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A MASS BALANCE MODEL TO ASSESS FOOD LIMITATION IN COMMERCIAL OYSTER NURSERIES

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ABSTRACT This work aims to provide oyster farmers a tool to estimate the stock biomass to hold in their nursery. Herein, a steady-state single-compartment mass balance model, which includes the feeding activity of oyster spat, was developed. This model applies to nurseries such as floating upweller systems or land-based tanks and estimates (1) the optimal stock as a function of external food concentration or (2) the food concentration required for a given stock. The model was implemented for the Pacific oyster (*Crassostrea gigas* Thunberg) and is available online: http://seaplusplus4.com/oysterspatbud.html. The model was evaluated using published data and further tested by simulating a general rule of thumb regarding the spat-holding capacity for a given nursery. According to a general rule of thumb, 1 hectare of a shallow pond can hold between 1 and 3 tons of spat. The model allows to further specify the rule depending on the spat grade to stock. If the spat is around 0.38 g, the model estimates a holding stock within the range of the rule of thumb; however, if the spat is around 0.04 g, the biomass stock sustained is lower (between 0.7 and 2 tons).

KEY WORDS: Pacific oyster, spat, nursery, mass balance, simple models, food limitation, carrying capacity

INTRODUCTION

Bivalves accounted for 21% of global aquaculture production by volume (excluding seaweeds) in 2015, of which oysters represent 36% of the bivalve total (FAO 2017). Aquaculture is the main source for oyster production worldwide (~97%, FAO 2017). According to FAO (2017) datasets, in 2015, Asia contributed around 95% of the global oyster farming volume (corresponding to about 81% in value); the remaining 5% of the oyster aquaculture production is from North and South America and Europe. Oyster farming is generally regarded as a sustainable sector within the aquaculture industry, and it is widely recognized that oyster production provides a set of ecosystem services such as nutrient cycling, reduction of eutrophication symptoms, habitat provision to other marine species, and restocking of wild populations (Coen et al. 2011, Ferreira et al. 2011, Gallardi 2014, Rose et al. 2014, Baker et al. 2015, Depiper et al. 2017). In addition, it can integrate the organic extractive component of integrated multitrophic aquaculture systems. Furthermore, shellfish farmers who grow these extractive species have a major interest in promoting good water quality to ensure industry sustainability (Dewey et al. 2011). Shellfish farming is promoted and recognized by some governmental stakeholders as providing social and economic benefits, as well as ecological benefits, e.g., NOAA established in 2011 the USA National Shellfish Initiative.

Most oyster farming practices depend on the natural environment, and like many other farmed species, oyster growth and production hinges on a complex interaction of factors such as temperature, salinity, freshwater flow/rainfall, current speed, density, food concentration and phytoplankton species composition, food partitioning with other species, and disease outbreaks. Modeling can be useful for understanding the feedback between the farming and environmental systems, and the effects on production. As an example, carrying capacity models are often applied for management and spatial planning of filter feeder production, as reviewed by Byron and Costa-Pierce (2013) and by Filgueira et al. (2015). Many other model applications exist for production management of oysters and other shellfish both at ecosystem and farm scales (Ferreira et al. 2008, 2011, Gangnery et al. 2011, Nobre et al. 2011, Saurel et al. 2014, Filgueira et al. 2015). Farmers are seldom the end users of these models. A strategy to make available simulation models that embed scientific research to farmers is to shift from (1) complex models (in terms of spatial and temporal resolutions, processes simulated), which allow detailed simulations but require datasets that might not be feasible to gather by a commercial unit, to (2) simple models or at least with simple interfaces that can be directly used by farmers and provide estimates of key questions for production; e.g., http://www.farmscale.org/ and Nobre et al. (2017).

Most developments of shellfish models are for adult animals, and there are only a few models that are suited to simulate initial development stages (Rico-Villa et al. 2010). Mass balance models can help estimate food requirements for a given spat stock (the initial seeding stock or the expected stock to harvest). Furthermore, spat are commonly reared in extensive nurseries that rely on natural seston concentration to feed the stock or are coupled with tanks designed to promote algal blooms (Helm & Bourne 2004). For these systems, it is more difficult to provide guidance on seed stock density given that local food concentration is variable, by contrast to hatcheries. For hatcheries and nurseries fed with algal cultures, there are manuals of oyster culture that include guidance for feed ration calculations (Breese & Malouf 1975, Helm & Bourne 2004, Wallace et al. 2008, Tetrault 2012). Guidance for cultivation practice in spat nurseries is provided based on rules of thumb about the typical number of seed per area or stock biomass to hold in each system, based on expert knowledge. On the other side of the

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spectrum is extensive research about the effects of body weight, temperature, food concentration, and feeding strategy, among others, on the filtration rate, assimilation efficiency, and growth of bivalves (Walne 1972, Winter 1978, Gerdes 1983a, Bacher & Baud 1992, Bougrier et al. 1995, Ward & Shumway 2004, Cranford et al. 2011, Tamayo et al. 2014).

Mass balance models that use simple user interfaces can help translating scientific knowledge into practical guidance for commercial nurseries. The goal of this article is to develop and evaluate this concept using Pacific oyster (*Crassostrea gigas* Thunberg) spat as a case study for model implementation and evaluation for structures such as a floating upweller system (FLUPSY) or land-based tanks, silos, or trays. The authors aim to make the model available online for wider use and to ensure it tackles two questions that arise when planning or managing an oyster nursery: (1) how much food is required to sustain a given stock and/or (2) for a typical range of food available in the surrounding environment, what is the maximum biomass that can be stocked.

METHODOLOGY

Conceptual Model Description

This model consists of a single-compartment mass balance at steady state for a given nursery (Fig. 1):

$$\mathrm{MF}_{\mathrm{Food\_in}} + \mathrm{MF}_{\mathrm{Phyto\_Growth}} = \mathrm{MF}_{\mathrm{Food\_out}} + \mathrm{MF}_{\mathrm{Food\_Cleared}}, \quad (1)$$

where, the mass fluxes (MF) are defined as $\mathrm{MF}_{\mathrm{Food\_in}}$ (Eq. 2) is the food inflow which can be an external natural food resource or feed ration; $\mathrm{MF}_{\mathrm{Phyto\_Growth}}$ (Eq. 4) is the phytoplankton community net growth rate to accommodate the case of nurseries with natural blooming ponds (as illustrated by Helm & Bourne 2004), otherwise $\mathrm{MF}_{\mathrm{Phyto\_Growth}}$ is set to zero; $\mathrm{MF}_{\mathrm{Food\_out}}$ (Eq. 5) is the food outflow; and $\mathrm{MF}_{\mathrm{Food\_Cleared}}$ (Eq. 6) is the food cleared by oysters. To allow model generality, the MF are expressed using several optional oyster food indicators, such as phytoplankton (using chl-*a* as a proxy), particulate organic matter (POM), or particulate organic carbon (POC). The corresponding units are shown in Table 1.

$\mathrm{MF}_{\mathrm{Food\_in}}$ (Eq. 2), is given by the external food concentration ($[\mathrm{Food}]_{\mathrm{External}}$, units defined in Table 1) multiplied by the water inflow rate (WaterInflow, in $\mathrm{m}^3\cdot\mathrm{day}^{-1}$):

$$\mathrm{MF}_{\mathrm{Food\_in}} = [\mathrm{Food}]_{\mathrm{External}} \cdot \mathrm{WaterInflow} \cdot \mathrm{M3toL}. \quad (2)$$

The user can define WaterInflow as the average flow rate or by the operational turnover rate (TurnoverRate, day^{-1}) multiplied by the nursery volume (Eq. 3):

$$\mathrm{WaterInflow} = \mathrm{TurnoverRate} \cdot V_{\mathrm{nursery}}. \quad (3)$$

$\mathrm{MF}_{\mathrm{Phyto\_Growth}}$ (Eq. 4) is given by the phytoplankton community net growth rate ($\mathrm{Growth}_{\mathrm{phyto}}$, day^{-1}) multiplied by the phytoplankton mass inside the nursery:

$$\mathrm{MF}_{\mathrm{Phyto\_Growth}} = \mathrm{Growth}_{\mathrm{phyto}} \cdot [\mathrm{Food}]_{\mathrm{nursery}} \cdot V_{\mathrm{nursery}} \cdot \mathrm{fraction}_{\mathrm{phyto/food}} \cdot \mathrm{M3toL}. \quad (4)$$

Here, $[\mathrm{Food}]_{\mathrm{nursery}}$ (units defined in Table 1) is the food concentration inside the nursery which is a constant because of the steady-state assumption. The sinks and sources of the mass balance are therefore solved to give that concentration in the nursery system. As reviewed by Cranford et al. (2011), it appears that several bivalve species regulate clearance rate to maximize energy. In accordance with their review, several authors indicate that a bivalve's clearance rate depends on food concentration, showing an initial peak at low concentrations followed by a decline with increasing seston concentrations. Thus, $[\mathrm{Food}]_{\mathrm{nursery}}$ is a key model parameter used in the model as the optimum concentration to maintain in the production unit. Depending on the available data, $[\mathrm{Food}]_{\mathrm{nursery}}$ can be parameterized as the minimum food concentration that maximizes ingestion or as the optimum concentration for growth. V_{nursery} (m^3) is the nursery water volume, and $\mathrm{fraction}_{\mathrm{phyto/food}}$ is the fraction of phytoplankton in the food. For the cases where the food indicator is POM or POC, the average fraction of phytoplankton in the food must be defined (otherwise $\mathrm{fraction}_{\mathrm{phyto/food}} = 1$).

