and 50% mussels). A clearance rate per unit leased area (CR_{Area} , $m^3 d^{-1} leased m^{-2}$) was then assigned to each lease category as per the information provided in Annex

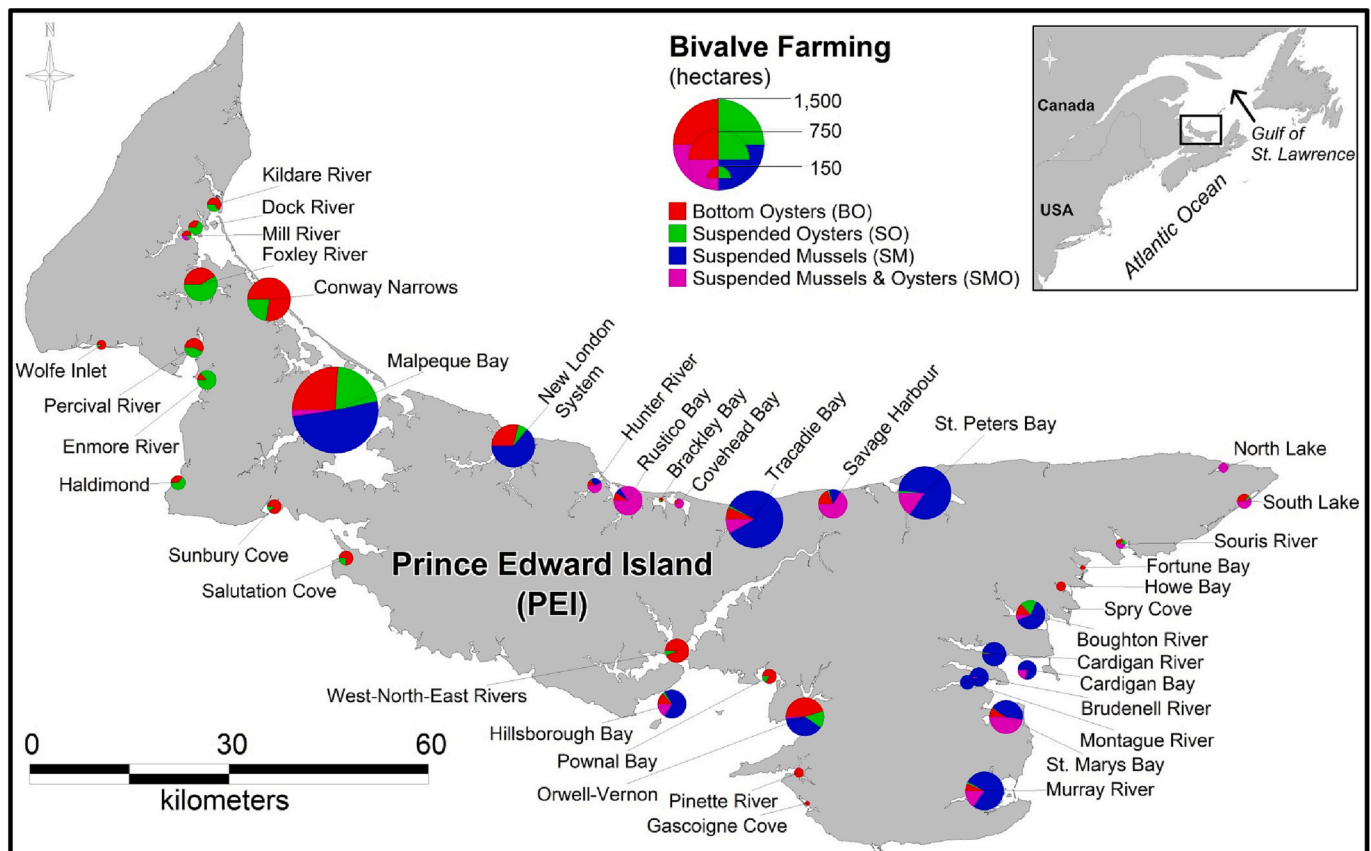


Fig. 1. Map of bivalve farming activity in Prince Edward Island, Canada. Data are for leases issued in 2020.

II.

Given the effect of temperature on the physiological response of organisms, CR_{Area} was corrected on a monthly basis according to the extended Arrhenius law (Kooijman, 2010):

$$\dot{k}(T) = \dot{k}_1 \times \exp\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right) \times s(T) / s(T_1) \tag{1}$$

$$s(T) = \left(1 + \exp\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right) + \exp\left(\frac{T_{AH}}{T} - \frac{T_{AH}}{T_H}\right)\right)^{-1} \tag{2}$$

where T is the absolute temperature (in degrees Kelvin, K), T_1 is the reference temperature (K), $k(T)$ is the physiological rate at temperature T , k_1 is the physiological rate at temperature T_1 , T_A is the Arrhenius temperature, T_L and T_H the lower and upper tolerance range, respectively, and T_{AL} and T_{AH} the rate of physiological rate decrease at lower and upper temperature boundaries, respectively. T represents monthly mean water temperature, computed from loggers (YSI Incorporated, OH, USA) moored in 5 culture systems in 2016–2017 (PEI Department of Agriculture and Fisheries). T_1 and k_1 were acquired from Comeau et al. (2015) and Comeau (2013) during CR measurements on *M. edulis* ($T_1 = 11.1$ °C) and *C. virginica* ($T_1 = 16.0$ °C), respectively. Remaining parameters (T_{AL} , T_L , T_{AH} , T_H , T_A) were derived from van der Veer et al. (2006) and Lavaud et al. (2021) for *M. edulis* and *C. virginica*, respectively.

CT (days) was calculated as follow:

$$CT = \frac{V_{System}}{\sum_{Category=1}^4 (CR_{Area,Category} \times L_{Area,Category})} \times (26.758 \times \mathbf{BF}_{cover}^{0.2016}) \tag{3}$$

where V_{System} represents the system’s volume (m³) and where the denominator summation term captures the 4 distinct culture categories indicated earlier. CT inherently assumes that individual bivalves are homogeneously distributed within a system and, therefore, that they have access to 100% of the available food supply. This simplification discounts any aggregation of cultured bivalves within culture units (e.g., sleeves, cages), and the confinement of these units to specific farm areas within systems. Such husbandry layouts forcibly increase localized water refiltration by the cultivated animals (Nielsen et al., 2016), and consequently increases CT at the system-scale level. For this reason a correction term highlighted in bold was added to Eq. (3) (see Annex III). This correction term increased CT as a function of the area of the system covered with leases (\mathbf{BF}_{cover}). Although the corrective term is based on a low sample size ($n = 3$), it offers useful insight into the magnitude of refiltration with increasing bivalve density.

