



Review

A review of existing eastern oyster filtration rate models



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ABSTRACT

Crassostrea virginica, the eastern oyster, is a suspension-feeding bivalve currently at low numbers in Chesapeake Bay, where it was once abundant. Accurately describing the filtration rate of these bivalves is essential to estuarine management and associated efforts to understand the impact of oyster populations on water quality. Here, the filtration rate equations for three existing models (Cercio and Noel, 2005; Fulford et al., 2007; Powell et al., 1992) are reviewed. We examine how each of the models define the maximum filtration rate and explore the various limitation factors that modify these maximum rates via environmental conditions that include salinity, temperature, and total suspended solids. Based on the individual model strengths assessed with a model comparison and literature review, we determine a maximum filtration rate of $0.17 (\pm 0.07) \text{ m}^3 \text{ g}^{-1} \text{ DW day}^{-1}$ for a 1 g DW oyster to describe this rate process, which is then modified by a combination of limitation factors taken from a variety of sources. These include those described by Fulford et al. (2007) for total suspended solids and salinity, and a newly developed function to describe temperature dependence. Differences in size are incorporated by using a basic allometric formulation where a weight exponent alters filtration rate based on individual oyster size.

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Contents

1. Introduction and objectives	202
1.1. Existing oyster models	202
1.1.1. Cercio and Noel (2005) oyster model	202
1.1.2. Fulford et al. (2007) oyster clearance model	203
1.1.3. Powell et al. (1992) population dynamics model	203
2. Methods	203
2.1. Model comparison	203
2.2. Filtration rate model	204
3. Results and discussion	205
3.1. Model comparison	205
3.1.1. Maximum filtration rates	205
3.1.2. Environmental limitation factors	206
3.1.3. 2009 filtration rate	207
3.1.4. Model sensitivity analysis	207
3.2. Filtration rate model	208
3.2.1. Individual-based maximum filtration rate	208
3.2.2. Limitation factors	209
3.2.3. Model equations	210
4. Conclusion	210
Acknowledgements	211
References	211

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1. Introduction and objectives

The eastern oyster, *Crassostrea virginica*, is a sessile suspension-feeding bivalve mollusk that can be classified as an ecosystem engineer (Gutierrez et al., 2003). According to Newell (1988), oysters filter water at a typical rate of $0.12 \text{ m}^3 \text{ g}^{-1}$ dry weight (DW) day^{-1} , removing suspended organic and inorganic particles from the water column to affect water column clarity and nutrient cycling. As autogenic engineers (Wilberg et al., 2013), oysters form reefs by accumulating shell. This shell provides substrate for oyster larvae settlement, as well as habitat for other organisms (Newell, 1988).

Current studies to document the spatial extent of oyster reefs point to a “functional extinction” (Beck et al., 2011), with regional estimates of ~63% reef loss since the late 1800s (Beck et al., 2011; Zu Ermgassen et al., 2012). At the local scale, many estuaries and bays have experienced declines of over 99% in the last century (Beck et al., 2011). For example, the Chesapeake Bay was home to a productive oyster fishery in the 1880s before a substantial decline, attributed to overfishing depleting the stock and dismantling the hard substrate that oysters need. In the 1950s, the outbreak of MSX (*Haplosporidium nelsoni*) and Dermo (*Perkinsus marinus*), parasitic diseases, further decreased the oyster population (Newell, 1988; Kemp et al., 2005). Recent modeling efforts to consider both fishery pressure and disease presence for *C. virginica* revealed the abundance of oysters in Chesapeake Bay has declined by 99.7% (Wilberg et al., 2011), greatly affecting the ecological services that oysters provide. These same causes of oyster population decline are also evident in other estuarine ecosystems (e.g. Harvell et al., 1999; Kirby, 2004; Zu Ermgassen et al., 2012).

Stock assessment models of native oyster populations, especially those that incorporate a term relating carrying capacity to habitat dependence for these reef building organisms (e.g. Wilberg et al., 2013), are valuable in integrating fishery and population dynamics with related habitat effects. However, there is still a need for model formulations that include the secondary role of these species as ecosystem engineers that filter the water column. Understanding the controls rates of filtration has implications for predicting the impact of oysters on water quality, and may inform models or management decisions relevant to restoration and aquaculture efforts.

Oyster filtration is regulated by the movement of cilia on the gills, decreasing or increasing pumping and particle uptake. Particles are first sorted at the gills and then reach the labial palps for further sorting. Those particles that are desired are delivered to the mouth and reach the digestive track. Particles that are rejected, either due to being undesirable or in excess of the digestive capacity of the oyster, are excreted as pseudofeces (Newell and Langdon, 1996; Tamburri and Zimmer-Faust, 1996; Ward et al., 1994). Waste products produced after digestion of desirable particles follow the alimentary system and are excreted as feces (Ward et al., 1994).

Numerous eastern oyster (*C. virginica*) models incorporating the feeding mechanism of oysters have been established, spanning a diversity of approaches that include the efforts of Powell et al. (1992), Cerco and Noel (2005), and Fulford et al. (2007). Cerco and Noel (2005) numerically model oyster growth in terms of changes in total carbon, and Fulford et al. (2007) predict filtration rates to determine clearance of phytoplankton. Powell et al. (1992) describe a bivalve growth and reproductive model applied specifically to *C. virginica* to calculate net production and changes in standing stock size structure. For oyster models describing bioenergetics (e.g. Powell et al., 1992; Cerco and Noel, 2005), the filtration rate is the major determinant of growth that in turn affects changes in oyster biomass. In addition to being a component of growth rate formulations, the filtration rate is also indicative of the impact oysters may have on the ecosystem via such processes

as phytoplankton clearance (Newell, 1988). The volume of water and associated particles that oysters can remove via filter-feeding is of interest to managers in ecosystems where nutrient pollution may lead to phytoplankton blooms and deteriorated water quality.

All too frequently, models are not thoroughly analyzed, even though sensitivity analyses and exploration of model dynamics are important to understand model strengths and weaknesses (Fulton et al., 2003). For example, Brush et al. (2002) finds that phytoplankton biomass, a state variable commonly used as currency in Nutrient–Phytoplankton–Zooplankton–Depth (NPZD) models, is often predicted correctly even though different models have different formulations for the rate process of primary production. In calculating primary production with these varied formulations, drastically different numbers are predicted and this diversity of output indicates great quantitative uncertainty in the mechanisms that drive primary production. Modelers rarely highlight these differences and focus instead on calibration, “tuning” or “fitting”, parameters so that output of state variables match available data. This results in greater uncertainty in what factors are driving a given rate process, and negate the utility of using modeling as a means to explore hypotheses via development and testing of the formulations themselves (see Ganju et al., in review). In the case of oysters, it is especially crucial that we provide reliable filtration rates as these formulations are critical in linking these organisms to the ecosystem services they provide in improving water clarity.

Our objective in this study was to compare three oyster models (Cerco and Noel, 2005; Fulford et al., 2007; Powell et al., 1992) with a focus on filtration rates. Here, we consider the oyster to be a perfect sieve of the water column, assuming no particles are released with the outflow of water. Therefore, clearance rates and filtration rates are considered synonymous. We acknowledge this assumption as a necessary simplification, as there is evidence for particle selectivity based on both size and food quality (e.g. Epifanio and Ewart, 1977; Haven and Morales-Alamo, 1970). However, only Fulford et al. (2007) provides a means of simulating this feature. Modeled filtration rates depend on both the critical selection of a maximum filtration rate and data-driven formulations that describe environmental limitation factors and mechanisms. Comparisons of these approaches, with further literature review, naturally leads to the development of a new filtration rate model and determination of weaknesses or data gaps that can be pursued in future empirical efforts.

1.1. Existing oyster models

1.1.1. Cerco and Noel (2005) oyster model

The Cerco and Noel (2005) bioenergetics oyster model describes changes in oyster biomass (O , g oyster C m^{-2}) with time (t , day) as:

$$\frac{dO}{dt} = [\text{POC Consumption}] - [\text{Respiration}] - [\text{Mortality}] \quad (1)$$

The particulate organic carbon (POC) consumption term is the amount of organic carbon oysters consume and incorporates a filtration rate that describes the rate oysters uptake water. This rate is a function of the maximum filtration rate, Fr_{max} , and limitations from temperature (T), salinity (S), total suspended solids (TSS), and dissolved oxygen (DO), which can be expressed as.

$$Fr = Fr_{\text{max}} * f(T) * f(S) * f(TSS) * f(DO) \quad (2)$$

The maximum filtration, Fr_{max} , is the maximum rate oysters can filter water ($\text{m}^3 \text{ g}^{-1}$ oyster C day^{-1}). Equations for each environmental limitation, $f(S)$, $f(T)$, $f(TSS)$, $f(DO)$, scaled between 0 and 1, are multiplied by the Fr_{max} . These environmental effects on filtration are listed in Table 1 (Cerco and Noel, 2005).