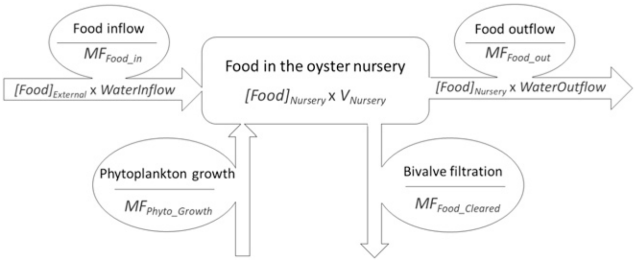


Figure 1. Conceptual model for the oyster nursery.

$\mathrm{MF}_{\mathrm{Food\_out}}$ (Eq. 5), is given by $[\mathrm{Food}]_{\mathrm{nursery}}$ multiplied by the water outflow rate (WaterOutflow, in $\mathrm{m}^3\cdot\mathrm{day}^{-1}$), which is considered equal to the WaterInflow:

$$\mathrm{MF}_{\mathrm{Food\_out}} = [\mathrm{Food}]_{\mathrm{nursery}} \cdot \mathrm{WaterOutflow} \cdot \mathrm{M3toL}. \quad (5)$$

$\mathrm{MF}_{\mathrm{Food\_Cleared}}$ (Eq. 6) is given by the $[\mathrm{Food}]_{\mathrm{nursery}}$ multiplied by the water volume cleared by the standing stock in a given period of time ($\mathrm{ClearanceRate}_{\mathrm{oyster}} \cdot \mathrm{Stock} \cdot \mathrm{DWtoFW} \cdot \mathrm{kg\_to\_mg}$):

$$\mathrm{MF}_{\mathrm{Food\_Cleared}} = [\mathrm{Food}]_{\mathrm{nursery}} \cdot \mathrm{ClearanceRate}_{\mathrm{oyster}} \cdot \mathrm{Stock} \cdot \mathrm{DWtoFW} \cdot \mathrm{kg\_to\_mg}. \quad (6)$$

Here, $\mathrm{ClearanceRate}_{\mathrm{Oyster}}$ ($\mathrm{L}\cdot\mathrm{mg\ DW}^{-1}\cdot\mathrm{h}^{-1}$) is the oyster-specific clearance rate, Stock (in kg) is the spat total biomass in the tanks, and DWtoFW (–) is the conversion ratio of dry weight (DW):fresh weight (FW) with shell. $\mathrm{ClearanceRate}_{\mathrm{Oyster}}$ is a function of seed weight and water temperature (Eq. 7) which must be parameterized per species (or if data are available for a strain within a line):

$$\mathrm{ClearanceRate}_{\mathrm{oyster}} = f(\mathrm{WaterTemperature}, \mathrm{SeedWeight}). \quad (7)$$

M3toL, kg_to_mg, and kg_to_g are conversion factors for unit consistency in Eqs. 2–8.

The overall aim of this model is to estimate (1) the required food inputs for a given stock biomass; and (2) the maximum stock biomass for a given typical external food concentration. To address that objective Eqs. 2–6 are replaced into the mass balance equation (Eq. 1) and solved for $[\mathrm{Food}]_{\mathrm{External}}$ (Eq. 8) and for TotalStock (Eq. 9) as follows:

TABLE 1.

Oyster food indicators and corresponding model units.

Oyster food indicator		Corresponding model units			
		Food concentration: $[\text{Food}]_{\text{External}}$ and $[\text{Food}]_{\text{nursery}}$		Food fluxes: $\text{MF}_{\text{Food\_in}}$, $\text{MF}_{\text{Phyto\_Growth}}$, $\text{MF}_{\text{Food\_out}}$, and $\text{MF}_{\text{Food\_Cleared}}$	
Phytoplankton (or a proxy chl-*a*)	Algae biovolume	Per water volume	mm^3 algae$\cdot\text{L}^{-1}$	Per time	mm^3 algae$\cdot\text{day}^{-1}$
	Cell count		algal cells$\cdot\mu\text{L}^{-1}$		10^6 algal cells$\cdot\text{day}^{-1}$
	Algal mass		mg algae$\cdot\text{L}^{-1}$		mg algae$\cdot\text{day}^{-1}$
	Chl-*a* mass		μg Chl-*a*$\cdot\text{L}^{-1}$		μg Chl-*a*$\cdot\text{day}^{-1}$
POM	Mass		mg POM$\cdot\text{L}^{-1}$		mg POM$\cdot\text{day}^{-1}$
POC	Mass		mg POC$\cdot\text{L}^{-1}$		mg POC$\cdot\text{day}^{-1}$

$$[\text{Food}]_{\text{External}} = [\text{Food}]_{\text{nursery}} \cdot \left(1 - \text{Growth}_{\text{phyto}} \cdot \frac{V_{\text{nursery}}}{\text{WaterInflow}} \cdot \text{fraction}_{\text{phyto/food}} + \frac{\text{ClearanceRate}_{\text{oyster}}}{\text{WaterInflow}} \cdot \text{Stock} \cdot \text{DWtoFW} \cdot \text{kg\_to\_g}\right) \tag{8}$$

$$\text{Stock} = \frac{[\text{Food}]_{\text{External}} \cdot \text{WaterInflow} + [\text{Food}]_{\text{nursery}} \cdot (\text{Growth}_{\text{phyto}} \cdot V_{\text{nursery}} \cdot \text{fraction}_{\text{phyto/food}} - \text{WaterInflow})}{[\text{Food}]_{\text{nursery}} \cdot \text{ClearanceRate}_{\text{oyster}} \cdot \text{DWtoFW} \cdot \text{kg\_to\_g}}. \tag{9}$$

To be useful for real farms, the model was extended to consider the simultaneous cultivation of several spat grades. Equations 8 and 9 are thus respectively replaced by the following equations:

(1) Equation 10 to estimate the required external food concentration considering the summation of the volume cleared per grade ($\sum \text{ClearanceRate}_{\text{Oyster\_PerGrade}} \cdot \text{Stock}_{\text{PerGrade}}$):

$$[\text{Food}]_{\text{External}} = [\text{Food}]_{\text{nursery}} \cdot \left(1 - \text{Growth}_{\text{phyto}} \cdot \frac{V_{\text{nursery}}}{\text{WaterInflow}} \cdot \text{fraction}_{\text{phyto/food}} + \frac{\sum \text{ClearanceRate}_{\text{Oyster\_PerGrade}} \cdot \text{Stock}_{\text{PerGrade}}}{\text{WaterInflow}} \cdot \text{DWtoFW} \cdot \text{kg\_to\_g}\right) \tag{10}$$

(2) Equation 11 to estimate the total maximum stock (TotalStock, in kg) considering a weighted clearance rate ($\sum \text{ClearanceRate}_{\text{Oyster\_PerGrade}} \cdot \text{Stock}_{\%\text{PerGrade}}$):

$$\text{TotalStock} = \frac{[\text{Food}]_{\text{External}} \cdot \text{WaterInflow} + [\text{Food}]_{\text{nursery}} \cdot (\text{Growth}_{\text{phyto}} \cdot V_{\text{nursery}} \cdot \text{fraction}_{\text{phyto/food}} - \text{WaterInflow})}{[\text{Food}]_{\text{nursery}} \cdot \sum \text{ClearanceRate}_{\text{Oyster\_PerGrade}} \cdot \text{Stock}_{\%\text{PerGrade}} \cdot \text{DWtoFW} \cdot \text{kg\_to\_g}}. \tag{11}$$

To provide outputs of interest to farmers, the final model equations (Eqs. 10 and 11) are solved for two values of phytoplankton growth ($\text{Growth}_{\text{phyto}}$) and two values of external food concentration ($[\text{Food}]_{\text{External}}$). With this approach, the outputs encompass the range of scenarios within which a nursery operates, given that these two parameters are highly variable within a day.

All the model parameters are given in Table 2.

As a case study, in this work, the model is applied to the Pacific oyster. Parameterization for this species is presented in Table 3.

Model Parameterization and Evaluation for the Pacific Oyster

$[\text{Food}]_{\text{nursery}}$, DWtoFW (–), and $\text{ClearanceRate}_{\text{Oyster}}$ are species specific and were parameterized (Table 3) for the Pacific oyster based on the published data of spat growth experiments.

$[\text{Food}]_{\text{nursery}}$ was parameterized for the Pacific oyster spat based on Tamayo et al. (2014) which tested three feed concentrations (0.5, 3, and 6 $\text{mm}^3\cdot\text{L}^{-1}$); the medium level was chosen, given it corresponded to the highest clearance rate (for the biological meaning of $[\text{Food}]_{\text{nursery}}$, see **Conceptual model description**). That concentration level (which converts to 44 algal cells$\cdot\mu\text{L}^{-1}$ as per rationale explained herein) is comparable with the range indicated by Walne (1972) as the optimum for growth, around 30–40 algal cells$\cdot\mu\text{L}^{-1}$. Tamayo et al. (2014) provide the conversion of the algal biovolume into POM and POC. Conversion into mg algal$\cdot\text{L}^{-1}$ considered that the algal cell has the same density of water following Suthers and Rissik (2009). For converting the biovolume ($\text{mm}^3\cdot\text{L}^{-1}$) into algal cell count (algal cells$\cdot\mu\text{L}^{-1}$), the average cell biovolume for the species used in the work by Tamayo et al. (2014), *Isochrysis galbana* Parke, of around 68 $\mu\text{m}^3\cdot\text{cell}^{-1}$ (Ishiwata et al. 2013) was considered. Finally, conversion into Chl-*a* was carried out using the general conversion ratio of C:Chl-*a* of around 50 (Reynolds 2006). All values are shown in Table 3.

Gerdes (1983a) carried out a set of experiments to study clearance rates of small-size oysters ranging from 0.005–0.811 g

TABLE 2.

