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ECOSYSTEMS

A Box Model for Ecosystem-Level Management of Mussel Culture Carrying Capacity in a Coastal Bay

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Abstract

The carrying capacity of shellfish aquaculture is determined by the interaction of cultured species with the ecosystem, particularly food availability to suspension feeders. A multiple box dynamic ecosystem model was constructed to examine the carrying capacity for mussel (*Mytilus edulis*) aquaculture in Tracadie Bay, Prince of Edward Island, Canada. Criteria for carrying capacity were based on chlorophyll concentration. The model was run in two different years (1998 and 1999) in which time series for three points inside the bay and a point outside the bay were available. This data set allows spatial validation of the ecosystem model and assessment of its sensitivity to changes in boundary conditions. The model validation process indicated that the differential equations and parameters used in the simulation provided robust prediction of the ecological dynamics within the bay. Results verified that mussel biomass exerts top-down control of phytoplankton populations. The model indicates that conditions observed during 1999 are more sensitive to grazing pressure from aquaculture than was observed during 1998, highlighting the importance of inter-annual variability in carrying capacity of the bay. This result is important from a management perspective because it emphasizes application of a precautionary policy and prediction in regulation of aquaculture activity in the bay. Retrospective scenarios showed that although the bay could yield greater mussel biomass production, stress on the environment would lead the ecosystem outside of its natural range of variation. Despite the spatial simplicity employed in the present model, it provides substantial management capability as well as an ecosystem-oriented approach to shellfish aquaculture.

Key words: ecosystem model; ecosystem management; shellfish aquaculture; carrying capacity; phytoplankton; depletion.

Introduction

Coastal areas such as estuaries or bays are commonly used for aquaculture activities, especially bivalve farming. In these ecosystems, the standing stock of bivalves exerts an important effect on the dynamics of particles and nutrients (Dame and Prins 1998). Bivalve filter feeders can clear large volumes of water of suspended particles, thereby potentially altering the flow of matter and energy (Dowd 2003). In the particular case of phytoplankton, filtration activity may also exert a top-down control of their populations (Dame and Prins 1998). Depletion removes particles used as food by zooplankton or other wild filter feeders (Grant and others 2005). On the other hand, bivalve populations consolidate small particles into feces and

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pseudofeces, which sink to the bottom, channelling energy flow towards benthic food webs instead of pelagic (Cloern 1982). This change may constitute a potential stress for benthic communities through organic loading (Grant and others 2005). With regard to the dynamics of nutrients, bivalves can accelerate the nitrogen (N) cycle (ammonia excretion, Dame and others 1991) and enhance the retention and remineralization of nutrients via sedimentation (Grant and others 1995). This effect on nutrient cycles may significantly accelerate phytoplankton turnover and production (Prins and others 1995), exerting a bottom-up nutrient control on phytoplankton populations (Cranford and others 2007).

The stress that aquaculture can exert on the environment compromises sustainability of an area, decreasing growth and survival rates of bivalves when cultured at high density. These impacts have stimulated the study of carrying capacity of cultivation areas, which may be defined as the maximum stock that can be maintained in an ecosystem without negative effects on bivalve growth rate (Carver and Mallet 1990). Alternatively and more recently, carrying capacity has been described as stocking density that maximizes annual production of commercial shell length of bivalves (Bacher and others 1998; Smaal and others 2001), or bivalve biomass that can be maintained in an ecosystem as a function of seawater residence time, primary production and clearance rate (Dame and Prins 1998). More generally, carrying capacity at an ecosystem scale relates to a process or variable that can be changed in a particular ecosystem without altering the structure and functioning beyond acceptable limits, established in terms of water quality and/or other parameters (Duarte 2003). The specific application of this concept to bivalve aquaculture area is the stocking density at which growth is not food limited, and/or some measure of ecosystem health is not compromised (Grant and others 2007). Carrying capacity studies can be applied to management of existing cultivation areas (Bacher and others 1998; Ferreira and others 1998; Duarte and others 2003; Grant and others 2007) or to increase profit at newly selected sites (Héral 1993). Moreover, these studies have demonstrated how carrying capacity has been exceeded in some cultivation areas (Héral 1993; Raillard and Ménesguen 1994; Smaal and others 2001).