Cerco and Noel (2005) estimate the change of oyster biomass in relation to environmental variables that affect the bioenergetics

Table 1

Environmental limitation factors for temperature ($f(T)$), salinity ($f(S)$), and total suspended solids ($f(TSS)$) for the Cerco and Noel (2005), Fulford et al. (2007), and Powell et al. (1992) models.

Function	Model		
	Cerco and Noel (2005)	Fulford et al. (2007)	Powell et al. (1992) ^a
$f(T)$	$= e^{(-0.015*(T-27))}$	$= e^{(-0.015*(T-27))}$	Incorporated in maximum filtration with oyster length
$f(TSS)$	$= 0.1$ when $TSS < 5 \text{ g m}^{-3}$ $= 1$ when $5 \leq TSS \leq 25 \text{ mg L}^{-1}$ $= 0.2$ when $25 < TSS < 100 \text{ mg L}^{-1}$ $= 0$ when $TSS > 100 \text{ mg L}^{-1}$	$= 0.1$ when $TSS < 4 \text{ mg L}^{-1}$ $= 1$ when $4 \leq TSS \leq 25 \text{ mg L}^{-1}$ $= 10.364 * \ln(TSS)^{-2.0477}$ when $TSS > 25 \text{ mg L}^{-1}$	$= 1 - 0.01 * \frac{\log\left(\frac{TSS}{1000}\right) + 3.38}{0.0418}$
$f(S)$	$= 0.5 * (1 + \tanh(S - 7.5))$	$= 0$ when $S < 5$ $= 0.0926 * S - 0.139$ when $5 \leq S \leq 12$ $= 1$ when $S > 12$	$= 0$ when $S \leq 3.5$ $= \frac{S-3.5}{4}$ when $3.5 < S < 7.5$ $= 1$ when $S \geq 7.5$

^a $f(S)$ came from Powell et al. (1994).

of the oyster population. This model approach is both similar to, and different from the following models, with the main difference a focus on carbon exchange and oyster growth in terms of total oyster carbon biomass in a square meter, rather than per individual organism.

1.1.2. Fulford et al. (2007) oyster clearance model

The Fulford et al. (2007) model objective is specifically targeted at understanding the effect of oysters on phytoplankton removal, rather than changes in biomass of oysters per unit area. Particle uptake is oyster size and particle size dependent. The main model equations describe clearance rate, or filtration rate if the oysters are a perfect sieve, with a formulation expressed similarly to Cerco and Noel (2005) (refer to Eq. (2)), but with a size dependent maximum filtration rate. This equation is

$$CR_{(i)} = CR_{\max(i)} * f(T) * f(S) * f(TSS) * f(DO) \quad (3)$$

where $CR_{(i)}$ is the oyster clearance rate ($\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$) dependent on the size (i) of the oyster, $CR_{\max(i)}$ is the maximum clearance rate ($\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$) for the oysters of size (i), and the functions of environmental variables or $f(T, S, TSS, DO)$ are limitation factors applied to the maximum clearance rate, scaled between 0 and 1 (Fulford et al., 2007). These environmental limitation functions are listed in Table 1.

Eq. (3) calculates the filtration rate for one size class of oyster. The mean filtration for a population is expressed as

$$CR_{pop} = \sum CR_{(i)} * P_{(i)} \quad (4)$$

where CR_{pop} is the mean clearance rate ($\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$) of the population, $CR_{(i)}$ is clearance rate ($\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$) of an oyster of size (i) (g DW), and $P_{(i)}$ is the proportion of the population that are size (i). Phytoplankton removal can then be calculated using the total filtration and ambient phytoplankton concentration. The clearance efficiency is also altered depending on the particle sizes with size classes of $<2 \mu\text{m}$, $2-4 \mu\text{m}$, and $>4 \mu\text{m}$ (Fulford et al., 2007).

This model examines the ecosystem effects of a population of oysters on phytoplankton removal rather than determining growth and changes in biomass. Unlike the Cerco and Noel (2005) model, Fulford et al. (2007) incorporates a different filtration rate depending on the sizes of oysters in the population.

1.1.3. Powell et al. (1992) population dynamics model

The Powell et al. (1992) model is a size-based bivalve population model specifically applied to oysters. Categories of oysters, such as juvenile and market sized, and the associated biomasses (g DW) make up 10 different size classes.

In the Powell et al. (1992) model, the change in standing stock of oysters, based on caloric units, is equal to the net production within the size class, additions to the size class from the larger or smaller size class, and losses to the larger and smaller size class. The governing equation for the change in the standing stock, O , (calories m^{-2}) of each size class (j) is:

$$\frac{dO_{(j)}}{dt} = Pg_{(j)} + Pr_{(j)} + (\text{gain and loss from/to } j - 1) + (\text{gain and loss from/to } j + 1) \quad (5)$$

where Pg is growth energy (calories $\text{m}^{-2} \text{day}^{-1}$), and Pr is reproductive energy (calories $\text{m}^{-2} \text{day}^{-1}$).

Filtration rate ($\text{mL individual}^{-1} \text{min}^{-1}$), Fr , which determines oyster food assimilation and contributes to the Pg value, is formulated as

$$Fr = Fr_{\max} * f(S) * f(TSS) \quad (6)$$

where Fr_{\max} is the maximum filtration rate ($\text{mL individual}^{-1} \text{min}^{-1}$). Fr_{\max} is dependent on the size of the oysters in each size class and temperature. This maximum filtration is then multiplied by limitation factors of $f(S)$ and $f(TSS)$. These environmental limitations are listed in Table 1. Dissolved oxygen is not a factor in the model (Powell et al., 1992).

The Powell et al. (1992) model is different from the other models in that it is a general bivalve population model, where the changes in size classes are the desired output. There is also no $f(T)$, as it is incorporated into the maximum filtration rate. Filtration rate is modeled on an individual basis rather than in units of carbon per square meter.

2. Methods

2.1. Model comparison

Filtration rate formulations were compared amongst the three models previously described. This comparative effort included identifying a data source for forcing functions to simulate each model's filtration rate using common conditions, contrasting the various limitation factors, and performing a sensitivity analysis to evaluate how simulated filtration rates responded to variations in T, S , and TSS . DO was assumed to be optimal and not a factor.

We first examined and analyzed the sources for each model's maximum filtration rate and the limitation functions they used. Each of the three models' filtration rate equations were then programmed in Simile (<http://www.simulistics.com/>), a modeling software. We calculated daily filtration rates ($\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$) for 1 g DW oysters with monitoring data from the lower Potomac River, a tributary of the Chesapeake Bay

where historical oyster reefs are located (Maryland Department of Natural Resources, 1997).

We obtained the Maryland Department of Natural Resources (MDNR)'s 2009 monthly monitoring water data for station LE 2.2 in the lower Potomac River. Data used as forcing functions included S , T , and TSS; with DO assumed optimal and set to a value of "1". We interpolated the data between sampling time frames to avoid missing values. This was done by computing moving averages and standard deviations at two-week increments, and randomly selecting a daily values within the constraints of the standard deviations for the given two-week period. Fig. 1 shows the interpolated daily water quality for T , S , and TSS.

Sensitivity of the models to changes in the environmental variables was also examined. Model sensitivity analysis was broken into two general approaches that included first determining how the magnitude of forcing functions affect filtration rate, and then testing how sensitive model output was to each of the limitation factors individually. To determine the effect of forcing function magnitude, we iteratively manipulated single environmental parameters from 2009 to have high, intermediate, and low values relative to the long term annual averages computed from the MD DNR station LE2.2 dataset between 1990 and 2010. "High" and "low" values were assigned using a range of 1 standard deviation from the long term mean in the twenty-year dataset. These newly interpolated forcing function values were then used to model filtration rates. We iteratively manipulated one environmental factor at a time to represent high or low values, keeping the other forcing functions set to average/intermediate conditions. For example, one model run for this sensitivity analysis would include using the high T values while keeping S and TSS forcing functions at the intermediate level.