List of model parameters.

Parameter type		Parameter (Unit)	Description
Farm parameters	General settings	V_{nursery} (m^3)	Water volume of the nursery. The boundaries of the system can be the volume encompassed by the FLUPSY area or can further include adjacent ponds for naturally grown phytoplankton communities.
		WaterInflow ($m^3 \cdot day^{-1}$)	Average water flow rate into the nursery.
		TurnoverRate (day^{-1})	Number of volume renewals per day. Should be consistent with the system boundary.
		WaterTemperature (°C)	An average value should be provided. Temperature inputs are limited to the range between 4 and 30°C.
		$\text{SeedWeight}_{\text{PerGrade}}$ (g)	
		Food indicator	To choose from Table 1.
	Model solved for $[\text{Food}]_{\text{External}}$	$\text{Stock}_{\text{PerGrade}}$ (kg)	Stock biomass per grade.
	Model solved for TotalStock	$\text{Stock\%}_{\text{PerGrade}}$ (-)	Fraction of the stock for a given grade relative to the total biomass.
		$[\text{Food}]_{\text{External}}$	Typical external food concentration or feed supplementation. The model implementation allows testing of two values. Units depend on the food indicator chosen (Table 1).
Biological parameters (advanced)	Species specific	$[\text{Food}]_{\text{nursery}}$	Optimum food concentration for oyster filtration. Units depend on the food indicator chosen (Table 1).
		DWtoFW (-)	Conversion ratio of DW:FW weight with shell.
		$\text{ClearanceRate}_{\text{Oyster}}$ ($L \cdot mg\ DW^{-1} \cdot h^{-1}$)	The clearance rate is a model parameter that in fact is a function of seed weight and water temperature and is species specific.
	Site specific	$\text{Growth}_{\text{phyto}}$ (day^{-1})	Specific local phytoplankton community growth rate. If values are not known, a range within two values can be tested.
		$\text{fraction}_{\text{phyto/food}}$ (-)	Average typical values of the fraction of phyto in the food applicable for the cases where food indicator is POM or POC. When food indicator is algae, this parameter is one.

DW and considering three different algal concentrations (50, 75, and 100 cells·μL^{-1}). In this work, the clearance rate allometric function defined by Gerdes (1983a) is used for a food concentration of around 50 cells·μL^{-1} (see function in Table 3), given that this is the concentration nearest to the assumption adopted in the model for $[\text{Food}]_{\text{nursery}}$ (around 44 cells·μL^{-1}, Table 3). For conversion between tissue DW and oyster total FW, the following were considered: (1) the value from Gerdes (1983b) of shell weight of about 97.3% of total DW and (2) an average conversion factor of live FW to total DW of around 0.5 based on Walne and Millican (1978). The resulting ratio of dry tissue weight:total fresh weight (DWtoFW) is around 0.014 (Table 3). The effect of temperature on clearance rate was included in this model (Table 3) based on a function by Bougrier et al. (1995). The Bougrier function for clearance rate (L·h^{-1}) is $[a - (b \times (T - c)^2)] \times DW^d$, *a to d* are constants where c is the temperature that corresponds to the maximum clearance rate ($a = 4.825$, $b = 0.013$, $c = 18.954$, $d = 0.439$; Bougrier et al. 1995). The Bougrier allometric function with the temperature effect was converted into a dimensionless function to account only for the effect of temperature, by dividing this general form by the function at optimum temperature (thus $T = c$). The resulting temperature dependence function $[1 - a/b \times (T - c)^2]$ is herein multiplied by the individual clearance rate as a function of seed weight (CR_W in Table 3) that results in a function of both temperature and weight ($CR_{W,T}$ in Table 3) and defines the following behavior: (1) the temperature for maximum clearance rate is around 19°C, which is within the range from other references for Pacific Oyster, e.g., literature revision by Barrett (1963) indicates the optimum at around 20°C and (2) the clearance rate at 5°C is about 50% of the clearance rate at 20°C, which is supported by the findings of Walne (1972). According to Barrett (1963), at around 3°C, the Pacific oyster ceases feeding, so the lower limit for model input for temperature is set to 4°C. The higher temperature limit for model input was set to 30°C.

The model was evaluated using data presented by Langton and McKay (1976). Langton and McKay (1976) experiments include feed supply at two levels: (1) daily supply of 180 algal cells·μL^{-1} × 250 L tank in Exp A and (2) 120 algal cells·μL^{-1} × 250 L in Exp B. Each daily algal cell concentration (Exp A and B) was supplied following four feeding regimes, ranging from all feed supplied at once or distributed continuously over 1 day as per Langton and McKay (1976) description. In this work, the model was applied to simulate the feeding regime that provides the two feeding levels with a 6-h interval. Within this regime, the feed is supplied in a concentration ($180/4 = 45$ algal cells·μL^{-1}; $120/4 = 30$ algal cells·μL^{-1}) that is most similar to the $[\text{Food}]_{\text{nursery}}$ set in the model (44 algal cells·μL^{-1}, Table 3). To mimic the

TABLE 3.

Model parameterization for Pacific oyster (*Crassostrea gigas* Thunberg).

Parameter		Value/function	Source
$[\text{Food}]_{\text{nursery}}$	(mm^3 algae·L^{-1})	3.0	Tamayo et al. (2014)
	(algal cells·μL^{-1})	44	Tamayo et al. (2014) and cell biovolume from Ishiwata et al. (2013)
	(mg algae·L^{-1})	3.0	Tamayo et al. (2014) and conversion factor from Suthers and Rissik (2009)
	(μg Chl-*a*·L^{-1})	12.5	Tamayo et al. (2014) and conversion factor from Reynolds (2006)
	(mg POM·L^{-1})	1.037	Tamayo et al. (2014)
	(mg POC·L^{-1})	0.63	Tamayo et al. (2014)
$\text{ClearanceRate}_{\text{Oyster}}$	(mL·mg DW^{-1}·h^{-1})	$\mathbf{CR_{W,T}}/(\text{SeedWeight}_{\text{PerGrade}} \times \text{DWtoFW} \times 1{,}000)$	
Individual clearance rate as a function of:			
Seed weight—$\mathbf{CR_W}$	(mL·h^{-1})	$17.8 \times \text{TissueDryWeight (mg)}^{0.79}$	From Gerdes (1983a) for a feed concentration of 50 cells. μL^{-1}
Seed weight and temperature (*T*)—$\text{CR}_{\text{W,T}}$	(mL·h^{-1})	$\text{CR}_\text{W}*[1 - 0.002694 \times (T - 18.954)^2]$	Based on Bougrier et al. (1995)
DWtoFW	(-)	0.014	Gerdes (1983b) and Walne and Millican (1978)

experimental setting, the model application includes only a single oyster grade whereby in each model run, the seed size is set to the same size obtained by Langton and McKay (1976) weekly observations for the 6 h on : 6 h off feeding regime (values taken from plots presented in Figs. 1 and 2 in Langton & McKay 1976). The stock biomass was calculated considering the density of 50 spat per liter multiplied by the tank volume (250 L) and by the seed size. An average temperature of 21°C was considered. A summary of the parameters used to drive the model that simulates Langton and McKay (1976) experiments is presented in Table 4. The model outputs for food requirement and maximum stock considering the settings for each of Langton and McKay's (1976) experiments were compared with the feed given and the stock of tanks and are presented in **Results**. The indication of whether feedd was limited was compared with the experimental outcomes and discussion carried out by Langton and McKay (1976).

MODEL APPLICATION AND USER INTERACTION

To promote widespread use, the model described in this work for Pacific oyster nurseries is made available online at http://seaplusplus4.com/oysterspatbud.html. It simulates several typologies of nursery systems such as a FLUPSY or land-based nurseries as reviewed by Helm and Bourne (2004). Nurseries that are interconnected with large natural blooming ponds (Helm & Bourne 2004) are also simulated because the mass balance includes, as an option, a source of food because of phytoplankton primary production. This model does not simulate field nursery systems, e.g., spat floating bags sitting in intertidal areas of coastal ecosystems.

This work describes the model user interface, including the menus for nursery setup (Fig. 2), output for food requirements (Fig. 3), output for optimum stock (Fig. 4), and advanced settings (Fig. 5). Examples on how to use the model for different case studies are also provided.

(1) The nursery setup menu (Fig. 2) is where the users enter their farm inputs such as flow rate (or turnover rate), water volume, water temperature, and if the nursery includes blooming tanks. This model simulates the nursery system as a single compartment, which means for instance, if the nursery has blooming tanks, the user should insert (a) in the "System volume" the sum of the volume of the oyster-holding unit and of the bloom tanks, (b) in the "Flow rate" or "Turnover rate" the water exchange with the surrounding waterbody, and (c) choose "Yes" in "With phytoplankton blooming tanks" box. Alternatively, that user can simulate only the oyster stock pond by inserting (a) in the "System volume" the volume of that pond, (b) in the "Flow rate" or "Turnover rate" the water exchange with the bloom tanks, and (c) choose "No" in "With phytoplankton blooming tanks" box. If the model is used to simulate a FLUPSY in an estuary, the user should insert (a) in the "System volume" the volume of the FLUPSY, (b) in the "Flow rate" or "Turnover rate" the water flow rate forced by the paddlewheel into the entire FLUPSY, not of the individual silos, and (c) choose "No" in "With phytoplankton blooming tanks" box. Alternatively, the user can simulate the individual silo inserting in the model its water volume and individual flow rate. Examples about system definition are provided in Table 5.

Besides system definition, the nursery setup menu (Fig. 2) is where the user inserts the average seed weight per grade. Default seed grades and average weights are provided, but the user can customize any of these by changing any of the boxes under "Oyster grades" and "Seed weight." "Choose food indicator" allows the user to select his preferred food indicator for model inputs/outputs.