Table 1

Water renewal times calculated from the tidal prism method and hydrodynamic models. ΔRT represents the level of disagreement between the two methods (see equation 5). The systems’ volumes were calculated for a state of Lower Low Water Large Tide (LLWLT).

System	Area (km ²)	System Volume LLWLT (m ³)	TIDAL PRISM				HYDRODYNAMIC MODEL					ΔRT (%)
			Neap Tide Range (m)	Neap Tide Period (h)	Spring Tide Range (m)	Spring Tide Period (h)	Water Renewal time (d)	Number of grid cells	Duration of simulation (d)	Maximum Water Renewal Time ¹ (d)	Mean Water Renewal Time ² (d)	
Brudenell	5.1	11,895,814	0.66	12.42	1.45	12.42	1.6	560	33	23.8	12.5	-87.4
Foxley	14.4	14,712,603	0.42	12.42	0.68	24.00	1.7	2186	87	34.8	19.6	-89.0
Malpeque	205.4	504,262,750	0.41	12.42	0.75	12.42	2.6	4479	91	89.0	41.6	-91.1
Mill	6.8	11,321,740	0.36	12.42	1.03	24.00	2.4	10,168	34	32.7	21.1	-93.7
Montague	4.9	12,257,638	0.66	12.42	1.45	12.42	1.7	481	33	18.9	11.0	-88.8
Orwell	9.5	1,934,573	0.68	12.42	2.08	12.42	0.3	1076	33	7.3	2.7	-84.8
Rustico Bay	9.2	13,021,412	0.22	12.42	1.01	24.00	2.7	8759	33	24.1	11.9	-89.3
St. Mary’s	18.8	27,398,857	0.53	24.00	1.57	24.00	2.3	2273	49	28.5	12.9	-77.3
St. Peter’s	15.7	36,880,705	0.23	12.42	1.13	24.00	4.1	2713	86	84.0	55.9	-82.2
Tracadie	19.6	43,379,325	0.28	24.00	0.98	24.00	5.6	2090	101	50.2	25.2	-92.7

¹ maximum time for a model cell within the grid to be renewed by Gulf of St. Lawrence water.

² mean renewal time of all grid cells, with each cell weighted by volume.

2.1.2. Water renewal time (RT)

Spatially-explicit hydrodynamic models were developed and validated for 10 PEI bivalve culture systems (Table 1). The common modeling approach that was adopted is already documented for three of the systems (Bacher et al., 2016; Grant et al., 2008; Guyondet et al., 2015). Work was carried out using the RMA10-RMA11 suite of finite element models (King, 1982, 2003). RMA10 is an hydrodynamic engine that solves the Reynolds form of the Navier-Stokes equations for momentum, the continuity equation and a convection-diffusion equation for transport of heat, salinity and any dissolved or suspended matter. It uses a Smagorinsky scheme (Smagorinsky, 1963) to estimate horizontal eddy diffusivities. The model grids contained 481 to 10,168 cells and covered the whole systems, as well as small portions of the Gulf of St. Lawrence (GSL) in the vicinity of each system’s mouth – offshore water junction. Water level data collected outside the systems were used to force the models, while inner stations with tidal gauges and ADCP current meters served as comparison points for model calibration. The shallow (< 8 m) systems were characterized by weak freshwater discharge and active wind mixing during the ice-free period. Therefore, a two-dimensional, vertically-averaged representation of the systems adequately captured the main features of their hydrodynamics. Simulation duration in a given system was set to ensure complete mixing; simulation duration among the 10 systems varied between 33 and 101 days. RT (days) was considered as the mean time of all model cells within a grid (system) to be renewed by GSL water (Koutitonsky et al., 2004); individual cells were weighted by volume prior to calculating the mean.

A second and simpler method for estimating RT is based upon the tidal prism. This method does not require hydrodynamic modeling expertise. The tidal prism is the amount of water that flows into and out of a system with the flood and ebb of the tide, excluding any contribution from freshwater inflows (Hume, 2005). It assumes complete mixing of the incoming tidal volume with the surrounding system volume, and the subsequent complete removal from the system of the tidal volume. Tidal ranges (m) and tidal periods (τ, h) were obtained from the same instruments that were deployed for full hydrodynamic modeling purposes. Tidal volumes (m³) were then computed separately for neap ($V_{tide\ neap}$) and spring ($V_{tide\ spring}$) tides: tide range (m) × system area (m²). Water renewal times (RT_{Prism}) in days was computed as follow:

$$RT_{Prism} = \frac{\frac{\tau_{neap}}{\ln\left(\frac{V_{System}}{V_{System}+V_{tide\ neap}}\right)} + \frac{\tau_{spring}}{\ln\left(\frac{V_{System}}{V_{System}+V_{tide\ spring}}\right)}}{2 \times 24} \tag{4}$$

where V_{System} (m³) represents the system volume at Lower Low Water

Large Tide (LLWLT) state; the 24 constant is meant to rescale from hours to days. Finally, in each system, the difference between the reference value (RT) and prism value (RT_{Prism}) was computed as follow:

$$\Delta RT = \frac{(RT_{Prism} - RT)}{RT} \times 100 \quad (5)$$

2.1.3. Phytoplankton turnover time (PT)

Information on phytoplankton dynamics is fundamental to any carrying capacity assessment for shellfish culture. However, one challenging issue is that baseline information is often no longer available for most estuarine systems due to coastal eutrophication (Beusen et al., 2016; Desmit et al., 2018; Erisman et al., 2013). In PEI, nutrient loading from agricultural practices over the past decades has increased primary production in several estuaries (Meeuwig et al., 1998; Meeuwig, 1999). Further complicating the issue was a concurrent development of bivalve culture in PEI, an activity that has led to significant top-down control of phytoplankton populations in some systems (Grant et al., 2008; Guyondet et al., 2015). In the present study, we attempted to gauge whether PT has changed against the backdrop of such anthropogenic confounders. In keeping with this objective, historical PT estimates were first computed using detailed information reported in a master's thesis. McIver (1972) measured primary production rates (PP_S , $\text{mgC m}^{-2} \text{d}^{-1}$) in 1969 and 1970 – a time when riverine nitrate loads were low or beginning to rise (Bugden et al., 2014), and suspended (intensive) culture was non-existent (Mallet and Myrand, 1995). McIver measured PP_S using a standard isotopic tracer (carbon-14) methodology (Strickland, 1960). Measurements were conducted at a bi-weekly to monthly interval during the ice-free period (May–Nov), specifically in the upper Bideford estuary ($46^\circ 37'02.6''\text{N}$, $63^\circ 55'00.5''\text{W}$) and also in the center of the Malpeque system ($46^\circ 33'47.6''\text{N}$, $63^\circ 48'06.6''\text{W}$). The Bideford site represented an elevated productivity level generally found in the nutrient-rich upper PEI estuaries, whereas the Malpeque site aligned more closely to a moderate productivity level typically found at the mouth of systems, where the tidal influx from the Gulf of St. Lawrence tends to reduce phytoplankton concentrations and dilute riverine nutrient inputs. Given that PEI bivalve farms are typically distributed across entire systems, McIver's data was pooled (monthly interval), averaged, and then projected (extrapolated) to 39 PEI systems by taking into account the photosynthesis capacity of each system. Specifically, McIver's PP_S values were converted into system-scale volumetric rates (PP_V , $\text{mgC m}^{-3} \text{d}^{-1}$) using the following equation:

$$PP_V = \frac{PP_S \times ES_{System}}{V_{System}} \quad (6)$$

where V_{System} (m^3) represents the volume of the system and ES_{System} (m^2) the euphotic surface area of the system. ES_{System} is defined as the surface of the system where a correction factor (α) has been applied in regions shallower than the euphotic depth to account for their limited potential for area-based primary production. Assuming that primary production followed the same exponential decrease with depth as light and that 10% of surface light remained at the bottom of the euphotic zone ($d_E = 3.7 \text{ m}$, Comeau et al. (2015)), the correction factor was estimated as:

$$\alpha = \frac{1 - e^{-K_D \times d}}{0.9} \quad \text{in regions of local depth } d \leq d_E \quad (7)$$

$$\alpha = 1 \quad \text{in regions of local depth } d \geq d_E \quad (8)$$

where the light attenuation coefficient $K_D = 0.622 \text{ m}^{-1}$ is set by the observed euphotic depth and the assumption of 10% surface light at d_E . Annex I shows that bottom depths are most commonly shallower than d_E , and therefore that the entire water column is illuminated during daytime.

Finally, for each culture system, PT (days) was calculated as:

$$PT = \frac{[P]_{System}}{PP_V} \quad (9)$$

where PT is the number of days needed for the phytoplankton biomass ($[P]_{System}$, mgC m^{-3}) to be renewed by local primary production (PP_V , $\text{mgC m}^{-3} \text{d}^{-1}$). The phytoplankton biomass to be renewed ($[P]_{System}$) was determined from historical chlorophyll *a* concentrations (Devi, 1980; McIver, 1972; Uyeno, 1966), measured at the same locations as indicated above and converted to carbon units assuming a carbon:chl of 50:1 (Nixon et al., 1986).

Historical PT estimates were compared against contemporary PT estimates. The latter estimates were intentionally founded on productivity levels recorded in intensive bivalve culture systems. With this approach the underlying rationale was to increase the likelihood of detecting a shift across the historical – contemporary timeline. Consequently 2011–2012 phytoplankton biomass and production data originating from St. Peter's Bay and Tracadie Bay, the most intensive culture systems in PEI, served the calculation of contemporary PT estimates. Specifically, these data, which were previously reported in Comeau et al. (2015), were pooled (monthly interval), averaged, and then projected to the 39 PEI systems by taking into account the physical characteristics of each system. Hence contemporary PT were computed using the same approach as described above for historical PT, with the exception that the underlying primary production parameterization, specifically $[P]_{System}$ and PP_V , originated from Comeau et al. (2015) instead of McIver (1972). Overall, this paper compares PT values deriving from a consistent methodology that integrated very contrasting levels of primary production, and presumably contrasting anthropogenic pressures.

2.2. Ecological carrying capacity (ECC) indices

ECC indices provide information on the capacity of bivalves to clear food particles against the capacity of the ecosystem to renew this food, either through water advection into the system or phytoplankton production within the system. Indices falling below 1 would be an indication that cultured bivalves are clearing phytoplankton faster than it is being advected into a system ($CT/RT < 1$) or produced internally within a system ($CT/PT < 1$). In practice for any given system, CT/RT would first be calculated. If determined that cultured bivalves may effectively control food resources from a water renewal perspective, an additional assessment would be conducted focusing on the system's internal food production and, more specifically, the CT/PT index. In the current study, the two ECC indices were computed at the system-scale for every month during the ice-free period (May–Nov). In keeping with a precautionary approach, the paper reports only the minimum CT/PT value attributed to each system, which may be interpreted as an indicator of the maximum grazing pressure exerted by the cultured bivalves that are present in the system.

Detailed phytoplankton data, including size-fractionated chlorophyll, was available for four systems that presented contrasting grazing pressures, specifically Brackley, Covehead, Foxley, and St. Peter's Bay. This field data, collected during intermittent expeditions (2011–2018), was examined to test a working hypothesis that intense grazing pressure may result in a community shift towards picophytoplankton, since bivalves inefficiently retain smaller phytoplankton cells (see Jiang et al., 2022; Ward and Shumway, 2004). With respect to field methodology, duplicate water samples (150 ml) were filtered through $3.0 \mu\text{m}$ and $0.2 \mu\text{m}$ membrane filters to determine the picophytoplankton ($0.2\text{--}3.0 \mu\text{m}$) and nanophytoplankton ($> 3.0 \mu\text{m}$) size fractions. Chl *a* was extracted in 90% acetone over a minimum of 24 h and thereafter measured using a Trilogy® benchtop fluorometer (Turner Designs, Sunnyvale, CA) following EPA protocol 445.0 (Arar and Collins, 1997). Size-fractionated primary production was measured using carbon isotope assimilation methods. Carbon 14 was used as a tracer in St Peter's as per the protocol in Comeau et al. (2015), whereas the stable isotope carbon 13 was

utilized in the other systems as per the protocol of Lefebvre et al. (2012). All results were expressed as the percentage of picophytoplankton contributing to the total biomass ($Biomass_{PICO}$) and total primary production ($Production_{PICO}$).