We then compared filtration rates affected by one limitation factor at a time, assuming the other environmental factors were optimal. For instance, the $f(T)$ would be dependent on the day of the year in the intermediate interpolated dataset, but the other functions of $f(TSS)$ and $f(S)$ were set at values of "1" and held constant over the time frame of the simulation.

2.2. Filtration rate model

After comparing the models, we defined an individual maximum filtration rate affected by T , S , and TSS limitations by searching the literature for empirically measured and modeled oyster filtration rates. Because filtration per unit weight varies with size, literature values required normalization for proper comparison and a 1 g DW oyster filtration rate was calculated.

When oyster length was given, it was first converted to g DW using an allometric relationship derived from laboratory measurements of oyster biomass (g DW individual⁻¹) and oyster lengths (mm). This equation was similar to that reported by Ross and Luckenbach (2006).

$$\text{g DW} = 0.00008 \times L^{2.175} \quad (7)$$

The published filtration rate in each study was then standardized to a 1 g DW oyster using the following relationship, where DW is either the original weight in the published study or the calculated value converted from length using Eq. (7):

$$FR_{1 \text{ g DW}} = \frac{FR_{pub}}{\text{g DW}^{-0.28}} \quad (8)$$

where $FR_{1 \text{ g DW}}$ is the corrected filtration rate for a 1 g DW oyster and FR_{pub} is the published filtration rate for a given study (after Fulford et al., 2007; Newell and Koch, 2004).

We then determined the maximum filtration rate for a 1 g DW oyster by computing the mean and standard deviation of the

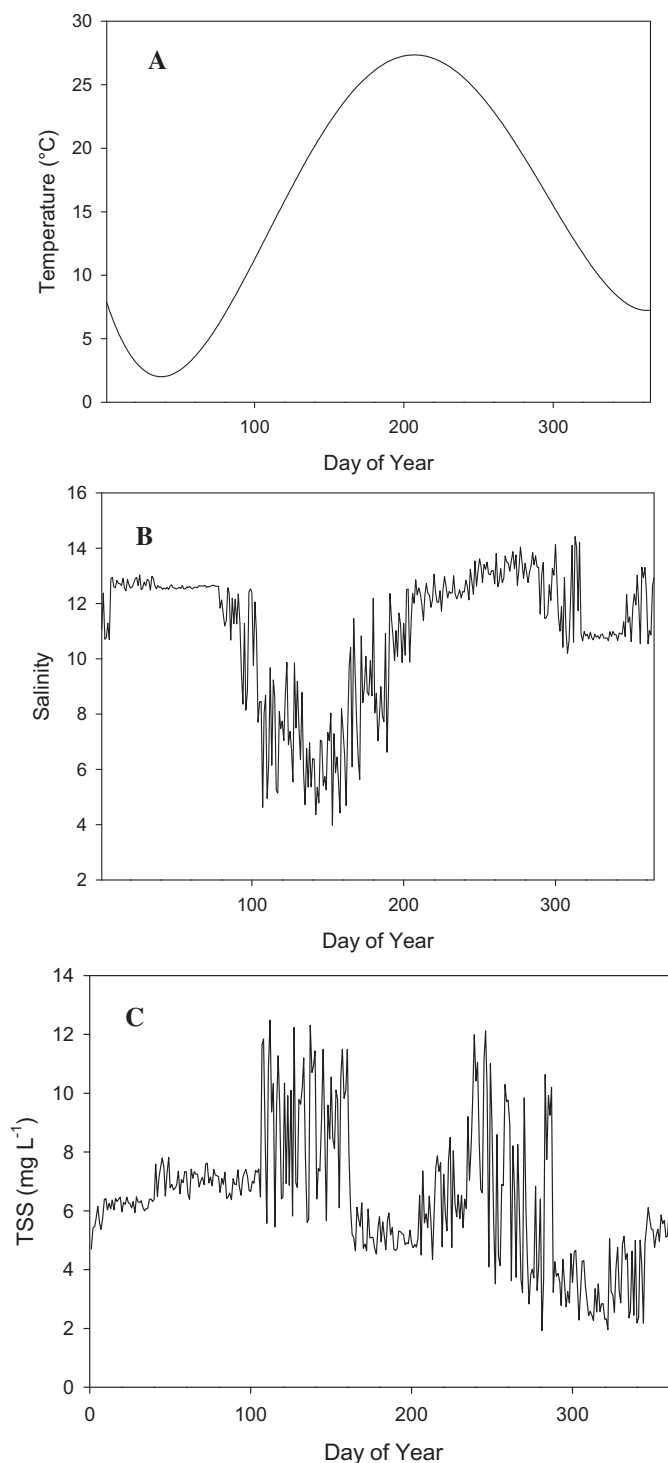


Fig. 1. Extrapolated daily forcing functions for 2009 used for model simulations including (a) temperature (°C), (b) salinity, and (c) TSS (mg L⁻¹).

published maximums, including those of the three models compared here.

Because individual size can alter the filtration rate (Newell and Langdon, 1996), we included allometric constraints. Oyster size or dry weight, W , is assumed to affect the maximum filtration, FR , represented by the power formula:

$$FR = a_f W^b \quad (9)$$

where a_f is a constant (Peters, 1983) related to filtration and b is the weight exponent (Newell and Langdon, 1996). In this case, a_f is the

maximum filtration rate for a 1 g DW oyster. We used a literature review to evaluate values of b .

After defining the individual maximum filtration rate in this final stage of the modeling analysis, we determined which limitation formulations and parameterizations from T , S , and TSS should affect the filtration by examining the source data from which these formulations were derived and the sensitivity to changes in variables. Results from model analyses were used to select a $f(TSS)$ and $f(S)$ to affect the new filtration rate maximum. Upon examination of maximum filtration rates, other studies surfaced that examine the effect of temperature on filtration rate. The $f(T)$ was formulated and re-parameterized based on model analysis and these other temperature vs. filtration rate empirical studies.

3. Results and discussion

3.1. Model comparison

3.1.1. Maximum filtration rates

The maximum filtration rate of an oyster is essential to parameterize as accurately as possible in any model that uses this value to simulate filtration in relation to environmental limitation factors. Cerco and Noel (2005) set the maximum filtration rate at $0.55 \text{ m}^3 \text{ g}^{-1} \text{ oyster C day}^{-1}$ based upon values reported by Jordan (1987) as weight specific biodeposition rates ($\text{mg g}^{-1} \text{ DW h}^{-1}$), and the clearance rates ($\text{L g}^{-1} \text{ DW h}^{-1}$) measured by Newell and Koch (2004). Both of these studies examine eastern oysters from the Choptank River, MD. Cerco and Noel (2005) calculate filtration rates from Jordan (1987) by dividing the measured biodeposition rates at varying water temperatures by the measured TSS concentrations (Cerco and Noel, 2005). The functional relationship between these filtration rates and temperature reveal the $0.55 \text{ m}^3 \text{ g}^{-1} \text{ oyster C day}^{-1}$ at 27°C maximum value used by Cerco and Noel (2005).

Similarly, Fulford et al. (2007) set the maximum at $0.55 \text{ m}^3 \text{ g}^{-1} \text{ oyster C day}^{-1}$, citing both Cerco and Noel (2005) and Newell and Langdon (1996), each with filtration rates originating from the Jordan (1987) empirical data. Unlike Cerco and Noel (2005), Fulford et al. (2007) alters this maximum rate by the size structure of a population. The individual (i) maximum filtration rate, $CR_{\max(i)}$ ($\text{m}^3 \text{ g}^{-1} \text{ oyster C day}^{-1}$), for an individual of weight, $W_{(i)}$ (g DW), adapted from Newell and Langdon (1996), is:

$$CR_{\max(i)} = 0.55 * (W_{(i)})^{-0.28} \quad (10)$$

In other words, as weight increases, the maximum filtration per unit weight decreases (Newell and Langdon, 1996). This is a common allometric function. Metabolic rates frequently scale with body size as a power function that exhibits quarter power scaling and the -0.28 exponent is indistinguishable from a theoretically predicted -0.25 value (Savage et al., 2004; Brown et al., 2004).

Unlike the Cerco and Noel (2005) and Fulford et al. (2007) models, the Powell et al. (1992) model maximum filtration rate is dependent on both oyster length, L (cm), and daily T ($^\circ\text{C}$). The individual (j) maximum filtration, $FR_{\max(j)}$ ($\text{mL individual}^{-1} \text{ min}^{-1}$) is calculated as:

$$FR_{\max(j)} = \frac{L_{(j)}^{0.96} T^{0.95}}{2.95} \quad (11)$$

These filtration rates originated from a study by Doering and Oviatt (1986), which used mesocosm experiments with different sized *Mercenaria mercenaria*, hard shell clams, and calculated filtration based on flow and ^{14}C concentration changes as a proxy for carbon removal.