Ecological system models are powerful decision-making tools because they simulate system organization, function and change (Odum and Odum 2000), increasing understanding and assessing the potential interactions within complex manipulated ecosystems (Dowd 2005). Ecosystem box models provide a valuable approximation for the study of bivalve growth and/or carrying capacity (Raillard and Ménesguen 1994; Dowd 1997; Bacher and others 1998; Ferreira and others 1998; Pastres and others 2001; Duarte and others 2003; Grant and others 2007) and ecosystem effects of the aquaculture activity (Chapelle and others 2000; Dowd 2005). Such models have the advantage of being computationally efficient, yet powerful enough to allow spatial realism in prediction. In this study, an ecosystem box model based on phytoplankton–zooplankton–nutrient (PZN) trophodynamics with the addition of mussel and seston submodels has been applied to Tracadie Bay, a shallow bar-built estuary on the north shore of Prince Edward Island (Canada) which supports extensive aquaculture activity. The focus of the study was carrying capacity of the bay and not individual bivalve growth per se. For this reason, a constant mussel biomass has been assumed in the whole bay, which implies that the mussel biomass interacts with the ecosystem model as a forcing function (Dowd 2005) rather than a response variable. By manipulating forcing by mussel biomass, we can examine other response criteria, for example, water quality as indicators of carrying capacity. With this assumption, some of the more uncertain steps of aquaculture activity are not required, for example, farming processes like harvesting and seeding, or bivalve size distribution. On the other hand, the bivalve mortality rate is not explicit in the model. In essence, this assumption means that the growth of the bivalves and seeding activity are compensated by mortality rate and harvesting, providing a constant biomass over time. The implication of this approach is that carrying capacity is defined as the stocking density at which given water or habitat quality criteria are met.

The energy flows in which the bivalves are involved depend on the supply of food to the cultivation area. Therefore, the boundary conditions will have a large influence on estimations of carrying capacity. Moreover, carrying capacity tends to be regarded implicitly as a fixed quantity, but temporal variation in boundary conditions over several time scales would influence its value. Specifically, interannual differences in boundary conditions may have a large impact on shellfish growth, an aspect of carrying capacity that has rarely been considered. In our previous field studies of mussel aquaculture (Waite and others 2005), we documented both different environmental conditions and consequent mussel growth in Tracadie Bay, Prince Edward Island (Canada). This led to speculation as to whether modelling could simulate observed biomass production as a function of these conditions. Moreover, it allows a test of carrying capacity determination as a function of interannual variability.

Due to the relative simplicity of box models, it should be possible to explore the effect of boundary conditions on carrying capacity estimations. This obvious extension of carrying capacity modelling has not been explored, although it is of clear importance to the industry. Based on these considerations, we conducted a set of simulations with the aim of answering the following questions:

1. What is the subsequent interannual variation in carrying capacity of mussel culture?
2. What is the optimal carrying capacity and how does it change as a function of interannual variation in boundary conditions?

Materials and Methods

Study Site

Tracadie Bay (Figure 1) is a small (13.8 km^2 at low tide), shallow (maximum depth 6 m) barrier beach inlet with predominantly diurnal tides with a range of 0.6 m. The embayment is located on the north shore of Prince Edward Island (Canada) and is open to the Gulf of St. Lawrence through a single narrow channel. Instantaneous exchange of bay with the offshore is up to 500 $m^3 s^{-1}$ (Dowd 2003), which results in a turnover of the entire volume of the Bay every 4–10 days (Dowd 2005). Based on bathymetry, the distribution of culture and our knowledge of the bay, we designate regions (boxes) for the purpose of model compartmentalization as follows. We designate Box 1 as the mouth of the bay, dominated by a large shallow tidal delta with extensive eelgrass beds, making mussel culture impossible at this location. Winter Harbour is a sub-basin of the larger bay, fed by Winter River which drains a large watershed but with low freshwater input most of the year (≈1 $m^3 s^{-1}$; see also Cranford and others 2007). Winter Harbour is used primarily for spat collection and adult mussel biomass in Box 4 is considered negligible. Longline mussel culture is carried out primarily in Boxes 2, 3 and 5, at depths ranging from 3 to 6 m. The mussel density in the innermost box is lower than in the central and northern box; therefore in the model, the mussel density in Box 5 is estimated to be half that of Boxes 2 and 3, which are considered similar to each other in terms of mussel density.

