



A fully-spatial ecosystem-DEB model of oyster (*Crassostrea virginica*) carrying capacity in the Richibucto Estuary, Eastern Canada



R. Filgueira^{a,b,*}, T. Guyondet^a, L.A. Comeau^a, J. Grant^b

^a Department of Fisheries and Oceans, Gulf Fisheries Centre, Science Branch, P.O. Box 5030, Moncton, NB E1C 9B6, Canada

^b Department of Oceanography, Dalhousie University, Halifax, NS B3H 4R2, Canada

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ABSTRACT

The success of shellfish aquaculture as well as its sustainability relies on adjusting the cultured biomass to local ecosystem characteristics. Oyster filter-feeding activity can control phytoplankton concentration, reaching severe depletion in extreme situations, which can threaten ecological sustainability. A better understanding of oyster–phytoplankton interaction can be achieved by constructing ecosystem models. In this study, a fully-spatial hydrodynamic biogeochemical model has been constructed for the Richibucto Estuary in order to explore oyster carrying capacity. The biogeochemical model was based on a classical nutrient–phytoplankton–zooplankton–detritus (NPZD) approach with the addition of a Dynamic Energy Budget (DEB) model of *Crassostrea virginica*. Natural variation of chlorophyll was used as a benchmark to define a sustainability threshold based on a resilience framework. Scenario building was applied to explore carrying capacity of the system. However, the complex geomorphology of the Richibucto Estuary and the associated heterogeneity in water residence time, which is integral in estuarine functioning, indicate that the carrying capacity assessment must be specific for each area of the system. The model outcomes suggest that water residence time plays a key role in carrying capacity estimations through its influence on ecological resistance.

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1. Introduction

Shellfish aquaculture constitutes 80% of global shellfish production (Shumway, 2011) and is an important ecosystem service provided by coastal environments (de Groot et al., 2012). However, densely cultivated populations of filter-feeders may alter the dynamics of both pelagic and benthic environments (e.g. Cloern, 1982; Dame and Prins, 1998; Holmer, 2010), potentially affecting the sustainability of other ecosystem services such as habitat, water quality, esthetics and recreation. Pelagic and benthic effects can be evaluated through time by developing in situ monitoring programs. Such programs constitute a valuable source of data for developing evidence-based management (Sutherland et al., 2004). Major drawbacks of monitoring programs are that they are expensive, time consuming, and spatially limited. Also, the information is generated a posteriori, lacking predictive capabilities.

In recent years, a series of mathematical models has been developed in order to generate a priori information for managing aquaculture. These models vary in complexity (see Dabrowski et al. (2013)) but in general they present the following commonalities: (1) integration of time and space, which is critical for understanding ecological dynamics and the provision of ecosystem services (Palmer et al., 2004); (2) scenario-building, which allows the exploration and

management of future situations (Nobre et al., 2010); and (3) optimization tools (e.g. Filgueira et al., 2010; North et al., 2010), which can be applied to these models to improve the efficiency of the system while maintaining a rational and transparent standpoint (Fisher et al., 2009).

The simplest of these modeling approaches is individual-based modeling, in which the growth of a single bivalve is predicted through time based on changing environmental conditions. These models rely on empirical (e.g. Gangnery et al., 2003; Riisgård et al., 2012), mechanistic (e.g. Kooijman, 2010; Willows, 1992) or mixed (e.g. Brigolin et al., 2009; Duarte et al., 2010) approaches. In recent years, there is a growing tendency to use Dynamic Energy Budget models (DEB; Kooijman, 2010) in the context of shellfish farming (see J. Sea. Res. special issues 62(2–3) and 66(4)), and several studies have successfully coupled DEB with hydrodynamic models (e.g. Dabrowski et al., 2013; Grangeré et al., 2010; Guyondet et al., 2010; Maar et al., 2009; Ren et al., 2012). This approach is particularly appealing, since it allows the investigator to explore complex interactions between different components of the ecosystem (Dowd, 2005), resulting in a powerful tool for understanding ecosystem functioning and predicting the implications of shellfish aquaculture on the environment.

The knowledge generated by these models can be used for marine spatial planning based on an ecosystem approach. The goal of Ecosystem-Based Management (EBM) is to maintain ecosystem functioning to provide the services that humans want and need (McLeod et al., 2005). In the context of shellfish aquaculture, a useful element

* Corresponding author. Tel.: +1 613 404 9683.
E-mail address: ramonf@dal.ca (R. Filgueira).

for guiding the EBM process is to estimate carrying capacity (CC), that is, the stocking density at which some measure of ecosystem health is not compromised (Grant et al., 2007). By focusing on the most relevant trophic interaction, shellfish feeding on phytoplankton, various indices of phytoplankton depletion have been developed to gauge CC (e.g. Ferreira et al., 2007; Grant et al., 2008). Nevertheless, setting the acceptable limits that guarantee sustainability remains a challenge (Duarte, 2003). Recently, Filgueira et al. (2013, 2014) have established sustainability thresholds for phytoplankton depletion based on a resilience framework. This approach assumes that phytoplankton depletion should remain within the bounds of natural variation in order to keep the system within resilience tipping points.

In the present study, a DEB model for the eastern oyster *Crassostrea virginica* has been coupled to a Nutrient–Phytoplankton–Detritus model and a hydrodynamic model with the following aims:

1. Developing and validating the first DEB model for *C. virginica*.
2. Determining whether the present level of oyster culture is within the carrying capacity of the system.
3. Evaluating the implications of local hydrodynamics on local- and bay-scale carrying capacity.

2. Material and methods

2.1. Study area

The Richibucto Estuary is a small (11.8 km²) bar-built river estuary located in southeastern New Brunswick, Canada, along the Northumberland Strait (46°41'N 64°50'W, Fig. 1a). It is a shallow embayment that can be divided into three areas: North Arm (max. 4 m depth), Central Harbour (max. 10 m depth) and Baie du Village (max. 3 m depth). These three areas are also characterized by different water residence times (Guyonnet et al., 2013), with the North Arm and Baie du Village areas having larger residence times than the Central Harbour (Fig. 1b). Two rivers discharge in the estuary. The Richibucto River runs into the Central Harbour and St. Charles River in the North Arm. The estuary is open to the Northumberland Strait through two permanent channels and a narrow breach (width 25–30 m and depth 1.2 m) in the center of the sand dunes located east of the main channel.

Oyster (*C. virginica*) farming occurs in all three areas of Richibucto Estuary (see polygons on Fig. 1b). Leases typically hold four year classes of oysters in floating-bags. As an average, the normalized bag contains 332 oysters and weights 6.1 kg (Comeau, 2013). Taking into account the total leased area and an average density of 904 oyster bags per hectare, the average standing stock biomass of oysters in Richibucto Estuary is about 1000 tons (total wet weight). This biomass estimate was used as the initial biomass in the modeling of the present aquaculture scenario. This biomass was homogeneously distributed among the oyster farms depicted in Fig. 1b. The initial weight and length of the oysters in each area (North Arm, Central Harbour and Baie du Village) was initialized according to the observations made during the field sampling (see Section 2.4).

2.2. Hydrodynamic model

A two-dimensional vertically averaged finite element model was developed for Richibucto Estuary using the RMA suite of models (<http://ikingrma.iinet.net.au>). A detailed description of the model, its validation and the passive tracer method used to compute the water renewal time may be found in Guyonnet et al. (2013). For the present application the model was forced by tides observed at both outer boundaries in the Northumberland Strait and by river discharges at both upstream boundaries (Fig. 1a). In addition to the spatial distribution of water renewal time shown in Fig. 1b, the hydrodynamic model provided the water level and current velocity data necessary for coupling with the ecosystem model.

2.3. *C. virginica* Dynamic Energy Budget model

The oyster submodel is based on DEB theory (Kooijman, 1986, 2010), which describes the individual in terms of three state variables: reserve(s), structure(s), and maturity/reproduction. The energy assimilated from food is stored as reserves; a fixed fraction of this energy (κ) is directed towards maintenance and growth of the structural body, and the remainder ($1-\kappa$) is directed towards maturation, gamete production and/or maintenance of the reproductive system depending on the life cycle stage of the organism. The mathematical formulation of the *C. virginica* model described in this paper is identical to Rosland et al. (2009) and follows the original notation by Kooijman (2000), in which $[\]$ denotes quantities expressed as per unit structural volume, $\{ \}$ denotes quantities expressed as per unit surface-area of the structural volume and a dot over a symbol denotes a rate, or a dimension per time. A brief description of the model is presented in Table 1 and a more thorough presentation of the model and the equations are given in Pouvreau et al. (2006) and Rosland et al. (2009). The emphasis of this section is on the minor modifications to Rosland's model that have been applied in this study as well as in the datasets that have been used to estimate the specific set of parameters required for *C. virginica* (Table 2). The procedures to estimate these parameters followed van der Veer et al. (2006) and consequently are not described in detail in the present paper.