2.3. Statistics

Statistical analyses were conducted using R version 4.0.2 (R Core Team, 2020-06-22) operating in the RStudio version 1.2.1335 environment. The paired *t*-test function in R's native stats function was used to determine whether RT differed according to the method of calculation (tidal prism versus full hydrodynamic model). The Shapiro-Wilk test was used to confirm that the differences of the pairs followed a normal distribution. As this normality assumption could not be met for other comparisons, distribution-free tests were used. Specifically, a Wilcoxon signed rank test on paired samples was used to compare PP_V and PT values generated by the two distinct parameterization schemes (historical vs. contemporary), whereas the sign-test was adopted for CT/PT because differences between paired samples were not distributed symmetrically around the median.

The effects of the 'system' on various phytoplankton metrics ($Biomass$, $Biomass_{PICO}$, $Production_{PICO}$) were evaluated using the *Anova()* function from the *car* package (Fox and Weisberg, 2019). Dependant variables were transformed to meet the assumptions of normality and homogeneity of variances; the specific type of transformation applied (log, square root or arcsine square root) is specified in the text for each analysis. Multiple comparisons between systems were performed using the *glht()* function from the *multcomp* package (Hothorn et al., 2008) with Tukey adjustments to the *p*-values. Where transformations failed to

stabilize the variances, the Welch's one-way test in R's native stats function was used and post-hoc testing was conducted by pairwise comparisons and Bonferroni adjustments to the *p*-values.

Significance for all statistical tests was set at 0.05. The measure of variability reported along with the mean values represents 1 standard error of the mean ($mean \pm SE$). The median and interquartile range (IQR) is reported for variables subjected to non-parametric statistics.

3. Results

3.1. Turnover rates

CT was substantially impacted by the corrective terms incorporated in this study (see Annex III). First, the 'refiltration' term added to the right side of Eq. (3) increased the system-scale CT by a factor of 10.7 to 22.3, with the exact magnitude being directly proportional to the farm coverage in a given system (BF_{cover}). In terms of seasonality, water temperatures were stable over a narrow range between $-1^\circ C$ and $0^\circ C$ for three consecutive months in winter, but they gradually rose to a summer peak of approximately $20^\circ C$ in August (Fig. 2A). In this seasonally changing environment CT varied on an annual basis by a factor of 38 to 141, exact number depending on the system and species being cultivated (Fig. 2B). Grazing was negligible in winter when CT rose to hundreds or thousands of days. By contrast, CT fell to values as low as 3 days in summer. Systems primarily allocated to *M. edulis* cultivation tended to have lower CTs than systems cultivating mainly *C. virginica*.

RT differed according to the modeling approach (Table 1). The tidal prism method indicated an RT of 2.5 ± 0.5 days across 10 PEI systems,

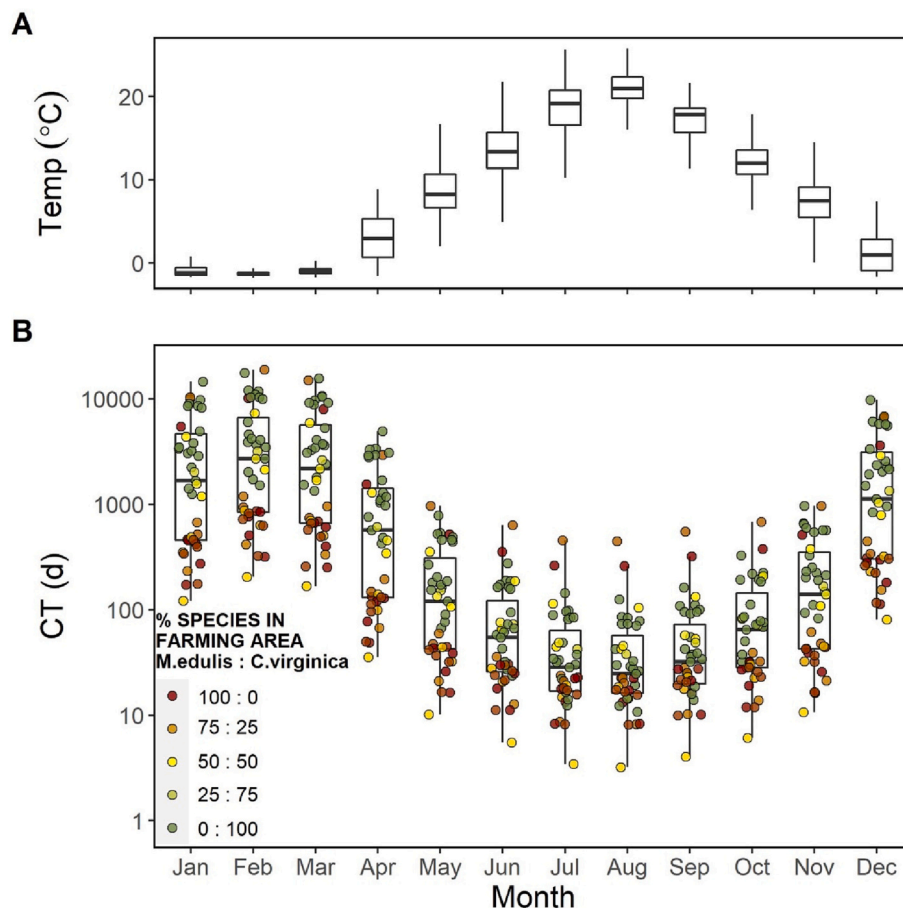


Fig. 2. Seasonal trends in water temperature (A) and cultivated bivalve clearance time (B); individual dots in panel B represent the 39 PEI systems and are colored to reflect the total farm area proportion allocated to *M. edulis* or *C. virginica*. Box plots show median values and IQR, with error bars extending to $1.5 \times IQR$.

whereas the detailed hydrodynamic model approach indicated 21.5 ± 5.1 days ($P < 0.01$, Paired t -test). The most striking shortfall of the tidal prism RT was its profound misrepresentation of the system's water fraction being renewed. When benchmarked against the hydrodynamic models, tidal prism RTs, which are assumed to indicate when the water of the systems is 100% renewed, corresponded to points in time when only $3.9 \pm 2.1\%$ (max of 22.1%) of the systems' volumes were actually renewed according to the hydrodynamic models (Fig. 3). Overall, the tidal prism approach substantially underestimated, with an inconsistent magnitude (77.3–93.7%), the amount of time needed for the renewal of water at bivalve culture sites.