The bay is cultured by a variety of growers, and the absolute distribution of cultured biomass is not

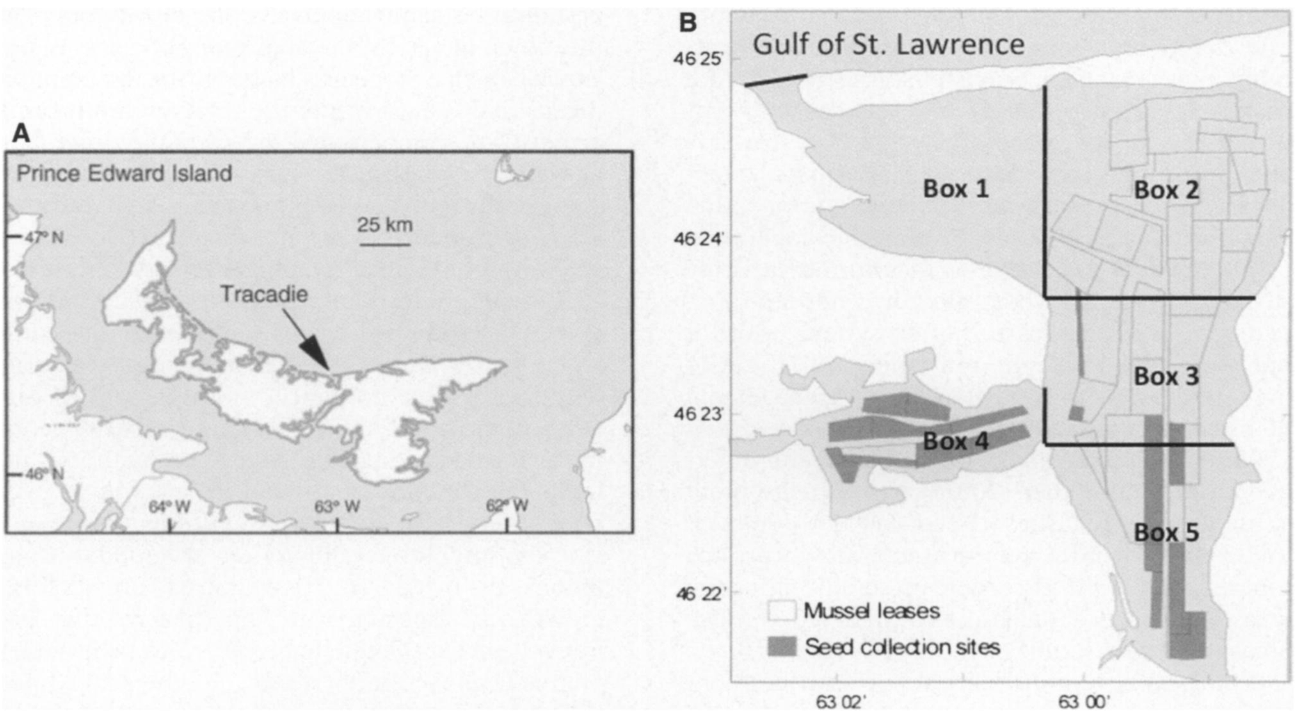

Figure 1. Map of Tracadie Bay including (**A**) location map in Eastern Canada and (**B**) location of culture sites and boxes considered in the model.