The shape coefficient (δ_v) determines how a specific length measurement relates to structural body mass. The estimation of the shape coefficient was based on data provided in Fig. 3 of Powell et al. (1995). Since these wet weight values include gonad mass and not only structural body mass, the dataset cannot be applied directly to estimate δ_v . In order to minimize this shortcoming the following steps were followed. Firstly, a virtual population was reconstructed by calculating the wet weight of 100 oysters of different lengths using the 18 available regressions (Powell et al., 1995), resulting in a pooled population of 1800 individuals, subsampled by selecting those oysters that are 5% lighter for a given length, following Dabrowski et al. (2013). Finally, this subsample was used to calculate the shape coefficient with the rationale that the structural body mass curve should lie below the total mass curve, which also includes reserves and gonad mass. This procedure resulted in a pooled shape coefficient of 0.20.

All of the physiological rates in DEB are corrected by using a function based on an Arrhenius function used by Rosland et al. (2009) and simplified in this study according to Saraiva et al. (2012):

$$k(T) = k_1 \exp\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right) \quad (1)$$

where T is the absolute temperature (K), T_1 is the reference temperature (K), $k(T)$ is the physiological rate at temperature T , k_1 is the physiological rate at temperature T_1 , and T_A is the Arrhenius temperature. The latter was calculated by using respiration data from Shumway and Koehn (1982). Only acclimated conditions (diagonal values in their Table 2) were used in this calculation, and provided a pooled value for T_A of 6292 K.

Ingestion rate is the balance between clearance rate, the volume of water cleared of particles per unit of time, and pseudofeces production rate, the amount of particles per unit of time that are cleared but rejected prior to ingestion. It has been suggested that ingestion rate is at a maximum when the production of pseudofeces begins (Winter, 1978). Hence the estimation of maximum surface area-specific ingestion rate, $\{p_{xm}\}$, was calculated as the product of clearance rate and the pseudofeces production threshold. Clearance rate measurements carried out on oysters from a neighboring cultivated population (Comeau, 2013) were combined with the pseudofeces threshold calculated from Haven and Morales-Alamo (1966) and the conversion factor 23.5 J mg⁻¹ for natural seston (Widdows et al., 1979), resulting in a $\{p_{xm}\}$ of 197.8 J cm⁻² d⁻¹ at 273. The maximum surface area-specific

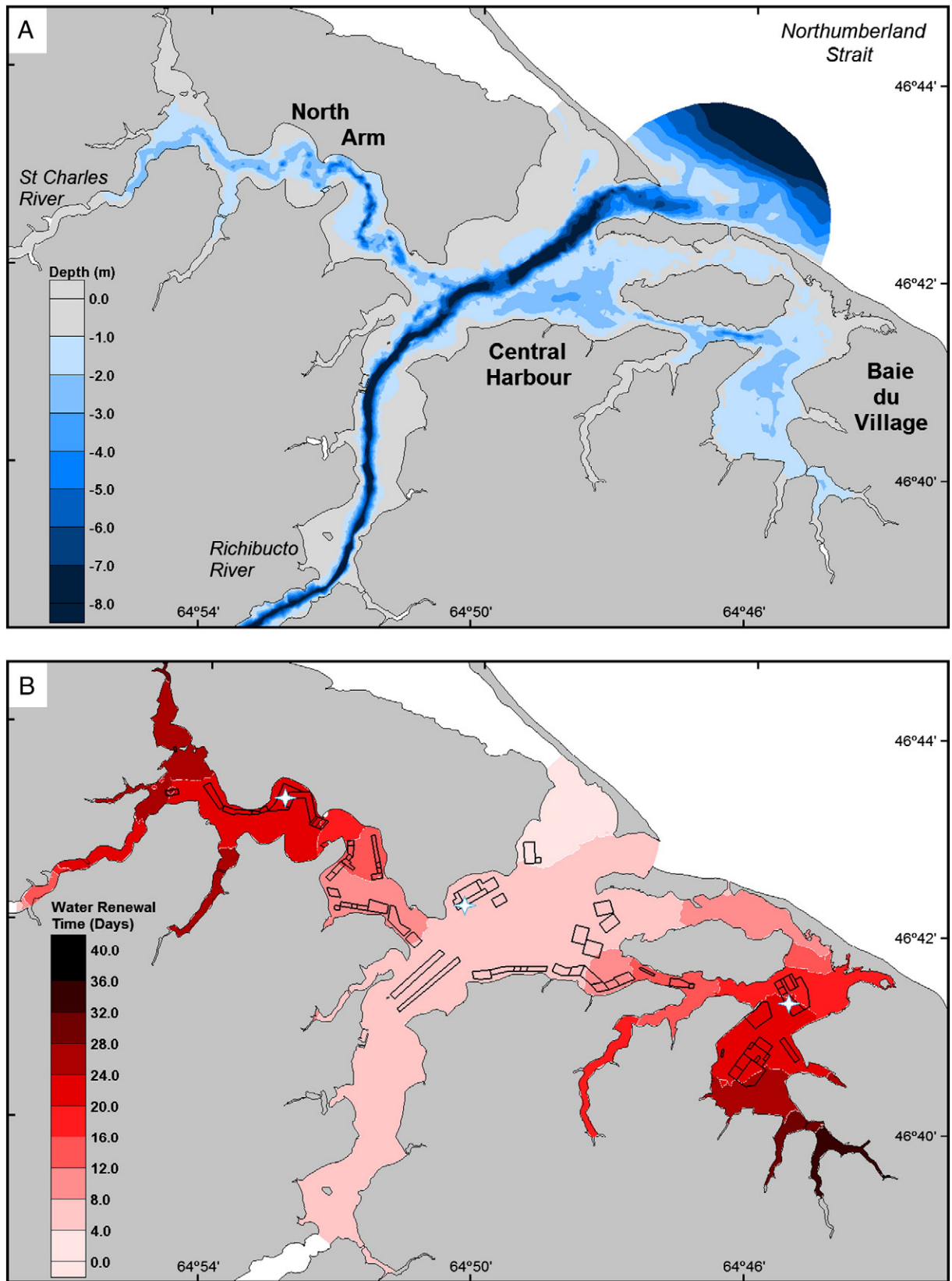


Fig. 1. Study area. A) Map of Richibucto Estuary with its three main areas (Central Harbour, North Arm and Baie du Village) and depth contours. B) Distribution of water renewal time over the study area also showing oyster farms (black polygons) and field sampling stations (white stars).

Table 1
Dynamic Energy Budget and ecosystem model description.