PP_V peaked in summer, regardless of the underlying primary production parameterization scheme (Fig. 4A). Historical PP_V summer peaks (blooms) were greater in magnitude than contemporary PP_V summer peaks. Across the entire series (May – Nov), historical PP_V (median = $148 \text{ mgC m}^{-3} \text{ d}^{-1}$, IQR = 228) was approximately two-fold higher than contemporary PP_V (median = $70 \text{ mgC m}^{-3} \text{ d}^{-1}$, IQR = 61); $P < 0.001$, Wilcoxon signed rank test on 273 paired samples (39 systems \times 7 months [May – Nov] = 273 historical vs. contemporary estimates). The contrasting PP_V outcomes had no apparent impact on PT (Fig. 4B), since the difference between the historical PT median (1.2 days, IQR = 1.7) and the contemporary PT median (1.6 days, IQR = 1.9) was not significant; $P > 0.05$, Wilcoxon signed rank test on 273 paired samples.

3.2. ECC indices

ECC indices were computed using system-scale CT estimates as per

Annex III. Moreover in keeping with a precautionary approach the reported indices represent minimum values for each system.

CT/RT values derived from the tidal prism approach were well above 1 across the 10 investigated systems (Fig. 5A); however, those calculated from the validated hydrodynamic models were generally closer to 1 and occasionally below 1, suggesting that cultured bivalves are theoretically capable of clearing phytoplankton cells faster than they are being renewed by advection in some PEI systems.

CT/PT values were consistently above 1 regardless of the underlying primary production parameterization scheme (Fig. 5B), suggesting that phytoplankton production rates within systems can outpace feeding rates by cultivated bivalves. The median CT/PT across all systems was 27.9 (IQR = 42.0) and 17.8 (IQR = 21.5) when parameterized using historical and contemporary PT, respectively. A paired-samples sign test showed that the difference between the two parameterization schemes was significant (number of pairs = 39 systems, $P < 0.001$). Nonetheless the two schemes produced a similar ranking of PEI systems across CT/PT spectrums (Fig. 5B).

Finally, field measurements were consistent with bivalves exerting a top-down control on phytoplankton populations in systems that ranked at the bottom end of the CT/PT spectrums. Fig. 5C reveals a significant effect of the 'system' on chlorophyll biomass [$F(3,103) = 12.96$, $P < 0.001$], with a definite tendency towards low biomass as CT/PT drops below approximately 15. Moreover, this depletion trend was accompanied by a community shift towards smaller phytoplankton cells (picophytoplankton), both in terms of biomass (Fig. 5D, [$F(3, 46) = 68.927$, $P < 0.001$]) and production (Fig. 5E, [$F(3, 105) = 3.968$, $P = 0.010$]).