explicitly known. The cultured mussel biomass in Tracadie Bay was calculated according to Grant and others (2008), who reported a density averaged over the farmed area of 20 individuals m^{-3} with approximately 50% being smaller first-year mussels. Therefore, only the density of second-year mussels (10 individuals m^{-3}) was considered in the model. The weight of the mussels was calculated according to Dowd (2003, 2005), who estimated a standing stock between 1 and 2 $\times$ 10^6 kg wet weight (WW) of mussels. The standing stock of 1.5 $\times$ 10^6 kg WW of mussels is considered the actual scenario in Tracadie Bay. Tissue weight was calculated assuming a condition index of 30%. Dry weight was calculated assuming water content of 80% and a carbon (C) content of 40% mussel dry weight.

Ecological Model

A multiple box ecosystem model was developed with highly configurable GUI-based software (Simile, http://www.simulistics.com) that allows explicit coupling between boxes representing regions of the bay. The model was analogous to a classical PZN model with the addition of mussel (M) and detritus (D) submodels. Given the minimal effect of zooplankton on the results, this submodel was turned off in subsequent scenarios. All stocks are characterized in terms of mg C m^{-3}, with the exception of dissolved nutrients, which are expressed in mg N m^{-3}. The equations of the model are based on Kremer and Nixon (1978) and a detailed description is given in Grant and others (1993, 2007, 2008) and Dowd (1997, 2005). A brief summary of the differential equations that define the submodels is given by:

$$\frac{dP}{dt} = +\text{growth} - \text{mortality} - \text{M grazing} \pm \text{mixing} \tag{1}$$

$$\frac{dN}{dt} = +\text{river source} + \text{M excretion} - \text{P uptake} \pm \text{mixing} \tag{2}$$

$$\frac{dD}{dt} = +\text{resuspension} + \text{M feces} + \text{P mortality} - \text{sinking} - \text{M grazing} \pm \text{mixing} \tag{3}$$

$$\frac{dM}{dt} = +\text{seeding} + \text{net growth} - \text{mortality} - \text{harvesting} = 0 \tag{4}$$

The mixing term includes exchange between boxes and exchange with the far field. The following modifications have been applied in this study. In the detritus equation, a fraction of the mussel feces and dead phytoplankton are channelled to the detritus compartment instead of exiting the water column to the bottom. It is assumed that 50% of mussel feces degrade enough to remain in the water column. For phytoplankton, it is assumed that 80% of senescent or dead cells can remain in suspension. The mussel compartment maintains a constant biomass through time. The term that interacts with the ecosystem, that is, net mussel growth (absorption minus respiration and excretion) is balanced by the farming practices (seeding and harvesting) and mussel mortality. This implies that the mussel compartment is fully functional in the model; however, its biomass remains constant through time.

The resuspension rate is an empirical relationship based on the wind velocity as follows. We have empirically measured the resuspension rate using an erosion device described in Walker and Grant (2009). An erosion rate of 15 g m^{-2} min^{-1} was considered a reasonable value for the whole bay according to the measurements by Walker and Grant (2009). The C content was calculated assuming an organic content of 10%, of which 40% is organic C. Our time series measurements from optical probes deployed in Tracadie Bay (unpublished) do not show clear dependence of resuspension on wind, although windy days in the bay create obviously turbid water. These data suggest that a wind speed threshold is reasonable for allowing resuspension to proceed using a conditional statement within Simile. According to the wind time series, a value of 5 m s^{-1} was considered a reasonable threshold to induce resuspension. Forcing is provided by actual wind data for the two study years. To check the sensitivity of the model to these empirical parameters, four scenarios were tested increasing and decreasing the threshold and the amount of resuspended detritus for both years.

Exchange Between Boxes

The ecosystem model is defined by five boxes (1: 5,531,365 m^3, 2: 16,668,880 m^3, 3: 7,694,318 m^3, 4: 8,660,180 m^3 and 5: 5,662,642 m^3) connected according to Figure 1. Each box is assumed homogeneous and the horizontal exchange between adjacent boxes is regulated by an exchange coefficient, K, which includes the physical processes that cause the water exchange. The K value is expressed in d^{-1} units and it can be interpreted as the percentage of water exchange per day that goes from the exit box to the entry. Given that the volumes of the boxes were different, two different coefficients were calculated for each boundary to conserve water and matter.