Equation	Terms and parameters	
<i>Dynamic Energy Budget (Pouvreau et al., 2006; Rosland et al., 2009; van der Veer et al., 2006)</i>		
$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$	E	Energy storage (J)
	\dot{p}_A	Assimilation rate (J d ⁻¹)
	\dot{p}_C	Mobilization rate of reserve energy (J d ⁻¹)
$\dot{p}_A = \{ \dot{p}_{Am} \} T_D f V^{2/3}$	$\{ \dot{p}_{Am} \}$	Maximum surface-area-specific assimilation rate (J cm ⁻² d ⁻¹)
	f	Michaelis–Menten term
	V	Structural volume (cm ³)
$f = \frac{X}{X + X_K}$	T_D	Arrhenius temperature function
	X	Chlorophyll concentration (µg l ⁻¹)
	X_K	Half-saturation constant (µg l ⁻¹)
$T_D = \exp\left(\frac{T_A}{T_I} - \frac{T_A}{T_K}\right)$	T_A	Arrhenius temperature (K)
	T_I	Reference temperature (K)
	T_K	Observed temperature (K)
$\dot{p}_C = \frac{[E]}{[E_C] + \kappa[E]} \left(\frac{[E_C] \dot{p}_{mC}}{[E_m]} V^{2/3} + \dot{p}_m \right)$	κ	Fraction of utilized energy to somatic maintenance and growth
	$[E_C]$	Volume-specific costs for structure (J cm ⁻³)
	$[E_m]$	Maximum storage density (J cm ⁻³)
$\dot{p}_m = [\dot{p}_M] V$	\dot{p}_M	Maintenance rate (J d ⁻¹)
	$[\dot{p}_M]$	Volume-specific maintenance costs (J cm ⁻³ d ⁻¹)
$\frac{dV}{dt} = (\kappa \dot{p}_C - p_M) / [E_C]$		
$\frac{dE_R}{dt} = (1 - \kappa) p_C - \left(\frac{1 - \kappa}{\kappa}\right) \cdot V \cdot [\dot{p}_M]$	E_R	Energy allocated to reproductive buffer (J)
$\frac{dE_R}{dt} = \kappa \dot{p}_C - \dot{p}_M \kappa \dot{p}_C - \dot{p}_M < 0$		Reproductive buffer dynamics when energy storage is too low
$L = \frac{V^{1/3}}{\delta_V}$	L	Oyster length (cm)
	δ_V	Dimensionless shape coefficient
<i>Ecosystem model (Dowd, 1997, 2005^b; Filgueira and Grant, 2009^c; Grant et al., 1993, 2007^a, 2008)</i>		
$\frac{dP}{dt} = +P_{growth} - P_{mortality} - O_{grazing} \pm P_{mixing}$	dP/dt	Phytoplankton change rate (mgC m ⁻³ d ⁻¹) ^a
	P_{growth}	Phytoplankton growth
	$P_{mort.}$	Phytoplankton mortality
	$O_{grazing}$	Oyster grazing on phytoplankton
	P_{mixing}	Exchange of phytoplankton with adjacent elements and/or far field
$\frac{dN}{dt} = +N_{river} + D_{remineralization} + O_{excretion} - P_{uptake} \pm N_{mixing}$	dN/dt	Nitrogen change rate (mgN m ⁻³ d ⁻¹) ^{a,b}
	N_{river}	Nitrogen river discharge
	$D_{remin.}$	Detritus remineralization
	$O_{excret.}$	Oyster nitrogen excretion
	P_{uptake}	Phytoplankton nitrogen uptake
	N_{mixing}	Exchange of nitrogen with adjacent elements and/or far field
$\frac{dD}{dt} = +O_{feces} + P_{mortality} - D_{sinking} - D_{remineralization} \pm D_{mixing}$	dD/dt	Detritus change rate (mgC m ⁻³ d ⁻¹) ^{a,c}
	O_{feces}	Oyster feces production
	$P_{mort.}$	Phytoplankton mortality
	$D_{sinking}$	Detritus removal by sinking
	$D_{remin.}$	Detritus remineralization
	D_{mixing}	Exchange of detritus with adjacent elements
$\frac{dO}{dt} = +O_{grazing} - O_{excretion} - O_{feces} - O_{mortality}$	dO/dt	Oyster change rate (mgC m ⁻³ d ⁻¹) ^{this study DEB}
	$O_{grazing}$	Oyster grazing on phytoplankton
	$O_{excret.}$	Oyster nitrogen excretion
	O_{feces}	Oyster feces production
	$O_{mortality}$	Oyster mortality

Table 2
Standard DEB parameters for *Crassostrea virginica*.

Parameter	Symbol	Unit	Value	Data used for estimation
Shape coefficient	δ_V	–	0.20	Powell et al. (1995)
Arrhenius temperature	T_A	K	6292	Shumway and Koehn (1982)
Reference temperature	T_I	K	293	–
Max. surf. area-specific ingestion rate	$\{ \dot{p}_{Am} \}$	J cm ⁻² d ⁻¹	197.8	Comeau, LA (unpub.), Haven and Morales-Alamo (1966)
Max. surf. area-specific assimilation rate	$\{ \dot{p}_{Am} \}$	J cm ⁻² d ⁻¹	148.4	$\{ \dot{p}_{Am} \} \cdot \kappa_A$
Assimilation efficiency	κ_A	–	0.75	Gerdes (1983)
Volume-specific costs for growth	$[E_C]$	J cm ⁻³	1521	Shellfish Monitoring Network
Maximum storage density	$[E_m]$	J cm ⁻³	2586	Shellfish Monitoring Network
Volume-specific maintenance costs	$[\dot{p}_M]$	J cm ⁻³ d ⁻¹	24	van der Veer et al. (2006)
Fraction of p_c to maintenance and growth	κ	–	0.506	van der Veer et al. (2006), Baqueiro-Cárdenas and Aldana-Aranda, 2007
Half-saturation constant	X_K	µg chl l ⁻¹	1.5	Auto-calibrated
% of reproduction buffer fixed in eggs	κ_R	–	0.9	Rosland et al. (2009)
Initial percentage of mass in E_R	κ_{IM}	–	0.2	This study
Structural dry weight: wet weight	DW:WW	–	0.12	Comeau, LA (unpub.)

assimilation rate, $\{\dot{p}_{Am}\}$, was derived from $\{\dot{p}_{xm}\}$ assuming an assimilation efficiency of 0.75 (Gerdes, 1983), which reported a value of $148.4 \text{ J cm}^{-2} \text{ d}^{-1}$.

Volume-specific costs for growth, $[E_G]$, were estimated by analyzing 4027 individuals collected by the Shellfish Monitoring Network (SMN), carried out by the Department of Fisheries and Oceans (DFO) in the southern part of the Gulf of St. Lawrence from 1995 to 2004 (Sonier et al., 2011). Allometric relationships measured in the laboratory were used to calculate a body mass index in terms of ash-free dry mass per volume (AFDM cm^{-3}) using the SMN dataset. The lowest value of this index is assumed to be the minimum somatic mass of an individual. In combination with the shape coefficient, 0.20, and the conversion factor, 21 J per mg of AFDM (van der Veer et al., 2006), $[E_G]$ was estimated at 1522 J cm^{-3} wet mass.

Maximum storage density, $[E_m]$, was estimated by comparing body mass index (AFDM cm^{-3}) of consecutive samplings in time collected in the Shellfish Monitoring Network (SMN) program. Given that in the SMN dataset gonad mass and somatic body mass have not been distinguished, a screening of the dataset was performed in order to discard samplings with high content in gonad mass which could introduce uncertainty in the analysis. The largest difference in body mass index between samplings of the same cohort was used to estimate $[E_m]$, which in combination with the shape coefficient, 0.20, and the conversion factor 21 J mg^{-1} of AFDM (van der Veer et al., 2006) yielded a value of 2586 J cm^{-3} wet mass.

In the absence of an appropriate starvation experiment for *C. virginica*, volume-specific maintenance costs, $[\dot{p}_M]$, were assumed to be $24 \text{ J cm}^{-3} \text{ d}^{-1}$, which is the common value suggested by van der Veer et al. (2006) for five bivalve species, including *Crassostrea gigas*. Once $[\dot{p}_M]$ was assumed, the fraction of utilized reserve to growth and maintenance κ , was derived from the theoretical relationship among maximum volumetric length, κ , $\{\dot{p}_{Am}\}$ and $[\dot{p}_M]$ (van der Veer et al., 2006):

$$V_m^{1/3} = \kappa \times \frac{\{\dot{p}_{Am}\}}{[\dot{p}_M]} \quad (2)$$

Volumetric length was calculated by multiplying the shape coefficient by the observed maximum length for *C. virginica*, 15.4 cm (Baquero-Cárdenas and Aldana-Aranda, 2007).

The last parameter of the basic parameter set, the half-saturation constant, X_K , was calibrated by using PEST (Model-Independent Parameter Estimation, Watermark Numerical Computing, <http://www.pesthomepage.org>), an optimization utility that uses the Gauss-Marquardt–Levenberg algorithm to estimate the value of a parameter, minimizing the discrepancies between the model results and a dataset chosen by the user. In this case, the optimization procedure was applied to two independent datasets in order to estimate X_K using shell length and dry meat mass as the optimization criteria. The two datasets are from a monitoring program carried out by Université de Moncton from 1990 to 1993 at six different sites in New Brunswick. Temperature ($^{\circ}\text{C}$), chlorophyll ($\mu\text{g l}^{-1}$), oyster shell length (cm) and dry meat (g) from Richibucto Estuary were retrieved from technical reports (Université de Moncton, 1991, 1992) generating two datasets: 1990 (21 May to 5 November) and 1991 (21 May to 7 October). Although monitoring started in May 1990, dry meat weight was initially missing in the report and consequently the modeling exercise started on 2 July. In 1991, intense spawning was observed at the beginning of July, therefore the dataset was shortened to 29 July–7 October in order to avoid the uncertainty that spawning could introduce in the estimation of X_K . The validation of the DEB model was carried out by using the three specific datasets collected in Richibucto Estuary as part of this study.

