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Ecological Modelling

Review

A review of existing eastern oyster filtration rate models

Melinda K. Ehrich*, Lora A. Harris

University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory, P.O. Box 38, Solomons, MD 20688, USA

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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 (Cerco 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) $m^3\,g^{-1}$ 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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* Corresponding author. Tel.: +1 540 6865365.
  E-mail address: forsyth@cbl.umces.edu (M.K. Ehrich).

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 m^3 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 1800 s (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:

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

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.

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

The maximum filtration, Fr_{max}, is the maximum rate oysters can filter water (m^3 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