Fig. 2a graphs Powell et al. (1992) individual maximum filtration rates ($\text{mL individual}^{-1} \text{ min}^{-1}$) against temperature for three

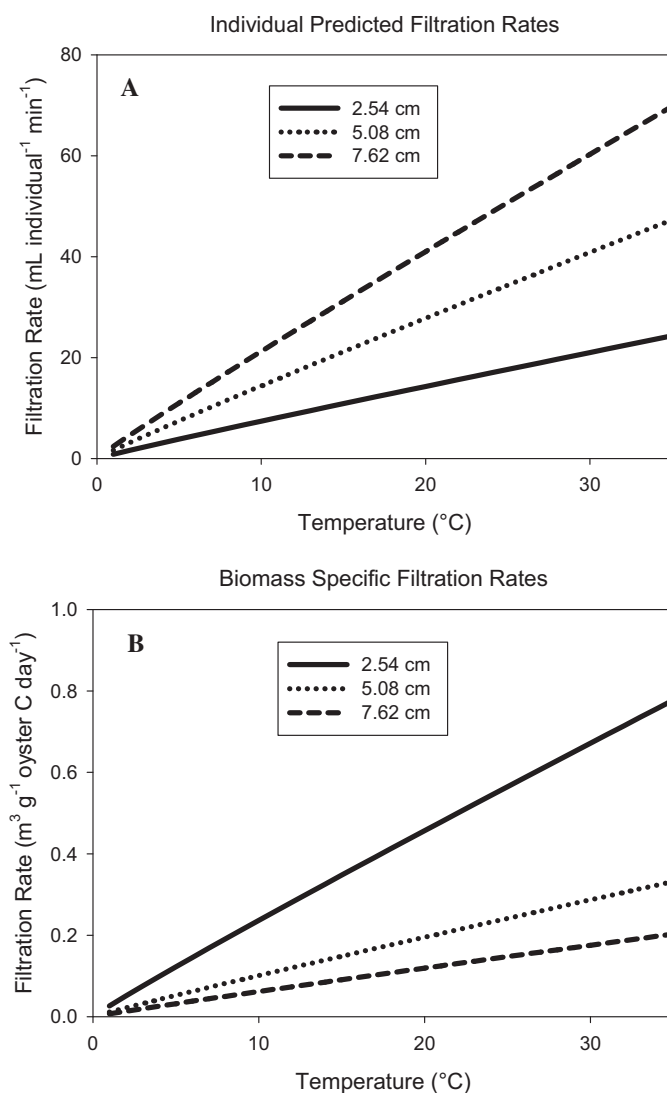


Fig. 2. (a) Predicted individual maximum filtration rates ($\text{mL individual}^{-1} \text{ min}^{-1}$) of the Powell et al. (1992) model for 1 in. (2.54 cm), 2 in. (5.08 cm), and 3 in. (7.62 cm) oysters and (b) filtration rates converted to biomass specific maximum filtration rates ($\text{m}^3 \text{ g}^{-1} \text{ oyster C day}^{-1}$) for the three oyster sizes.

different lengths of oysters, representing 1, 2, and 3 year old oysters, showing increased filtration with increasing oyster size. For comparison to Cerco and Noel (2005) and Fulford et al. (2007) models, these filtration rates were converted to be biomass specific ($\text{m}^3 \text{ g}^{-1} \text{ oyster C day}^{-1}$), which are graphed against temperature in Fig. 2b. With this normalization, the pattern of size with filtration rate is reversed. A 1 g DW, 7.62 cm, oyster at 27°C has a filtration rate of $0.16 \text{ m}^3 \text{ g}^{-1} \text{ oyster C day}^{-1}$, which is 3–4-fold lower than the $0.55 \text{ m}^3 \text{ g}^{-1} \text{ oyster C day}^{-1}$ filtration of the other two models. It is also important to note the effect of oyster size on filtration as a result of the power function (Eq. (11)) as shown in Fig. 2b where smaller oysters have a larger filtration rate per unit size than $0.16 \text{ m}^3 \text{ g}^{-1} \text{ oyster C day}^{-1}$.

The maximum filtration rate used for both Cerco and Noel (2005) and Fulford et al. (2007) both originate from oyster studies. Powell et al. (1992) suggested that modeled filtration rates for bivalves are often too high and unrealistic and are not continuously maintained, and proceeded to use the *M. mercenaria* maximum filtration rate. Yet, hard clams, which use siphons (Doering and Oviatt, 1986), and eastern oysters have different filtration rates. For example, Riisgard (1988) reports oyster filtration and clam filtration rates (L h^{-1}) as

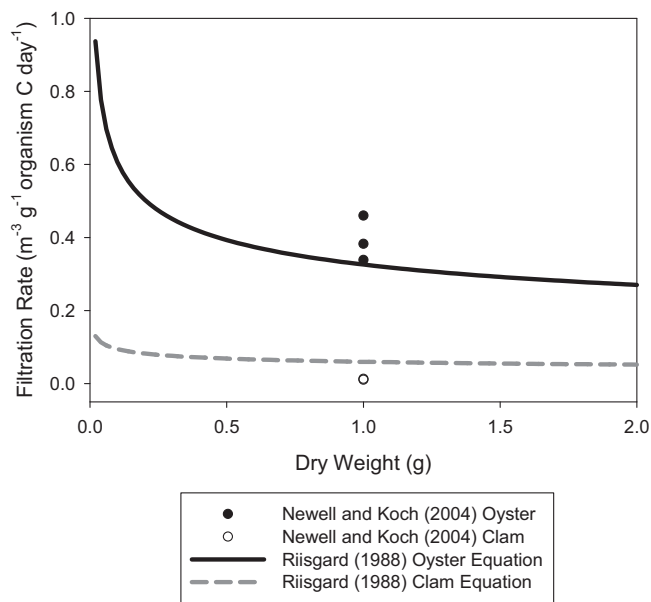


Fig. 3. Comparison of predicted and measured filtration rates for oysters and clams. Regression lines of filtration rates for clams and oysters vs. the individual g DW by Riisgard (1988) and data points of filtration rates for 1 g DW oysters and clams at 25 °C found by Newell and Koch (2004).

$FR = 6.79W^{0.73}$ and $FR = 1.24W^{0.8}$ respectively, where W is individual biomass in units of g DW (Riisgard, 1988).

Fig. 3 graphs the computed filtration rate in units of $m^3 g^{-1} organism C day^{-1}$ for clams and oysters using the equations of Riisgard (1988) and measured filtration rates from Newell and Koch (2004) at 25 °C, corrected for 1 g DW of bivalve. Oysters have much higher filtration rates than clams on a dry weight basis. This result informs my assessment that Powell et al. (1992) underestimate filtration rates simulated for oysters, a finding that conflicts with their conclusions.

3.1.2. Environmental limitation factors

In each of the reviewed oyster models, maximum filtration rates are affected by environmental limitation factors, listed in Table 1, and results below consider the model sensitivity to functions for T , TSS, and S .

3.1.2.1. Temperature limitation factors. Generally, oysters increase filtration with temperature up to an optimum. In a temperate climate, oysters are exposed to a broad range of water temperatures, which can have a great impact on filtration. Cerco and Noel (2005) and Fulford et al. (2007) employ the same function of temperature, or $f(T)$, as listed in Table 1 and graphed in Fig. 4. Cerco and Noel (2005) formulate the $f(T)$ by comparing filtration rates with temperature from the Newell and Koch (2004) and Jordan (1987) studies, and Fulford et al. (2007) acquire their $f(T)$ from Cerco and Noel (2005).

The Powell et al. (1992) model has temperature as a component of the maximum filtration equation, as described previously and adopted from the study by Doering and Oviatt (1986), thus there is no standalone $f(T)$. The weight standardized filtration rates ($m^3 g^{-1} oyster C day^{-1}$) for 1 g DW or 7.62 cm oysters are graphed against temperature in Fig. 4. Unlike the other models, the Powell et al. (1992) model does not exhibit a decrease in filtration at higher temperatures. Rather, rates increase near linearly. Predicted filtration rates vary from 0 to above $0.2 m^3 g^{-1} oyster C day^{-1}$, over a range of realistic water temperatures (Fig. 4).