The initial mass allocated towards structural body was calculated as a function of oyster length and shape coefficient (Table 1). The remaining mass, that is, observed oyster mass minus mass allocated towards structural body, was divided between reproduction buffer and reserves.

Given that gonad mass and somatic body mass were not distinguished during the initial oyster sampling, and that all simulations began after spawning events, the initial percentage of mass in reproduction buffer energy, E_R , was assumed 0.2, allocating the remaining 0.8 to reserve energy, E .

2.4. Ecosystem model

The hydrodynamic model developed in RMA-10 was coupled to a biogeochemical model constructed in Simile (Simile, <http://www.simulistics.com>) following a first-order upwind scheme as described in Filgueira et al. (2012). The biogeochemical model contains the following submodels: Phytoplankton (P), Nutrients (N), Oyster (O) and Detritus (D) submodels. The model is characterized in terms of mgC m^{-3} , with the exception of dissolved nutrients, which are expressed in mg N m^{-3} . Table 1 provides a brief description of the model, which follows Grant et al. (1993, 2007, 2008), Dowd (1997, 2005) and Filgueira and Grant (2009). The mussel submodel described in these papers has been substituted by the Dynamic Energy Budget (DEB) model parameterized in this study for *C. virginica*. An individual DEB model has been run in each element in which a farm is allocated. The extrapolation from the individual to the population level has been carried out as a product of DEB individual rates and number of animals. The number of individuals has been modeled with a simple population model in which mortality was considered as the only significant process due to the short time period that has been simulated. Given that this version of DEB only considers chlorophyll as a food source for oysters, the detritus compartment only interacts with the other submodels via nutrient remineralization ($D_{\text{remineralization}}$, Table 1). Therefore this submodel has been simplified and prescribed as a forcing function to deliver $D_{\text{remineralization}}$ based on field measurements of seston rather than a dynamic balance, an approach followed by Filgueira et al. (2014). A sensitivity test has been performed to evaluate the effects of different DEB parameters on model performance. The fully-coupled model was run from 1 August 2012 to 19 September 2012 (50 days) in order to avoid the spawning period, which typically occurs in early July. The end of the simulated period was determined by the lack of far field nutrient data beyond that date. This simulated period has been used for both validation of the fully-coupled ecosystem model as well as carrying capacity simulations.

2.5. Boundary conditions and field data

Chlorophyll and temperature time series for the simulated period (1 August 2012 to 19 September 2012) were constructed by using daily time series of 4 km MODIS-Aqua chlorophyll averaged within a region located just outside of Richibucto Estuary defined by the coordinates $64^{\circ} 46' 58'' \text{ W}$ to $64^{\circ} 42' 42'' \text{ W}$ and $46^{\circ} 45' 25'' \text{ N}$ to $46^{\circ} 42' 44'' \text{ N}$. Missing data were interpolated by using linear regression. Chlorophyll concentration was converted to carbon units assuming a carbon:chl ratio of 50:1.

River flows were obtained from Environment Canada (<http://www.ec.gc.ca>). Nutrient time series were generated by using the Environment Canada database. For the St. Charles River, nutrient data from 1996 to 1998 were combined to generate time series for the period 9 May to 20 November. In the case of the Richibucto River, studies from 1996 to 2007 generated a temporal series from 29 May to 20 November. Nutrient data for the far field came from sampling carried out in the Southern Gulf of Saint Lawrence between 1993 and 1996 (Waite et al., 1997a,b,c,d). The closest stations to the Richibucto Estuary were pooled to generate average far-field conditions between 7 June and 19 September. Missing data were interpolated by using linear regression.

Monthly chlorophyll and seston samples were collected at three stations inside the bay (Fig. 1) from 11 July to 15 October 2012. Duplicate chlorophyll samples were filtered through 25 mm Whatman GF/F filters, kept frozen (-20°C) and analyzed following EPA Method

445.0. Duplicate Total Particulate Matter (TPM) samples were analyzed gravimetrically on pre-ashed (500 °C, 4 h) 47 mm Whatman GF/F filters. The filters were dried at 70 °C for 24 h and weighed to determine the TPM. Particulate Organic Matter (POM) was determined after ashing the filters for 6 h at 500 °C.

Oyster sampling was performed simultaneously with water sampling. Central Harbour sampling concluded a month earlier than the other two locations due to logistic problems. At each station a cage with 2 Vexar bags, each containing approximately 150 oysters, were deployed. At each sampling date, 15 oysters from each bag were collected, weighed and measured to 0.01 mm resolution. After that, the individuals were dissected and dried at 75 °C for 24 h to determine dry weights.

2.6. DEB-IBM and ecosystem model validation procedures

The agreement between simulations and observations of DEB-Individual Based Model (DEB-IBM) and fully-coupled ecosystem model has been tested on oyster tissue mass and shell length using the deviation (F) following Rosland et al. (2009):

$$F = \frac{100}{2T} \left(\sum_{t=1}^T \frac{|M_m(t) - M_o(t)|}{M_o(t)} + \sum_{t=1}^T \frac{|L_m(t) - L_o(t)|}{L_o(t)} \right) \quad (3)$$

Where t is the time index, T the total number of observations in the dataset, M_m and M_o the modeled and observed tissue mass, and L_m and L_o the modeled and observed shell length. A similar formulation has been applied to calculate the deviation of chlorophyll values between simulations and observations:

$$F = \frac{100}{T} \left(\sum_{t=1}^T \frac{|C_m(t) - C_o(t)|}{C_o(t)} \right) \quad (4)$$

Where C_m and C_o are the modeled and observed chlorophyll concentration.

Both models have been tested for sensitivity to changes in some parameters by alternating the original value of the parameter by + 10%/– 10%. The sensitivity has been evaluated as the relative difference in tissue mass and shell length at the end of the model simulation following:

$$S = \frac{O_{alt} - O_{ori}}{O_{ori}} \times 100 \quad (5)$$

Where O_{alt} and O_{ori} are the final oyster tissue mass or shell length for the simulation with alternated and original parameter values respectively.

2.7. Phytoplankton depletion and sustainability threshold

In addition to the simulation that represents the current conditions in Richibucto, five additional scenarios were run by increasing the standing stock biomass 2, 3, 4, 5 and 6 times the present standing stock biomass allocated in the bay with the aim of exploring the carrying capacity of the bay. The results were computed in terms of phytoplankton depletion index (%), which was calculated according to Filgueira et al. (2014):

$$\text{Phytoplankton depletion index} = \frac{[Chla]_i}{[Chla]_{far\ field}} \times 100 - 100 \quad (6)$$

where $[Chla]_i$ and $[Chla]_{far\ field}$ are the chlorophyll concentration ($\mu\text{g chl l}^{-1}$) in element i and far field, respectively. Values below 0% indicate

depletion and above 0% indicate enrichment of chlorophyll in element i compared to the far field. Similarly, a bay-scale depletion index was calculated as follows:

$$\text{Bay-scale depletion index} = \frac{\sum_i [Chla]_i \times Vol_i / \text{Bay volume}}{[Chla]_{far\ field}} \times 100 - 100 \quad (7)$$

where Vol_i and Bay volume are the volume (l) of element i and the volume of the bay, respectively. An inter-annual coefficient of variation of chlorophyll concentration was calculated for August–September using a multi-year (2002–2011) satellite remote sensing dataset, which yielded a value of 32.5%. Consequently, the threshold of sustainability based on resilience within natural variation was established at – 32.5%. These depletion indices have asymmetrical distributions, with – 100% representing the total depletion of the bay, but with enrichment having no upper limit. Consequently, medians were used as time averaged measures instead of means.

3. Results

3.1. *C. virginica* DEB model calibration

The auto-calibration procedure of the half-saturation constant, X_K , was in good agreement with both Université de Moncton datasets, showing a deviation of 6.9 and 9.6% for 1990 and 1991, respectively. The optimized X_K values ranged from 1.1 to 1.9 $\mu\text{g chl l}^{-1}$ and consequently the mean value, 1.5 $\mu\text{g chl l}^{-1}$ was used in the standard set of parameters. Using this X_K value, the deviation of both simulations increased to 7.9 and 9.8% for 1990 and 1991, respectively. Nevertheless, the simulated tissue mass and shell length were generally within the range of the observed standard deviation (Fig. 2). A sensitivity analysis (Table 3) was performed for all the parameters of the model using the 1990 dataset. Three of these parameters, δ_v , $\{\dot{p}_{Xm}\}$ and $[\dot{p}_M]$, were used to determine other parameters (See Section 2). Consequently, two sensitivity tests were carried out for these parameters, one in which the tested parameter had no influence on the other ones, and a second one in which the new value of the tested parameter was used to recalculate the other parameters (* values in Table 3). These sensitivity tests are especially important in the case of the shape coefficient, δ_v , given that it is used in the calculation of three parameters, $[E_G]$, $[E_m]$ and κ . Consequently, when the alternative value of δ_v was also used to recalculate these parameters, the change in tissue mass reached 20.3%, the largest change of all the standard set of parameters. The second most sensitive parameter was $\{\dot{p}_{Xm}\}$, maximum surface area-specific ingestion rate, causing a maximum change in tissue mass of 13.6%. The effects on the remaining parameters were always lower than 5.5%.