(2) In the output for food requirements menu (Fig. 3) is presented the result regarding the food required for a given stock, which is expressed in the units chosen by the user in the previous menu. The user should insert in this menu below "Stock per grade ($\times 10^3$ seeds)" the amount of seeds per grade. If the nursery includes blooming tanks, then two

TABLE 4.

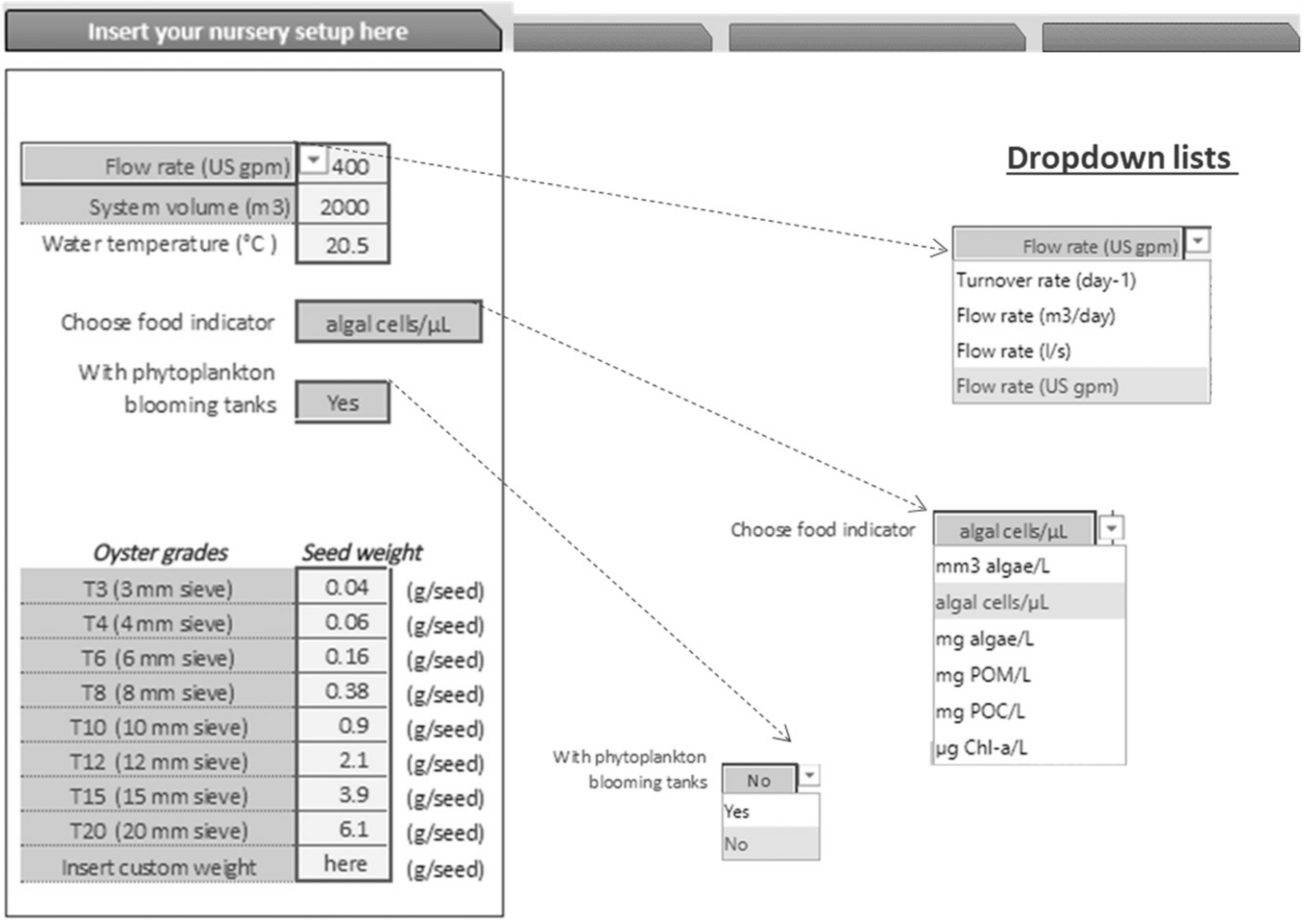
Model settings to simulate the Langton and McKay (1976) experiments.

	Model setting to simulate Langton and McKay (1976) experimental conditions at:							
	Week 0		Week 2		Week 3		Week 6	
	Exp. A	Exp. B	Exp. A	Exp. B	Exp. A	Exp. B	Exp. A	Exp. B
$V_{nursery}$ (m^3)	0.25							
TurnoverRate (day^{-1})	1							
WaterTemperature (°C)	20.5							
Food indicator	algal cells·μL^{-1}							
$[Food]_{nursery}$	Pacific oyster parameterization (in Table 3)							
DWtoFW (-)								
$ClearanceRate_{Oyster}$								
$Growth_{phyto}$ (day^{-1})	0							
$fraction_{phyto/food}$ (-)	1							
SeedWeight (mg)*	0.75		4		6	5	19	11
Estimated stock (g) in the 250 L tanks	9.4		50		75	63	238	138
Feed given ($[Food]_{External}$) algal cells·μL^{-1}	180	120	180	120	180	120	180	120

* Wet weight taken from plots shown in Figure 1 (Exp A) and Figure 2 (Exp B) of Langton and McKay (1976) for feeding regime 6 h on : 6 h off.

outputs are shown that encompass a low and a high phytoplankton growth scenario.

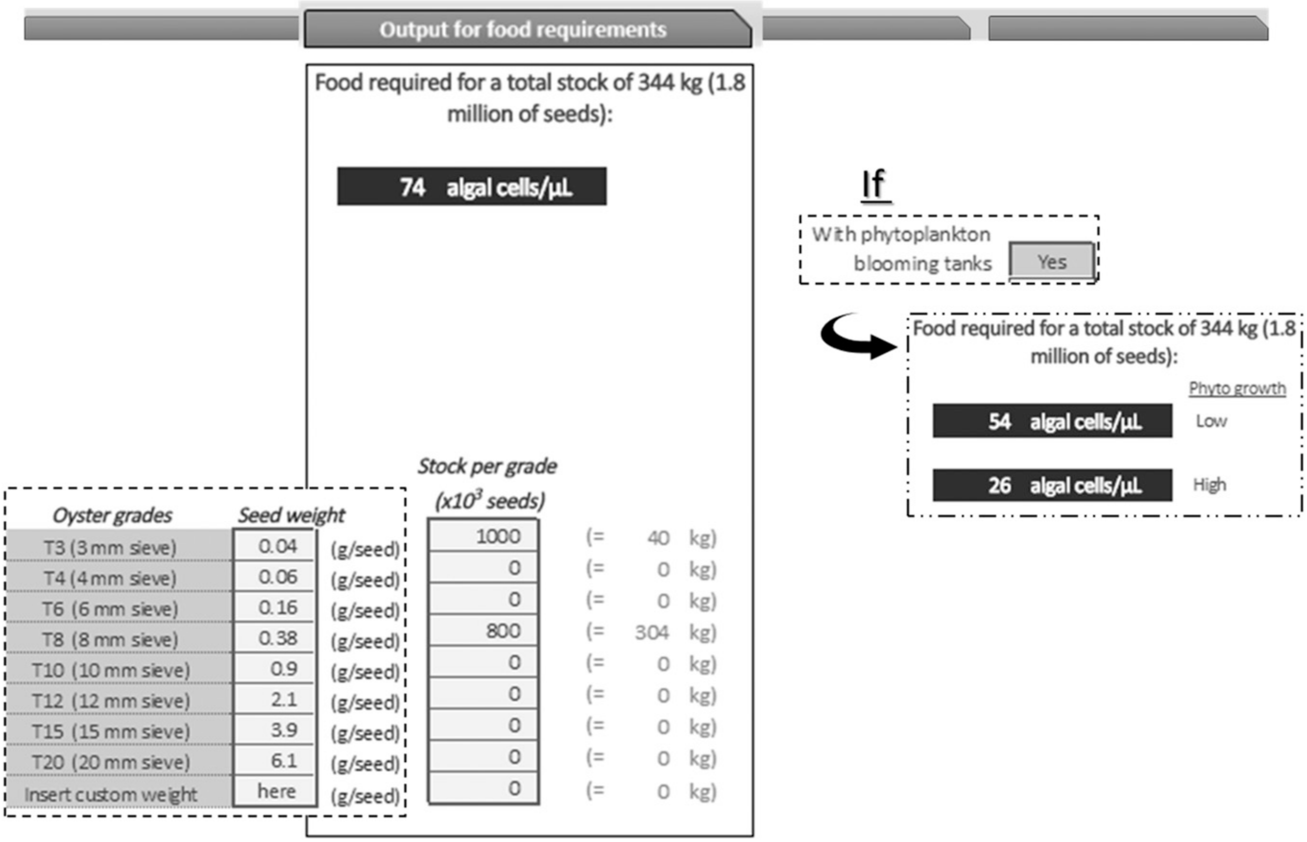
(3) In the output for optimum stock menu (Fig. 4), the results are presented concerning the maximum stock sustained, expressed as overall biomass and as the number of seeds per grade, for two scenarios of available food. The model needs to "know" the oyster biomass distribution per grade that the farmer aims, for instance, 100% of small 0.04 g spat or 50%


Insert your nursery setup here

Flow rate (US gpm): 400
System volume (m3): 2000
Water temperature (°C): 20.5
Choose food indicator: algal cells/µL
With phytoplankton blooming tanks: Yes

Oyster grades	Seed weight	
T3 (3 mm sieve)	0.04	(g/seed)
T4 (4 mm sieve)	0.06	(g/seed)
T6 (6 mm sieve)	0.16	(g/seed)
T8 (8 mm sieve)	0.38	(g/seed)
T10 (10 mm sieve)	0.9	(g/seed)
T12 (12 mm sieve)	2.1	(g/seed)
T15 (15 mm sieve)	3.9	(g/seed)
T20 (20 mm sieve)	6.1	(g/seed)
Insert custom weight	here	(g/seed)

Figure 2. Nursery parameters menu. Full online interface available at http://seaplusplus4.com/oysterspatbud.html.