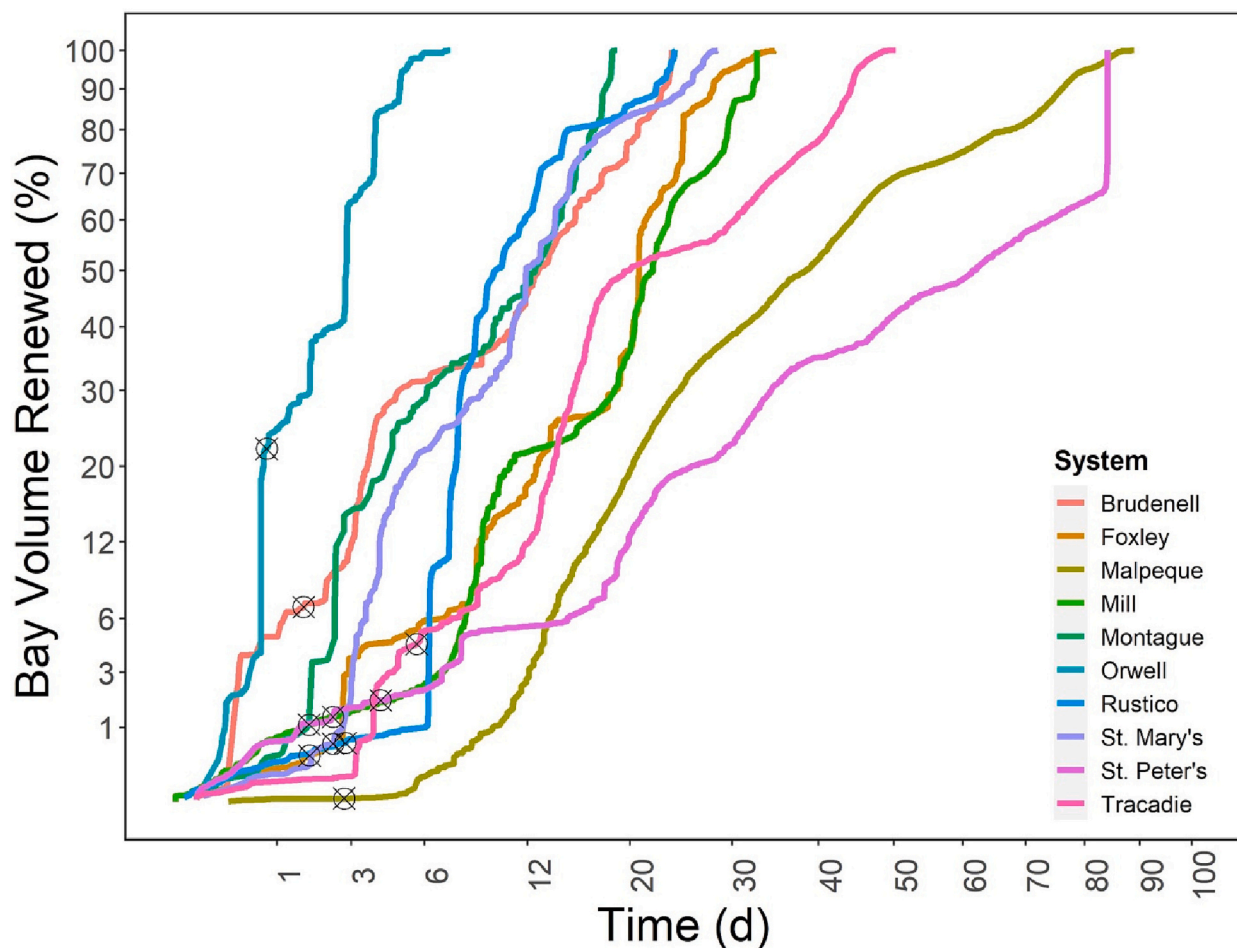


Fig. 3. System volume renewed by external (Gulf of St. Lawrence) water over time. Results from full hydrodynamic models are in solid lines; black circles denote complete renewal times predicted by the tidal prism method.

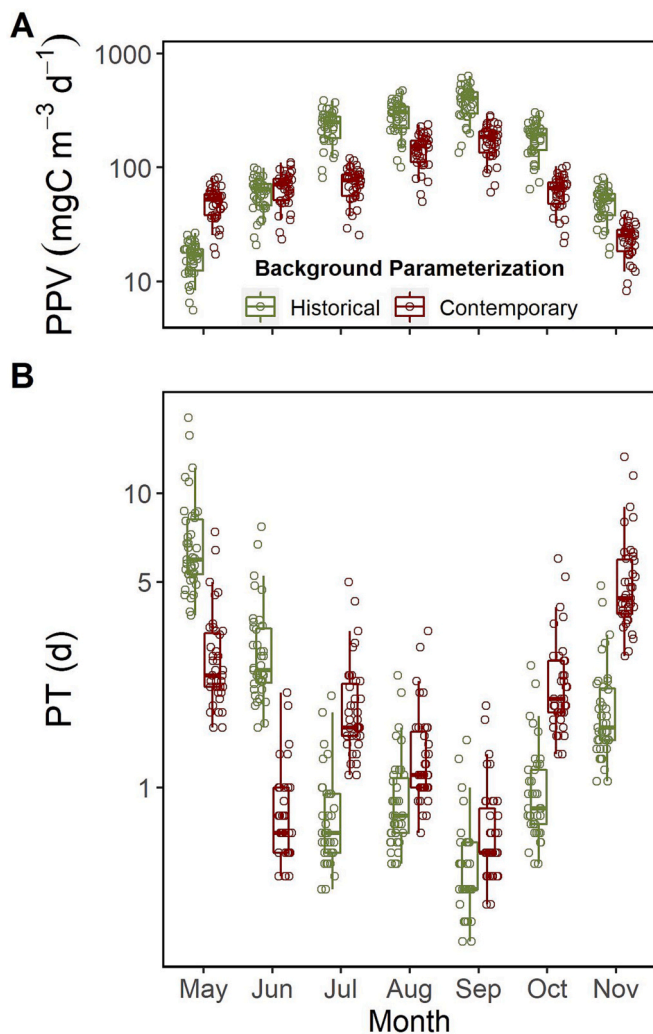


Fig. 4. Seasonal trends in phytoplankton production rates (A) and production times (B) computed using historical and contemporary datasets; individual dots represent the 39 PEI systems.

4. Discussion

Bivalve culture ECC indices rely exclusively on arithmetic ratios of CT, RT, and PT that represent an ecosystem as dimensionless and simplistic. Though these conceptually simple methods are appealing for coastal planning and eco-certification purposes, the present study highlights the true complexities of turnover rate parameterization. We reveal that such underlying details can substantially impact ECC indices and assessments of sustainable bivalve aquaculture development.

4.1. Turnover rates

The simple tidal prism method should not be used for RT parameterization; the method ignores coastal morphology, thus oversimplifying estuarine mixing (Filgueira et al., 2013) and systematically underestimating actual water renewal times (Hume, 2005; Luketina, 1998). PEI culture systems were poorly modeled with this method; the tidal prism method grossly underestimated the RT and predicted full renewal when actual renewal was only $\sim 3.9\%$ (max 22.1%) of system volume based on validated hydrodynamic models. The tidal prism method consistently underestimates water renewal times and produces overly optimistic ECC assessments in bivalve culture. A simple corrective term cannot rescue the validity of the prism method because the differences between the tidal prism and full hydrodynamic models are inconsistent

between systems. Thus, elaborate hydrodynamic models are needed when assessing RT, after which RT must still be reduced by choice to a single system-scale value. The maximal RT in the model grid may be overly cautious and unrepresentative because such maxima are typically associated with low-volume grid cells located at the shallow inner edges of systems. In the current study, RT is the mean renewal time of all model cells (by Gulf water), with individual cells weighted by volume prior to calculating the mean. Such weighting-by-volume approaches may be unrepresentative because grazing elements (leaves) are not necessarily contained within the bulk volume of a system.

Secondly, the study highlights that CT parameterization should include husbandry considerations by adjusting for the effects of densely aggregated bivalves. In aggregations such as mussel ropes, neighboring mussels reduce each other's food supplies (Nielsen et al., 2016) and this phenomenon increases local clearance times around the aggregate, thus increasing the system-scale CT. To date, refiltration effects have been considered at intermediate or farm scales in calculating realized clearance rates within a longline mussel farm (Aure et al., 2007; Nielsen et al., 2016) and Spanish mussel raft (Cranford et al., 2014; Petersen et al., 2008). Here we applied such a correction at the ecosystem scale (Annex III) by exploiting hydrodynamic-biogeochemical model outcomes from contrasting aquaculture systems (Malpeque and St. Peter's). Model resolution scales were several meters, which was insufficient to capture refiltration effects at the growing unit scale. However, such localized effects were implicitly accounted for in model validation by integrating a CT term for the cultured bivalve component with modeled vs. measured bay-scale phytoplankton biomass observations (Filgueira et al., 2015b; Guyondet et al., 2015); this corrective CT was applied to all 39 PEI systems (Annex III). Though this correction scheme is likely region specific and somewhat inaccurate because it excludes bay morphology, the results inform on the magnitude of the scaling problem (i.e., individual - > growing unit - > farm - > bay). Such corrections increased CT by a factor of 10.7 to 22.3 with the most intensive culture systems receiving the largest adjustments; these denser culture systems (where farm coverage area reaches 40%) likely have higher rates of refiltration and drag. There is a growing consensus (this study; Nielsen et al., 2016 and references therein) that CT parameterization should consider filter-feeder aggregation and food competition across scales rather than using unrealistic idealized assumptions about bivalve distribution and food mixing that dramatically reduces system-scale CT estimates.