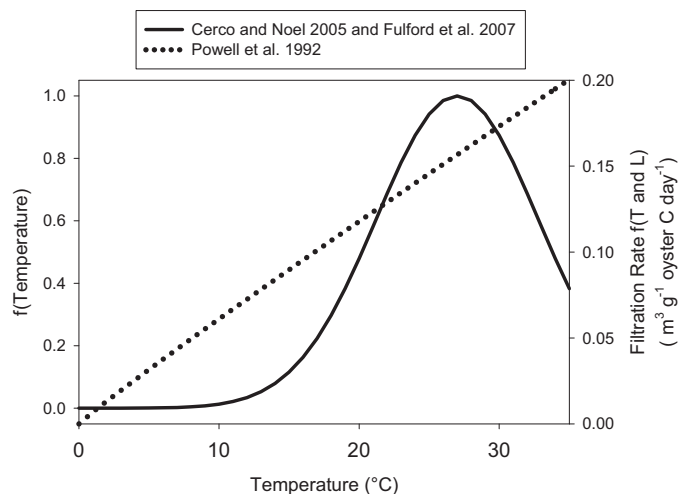


Fig. 4. Model temperature limitation functions. The $f(T)$ for the Cerco and Noel (2005) and Fulford et al. (2007) models, and the Powell et al. (1992) model's temperature dependent weight based filtration rate ($m^3 g^{-1} oyster C day^{-1}$) for a market sized oyster.

3.1.2.2. Salinity limitation factors. The $f(S)$ selected for each of the models illustrates the general mechanistic response of oysters where higher salinities favor higher filtration rates. These salinity limitation functions are listed in Table 1, and vary from a single equation to stepwise functions. A comparison of the functional form of these limitation formulations is graphed in Fig. 5.

The salinity limitation functions for each model are derived from different sources. Cerco and Noel (2005) adopt a formulation of $f(S)$ found in other parts of the Chesapeake Bay Environmental Model Package for which the oyster model is a component, parameterized using the functional response with salinity reported by Loosanoff (1953). Powell et al. (1992) also cite Loosanoff (1953), where filtration begins decreasing below a salinity of 7.5 and ceases below a salinity of 3.5. Powell et al. (1992) then formulate a $f(S) = 0$ for S less than 3.5, a $f(S) = 1$ for S greater than 7.5, and a linear increase from $f(S) = 0$ to $f(S) = 1$ between the salinities of 3.5 and 7.5. Fulford et al. (2007) cite R.I.E. Newell's unpublished data.

The models differ most in the mid-range salinities (4–12) where the increase from a $f(S) = 0$ to a $f(S) = 1$ occurs, shown in Fig. 5. The model differences of these mid-range salinities are notable at a salinity of 7, where Cerco and Noel (2005) predict a $f(S) = 0.27$, Fulford et al. (2007) a $f(S) = 0.51$, and Powell et al. (1992) a $f(S) = 0.86$.

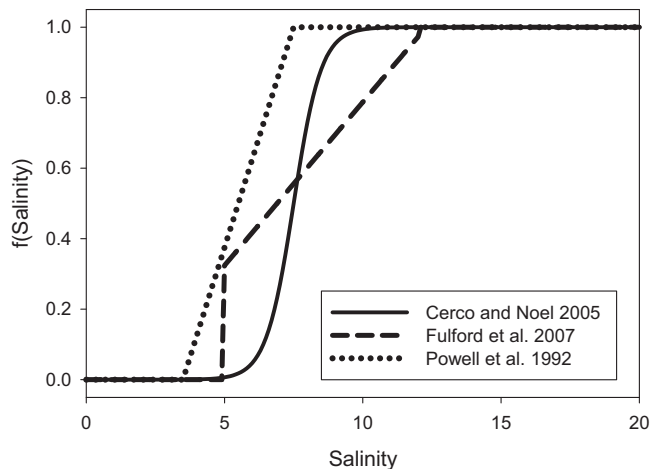


Fig. 5. Model salinity limitation functions. The $f(S)$ over different salinity ranges for the three different models.

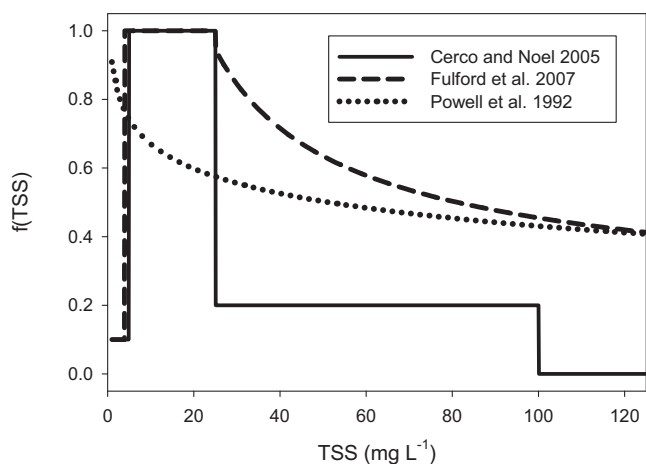


Fig. 6. Model TSS limitation functions. The $f(TSS)$ over different total suspended solid ranges for the three different models.

This near 3-fold difference in predicted limitation effects deserves additional study.

3.1.2.3. Total suspended solids limitation factors. Very high and very low levels of particulate load or TSS decrease filtration. TSS consists of both inorganic and organic particles, and oysters feed on the phytoplankton that make up a portion of these organic particles. Low TSS indicates there is low availability of phytoplankton, so oysters decrease their feeding activity (Cercio and Noel, 2005). At higher TSS levels, there may be physiological issues that decrease filtration (Loosanoff, 1962) such as clogging of the gills (Newell and Langdon, 1996).

The models' various $f(TSS)$ equations are listed in Table 1 and graphed in Fig. 6. Cercio and Noel (2005) use the Jordan (1987) biodeposition rates measured under varying TSS to formulate a general stepwise function. Fulford et al. (2007) formulate $f(TSS)$ using results from Loosanoff (1962), which examined the effect of different concentrations and types of seston on the filtration of Long Island Sound oysters. Fulford et al. (2007) also cite Newell and Langdon (1996), who describe clearance rates that increase until TSS reaches about 25 mg L^{-1} , a conclusion that can also be drawn from analyzing Jordan (1987) data. Powell et al. (1992) formulate the $f(TSS)$ using Loosanoff and Tommers (1948), which is a brief article on silt effects on feeding, expanded upon in Loosanoff (1962), which the Fulford et al. (2007) model cites. In general, these studies all appear to depend on a few experiments that indicate minimum and saturating bounds to rates of filtration in response to suspended particle concentrations.

As seen in Fig. 6, Fulford et al. (2007) and Cercio and Noel (2005) have similar responses of filtration to TSS up to a concentration of 25 mg L^{-1} , at which point the two functions diverge. Cercio and Noel (2005) eventually predicts a value of 0, while the function of Fulford et al. (2007) levels out around a value of 0.4.

Powell et al. (1992) do not predict negative impacts of low TSS on filtration like the other models (Fig. 6; Table 1). Rather, they use a logarithmically decreasing function, which produces limitations similar to that of Fulford et al. (2007) at higher TSS levels. The differences among all three models for $f(TSS)$ is highlighted in Table 2, where different levels of TSS can have very different outcomes of $f(TSS)$ depending on the model used.

3.1.3. 2009 filtration rate

The daily computed filtration rates for the three models using the 2009 forcing function dataset are graphed for comparison in Fig. 7, all showing a pattern of increased filtration during warmer

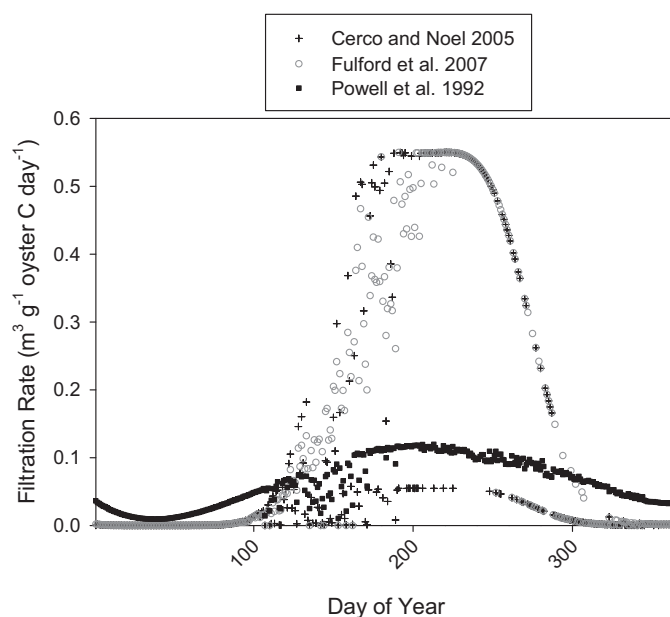


Fig. 7. Simulated 2009 biomass specific daily filtration rates ($\text{m}^3 \text{ g}^{-1} \text{ oyster C day}^{-1}$) for each model.

months. The yearly pattern for Cercio and Noel (2005) and Fulford et al. (2007) are quite similar, with variability in the daily simulated output ranging between 0 and maximum values. In contrast, Powell et al. (1992) is substantially different than the other models, having 3–4-fold consistently lower filtration in the summer months and substantially less variability. The extremes in predicted filtration rates in the late spring and summer months for all the models are likely due to variability in the salinity forcing function.