Food required for a total stock of 344 kg (1.8 million of seeds):

74 algal cells/µL

If

With phytoplankton blooming tanks: Yes

Food required for a total stock of 344 kg (1.8 million of seeds):

	Phyto growth
54 algal cells/µL	Low
26 algal cells/µL	High

Oyster grades	Seed weight		Stock per grade ($x10^3$ seeds)		
T3 (3 mm sieve)	0.04	(g/seed)	1000	(= 40	kg)
T4 (4 mm sieve)	0.06	(g/seed)	0	(= 0	kg)
T6 (6 mm sieve)	0.16	(g/seed)	0	(= 0	kg)
T8 (8 mm sieve)	0.38	(g/seed)	800	(= 304	kg)
T10 (10 mm sieve)	0.9	(g/seed)	0	(= 0	kg)
T12 (12 mm sieve)	2.1	(g/seed)	0	(= 0	kg)
T15 (15 mm sieve)	3.9	(g/seed)	0	(= 0	kg)
T20 (20 mm sieve)	6.1	(g/seed)	0	(= 0	kg)
Insert custom weight	here	(g/seed)	0	(= 0	kg)

Figure 3. Model outputs menu for minimum external food concentration for a given stock. Full online interface available at http://seaplusplus4.com/oysterspatbud.html.

of the biomass stock with small spat and 50% with bigger 0.9 spat. The user can insert that input under "Biomass % per grade" or the model calculates distribution per grade based on data about "Stock per grade ($\times 10^3$ seeds)" inserted in the previous menu (Fig. 3). To test the effect of different food levels at the water intake from the surrounding ecosystem, the user must specify a lower and an upper food concentration. If the nursery includes blooming tanks, then two outputs that encompass a low and a high phytoplankton growth scenario are shown for each food concentration.

(4) The advanced settings menu (Fig. 5) allows the user to change the optimum food concentration for oyster filtration. That parameter ($[\text{Food}]_{\text{nursery}}$) is detailed in the model description and it is not foreseen that the common user will have the data required to change this value. This menu also presents the model estimates for the clearance rate based on an allometric filtration rate function (Gerdes 1983a) and the temperature dependence effect that assumes optimum filtration rate for the Pacific oyster at 19°C (Bougrier et al. 1995). If the nursery includes blooming tanks, the user can change in this menu the phytoplankton growth rate values. The model allows the user to specify a low and a high phytoplankton growth rate to test the range of community net primary production scenarios typical of the nursery's blooming tanks. Also in this menu is where the user specifies the value for the phytoplankton fraction in POM or POC, for the cases that POM or POC concentration were chosen as food indicator.

Model limitations include the following:

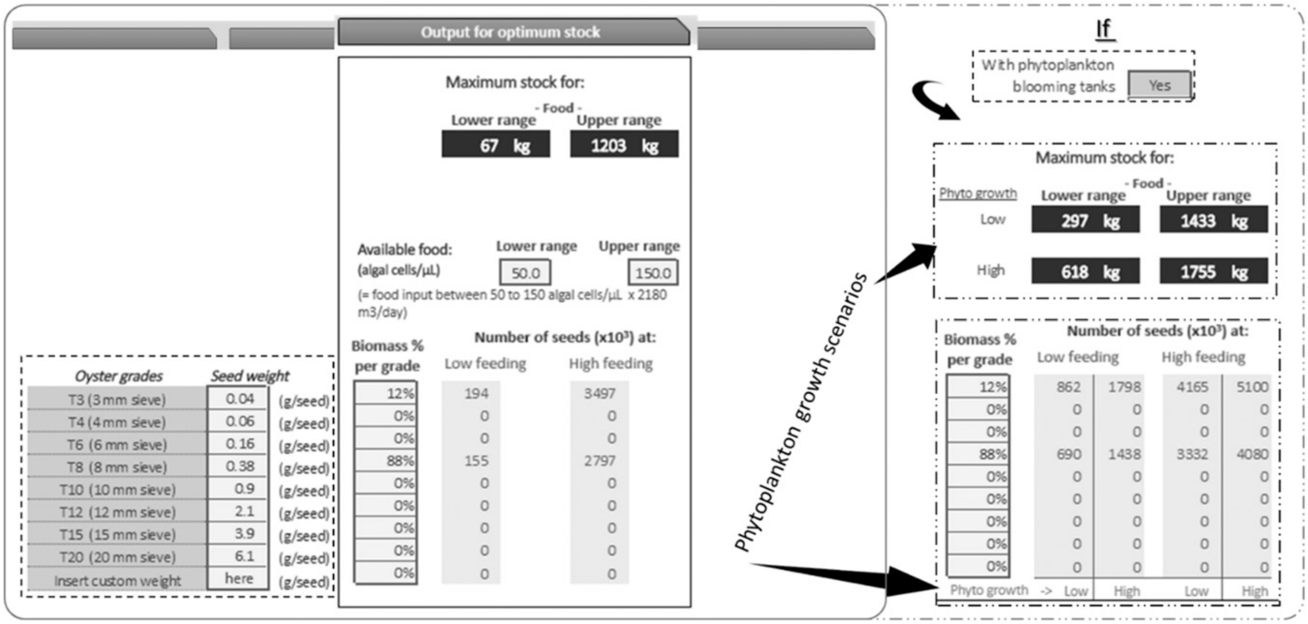
(1) Important effects that occur at smaller scale are not simulated in the model, e.g., changes in the water flow rate due to oyster size/densities or tank shape.
(2) The option with bloom tanks assumes these are interconnected with the oyster-holding tank, which together are the simulated unit. In this case, the water flow is the water that enters from the outside (an adjacent ecosystem for instance) into the bloom tanks forced by tidal height or pumped.
(3) The salinity effects on filtration rate are not simulated and thus it is assumed that water salinity is higher than 20.

RESULTS

Model Evaluation

The model settings to simulate the Langton and McKay (1976) experiments are systematized in Table 4 and the results are presented in Table 6.

For a spat of 0.75 mg and a stock of approximately 9 g in the 250-L containers, which corresponds to the conditions at the beginning (week 0) of both experiments (A—high and B—low feed level), the estimated food requirement is around 70 algal cells·μL^{-1}. For this spat weight and considering the two feed levels supplied, i.e., 180 algal cells·μL^{-1} in Exp A and 120 algal cells·μL^{-1} in Exp B, the model estimates a maximum stock of 50 g and 28 g, respectively. The outputs of this model run



Oyster grades	Seed weight	
T3 (3 mm sieve)	0.04	(g/seed)
T4 (4 mm sieve)	0.06	(g/seed)
T6 (6 mm sieve)	0.16	(g/seed)
T8 (8 mm sieve)	0.38	(g/seed)
T10 (10 mm sieve)	0.9	(g/seed)
T12 (12 mm sieve)	2.1	(g/seed)
T15 (15 mm sieve)	3.9	(g/seed)
T20 (20 mm sieve)	6.1	(g/seed)
Insert custom weight	here	(g/seed)

Maximum stock for:

	- Food - Lower range	Upper range
	67 kg	1203 kg

Available food: (algal cells/µL) Lower range 50.0 Upper range 150.0

(= food input between 50 to 150 algal cells/µL x 2180 m3/day)

Biomass % per grade	Number of seeds (x10³) at: Low feeding	High feeding
12%	194	3497
0%	0	0
0%	0	0
88%	155	2797
0%	0	0
0%	0	0
0%	0	0
0%	0	0
0%	0	0

With phytoplankton blooming tanks: Yes

Maximum stock for:

Phyto growth	- Food - Lower range	Upper range
Low	297 kg	1433 kg
High	618 kg	1755 kg

Biomass % per grade	Number of seeds (x10³) at: Low feeding		High feeding	
12%	862	1798	4165	5100
0%	0	0	0	0
0%	0	0	0	0
88%	690	1438	3332	4080
0%	0	0	0	0
0%	0	0	0	0
0%	0	0	0	0
0%	0	0	0	0
0%	0	0	0	0
Phyto growth ->	Low	High	Low	High

Figure 4. Model outputs for maximum stock that can be sustained for a given food input and considering a given stock distribution per grades. Full online interface available at http://seaplusplus4.com/oysterspatbud.html.