Thirdly, the study revealed the importance of accounting for seasonality at temperate latitudes. For PEI, monthly CT estimates varied by a factor of 38 to 141, depending on the individual system and species being cultivated. Seasonal trends in local stocking practices were included in the CT calculations but cannot explain all the observed CT variability; PEI stocking densities are relatively stable and vary seasonally only by a factor of two. Maximum biomass is reached in autumn (Comeau et al., 2017). Hence it appears that water temperature drives CT seasonality. CT was highest in winter when near-freezing waters curtail metabolic and clearance rates in both cultivated species (Comeau et al., 2008; Comeau et al., 2017; Pernet et al., 2007), particularly in *C. virginica*, which is largely quiescent in winter (Comeau et al., 2012). As the thick (~ 1 m) ice cover melts in April, food demand increases in both species and peaks in summer with a system-wide decrease in CT.

Finally, PT was not significantly influenced by a contrasting phytoplankton parameterization; historical (1969–1970) and contemporary (2011–2012) phytoplankton datasets led to similar PT outcomes. We consider the 'historical PT' from this study (1.2 days; IQR = 1.7) as an ecological baseline for PEI because those parameterization data were collected prior to the rise of anthropogenic confounders such as agricultural nutrient loading (1970s) and intensive aquaculture development (1980s) (Bugden et al., 2014; Mallet and Myrand, 1995). Surprisingly, our contemporary phytoplankton turnover rates (1.6 days, IQR = 1.9) closely matched the ecological baseline, possibly because the