We summed the daily filtration rates to obtain the total 2009 filtration ($\text{m}^3 \text{ g}^{-1} \text{ oyster C}$), which was 45.51, 56.96, and $22.59 \text{ m}^3 \text{ g}^{-1} \text{ oyster C}$ for Cercio and Noel (2005), Fulford et al. (2007), and Powell et al. (1992) respectively. The total filtration for the Powell et al. (1992) model is about half that of the Cercio and Noel (2005) total. As shown in Fig. 7, the Powell et al. (1992) model has higher filtration in the cooler months than the other models, so even though the maximum rate is 3–4-fold less than the other two models, the yearly filtration for Powell et al. (1992) is only about 2-fold lower. In terms of uptake capabilities, this may not result in more uptake due to low food particle concentrations associated with these cooler months.

3.1.4. Model sensitivity analysis

Two types of sensitivity analyses were performed with the three models, the first altering one environmental variable to be “high”, “intermediate”, and “low” levels, while keeping other variables constant, and the second multiplying one environmental variable at a time by the maximum filtration, assuming other conditions were optimal. Sensitivity to these changes varied for the models depending on the environmental parameters tested.

Table 2
Model comparison of calculated $f(TSS)$ s for different TSS level.

Model	TSS		
	20 mg L^{-1}	30 mg L^{-1}	120 mg L^{-1}
Cercio and Noel (2005)	1	0.2	0
Fulford et al. (2007)	1	0.86	0.42
Powell et al. (1992)	0.6	0.56	0.41

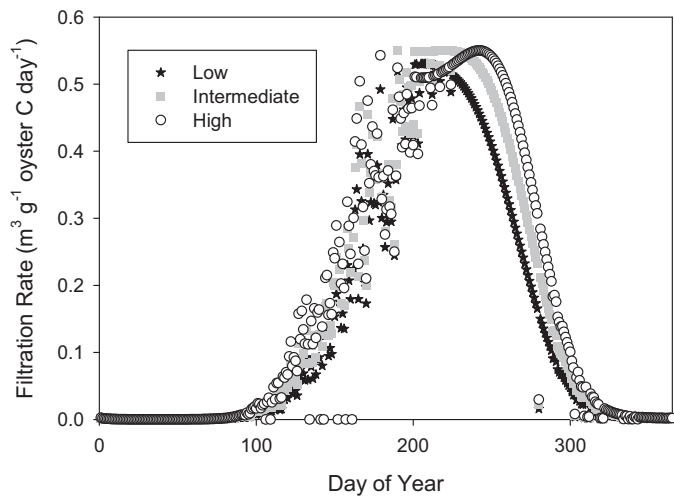


Fig. 8. Sensitivity results of daily simulated filtration rates ($\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$) for the Fulford et al. (2007) model at three levels of T interpolated to represent average conditions (“intermediate”), as well as “low” and “high values”.

3.1.4.1. Temperature. Higher temperatures increased the filtration for all models, as expected from the $f(T)$ definitions (Table 1). However, when temperature is too high, the Cerco and Noel (2005) and Fulford et al. (2007) models exhibit a dip in filtration, as depicted in Fig. 8, which graphs the results of manipulating the field-based environmental forcing conditions to reflect low, intermediate, and high conditions for the Fulford et al. (2007) model.

3.1.4.2. Salinity. For Powell et al. (1992), there are only slight differences with changes in salinity. However, low salinity decreases filtration for both the Fulford et al. (2007) model and Cerco and Noel (2005) models as shown in Fig. 9 that graphs the outcome of altering the forcing conditions.

To further isolate the effect of salinity on maximum filtration, Fig. 10 examines the effect of this limitation factor on filtration rates while keeping the other factors at an optimal value of “1”. It is clear that low salinity affected filtration between days 100 and 200 for the Fulford et al. (2007) and Cerco and Noel (2005) models. The limiting effect of salinity is greater for Cerco and Noel (2005) due to the steeper slope from $f(S)=1$ to $f(S)=0$ in the salinity limitation equation. This contrasts with a second period of lower $f(S)$ between days 300 and 365 for Fulford et al. (2007) that lowers filtration, which does not appear in the predictions of Cerco and Noel (2005). The $f(S)$ slope for Fulford et al. (2007) affects a wider range of salinities, and during the days of 300–365, Cerco and Noel (2005) considers the S optimal and Fulford et al. (2007) does not.

3.1.4.3. Total suspended solids. When TSS was altered to be low, medium, and high, Powell et al. (1992) demonstrates a clear decrease in filtration with the increase in TSS (Fig. 11), where the filtration rate for a 7.6 cm oyster is plotted over the time period of the simulation. Cerco and Noel (2005) and Fulford et al. (2007) show minimal changes in filtration rate in response to the TSS levels forced in this simulation exercise. When $f(\text{TSS})$ is only multiplied by the maximum filtration, some variability between Cerco and Noel (2005) and Fulford et al. (2007) is evident. Generally, the TSS is in the optimal range for both the Cerco and Noel (2005) and Fulford et al. (2007) models, but there are some days with suboptimal TSS levels. These suboptimal days are more frequent when using the $f(\text{TSS})$ provided by Cerco and Noel (2005). In this instance, the sub-optimal TSS levels are created from TSS concentrations that are at the lower TSS threshold of the $f(\text{TSS})$ functions, and the difference between the number of days between the models was due to Cerco

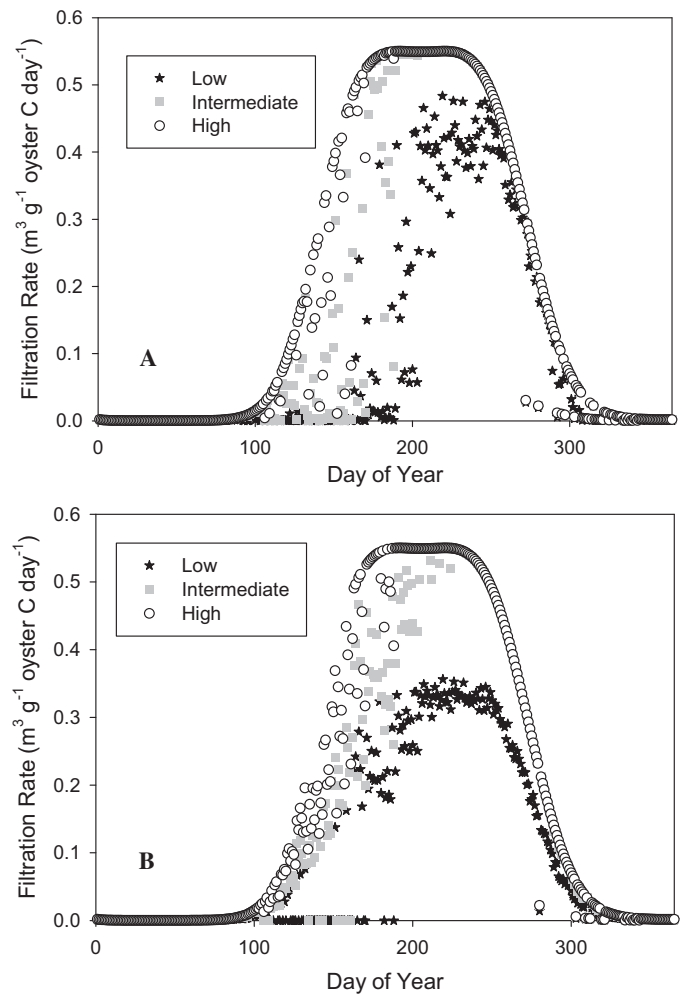


Fig. 9. Sensitivity results of daily simulated filtration rates ($\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$) for the (a) Cerco and Noel (2005) and (b) Fulford et al. (2007) models at three levels of S.

and Noel (2005) encompassing concentrations less than 5 mg L^{-1} in the low range while Fulford et al. (2007) has low concentrations as less than 4 mg L^{-1} (Table 1).