The K values were calculated according to the far-field exchange with the Gulf of St. Lawrence and the exchange between boxes was calculated following the methodology described in Dowd (2005). To check if the water exchange was correct, the box model was run introducing an arbitrary conservative tracer across the estuary mouth. The relative concentration of the conservative tracer with regard to the boundary concentration was examined in Boxes 1 and 2 (Figure 2). Equilibrium time, the day in which the conservative tracer reached a relative concentration of 95%, was measured and compared with the results observed by Grant and others (2005). In the latter study, a numerical model of circulation for Tracadie Bay was developed using Aquadyn (Hydrosoft Energie Inc., Montreal, Canada), reporting an equilibrium time of 8–9 days in the mouth of the estuary and 16 days at a point located inside Box 2. The results observed in the present simulation showed an equilibrium time of 7 and 22 days for Boxes 1 (mouth) and 2, respectively. Both results are in a good agreement, and the differences can be caused by the larger area included in the box model, compared to the numerical model developed in Aquadyn, which calculates the conservative tracer concentration at a discrete point.

Boundary Conditions and Field Data

The chlorophyll, particulate organic matter (POM) and temperature data in the far-field and Boxes 2, 3 and 5 were taken from Waite and others (2005). In 1998, the sampling began on 12th May and was extended for 191 days, taking samples every 3 weeks. In 1999, the sampling schedule began on 6th May and was extended for 145 days, taking samples every month. The chlorophyll concentration was converted to C units assuming a C:chl of 50:1. The detrital C was calculated multiplying the POM value by 0.5 and subtracting the phytoplankton C. Nutrient data were taken from Cranford and others (2007) using an average value of 2 years (June to November for 2002 and 2003) and repeating it for River flow, which was obtained from the Environment Canada hydrometric database (http://www.wsc.ec.gc.ca). Wind data for each year were taken from Dowd and others (2001) and the time series completed with data from the Canadian Weather Office (http://www.climate.weatheroffice.ec.gc.ca) after confirming that the modulus of wind velocity was similar between the two sources of data in a common period. The first value of the time series was used as the initial value of the state variables.

Groundtruthing

The overall correspondence between observed and modelled values was analyzed with regression analysis following a protocol similar to that of Duarte and others (2003). The major axis regression method (RMA) was applied to the relationship between observed and modelled results for chlorophyll and detritus content in Boxes 2, 3 and 5. ANOVA was used to test the significance of the regression. A significant regression means that the model explains a significant percentage of the variance. A subsequent comparison of the slope with the theoretical value of 1 was carried out following Zar (1984). When the slope is not significantly different from 1, both time series follow the same pattern. Furthermore, if the intercept of the regression is not significantly different from 0, the modelled and the observed values are in a good agreement.

Results

Groundtruthing

The results of the model are first considered in terms of chlorophyll and detritus concentration in comparison to observed values in Boxes 2, 3 and 5.

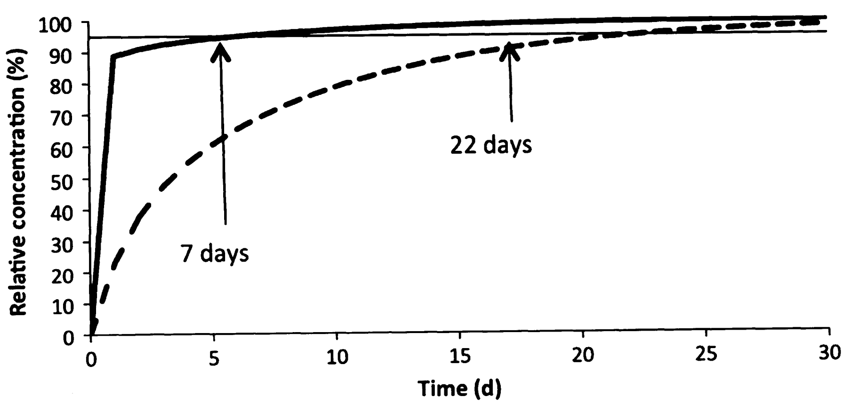

Figure 2. Relative concentration of a conservative tracer and equilibrium time in Box 1 (*solid line*) and 2 (*dashed line*).