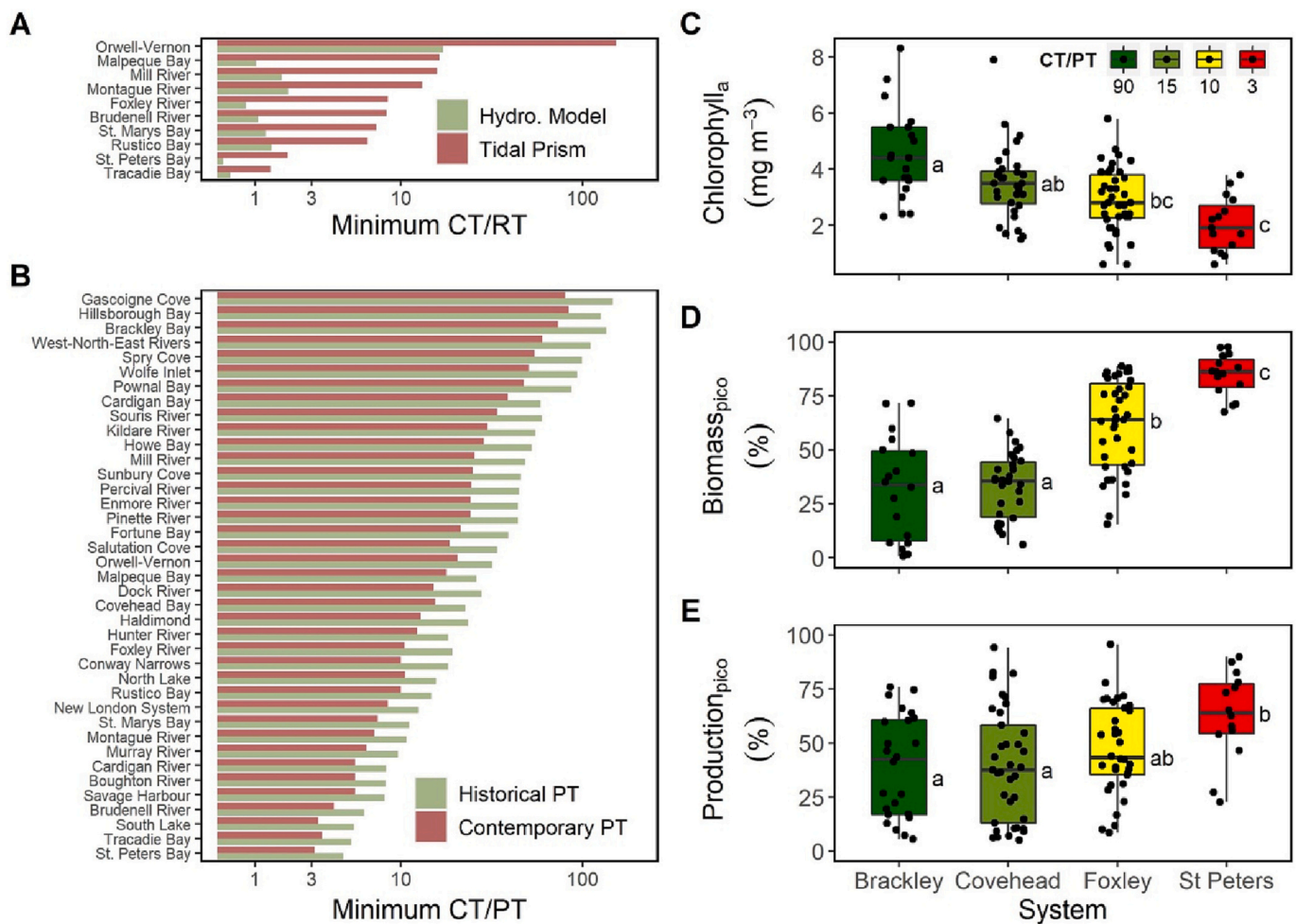


Fig. 5. A) Minimum CT/RT values for 10 PEI systems parameterized using hydrodynamic models and tidal prisms. B) Minimum CT/PT values for 39 PEI systems parameterized using historical and contemporary phytoplankton datasets. C–E) Phytoplankton measurements across four systems with contrasting CT/PT values; each point represents an individual date during the ice-free period (May–November 2011–2018). Chlorophyll *a* biomass is reported for cells larger than 0.2 μm (panel C) and for small cells (picophytoplankton, 0.2–3.0 μm) (panel D). The contribution of picophytoplankton cells to primary production rates (panel E) was measured using carbon isotope tracers. System effects were evaluated by ANOVAs. Dependent variables were transformed to square root (panel C) or arcsine square root (panel E) to meet the assumptions of normality and homogeneity of variances. Letters report multiple comparison testing (Tukey-adjusted) for system effects ($P < 0.05$). In panel D, homoscedasticity could not be attained and system effects were tested by Welch's ANOVA on the original (untransformed) data; letters report pairwise comparison testing scenario effects ($P < 0.05$, Bonferroni-adjusted). Box plots show median values and IQR, with error bars extending to $1.5 * \text{IQR}$.

bottom-up anthropogenic effects (nutrient loading) balanced the top-down anthropogenic effects (cultured bivalves). Alternatively, contemporary PTs may reflect the rapid replenishment of depleted phytoplankton biomass with a community shift towards picophytoplankton, as cultivated bivalves disproportionately retain larger nanophytoplankton cells (Caroppo, 2000; Cranford et al., 2014; Froján et al., 2014; Prins et al., 1998; Smaal et al., 2013). The latter interpretation is consistent with our contemporary phytoplankton biomass and cell-size observations and also with numerical models applied to PEI, which revealed that the energy cycle in intensive mussel culture systems is largely restricted to a nitrogen-phytoplankton-cultured bivalves loop that leaves few resources for higher trophic levels (Cranford et al., 2007; Filgueira and Grant, 2009; Guyondet et al., 2015). Cultured bivalves can likely alter phytoplankton dynamics at the ecosystem scale, though the sensitivity of the PT metric to these dynamics is unclear; PT depends on the combination of both stock and production variables. Exclusive reliance on PT may be misleading because high turnover rates do not directly indicate healthy phytoplankton populations (this study).

4.2. Indices

System-wide water circulation cannot be easily summarized with a single metric (see 4.1), so we are cautious in our use of RT and the CT/RT ratio. Our only conclusion is that PEI phytoplankton cells are being cleared by cultured bivalves more quickly than advection renews them. Under such circumstances, Smaal and Prins (1993) suggested that CT/PT should be >3 because this allows the algal buffer stock to reach a certain level of primary production and also considers unknown natural grazers in the system. Similarly, Gibbs (2007) suggested that production carrying capacity is reached as CT/PT approaches 1 and the pelagic food web collapses into a nutrient-phytoplankton-cultured bivalve loop with few phytoplankton cells remaining for natural grazers (Gibbs, 2004). Such thresholds are cautionary tipping points, rather than fixed ecological requirements, in risk-management decision-making; they are useful for identifying sites most sensitive to aquaculture development and optimizing resource allocation for field monitoring and hydrodynamic/ecological modeling.

In this study, we cautiously retained the lowest seasonal CT/PT value for each system, which reflects the maximum grazing intensity that a cultured bivalve system imposes on phytoplankton populations. We

found that all PEI systems currently meet the ECC sustainability score mentioned earlier (CT/PT > 3), though our data suggest that PEI phytoplankton biomass and community composition may be impacted at CT/PT < 15 (Fig. 5C–E); the underlying reason for such a high CT/PT inflection point is unclear.

We do not endorse any thresholds or scores as definite ecological standings; their utility is uncertain without broadly adopted and validated methods and standards for parameterization. As we demonstrated, turnover rates (particularly CT) are highly sensitive to parameterization details that require in-depth knowledge of local husbandry practices and hydrodynamic/physiological processes. Consequently, CT/PT absolute values may reflect these parameterization choices rather than the actual ecological impacts of cultured bivalve grazing; sustainability classifications based on CT/PT threshold values should thus be regarded with caution. The multi-site method standardization used here essentially provides a CT/PT ranking spectrum to identify systems requiring additional monitoring or modeling resources; the standardization approach can also provide insights on future farm scenarios. For instance, the approach suggests a potential for additional suspended oyster leases in our study area (Annex IV, panel A) because sea surface warming (Galbraith et al., 2020) will favor *C. virginica* over *M. edulis* (Steeves et al., 2018), a shift that significantly reduces expected phytoplankton resource demands (Annex IV, panel B). Finally, climate change must be considered when setting baselines for ‘natural’ phytoplankton populations, especially because picophytoplankton and other small taxa are already expanding in response to global warming (Correia-Martins et al., 2022; Daufresne et al., 2009; Mousing et al., 2014).

5. Conclusion

While practical system-scale ECC indices are understandably popular, our data demonstrate the inaccuracy of simplistic parameterization methods and caution against their use in assessing organically extractive aquaculture sustainability. The tidal prism method seriously underestimates RT, leading to overly optimistic assessments of carrying capacity and excesses in licensing that have consequences for production and trophic interactions. Full hydrodynamic models require considerable resources and therefore are incompatible with scoping assessments. Other system-scale turnover rates have intrinsic complexities: CT must consider non-linear/system-scale refiltration effects, and PT provides insufficient granularity on microalgae biomass replacement. Thus, accurate CT/PT values are challenging to obtain and interpret; they may be best used for early precautionary scoping of systems in need of full hydrodynamic/ecological modeling resources.

CRediT authorship contribution statement

Luc A. Comeau: Conceptualization, Funding acquisition, Project administration, Methodology, Formal analysis, Writing – original draft. **Thomas Guyondet:** Conceptualization, Funding acquisition, Methodology, Writing – review & editing. **David Drolet:** Validation, Writing – review & editing. **Rémi Sonier:** Funding acquisition, Investigation, Writing – review & editing. **Jeff C. Clements:** Writing – review & editing. **Réjean Tremblay:** Investigation, Writing – review & editing. **Ramón Filgueira:** Conceptualization, Funding acquisition, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.aquaculture.2023.739911>.

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