3.2. Filtration rate model

3.2.1. Individual-based maximum filtration rate

The three models we assessed are examples of filtration rate formulations in the literature, but other filtration rate empirical studies and models were also explored to more fully determine what might be the best way of simulating this process in oysters. A compilation of this literature review is presented in Table 3, listing those studies and models examining oyster filtration, including a range of filtration rates ($\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$), maximum filtration rates ($\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$) corrected for 1 g DW oysters, the variable examined in the study, and the method of measurement.

The three models and the studies listed in Table 3 report a range of 0.08–0.54 for 1 g DW oyster maximum filtration rates ($\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$). This is an extraordinarily wide range of values. Some of this variation may be attributed to the way the filtration rate is measured.

To find a maximum filtration rate for the purposes of this modeling effort, we calculated the mean maximum rate from the sources in Table 3 and the three models used in the comparison, excluding Comeau et al. (2008) that experimented with low temperatures. This mean rate is calculated to be 0.34

Table 3

A review of oyster filtration rates. This table compiles filtration rates from a number of studies and includes the study's citation, filtration rate ($\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$), oyster size, filtration rate standardized for a 1 g DW oyster ($\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$), method used to measure filtration rate, and the parameter tested in each study.

Source	Filtration rate range ^a	Study oyster size ^{**}	Maximum rate ^a	Measurement method	Experimental condition
Barrera-Escorcia et al. (2012)	0.02–0.07	1.38	0.08	Change in algal cells using a Neubauer chamber	NA
Comeau et al. (2008)	0.01–0.12	1.1	0.12	Change in particles using a Coulter counter	T 0–9 °C
Gerritsen et al. (1994)	0.24	1	0.24	Literature search	NA
Grizzle et al. (2008)	0–0.48	0.19	0.30	In situ chlorophyll- <i>a</i> changes	NA
Langefoss and Maurer (1975)	0.13–0.40	0.21–0.42	0.28	Change in algal cells using a Coulter counter	Food content
Loosanoff (1958)	0–0.39	1.99	0.47	Kymograph	T 2–38 °C
Loosanoff and Nomejko (1946)	0.32–0.46	1.87	0.54	Dockside kymograph	Tide/light
Newell et al. (2005)	0–0.46	1	0.46	Interpretation of Jordan (1987)	NA
Newell and Koch (2004)	0.04–0.46	1	0.46	Change in light measurements	T 15–25 °C
Palmer (1980)	0–0.26	1	0.26	Change in algal cells using a Coulter counter	Light and food type
Riisgard (1988)	0.33–0.69	0.06–0.99	0.33	Change in particles using a Coulter counter	NA

^a $\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$.

^{**} g DW.

^a Standardized for 1 g DW oyster in units of $\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$.

(± 0.14) $\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$ for a 1 g DW oyster, comparable to the maximum rate reported by Riisgard (1988) (Table 3). For simplicity in modeling oyster filtration, this rate is converted from per g oyster C to per g DW using the conversion of 0.5 g C: 1 g DW (Cercio and Noel, 2005), resulting in a maximum filtration rate of 0.17 (± 0.07) $\text{m}^3 \text{g}^{-1} \text{DW day}^{-1}$. We strongly recommend that simulations using this mean value also incorporate the uncertainty of

this estimate into their simulations by applying some stochasticity to this parameter, using the standard deviation reported here to constrain the variability of the reported literature values.

We adapted the size-dependent allometric formulation common to other studies and determined the weight exponent, *b*, from the literature. This formulation is also common in the metabolic theory of ecology in which the exponent *b* has been found to fall between $2/3$ and 1, with $3/4$ being the standard and theoretically derived value (Sibly et al., 2013; Brown et al., 2004; Savage et al., 2004). We thus decided to use 0.75 following the metabolic theory of ecology. A value of 0.72 has been confirmed in a range of filter-feeding bivalves reviewed by Cranford et al. (2011), providing further support for an exponent following the MTE predictions. From these findings, the maximum filtration formulation of $FR = aW^b$ is parameterized using a value of 0.75 for the weight exponent, *b*, and the constant *a* is defined as the maximum filtration rate, 0.17 $\text{m}^3 \text{g}^{-1} \text{DW day}^{-1}$. This can be used to determine the filtration rate of an individual of weight, *W* (g DW).

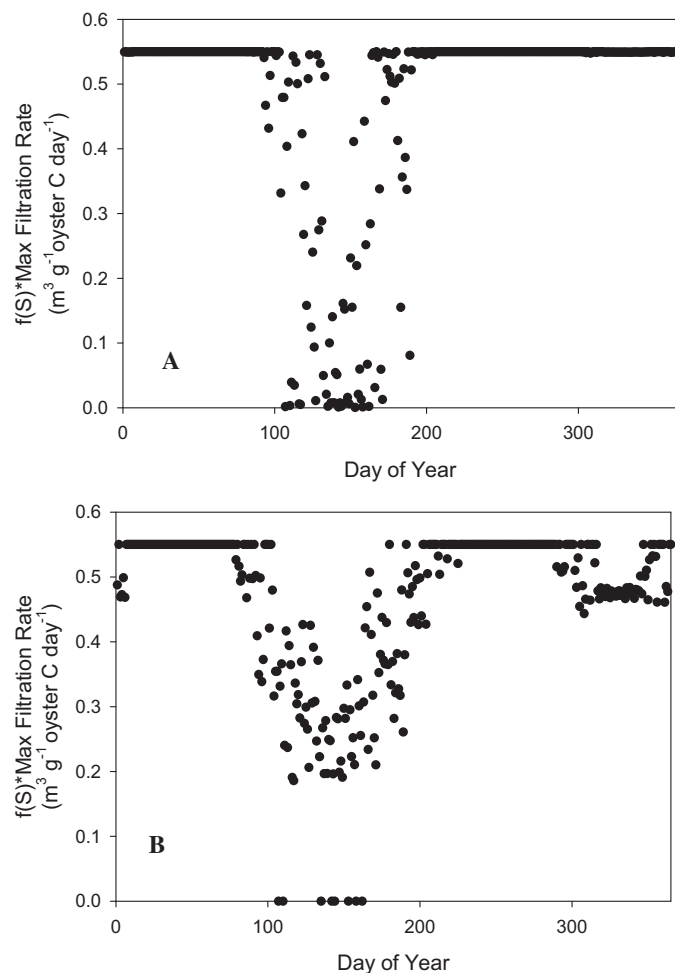


Fig. 10. Sensitivity results of salinity influenced simulated filtration rates ($\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$) for the (a) Cercio and Noel (2005) and (b) Fulford et al. (2007) models.

3.2.2. Limitation factors

We assessed the limitation factors for which functions we feel should be included in the new model. For this model, DO is assumed optimal and is not incorporated. The model comparison resulted in the conclusion that the temperature function needs to be modified from the Cercio and Noel (2005) and Fulford et al.

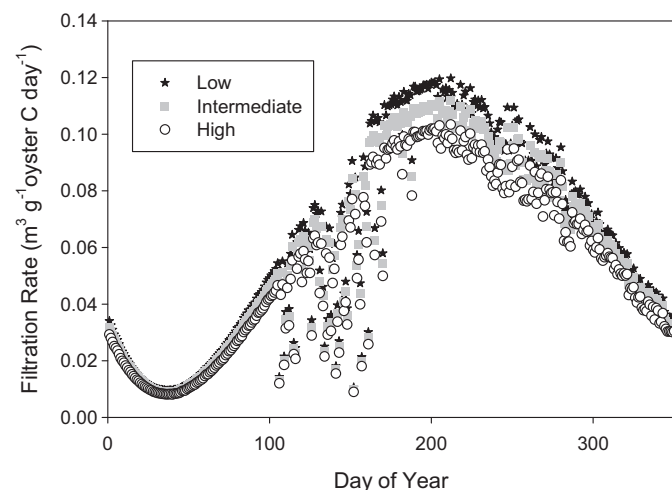


Fig. 11. Sensitivity results of daily simulated filtration rates ($\text{m}^3 \text{g}^{-1} \text{oyster C day}^{-1}$) for the Powell et al. (1992) model at three levels of TSS.