3.2. *C. virginica* DEB model validation

The period between the first and second sampling on North Arm and Central Harbour stations was not modeled due to the observed spawning events and the lack of spawning parameterization in this current DEB model. Therefore at these two stations the model was initialized on 10 August instead on 11 July, which is the starting point at Baie du Village. The simulation at Central Harbour was ended a month earlier (14 September) than at the other stations (15 October) due to the lack of data as explained above. DEB-IBM provided a prediction of oyster growth that is in good agreement with the observed values (Fig. 3). Simulated values of tissue mass and shell length are within the observed standard deviation in all sampling for all stations. The averaged deviation (Eq. (3), Table 4) for the three datasets pooled together is 10.2%, with the best agreement (8.0%) occurring in North Arm, and the poorest (13.1%) in Central Harbour.

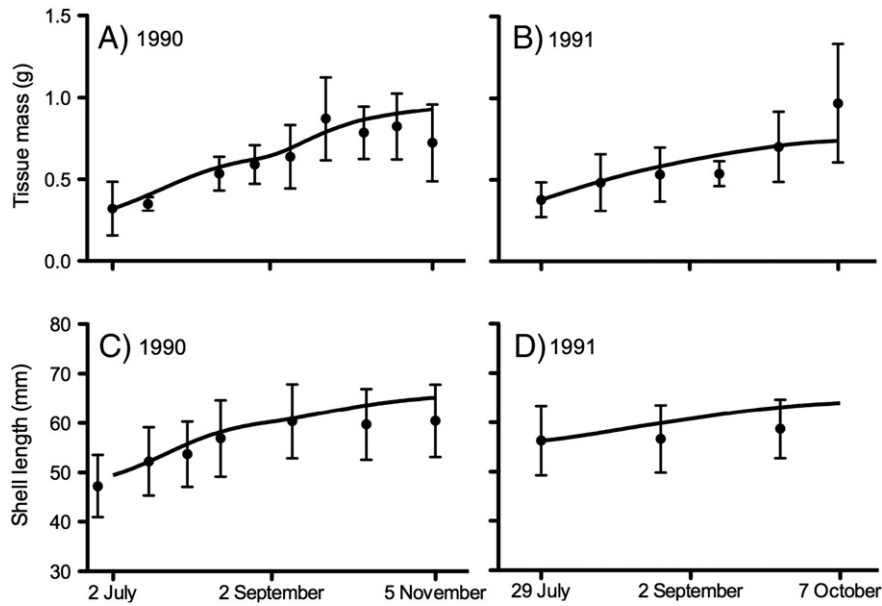


Fig. 2. Simulated (line) and observed (dots with bars for standard deviation) tissue mass (g) for 1990 (A) and 1991 (B) Université de Moncton datasets as well as shell length for the same locations (C and D respectively).

3.3. Ecosystem model validation

Groundtruthing of the ecosystem model was carried out by comparing modeled and observed values of chlorophyll concentration and oyster growth at three sampling stations (Fig. 1). For chlorophyll, the reduced major axis (RMA) regression between modeled and observed values at the three sampling stations reported a significant relationship ($r^2 = 0.72$, $F = 10.039$, $p < 0.05$) with a slope of 0.53 ± 0.39 and an intercept of 3.98 ± 3.33 . The analysis of chlorophyll deviation (Eq. (4), Table 4) showed the best results in Baie du Village, 8.9%, and the poorest performance in Central Harbour, 30.9%. The RMA analysis for oyster weight reported a significant regression ($r^2 = 0.77$, $F = 18.504$, $p < 0.05$) with a slope of 0.80 ± 0.47 and an intercept of 0.12 ± 0.20 . For oyster length, the RMA regression was also significant ($r^2 = 0.86$, $F = 24.468$, $p < 0.01$) with a slope of 0.66 ± 0.34 and an intercept of 10.10 ± 21.47 .

The simulated weight and length obtained with the fully-coupled model is also presented in Fig. 3. Note that the simulations in the fully-coupled model were initialized on 1 August instead of 10 August

Table 3

Standard DEB sensitivity test in 1990 Université de Moncton dataset. Percentage of change (%) on final tissue mass and shell length between the standard model and the model alternating one parameter by $+10/-10\%$. * values: the new value of the tested parameter was used to recalculate the other parameters (see text).

Parameter	Tissue mass		Shell length	
	+10%	-10%	+10%	-10%
δ_V	3.7/20.3*	-3.7/-16.4*	-6.8/4.1*	8.6/-4.0*
T_A	0.0	0.3	0.0	0.1
T_I	-	-	-	-
$\{P_{Xm}\}$	13.6/9.0*	-12.4/-8.9*	4.8/0.6*	-4.8/-0.7*
$\{P_{M}\}$	-	-	-	-
K_A	-	-	-	-
$[E_C]$	-2.2	2.5	-1.2	1.3
$[E_M]$	-1.1	1.2	-1.2	1.3
$[P_M]$	-5.1/-1.4*	5.5/1.1*	-2.8/1.2*	2.9/-1.3*
K	4.0	-4.1	4.0	-4.3
X_K	-3.8	4.1	-1.2	1.3
K_R	3.5	-3.5	0.0	0.0
K_{IM}	-0.7	0.7	-0.6	0.6
DW:WW	1.3	-1.3	-0.4	0.3

as it was done for DEB-IBM simulations. This extended simulated period was chosen in order to maximize the available time series to force the fully-coupled model. The fully-coupled model was ended on 19 September due to the lack of forcing datasets after that day (see above). The pooled deviation of oyster growth (Eq. (3), Table 4) in the fully-coupled model, 14.8%, was higher than in the individual based model (IBM), 10.2%. This outcome can be partially explained by the use of slightly different simulated periods between modeling approaches. Nevertheless, a better agreement of the DEB-IBM was expected given that the oyster growth in the fully-coupled model was forced by estimated chlorophyll, while field measurements were used in the IBM, which ensures a better description of food availability. The better agreement in North Arm and Baie du Village in the fully-coupled model was not anticipated but within the range of the expected error of model predictions. The pooled deviation for oyster growth, 14.8%, was smaller than for chlorophyll, 20.7%, which could be related to a high frequency variation in chlorophyll measurements compared to oyster growth.

Sensitivity tests (Table 5) were performed for the following parameters: X_K , bivalve mortality, phytoplankton growth rate, phytoplankton mortality and detritus remineralization ($D_{remineralization}$). Two scenarios were run for each parameter, i.e. by increasing and decreasing the parameter value by 10%. The response of the model to these parameters was evaluated by observing the relative change in these simulations compared to present scenario values. The following response variables were analyzed: final bivalve biomass (total biomass of bivalves in the bay), individual bivalve dry weight, length and condition index as well as phytoplankton depletion. Phytoplankton depletion was in all cases the most affected response variable and $D_{remineralization}$ the only sensitive parameter, causing $+9.69/-9.70\%$ change when the parameter varied $+10/-10\%$. Phytoplankton mortality was not a sensitive parameter, with maximum changes around 2% in phytoplankton depletion. Oyster performance was not sensitive to these parameters, observing a maximum change of 0.63% in bivalve biomass and dry weight when X_K was reduced by 10%.