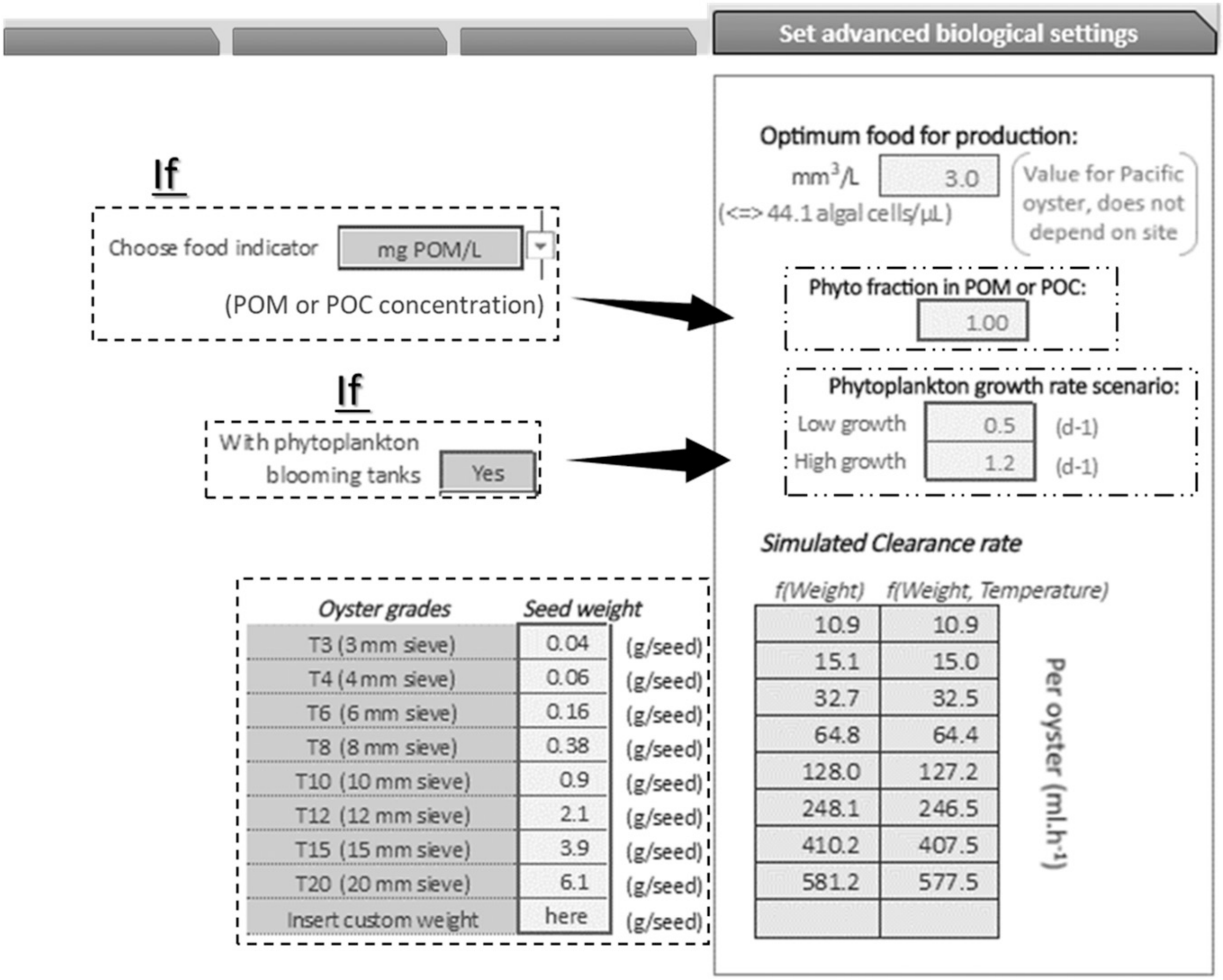
indicate that at week 0, the feed supplied is much higher than the stock requirements.

The model outputs for the run that simulates week 2 indicate a food requirement around 139 algal cells·μL^{-1} for the 50 g stocked in the 250 L containers (spat around 4 mg). According to the outputs of this simulation, the feed level supplied in Exp A is still enough; nevertheless, oysters in the containers of Exp B are fed less than the optimum.

In week 3, the feed level supplied is near the threshold in Exp A and does not meet the oyster requirements in Exp B, which according to the model outputs should be 175 and 158 algal cells·μL^{-1} in Exp A and B, respectively. According to Langton and McKay (1976), the spat average weight in week 3 (6 and 5 mg in Exp A and B, respectively) already exhibits a slower growth for Exp B. In subsequent weeks, the higher feed limitation experienced in Exp B (since week 2) is translated into lower weights, in week 4, the spat weight is around 7.5 mg in Exp B compared with 13 mg in Exp A, and by week 6, the weight is around 11 mg in Exp B compared with 19 mg on Exp A (Langton & McKay 1976). These different growth rates measured in Exp A and B (Langton & McKay 1976) support the model predictions for food limitation. The model results also agree with Langton and McKay (1976), according to which in the first 2 wk, the oyster spat are not feed limited.

Model Application to Farms

The fact that the model implementation allows testing of ranges of values for the external food concentration ($[\text{Food}]_{\text{External}}$) and the phytoplankton growth rate ($\text{Growth}_{\text{phyt}}$) means that model outputs provide a range of possible scenarios within which the nursery is operating. This facilitates model application into a given nursery whereby the user needs to provide the boundaries for this highly variable parameter (when dependent on food concentration in the surroundings). In extensive oyster nurseries, such seston concentration is unlikely to be monitored frequently. Therefore, in spite of the model simplification, it can still provide guidance for managing stock and food limitation in natural feeding oyster nurseries. These model functionalities contribute to support management of oyster nurseries. In particular, this model allows quantification of general rules of thumb regarding the spat-holding capacity for a given nursery. For instance, according to Helm and Bourne (2004), determining the biomass of spat that can be held in a pond system is largely a matter of trial and error. A general rule is that 1 hectare surface area of shallow pond will support the production of between 1 and 3 tons biomass of seed, depending on levels of algal productivity, over the course of a growing season. This represents the maximum sustainable biomass that can be maintained with careful management." To apply the model for the described rule of thumb, the following assumptions are made: (1) a water renovation with the external system of around 10%, (2) a system volume of about 10,000 m^3 corresponding to a surface area of 10,000 m^2 for the bloom pond +1,000 m^2 for the stock pond and a 1 m water depth, (3) a water temperature around 19°C, (4) a phytoplankton concentration in the external waterbody within the range of about 0.5–2 µg Chl-*a*·L^{-1}, and (5) phytoplankton growth rate that ranges between 0.5 and 1.2 day^{-1}. The total biomass stock that can be sustained will depend on the spat grades. In accordance with the model outputs for this setup (Fig. 6A), if the farmer aims to stock spat of about 0.38 g, the nursery can hold in those conditions between 1 and 3 tons (Fig. 6B) of total seed biomass (corresponding to around 3–8 million seeds). These estimates fit well within the rule of thumb described by Helm and Bourne (2004); however, considering the same conditions but targeting to stock smaller spat of around 0.04 g, the biomass stock sustained is lower (Fig. 6C), between 0.7 and 2 tons (corresponding to around 17–47 million seeds). The application of the model allows to improve the rule of thumb for a given set of conditions



Choose food indicator: mg POM/L
(POM or POC concentration)

With phytoplankton blooming tanks: Yes

Optimum food for production:
mm^3/L: 3.0
(<=> 44.1 algal cells/µL)
Value for Pacific oyster, does not depend on site

Phyto fraction in POM or POC: 1.00

Phytoplankton growth rate scenario:
Low growth: 0.5 (d-1)
High growth: 1.2 (d-1)

Oyster grades	Seed weight	
T3 (3 mm sieve)	0.04	(g/seed)
T4 (4 mm sieve)	0.06	(g/seed)
T6 (6 mm sieve)	0.16	(g/seed)
T8 (8 mm sieve)	0.38	(g/seed)
T10 (10 mm sieve)	0.9	(g/seed)
T12 (12 mm sieve)	2.1	(g/seed)
T15 (15 mm sieve)	3.9	(g/seed)
T20 (20 mm sieve)	6.1	(g/seed)
Insert custom weight	here	(g/seed)

Simulated Clearance rate

Per oyster (ml.h^{-1})

f(Weight)	f(Weight, Temperature)
10.9	10.9
15.1	15.0
32.7	32.5
64.8	64.4
128.0	127.2
248.1	246.5
410.2	407.5
581.2	577.5

Figure 5. Advanced biological parameters menu. Full online interface available at http://seaplusplus4.com/oysterspatbud.html.

and thus to lower the set of trials and errors required to determine the biomass of spat to hold in a pond system.

A wide range of other scenarios can be tested by any user in the online model (http://seaplusplus4.com/oysterspatbud.html) to better adjust a general rule of thumb to their own nursery conditions; for instance, and considering the aforementioned example, what are the changes regarding the stock biomass or number of seeds per grade that can be sustained due to lower or higher temperatures, typical of the local winter/summer? What if the local phytoplankton community growth rate can be as low as 0.2 day^{-1}?

DISCUSSION

The inclusion in the model of a minimum concentration at the tanks that must be ensured to maximize ingestion ($[\text{Food}]_{\text{nursery}}$) is one of the key elements in solving the mass balance at the steady state. The practical implications of this assumption are that the model outputs provide (1) the food input requirements to ensure minimum concentration in the nursery; considering a given water inflow, oyster filtration rate at a given stocking and seed weight, and if applicable, phytoplankton natural production within the nursery; and (2) the maximum biomass that can be stocked to ensure that minimum concentration at the nursery and thus ensure an optimized growth; considering a given food input, oyster seed weight and distribution among the oyster grades, and if applicable, phytoplankton natural production within the nursery. The value adopted in the Pacific oyster model (3 mm^3·L^{-1} as per rational explained in **Model Parameterization and Validation for the Pacific Oyster**) was chosen from within a set of three tested concentrations (0.5, 3, and 6 mm^3·L^{-1}) from Tamayo et al. (2014). It is possible that within the interval between these values, other solutions maximize ingestion. Further research should be developed to more accurately estimate the $[\text{Food}]_{\text{nursery}}$. Given that other factors influence filtration efficiency dependence on food concentration, such as the algae size (Winter 1978), further research should also include different feeds. For nurseries that provide cultivated algae, they can improve their own model application by changing the $[\text{Food}]_{\text{nursery}}$ parameter (in http://seaplusplus4.com/oysterspatbud.html) and inserting the value that best suits their own facility.