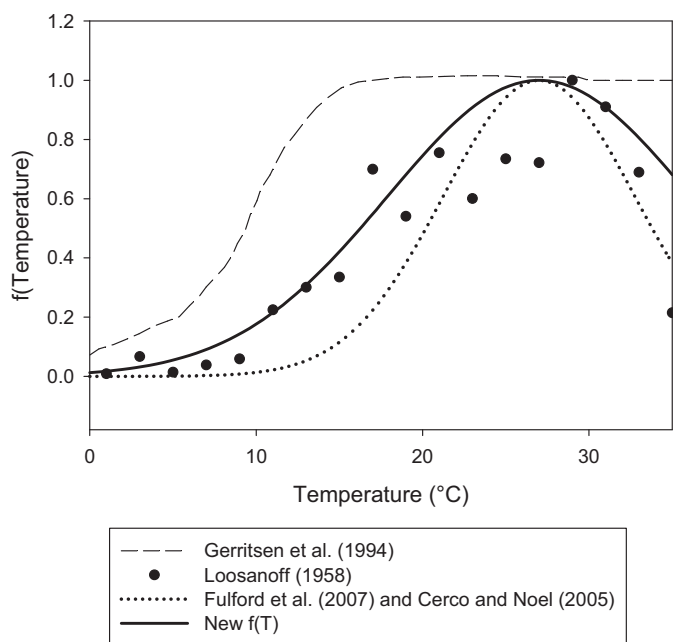


Fig. 12. Comparison of temperature limitations, including the $f(T)$ found in Gerritsen et al. (1994), Fulford et al. (2007) and Cerco and Noel (2005), and Loosanoff (1958), and the new $f(T)$.

(2007) models. These models have very low filtration in the winter months and high filtration in the summer, while Powell et al. (1992) has more filtration during the winter months than the other models. According to Comeau et al. (2008) (Table 3), at low temperatures, there should be some filtration. This is better represented by the Powell et al. (1992) predictions. Upon examining the filtration rates calculated by Cerco and Noel (2005) using a temperature function derived from the Jordan (1987) study, oysters exhibit a slightly higher filtration rate than Cerco and Noel (2005)'s $f(T)$ approximated at lower temperatures. The $f(T)$ is formulated to be essentially 0 in the winter months, but in reality we know from Comeau et al. (2008) that some filtration continues to occur. On the other hand, this filtration change may not lead to drastic uptake changes in modeled output because food is limited in the winter months as well.

Given these considerations, we parameterized a new $f(T)$, adapting the Cerco and Noel (2005) and Fulford et al. (2007) formulation for $f(T)$, for simplicity here referred to as Fulford et al. (2007). Upon researching other maximum filtration rates, additional temperature functions surfaced. Fig. 12 graphs the $f(T)$ for Gerritsen et al. (1994) (Table 3), which reports general bioenergetics bivalve equations, and Fulford et al. (2007). Fig. 12 also shows Loosanoff (1958) (Table 3) filtration rates, dependent on temperature, translated into fractions of the maximum rate. Upon examining these studies, each with varying temperature functions, the $f(T)$ formulation was re-parameterized to give a new $f(T)$, one that falls mid-way between the data points, which are also plotted in Fig. 12:

$$f(T) = e^{(-0.006*(T-27)^2)} \quad (12)$$

Fulford et al. (2007) limitations for S and TSS (Table 1) are incorporated in the new model. The $f(S)$ captures more variability in filtration from salinity changes, and there are less drastic decreases in filtration, which occur using the Cerco and Noel (2005) model for salinities of 7–10. We see these as more suitable qualities for limitation functions, providing there is not a biologically justifiable reason for more sensitive responses (for example in the case of the drop in filtration rate to zero at high suspended solids concentrations).

The Fulford et al. (2007) TSS limitation combines the components of the limitations of Cerco and Noel (2005) and Powell et al. (1992), which we see as preferable from our analysis. There is no filtration at very low concentrations, in agreement with Cerco and Noel (2005), but it also incorporates a logistic decrease at higher concentrations, similar to Powell et al. (1992). High TSS can significantly decrease the filtration rate (Table 1; Fig. 6), but this was not seen in the sensitivity analysis as the TSS did not reach these levels. The Fulford et al. (2007) model's use of a logarithmic function after 25 mg L^{-1} , reaching a $f(\text{TSS})$ of about 0.4 for the higher TSS levels, would give less drastic effects on filtration than the Cerco and Noel (2005) model (Table 1; Fig. 6).

In this discussion of functional responses of oyster filtration to physical and chemical forcings, questions may arise regarding local adaptation of populations to temperature, salinity, or other environmental conditions. Whether populations of eastern oysters vary in their response to the limitation factors identified here is an open question, and likely deserves greater attention and experimental efforts. To date there is only one published study of local adaptation in oysters (Burford et al., 2014) and insufficient empirical data to consider parameterization of limitation factors that might be applied to a specific genotype. Future research might consider borrowing from the agricultural approach of "common garden" experiments, where different oyster genotypes are identified and exposed to a gradient of T , S , and TSS conditions.

3.2.3. Model equations

Combining all the elements of the above analysis together, and assuming there is no limit on oxygen, results in an amended filtration rate model $FR_{(i)}$ ($\text{m}^3 \text{ oyster}^{-1} \text{ day}^{-1}$) that includes limitation factors for T , S , and TSS for and individual (i) of weight, W (g DW):

$$FR_{(i)} = 0.17 * W^{0.75} * f(T) * f(S) * f(\text{TSS}) \quad (13)$$

The environmental limitation equations include:

$$f(T) = e^{(-0.006*(T-27)^2)} \quad (12)$$

$$f(S) = 0 \text{ when } S < 5; 0.0926 * S - 0.139 \text{ when } 5 \leq S \leq 12; \\ 1 \text{ when } S > 12 \quad (14)$$

(Fulford et al., 2007)

$$f(\text{TSS}) = 0.1 \text{ when } \text{TSS} < 4 \text{ mg L}^{-1}; 1 \text{ when } 4 \leq \text{TSS} \leq 25 \text{ mg L}^{-1}; \\ 10.364 * \log(\text{TSS})^{-2.0477} \text{ when } \text{TSS} > 25 \text{ mg L}^{-1} \quad (15)$$

(Fulford et al., 2007)

4. Conclusion

Our review identifies a remarkably diverse array of approaches for modeling eastern oyster filtration rates. Our retrospective simulation analysis of these filtration rate models has permitted a "Goldilocks" assessment, selecting aspects of each formulation to improve model oyster filtration rates. Cerco and Noel (2005) and Fulford et al. (2007) predict high maximum filtration rates in comparison to other literature values, while Powell et al. (1992) uses a relatively low maximum filtration rate, which was based on clams, not the eastern oyster. Fulford et al. (2007) simulate a more temperate response of oyster filtration to changes in S and TSS when compared to Cerco and Noel (2005). Fulford et al. (2007) and Cerco and Noel (2005) did not capture winter filtration with their $f(T)$, while Powell et al. (1992) showed higher filtration in the cooler months. Our proposed filtration rate model combining elements of

these formulations with a re-parameterized temperature function takes a conservative approach in selecting less sensitive features of the published models and incorporating some of the variability inherent in published maximum filtration rates.

Accurate filtration rates are imperative to understanding the impacts oysters can have on water quality, thus analysis of these models allowed us to delve into how various aspects of the mechanisms and structure of filtration rate formulations may vary. Our thorough literature search revealed a remarkably wide range of measured maximum filtration rates, and we conclude this study by proposing a maximum filtration of $0.17 (\pm 0.07) \text{ m}^3 \text{ g}^{-1} \text{ DW day}^{-1}$ for a 1 g DW oyster while cautioning model practitioners to consider the sensitivity of these formulations to selection of this value. We strongly recommend that the differences revealed in this review warrant further exploration, in some cases revisiting basic laboratory experiments to more unequivocally determine how eastern oysters respond to their environment. Such experiments could be combined with efforts to describe the genetic diversity of populations and its effects on rate processes.

In addition to more rigorously considering the formulation and parameterization used to model filtration rates in oysters, estimating the impact of oysters on water quality also requires accurate estimates of oyster population size, and an understanding of the impact of associated fauna that impact biogeochemical processing on oyster reefs (e.g. Kellogg et al., 2013; Gedan et al., 2014). Given the uncertainty associated with estimating each of these factors, it is particularly important that we approach predictions of any one factor with care. Any application of existing filtration rate models must incorporate understanding of the responsiveness of those models explored here along with a careful consideration of how population size and ecosystem effects may impact modeled estimates.

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