3.4. Present aquaculture scenario

The bay-scale depletion index through time (Fig. 4) highlighted that under the present aquaculture conditions Richibucto Estuary was most of the time enriched in phytoplankton compared to conditions

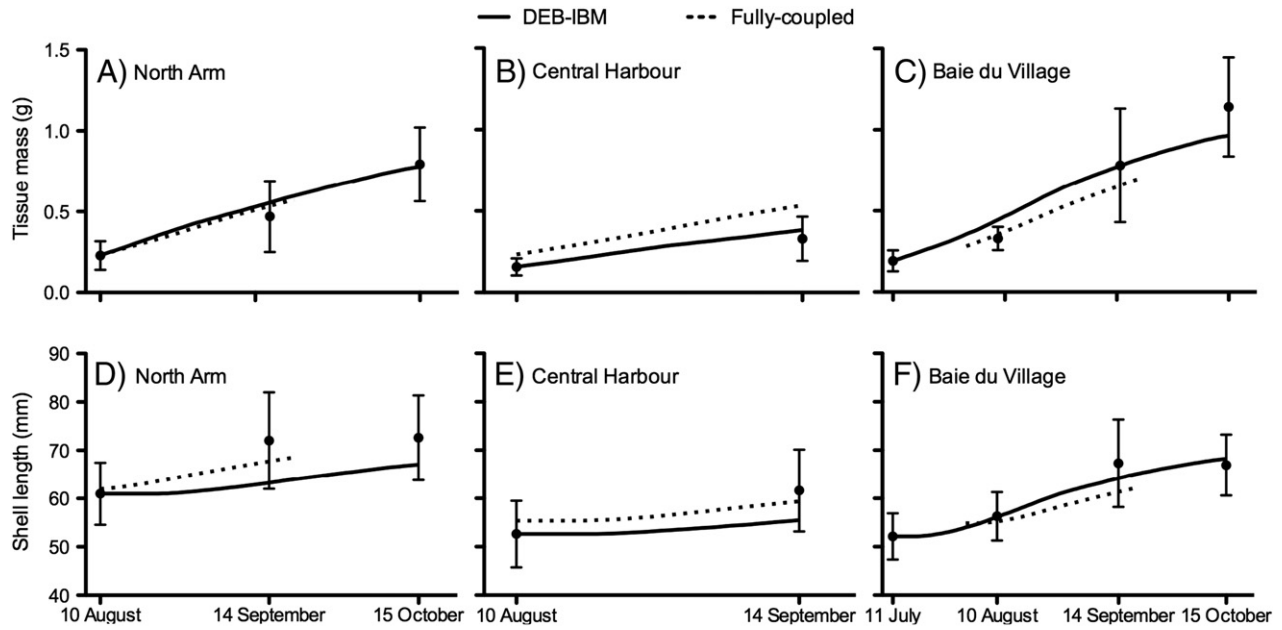


Fig. 3. Simulated (line) and observed (dots with bars for standard deviation) tissue mass (g) for North Arm (A), Central Harbour (B) and Baie du Village (C) as well as shell length for the same locations (D, E and F respectively).

immediately outside the estuary. There was only a short period of time in mid-September when the depletion index fell below the threshold of sustainability, -32.5% . The median bay-scale depletion over the whole simulation was 64.2% which reflects phytoplankton enrichment in the estuary. The spatial distribution of the depletion index (Fig. 5a) showed that although the whole system was enriched in phytoplankton, the areas with the longest residence time, North Arm and Baie du Village (Fig. 1b) corresponded with the highest accumulation of phytoplankton.

3.5. Carrying capacity analysis

A series of simulations were carried out to further explore the carrying capacity of Richibucto Estuary by increasing the oyster standing stock biomass and evaluating the consequences for phytoplankton populations. Five scenarios were run by increasing the standing stock biomass 2, 3, 4, 5 and 6 times the present standing stock biomass allocated in the bay (Fig. 5b,c,d,e and f respectively). When oyster biomass was doubled (Fig. 5b) the bay scale depletion index dropped to 31.0% , which suggests that even at this culture density the median bay would be enriched in phytoplankton compared to adjacent waters. The spatial distribution of phytoplankton was slightly different than the present scenario, yielding an incipient depletion in North Arm and Baie du Village, although the spatial variability was maintained at the same level (16.7 versus 17.0%). The bay-scale depletion index dropped to 6.9% when the stocking biomass was increased by three times (Fig. 5c). Although this depletion index suggests enrichment in phytoplankton at the bay-scale, the high spatial variability, 30.0% (Fig. 5c), highlights an extreme change in performance at local scale. In this

sense, North Arm and Baie du Village median depletion index fell below the sustainability threshold, -32.5% , while Central Harbour was still enriched in phytoplankton. The same pattern but with more extreme spatial gradients, 47.3% spatial variability, was observed when the oyster biomass was increased by a factor of four (Fig. 5d). In the latter scenario most of the area in North Arm and Baie du Village was completely depleted in phytoplankton although the bay-scale depletion index indicated a depletion, -13.2% , still within the sustainability range. An increase of five times the present biomass led some areas of Central Harbour to values below the sustainability threshold (Fig. 5e). Nevertheless, the bay-scale depletion index, -27.3% , was still within the sustainability range. It would be necessary to increase the oyster biomass by six times to obtain a drop of the bay-scale depletion index below the sustainability threshold (Fig. 5f).

4. Discussion

Shellfish aquaculture sites are characterized by a complex interaction of biological and physical processes. The filter feeding activity of the cultured population can clear large volumes of water of suspended particles, thereby altering the natural flow of matter and energy (Dowd, 2003). In particular, this filtration capacity can exert a strong top-down control on phytoplankton populations (Dame and Prins, 1998). The top-down control can reach a threshold in which the cultured population causes a severe depletion of phytoplankton, compromising ecosystem sustainability. Exploring this level of depletion and framing it in the context of ecosystem sustainability is the focus of this study. Nevertheless, the biological processes involved in aquaculture sites have a much broader scope than the sole pelagic effect just mentioned. Bivalves consolidate small particles into feces and pseudofeces that sink to the bottom, which may significantly increase organic loading in benthic communities (Grant et al., 2005). The remineralization of this organic material plus ammonia excreted by the oysters can exert a significant effect on nutrient availability, accelerating phytoplankton turnover and production and ultimately exerting a bottom-up nutrient control on phytoplankton populations (Cranford et al., 2007). These biological processes are largely influenced by coastal hydrodynamics. For example, strong water currents in a bivalve farm can rapidly replenish phytoplankton, minimizing local depletion. The impact of hydrodynamics is even more important in heterogeneous

Table 4
Deviations (%) between simulations and observations in oyster growth (Eq. (3)) in both DEB Individual Based Model (IBM) and fully-coupled model as well as deviation of chlorophyll concentration (Eq. (4)) in the fully-coupled model.

	Oyster		Chlorophyll
	IBM	Fully-coupled	Fully-coupled
North Arm	8.0	5.9	22.2
Central Harbour	13.1	29.9	30.9
Baie du Village	9.6	8.5	8.9
Pooled	10.2	14.8	20.7

Table 5
Sensitivity test of model parameters on total biomass of bivalves in the bay, bivalve performance and chlorophyll depletion index.

Parameter	Parameter change (%)	Percentage of change in response variable (%)				
		Bivalve biomass	Bivalve dry weight	Bivalve length	Bivalve CI	Chlorophyll depletion
X_K	+10	-0.62	-0.62	-0.11	-0.38	0.37
	-10	0.63	0.63	0.11	0.39	-0.36
Bivalve mortality	+10	-0.38	0.09	0.02	0.03	0.21
	-10	0.38	-0.09	-0.02	-0.03	-0.21
Phytoplankton growth rate	+10	0.01	0.01	0.00	0.00	0.72
	-10	-0.01	-0.01	0.00	-0.01	-0.88
Phytoplankton mortality	+10	0.02	0.02	0.00	0.01	-1.99
	-10	-0.02	-0.02	0.00	-0.01	2.03
$D_{remineralization}$	+10	0.07	0.08	0.01	0.05	9.69
	-10	-0.08	-0.08	-0.01	-0.05	-9.70

systems such as the Richibucto Estuary, in which different parts of the system are characterized by different water residence time. In this work, these biological processes are dynamically simulated by means of a fully-coupled biogeochemical–hydrodynamic model, allowing an exploration of the effect of water residence time on ecosystem performance.