Nevertheless, the value adopted in the model parameterization for the Pacific oyster for the minimum food concentration

TABLE 5.

Examples of nursery system definition for different types of nurseries (FLUPSY, land-based with blooming tanks and closed systems).

Type of nurseries	FLUPSY in an estuary		Land-based with blooming tanks (10% renovation with external waterbody)		Closed system (Renovates the water every-one day)
Simulation options:	All system	Only one of the silos	All system	Only the seed holding pond	
"System volume"	Oyster-holding units	1 of the silos	Oyster-holding unit + blooming tanks	Oyster-holding unit	Oyster-holding unit
"Flow rate"/"Turnover rate"	"Flow rate" = flow rate forced by paddlewheel	"Flow rate" = Water flow rate into one silo	"Turnover rate" = 0.1 day^{-1}	"Flow rate" = Water flow rate from the blooming tanks	"Turnover rate" = 1 day^{-1}
"With phytoplankton blooming tanks"	No	No	Yes	No	No

that maximizes ingestion, i.e., $[\text{Food}]_{\text{nursery}}$ (44 algae cells·µL^{-1}, Table 3) is also in agreement with experiments by Langton and McKay (1976) whereby the growth was maximized for the feed supplied (120 or 180 algae cells·µL^{-1}) with 6-h intervals, which corresponds to 30 (=120/4) and 45 (=180/4) algae cells·µL^{-1}.

CONCLUSIONS

The model presented provides an assessment of the seed stock boundary ranges within a commercial extensive oyster nursery which can operate regarding food limitation. This model is built based upon a simplification of the oyster biological processes, the nursery systems and timescales of interaction. The model evaluation for the Pacific oyster using an experimental dataset (Langton & McKay 1976) indicates that it can provide valid guidance on boundaries for maximum stock at a given nursery setting or feeding requirements for a given seed stock for optimum rearing conditions. In this work, it is also exemplified how to use the model to improve the application of general rules of thumb for planning the oyster spat–holding capacity within a nursery. Although there is extensive literature on ecological models, these are seldom used directly by farmers. This model is targeted to managers of commercial operations and can be used online: http://seaplusplus4.com/oysterspatbud.html. Shellfish farmers are major stakeholders for the sector sustainability and thus can benefit with the application of models to manage production and understand environmental interactions. Further developments to the model can be made based on feedback from farmers regarding usefulness of the model. Moreover, other features they find important could be included, as well as other oyster species, such as eastern oyster (*Crassostrea virginica* Gmelin), European flat oyster (*Ostrea edulis* Linnaeus), Olympia oyster (*Ostrea lurida* Carpenter), Portuguese oyster (*Crassostrea angulata* Lamarck), slipper cupped oyster (*Crassostrea iredalei* Faustino), and Sydney rock oyster (*Saccostrea glomerate* Gould).

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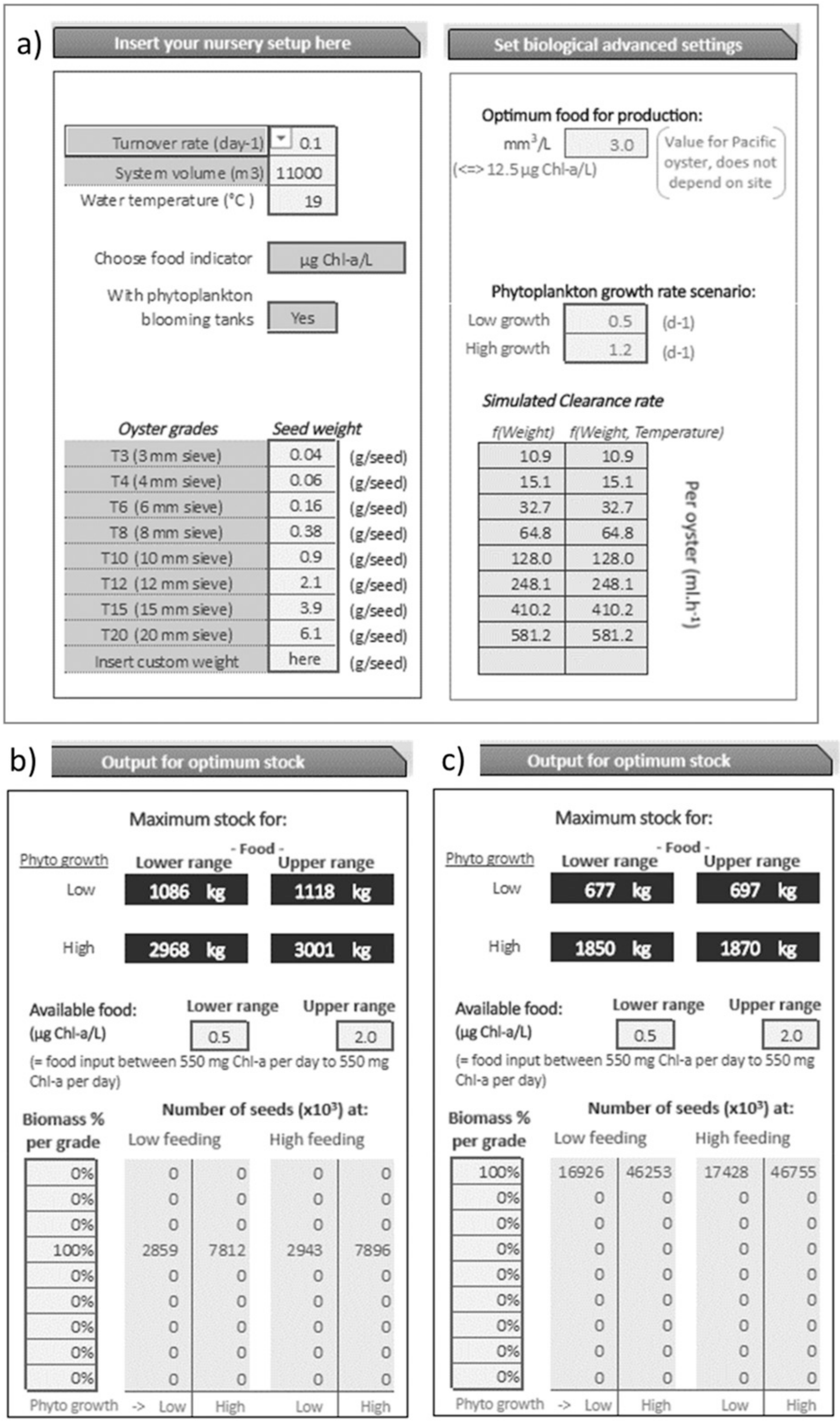
TABLE 6.

Model outputs for Langton and McKay (1976) experiments.

Langton and McKay (1976) experimental conditions:		*Seed weight (mg)	Simulated clearance rate (L·h^{-1}. mg DW^{-1})	Model outputs: Food requirements		Model outputs: Max stock	
				Minimum algal cells·µL^{-1} required	*Considering a stock (g) of:	Maximum stock (g)	*Considering a feed level (algal cells·µL-1) of:
Week 0	Exp. A	0.75	0.047	70	9	50	180
	Exp. B					28	120
Week2	Exp. A	4	0.033	139	50	71	180
	Exp. B					40	120
Week 3	Exp. A	6	0.031	175	75	78	180
	Exp. B	5	0.032	158	63	42	120
Week 6	Exp. A	19	0.024	370	238	99	180
	Exp. B	11	0.027	256	138	49	120

* Settings from Langton and McKay (1976) experiments (6 h on/off feeding).



Insert your nursery setup here

Turnover rate (day-1)	0.1
System volume (m3)	11000
Water temperature (°C)	19
Choose food indicator	µg Chl-a/L
With phytoplankton blooming tanks	Yes

Oyster grades	Seed weight	
T3 (3 mm sieve)	0.04	(g/seed)
T4 (4 mm sieve)	0.06	(g/seed)
T6 (6 mm sieve)	0.16	(g/seed)
T8 (8 mm sieve)	0.38	(g/seed)
T10 (10 mm sieve)	0.9	(g/seed)
T12 (12 mm sieve)	2.1	(g/seed)
T15 (15 mm sieve)	3.9	(g/seed)
T20 (20 mm sieve)	6.1	(g/seed)
Insert custom weight	here	(g/seed)

Set biological advanced settings

Optimum food for production:
mm^3/L 3.0 (<=> 12.5 µg Chl-a/L)
Value for Pacific oyster, does not depend on site

Phytoplankton growth rate scenario:
Low growth 0.5 (d-1)
High growth 1.2 (d-1)

Simulated Clearance rate

Per oyster (ml.h^{-1})

f(Weight)	*f(Weight, Temperature)*
10.9	10.9
15.1	15.1
32.7	32.7
64.8	64.8
128.0	128.0
248.1	248.1
410.2	410.2
581.2	581.2

b) **Output for optimum stock**

Maximum stock for:

Phyto growth	- Food - Lower range	Upper range
Low	1086 kg	1118 kg
High	2968 kg	3001 kg

Available food: (µg Chl-a/L) Lower range 0.5 Upper range 2.0
(= food input between 550 mg Chl-a per day to 550 mg Chl-a per day)

Biomass % per grade	Number of seeds (x10^3) at: Low feeding		High feeding	
0%	0	0	0	0
0%	0	0	0	0
0%	0	0	0	0
100%	2859	7812	2943	7896
0%	0	0	0	0
0%	0	0	0	0
0%	0	0	0	0
0%	0	0	0	0
0%	0	0	0	0
Phyto growth ->	Low	High	Low	High

c) **Output for optimum stock**

Maximum stock for:

Phyto growth	- Food - Lower range	Upper range
Low	677 kg	697 kg
High	1850 kg	1870 kg

Available food: (µg Chl-a/L) Lower range 0.5 Upper range 2.0
(= food input between 550 mg Chl-a per day to 550 mg Chl-a per day)

Biomass % per grade	Number of seeds (x10^3) at: Low feeding		High feeding	
100%	16926	46253	17428	46755
0%	0	0	0	0
0%	0	0	0	0
0%	0	0	0	0
0%	0	0	0	0
0%	0	0	0	0
0%	0	0	0	0
0%	0	0	0	0
0%	0	0	0	0
Phyto growth ->	Low	High	Low	High

Figure 6. Model application for quantification of general rules of thumb about biomass stock that can be sustained by blooming ponds: (A) model setup, (B) model outputs considering spat of about 0.38 g, and (C) model outputs considering spat of about 0.04 g.