For chlorophyll values, the modelled and observed values are in good agreement and the pattern through time is well reproduced by the model for both years, with the exception of the values for Box 5 in 1999 (Figure 3A), which showed an earlier and lower phytoplankton bloom compared to the observed values. In addition, at the end of the time series, the modelled chlorophyll concentration is

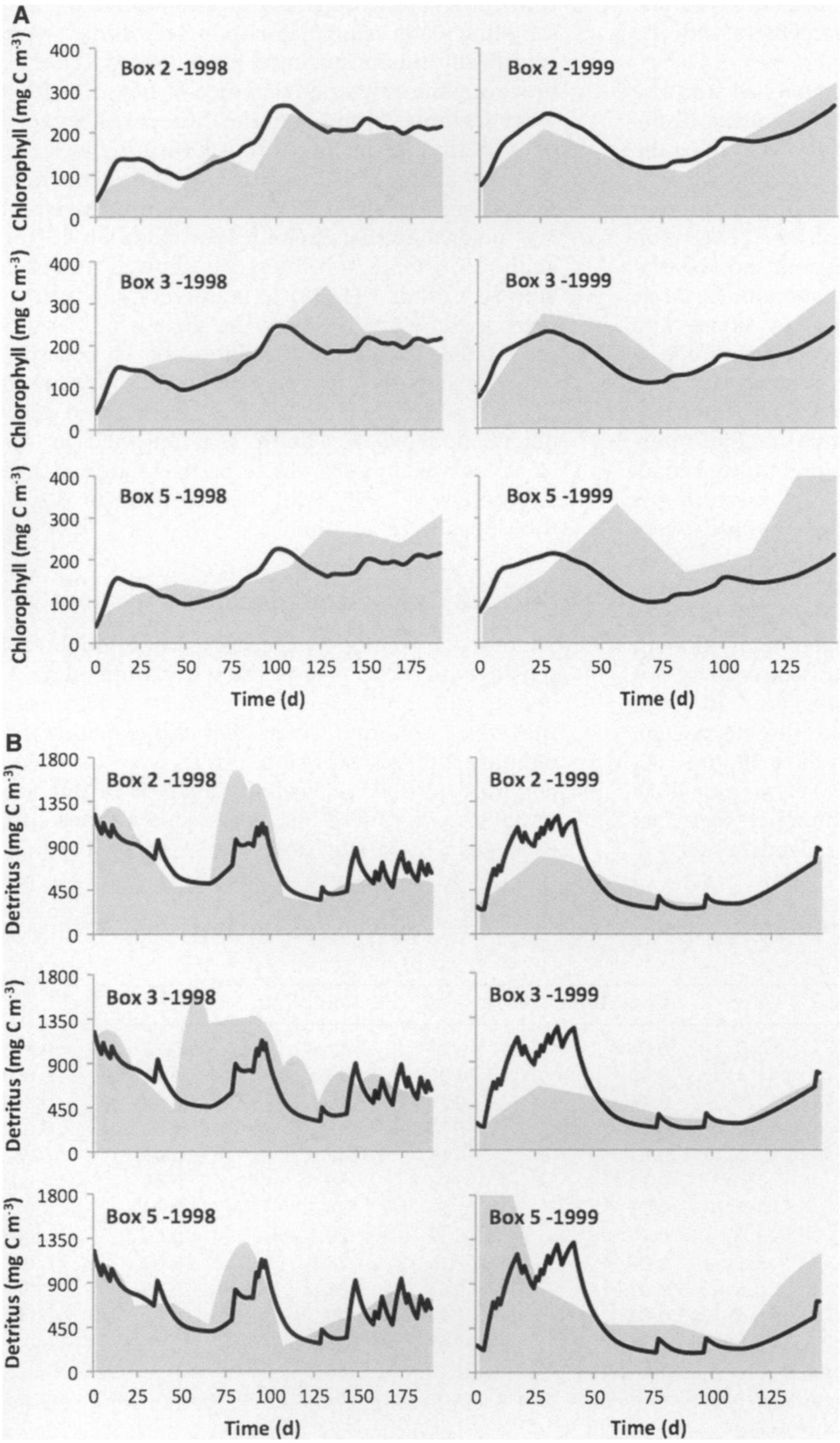

Figure 3. Observed (*grey area*) and modelled (*solid line*) values of chlorophyll (**A**) and detritus (**B**) in both years for Boxes 2, 3 and 5.

lower than observed; however, it could be influenced by an outlier in the observations. The data set is composed of monthly samples extrapolated to each day by means of linear regression between two consecutive days. Therefore, when the last 30 days were removed from the latter analysis, the modelled values were in better agreement with the observed.

The agreement between the modelled and the observed values can be analyzed by means of the RMA (Table 1). The ANOVAs showed that the regressions were statistically significant in all cases, that is, the model explained a significant percentage of the variance. With the mentioned exception of Box 5 in 1999, Pearson's coefficient showed that the model explained 60% of the variance in terms of chlorophyll. The analysis of the slopes and intercepts indicated that the modelled chlorophyll in Box 2 for 1998 was in very good agreement with observed values, showing a slope that is not statistically different from 1 ($P > 0.05$) and an intercept close to 0. The other regressions showed in all cases a slope greater than 1 and an intercept less than 0, which means that modelled values were proportional to the observed ones.

For detritus values, the comparison of the modelled results with the observed values showed, as for chlorophyll, a very good agreement in both years (Figure 3B). However, in this case, there is a different pattern depending on the year. In 1998, the model showed values less than those expected, especially in the period between days 50 and 