4.1. A set of parameters for *C. virginica* DEB model

The parameters of the DEB model were estimated based on literature review and not on specific experiments, which could introduce uncertainty in some cases. For example, the shape coefficient is based on the assumption that 5% of the lighter individuals for a given length would represent the structural weight vs. length relationship. A similar approach was followed by Rosland et al. (2009) and Dabrowski et al. (2013) but specific experiments would improve the estimation and reduce uncertainty in this parameter. The estimation of maximum surface area-specific ingestion rate, $\{\dot{p}_{X_m}\}$, assumes that ingestion is maximum when pseudofeces are being produced (Winter, 1978) but this assumption does not consider the capacity of bivalve suspension feeders to finely adjust clearance rate under different environmental conditions (Cranford et al., 2011). Therefore, the estimation of $\{\dot{p}_{X_m}\}$ presents uncertainty due to the variability in clearance rate estimations as well as the complexity of selection and sorting processes carried out by bivalves, which can respond to physical, quantitative and qualitative aspects of the seston as well as be affected by intraspecific differences in feeding-organ morphology (Ward and Shumway, 2004). Regarding maximum storage density, $[E_m]$, the best dataset available to indirectly calculate its value does not distinguish between somatic and gonad mass. Although the data were carefully pre-analyzed in order to minimize the effect of gonad mass by removing specific points from the analysis, there may be a residual effect on $[E_m]$ estimation. Nevertheless, all the parameters estimated for *C. virginica* in this study are in the range of other related species (e.g. van der Veer et al., 2006). According to

sensitivity tests, the shape coefficient δ_v , and maximum surface area-specific ingestion rate, $\{\dot{p}_{X_m}\}$, have the highest impact on model results and consequently should be improved via further experimentation. Nevertheless, validation of the individual-based model despite components from different datasets suggests that the estimated set of parameters could be used in further modeling exercises for *C. virginica*.

4.2. Ecosystem model validation

The fully-coupled model has been validated by comparing modeled and observed values of chlorophyll concentration and oyster growth at three sampling stations (Fig. 1). Although the reduced major axis (RMA) regression for chlorophyll was statistically significant, the slope was different than 1, which suggests that the model can explain a significant proportion of the variance but there is not a full agreement between modeled and observed values (Duarte et al., 2003). The lack of full agreement in chlorophyll concentration could be caused by (1) the use of a fixed carbon:chlorophyll ratio, and/or (2) high frequency variation of chlorophyll. One of the assumptions of the model is a constant carbon:chl ratio of 50:1. However, it is well known that this ratio is highly variable depending on phytoplankton assemblages and environmental conditions such as temperature, daily irradiance and nutrient availability (Cloern et al., 1995). Given that the fully-coupled model is constructed in carbon units, the use of a constant ratio could lead to over- or under-estimation of chlorophyll concentration. A second cause is related to the fact that the ecosystem model is being forced by daily time series but field observations were collected at a specific time of the tidal cycle. It is well known that chlorophyll concentration in coastal bays can depend on tidal cycle (e.g. Grant et al., 2008). Consequently, the isolated samples collected in the field at a certain moment of the tidal cycle do not necessarily match the average daily values reported by the ecosystem model. Given that chlorophyll can abruptly change over a short period of time and the fact that bivalve growth integrates the effects of changing environmental conditions over time, the groundtruthing based on oyster growth can provide a better assessment of the ecosystem model performance in long-term simulations (Filgueira et al., 2014). The RMA regressions for oyster weight and length reported that both slopes and intercepts were statistically similar to 1 and 0 respectively, indicating a good agreement between modeled and observed values (Duarte et al., 2003). The good agreement of oyster growth suggests that the model is able to successfully simulate the main trophic interactions between oysters and phytoplankton in Richibucto. Nevertheless, further research is necessary to include a proper characterization of the carbon:chlorophyll ratio of phytoplankton as well as high frequency sampling of chlorophyll in order to reduce uncertainty not only in chlorophyll outcomes but also in oyster growth. Chlorophyll is used as a proxy of food availability in this current version of DEB, but a changing carbon:chlorophyll ratio can introduce uncertainty in oyster growth estimations. Special emphasis is being made nowadays to improve this aspect of DEB by using different food proxies (Bourlès et al., 2009; Grangeré et al., 2009), including different food sources in the

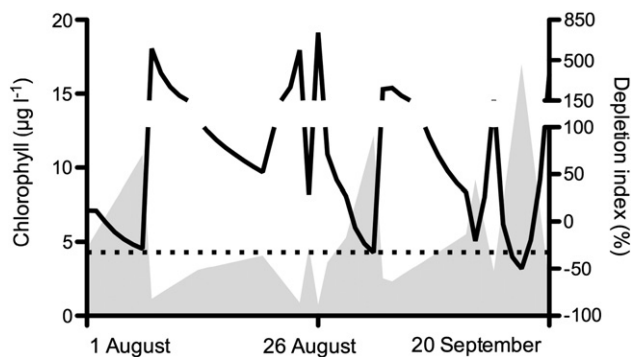


Fig. 4. Bay-scale depletion index (%) through time in the present aquaculture scenario. Dashed line represents the depletion index sustainable threshold, i.e. -32.5%, and gray area observed far field chlorophyll concentration ($\mu\text{g l}^{-1}$).

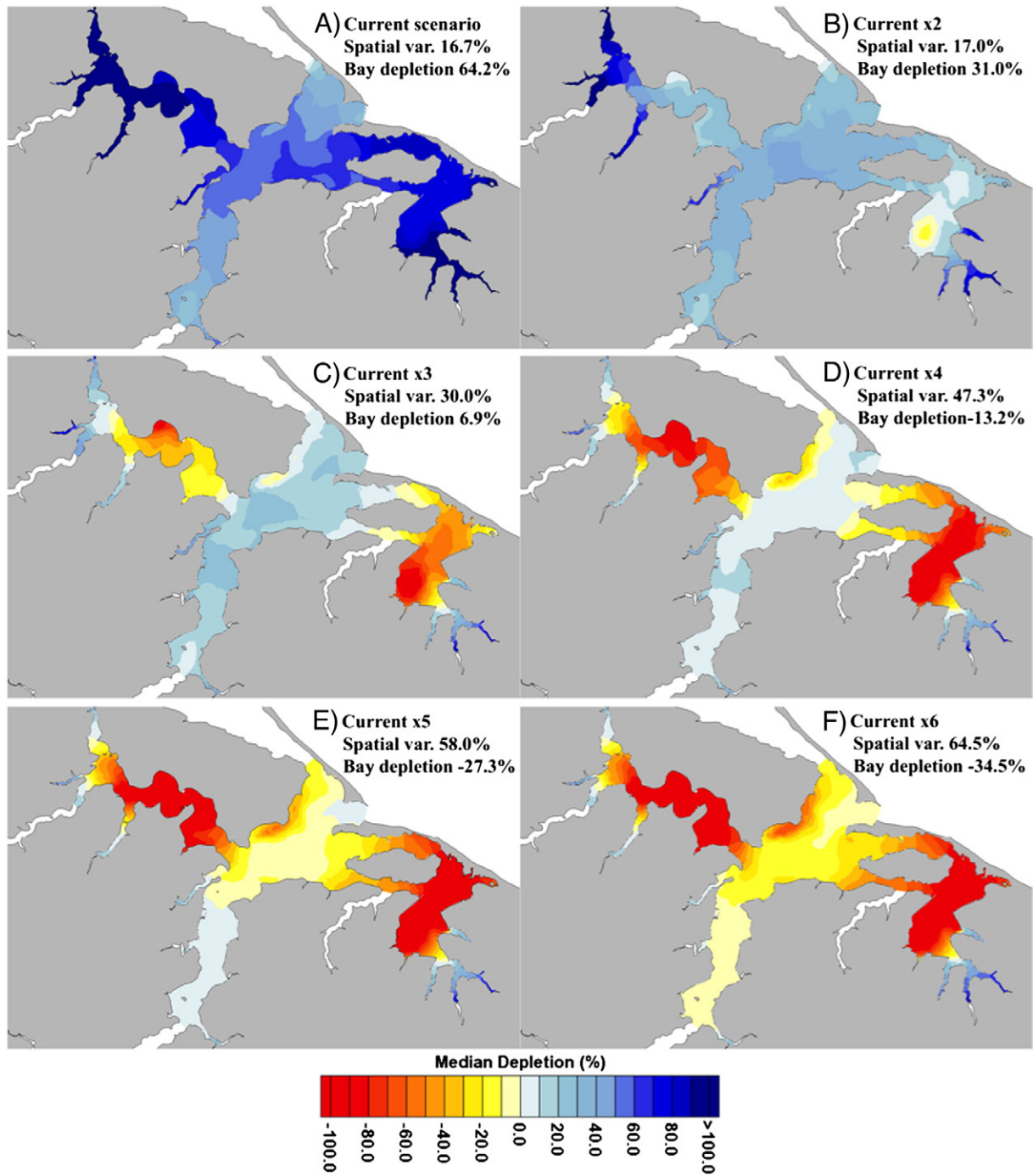


Fig. 5. Median values of depletion index (%) for each element over the simulated period in the present aquaculture scenario (A) and in five scenarios with increasing stocking biomass 2, 3, 4, 5 and 6 times the present biomass (B, C, D, E and F respectively). Spatial variability (Mean of medians/Std. Dev. $\times 100$, %) and Bay-scale depletion index (%).

ingestion law (Alunno-Bruscia et al., 2011) or making use of the concept of “synthesizing units” (Saraiva et al., 2011).