LITERATURE CITED

Bacher, C. & J. P. Baud. 1992. Intensive rearing of juvenile oysters *Crassostrea gigas* in an upwelling system: optimization of biological production. *Aquat. Living Resour.* 5:89–98.

Baker, S., K. Grogan, S. Larkin & L. Sturmer. 2015. "Green" clams: estimating the value of environmental benefits generated by the hard clam aquaculture industry in Florida. Project Report. University of Florida IFAS research and extension faculty. 10 pp. Available at: http://shellfish.ifas.ufl.edu/wp-content/uploads/environmental-benefits.pdf.

Barrett, E. M. 1963. The California oyster industry. Fish bulletin, 123. 103 pp. State of California, Department of Fish and Game. Available at: http://content.cdlib.org/view?docId=kt629004n3;NAAN=13030&chunk.id=d0e272&toc.id=d0e269&toc.depth=1&brand=calisphere&anchor.id=tab3.

Bougrier, S., P. Geairon, J. M. Deslous-Paoli, C. Bacher & G. Jonquières. 1995. Allometric relationships and effects of temperature on clearance and oxygen consumption rates of *Crassostrea gigas* (Thunberg). *Aquaculture* 134:143–154.

Breese, W. P. & R. E. Malouf. 1975. Hatchery manual for the Pacific oyster. Oregon State University, Sea Grant College Program. Agricultural Experiment Station. Publication no. ORESU-H-75-002. Special Report No. 443. Available at: http://ir.library.oregonstate.edu/xmlui/bitstream/handle/1957/6637/?sequence=1.

Byron, C. J. & B. A. Costa-Pierce. 2013. Carrying capacity tools for use in the implementation of an ecosystems approach to aquaculture. In: Ross, L. G., T. C. Telfer, L. Falconer, D. Soto & J. Aguilar-Manjarrez, editors. Site selection and carrying capacities for inland and coastal aquaculture, pp. 87–101. FAO/Institute of Aquaculture, University of Stirling, Expert Workshop, 6–8 December 2010. Stirling, the United Kingdom of Great Britain and Northern Ireland. FAO Fisheries and Aquaculture Proceedings No. 21. Rome: FAO. 282 pp.

Coen, L. D., B. R. Dumbauld & M. L. Judge. 2011. Expanding shellfish aquaculture: a review of the ecological services provided by and impacts of native and cultured bivalves in shellfish-dominated ecosystems. In: Shumway, S. E., editor. Shellfish aquaculture and the environment. Oxford, United Kingdom: Wiley Science Publishers. pp. 239–295.

Cranford, P. J., J. E. Ward & S. E. Shumway. 2011. Bivalve filter feeding: variability and limits of the aquaculture biofilter. In: Shumway, S. E., editor. Shellfish aquaculture and the environment. Oxford, United Kingdom: Wiley Science Publishers. pp. 81–124.

Depiper, G. S., D. W. Lipton & R. N. Lipcius. 2017. Valuing ecosystem services: oysters, denitrification, and nutrient trading programs. *Mar. Resour. Econ.* 32:1–20.

Dewey, W., J. P. Davis & D. C. Cheney. 2011. Shellfish aquaculture and the environment: an industry perspective. In: Shumway, S. E., editor. Shellfish aquaculture and the environment. Oxford, United Kingdom: Wiley Science Publishers. pp. 33–50.

FAO. 2017. Fishery and aquaculture statistics. Global aquaculture production 1950–2015 (FishstatJ). In: FAO Fisheries and Aquaculture Department [online]. Rome. Updated 2017. Available at: www.fao.org/fishery/statistics/software/fishstatj/en.

Ferreira, J. G., A. J. S. Hawkins & S. B. Bricker. 2011. The role of shellfish farms in provision of ecosystem goods and services. In: Shumway, S. E., editor. Shellfish aquaculture and the environment. Oxford, United Kingdom: Wiley Science Publishers. pp. 3–31.

Ferreira, J. G., A. J. S. Hawkins, P. Monteiro, H. Moore, M. Service, P. L. Pascoe, L. Ramos & A. Sequeira. 2008. Integrated assessment of ecosystem-scale carrying capacity in shellfish growing areas. *Aquaculture* 275:138–151.

Filgueira, R., L. A. Comeau, T. Guyondet, C. W. McKindsey & C. J. Byron. 2015. Modelling carrying capacity of bivalve aquaculture: a review of definitions and methods. In: Meyers, R. A., editor. Encyclopedia of sustainability science and technology. New York, NY: Springer. pp. 1–33.

Gallardi, D. 2014. Effects of bivalve aquaculture on the environment and their possible mitigation: a review. *Fish. Aquac. J.* 5:105.

Gangnery, A., C. Bacher & D. Buestel. 2011. Assessing the production and the impact of cultivated oysters in the Thau lagoon (Mediterranee, France) with a population dynamics model. *Can. J. Fish. Aquat. Sci.* 58:1012–1020.

Gerdes, D. 1983a. The Pacific oyster *Crassostrea gigas*: part I. Feeding behaviour of larvae and adults. *Aquaculture* 31:195–219.

Gerdes, D. 1983b. The Pacific oyster *Crassostrea gigas*: part II. Oxygen consumption of larvae and adults. *Aquaculture* 31:221–231.

Helm, M. M. & N. Bourne. 2004. Hatchery culture of bivalves—a practical manual. FAO Fisheries Technical Paper 471. Rome: FAO. 178 pp.

Ishiwata, Y., N. Ohi, M. Obata & S. Taguchi. 2013. Carbon to volume relationship of *Isochrysis galbana* (Prymnesiophyceae) during cell divisions. *Plankton Benthos Res.* 8:178–185.

Langton, R. W. & G. U. McKay. 1976. Growth of *Crassostrea gigas* (Thunberg) spat under different feeding regimes in a hatchery. *Aquaculture* 7:225–233.

Nobre, A. M., S. B. Bricker, J. G. Ferreira, X. Yan, M. de Wit & J. P. Nunes. 2011. Integrated environmental modeling and assessment of coastal ecosystems: application for aquaculture management. *Coast. Manage.* 39:536–555.

Nobre, A. M., L. V. Valente & A. Neori. 2017. A nitrogen budget model with a user-friendly interface, to assess water renewal rates and nitrogen limitation in commercial seaweed farms. *J. Appl. Phycol.* doi: 10.1007/s10811-017-1164-9

Reynolds, C. S. 2006. The ecology of phytoplankton. Ecology, biodiversity and conservation. Cambridge, UK: Cambridge University Press. 437 pp.

Rico-Villa, B., I. Bernard, R. Robert & S. Pouvreau. 2010. A dynamic energy budget (DEB) growth model for Pacific oyster larvae, *Crassostrea gigas*. *Aquaculture* 305:84–94.

Rose, J. M., S. B. Bricker, M. A. Tedesco & G. H. Wikfors. 2014. A role for shellfish aquaculture in coastal nitrogen management. *Environ. Sci. Technol.* 48:2519–2525.

Saurel, C., J. G. Ferreira, D. Cheney, A. Suhrbier, B. Dewey, J. Davis & J. Cordell. 2014. Ecosystem goods and services from Manila clam culture in Puget Sound: a modelling analysis. *Aquacult. Environ. Interact.* 5:255–270.

Suthers, I. & D. Rissik. 2009. Plankton: a guide to their ecology and monitoring for water quality. Collingwood, Australia: CSIRO Publishing. 272 pp.

Tamayo, D., I. Ibarrola, I. Urrutxurtu & E. Navarro. 2014. Physiological basis of extreme growth rate differences in the spat of oyster (*Crassostrea gigas*). *Mar. Biol.* 161:1627–1637.

Tetrault, K. 2012. Reference manual for SPAT oyster gardeners. SPAT—Southold Project in Aquaculture Training. Cornell Cooperative Extension of Suffolk Marine Program. 75 pp. Available at: https://s3.amazonaws.com/assets.cce.cornell.edu/attachments/9506/SPAT_Manual.pdf?1435065245.

Wallace, R., P. Waters & F. S. Rikard. 2008. Oyster hatchery techniques. Southern Regional Aquaculture Center. SRAC Publication No. 4302. 6 pp. Available at: http://fisheries.tamu.edu/files/2013/09/SRAC-Publication-No.-4302-Oyster-Hatchery-Techniques.pdf.

Walne, P. R. 1972. The influence of current speed, body size and water temperature on the filtration rate of five species of bivalves. *J. Mar. Biol. Assoc. U.K.* 52:345–374.

Walne, P. R. & P. F. Millican. 1978. The condition index and organic content of small oyster spat. *J. Cons. Cons. Int. Explor. Mer* 38:230–233.

Ward, J. E. & S. E. Shumway. 2004. Separating the grain from the chaff: particle selection in suspension- and deposit-feeding bivalves. *J. Exp. Mar. Biol. Ecol.* 300:83–130.

Winter, J. E. 1978. A review of the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. *Aquaculture* 13:1–33.