The success of a modeling exercise relies heavily on the correct parameterization of general and specific parameters. One of the challenges in shellfish aquaculture modeling is the characterization of the initial standing stock biomass. Different farmers in the same area can follow slightly different practices, e.g. different stocking density, and timing of market cycle. In addition, the cultivated biomass changes through time as the population grows. This leads to high uncertainty when determining the stocked biomass in a bay at a given time. If the initial biomass in the model is not correctly parameterized and/or the

population growth is not properly modeled, a disagreement between model and observations can be expected but a change of the disagreement level through time as the population grows is also expected. The present modeling exercise has provided a good agreement between modeled and observed values though time. Nevertheless, a detailed characterization of the standing stock biomass at different times during the simulated period would significantly reduce the uncertainty of the model outputs. An optimal method to validate model outputs is by comparing predicted and declared harvest. Although harvested biomass would perfectly complement the information collected to determine individual growth, it requires a close collaboration, training and

implication of farmers and authorities. The individual growth data together with the harvested information would allow the model validation at both individual and population levels.

Another source of uncertainty in the study of the phytoplankton bivalve trophic interaction is related to natural populations of filter-feeders. This effect at the estuary scale should not be significant because the biomass of natural populations is dramatically smaller than the cultured biomass. However, oyster beds could have an important role at the local scale, interacting with phytoplankton and cultured bivalves. Therefore, the effect of natural populations on bay-scale carrying capacity is not expected to be significant but competition with cultured bivalves could exist at a local scale.

4.3. Implications of local hydrodynamics on ecological resistance

Water circulation is integral in the performance of coastal embayments (Elliot and Whitfield, 2011), affecting phytoplankton and other trophic dynamics (Paerl et al., 2006). Consequently, most of the mathematical tools developed to explore carrying capacity of bivalve aquaculture sites have included some form of hydrodynamics. For example, simple food depletion indices not only have been used to assess carrying capacity by incorporating the residence time of the water body (e.g. Dame and Prins, 1998) but also by using 2D or 3D hydrodynamic models (e.g. Cugier et al., 2010; Filgueira et al., 2013; Nunes et al., 2011).

The complex geomorphology of the Richibucto Estuary suggests that detailed spatial resolution is needed in order to successfully characterize local hydrodynamics (Guyondet et al., 2005; Koutitonsky et al., 2004). Koutitonsky et al. (2004) carried out a study in the North Arm of Richibucto Estuary and suggested that the use of a 3D hydrodynamic model constitutes a major improvement over conventional renewal estimates using tidal prism models. The use of a fully spatial model allowed the identification of areas enriched in phytoplankton, North Arm and Baie du Village, which also showed the longest residence time (Fig. 1b). The discharge of river nutrients in these areas in combination with the long residence time triggered phytoplankton build up and accumulation. On the contrary, river nutrient discharge in the Central Harbour did not have an impact on phytoplankton concentration because the short residence time in this area of the bay (Fig. 1b) prevented accumulation. Phytoplankton and nutrients were rapidly diluted and transported to the outer part of the harbour due to the strong water exchange. Consequently, phytoplankton concentration in the Central Harbour was governed by mixing of different water characteristics following the main axis of the estuary: (1) the area closest to the river, with low phytoplankton due to the influence of river discharge as a negligible source of phytoplankton; (2) the central part, with high phytoplankton, being the confluence of the two water bodies enriched in phytoplankton, North Arm and Baie du Village; and (3) the most seaward area, with low phytoplankton due to the short residence time (Fig. 1b) and strong mixing with the far field. Guyondet et al. (2005) performed a similar fully-spatial modeling approach for the south channel connecting Central Harbour and Baie du Village. Consecutively, renewal time calculations were used to calculate an index of food depletion based on Dame and Prins (1998) and different aquaculture scenarios were explored to assess potential aquaculture development in this region of the Richibucto Estuary. More recently, Guyondet et al. (2013) have followed the framework proposed by Dowd (2003) and constructed a 2D hydrodynamic model coupled to a tracer advection dispersion module to simulate transport, production and consumption of seston. This model has been used to estimate a seston depletion index (SDI) and assess carrying capacity in the Richibucto Estuary. The depletion index calculated in the present study cannot be directly compared to the values estimated by Guyondet et al. (2013) because SDI values are not intended to represent an actual depletion but rather form a relative criterion allowing for the identification of potentially sensitive areas (Guyondet et al., 2013). Nevertheless both studies agreed in the

identification of the inner parts, those areas with the longest residence time and highest accumulation of phytoplankton.

The influence of water residence time on ecosystem performance can be observed in the scenario analysis directed at exploring the carrying capacity of the system (Fig. 5). These scenarios were designed by increasing oyster biomass evenly among the farms, which are primarily located in the North Arm and Baie du Village. However the response of phytoplankton depletion was not homogeneous but strongly influenced by the residence time of the different areas. In this sense, phytoplankton depletion in response to increasing oyster biomass (Fig. 5) was particularly evident in areas covered with farms and having the longest residence times, i.e., the North Arm and Baie du Village (Fig. 1b). This result demonstrates the crucial role of local hydrodynamics in ecosystem performance. In detail, residence time affected ecological resistance, that is, the magnitude of external forces needed to displace an ecosystem a given amount (Zell and Hubbart, 2013) or in other words, how “resistant” the ecosystem is to change (Walker et al., 2004). Resistance is a key aspect of resilience theory, complementing the understanding of stability and shift. For example, an ecosystem with low resilience, in which a small shift on equilibrium state causes dramatic changes in functioning, can be very stable against perturbations if its resistance is high. Therefore water residence time is also a key for ecological carrying capacity because it becomes essential for keeping phytoplankton concentration unchanged when a stressor such as aquaculture level is increased. The importance of hydrodynamics in estuarine function allows for simple approaches such as the one followed by Guyondet et al. (2013), which mostly relies on 2D hydrodynamics with the addition of a limited set of biological processes. This becomes a valuable option for addressing important management issues such as site selection, susceptibility to food limitation and interactions among farms (disease and invasive species propagation). The increase in complexity of the biogeochemical model constructed in this study allows exploration of ecological carrying capacity but the simpler approach developed by Guyondet et al. (2013) seems to be a good approach for early stages of modeling programs.

4.4. Managing heterogeneous ecosystems within carrying capacity

The bay-scale depletion index above the sustainability threshold (Fig. 4) and the consistency of high phytoplankton concentration along the whole estuary suggests that the present aquaculture activity in Richibucto Estuary is within the range of carrying capacity. The analysis of alternative scenarios with higher oyster biomass suggests that the estuary could hold a larger population of oysters without major impact on phytoplankton populations. However, a detailed assessment should be performed with the exact location of new leases because they (1) can exert negative impacts on nearby farms and (2) can be significantly influenced by local hydrodynamics and water depth. The interaction among farms and the effect of hydrodynamics have been demonstrated above. Oyster culture is usually carried out in shallow waters (~1.85 m in Richibucto Estuary). Shallow bathymetry implies increased oyster density per unit volume and consequently enhanced phytoplankton depletion (Wheat and Ruesink, 2013). In addition to phytoplankton depletion, other aspects such as benthic impacts (e.g., Mallet et al., 2006; Skinner et al., 2013) should be considered, preferably in parallel with the local hydrodynamics given their role in the re-suspension of feces and pseudofeces.

In conclusion, the outcomes of the coupled biogeochemical–hydrodynamic model in which a new Dynamic Energy Budget (DEB) model for *C. virginica* has been developed, suggest that oyster culture in the Richibucto Estuary is presently within the bounds of the carrying capacity. The carrying capacity has been analyzed in the context of ecological resilience with emphasis on the effect of water residence time on ecological resistance. The model results highlighted that the complex geomorphology of the system and the associated heterogeneity of local hydrodynamics and consequently water residence time, call for a

management strategy carried out independently in three zones of the Richibucto Estuary: North Arm, Central Harbour and Baie du Village. The simulations carried out in this modeling exercise suggest that water bodies with a short residence time are more resistant to ecosystem shifts than areas with large residence time. Consequently, this study proves the integral effect of water residence time in estuarine functioning, ultimately influencing ecological resistance. Consequently, water residence time must be considered as a key characteristic in the development of effective management strategies of heterogeneous marine systems.

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