100. This was more evident in Box 3 between days 50 and 75, in which the largest differences between modelled and observed values were observed. Model results from 1999 showed that the modelled values were higher than the observed values at the beginning of the simulated period. Once again, the observed values of Box 5 in 1999 showed a different behavior compared with the other boxes, showing a peak of detritus concentration in the first sampling date. The major axis regressions were statistically significant in all cases (RMA, Table 1); however, the explained variance of Box 5 in 1999 was again low. In addition, the differences between days 50 and 75 of Box 3 in 1998 caused a sharp decrease in the explained variance. The remaining regressions explained 55% of the detritus variance, 5% lower than that explained for chlorophyll. The analysis of slopes and intercepts showed modelled detritus in Box 5 (1998) to be in very good agreement with observed values; the slope is similar to 1 ($P > 0.05$), although the intercept is negative, which means that the modelled values are below the observed. The different pattern between years described above for detritus is reflected in the slopes as well; in 1998, the slopes were greater than 1, whereas in 1999, with the exception of Box 5, the slopes were less than 1.

Sensitivity of Resuspension Equation

The model results for detritus are undoubtedly sensitive to how resuspension is parameterized, because this process generates fluxes of detritus to the water column. Given that the equation for defining the resuspension events was based on empirical results, a sensitivity analysis of this formulation was carried out. Four scenarios were run each year, increasing and decreasing by 10% the

Table 1. RMA Between Observed and Modelled Values in Both Years for Chlorophyll and Detritus in Different Boxes

Year	State variable	Box	*b*	Conf. limit	*a*	Conf. limit	R^2	*P*
1998	Chlorophyll	2	1.0	0.06	17	11.4	0.82	<0.001
		3	1.3	0.13	−106	23.5	0.51	<0.001
		5	1.6	0.16	−139	26.1	0.52	<0.001
	Detritus	2	1.9	0.18	−775	128.7	0.56	<0.001
		3	1.5	0.21	−718	142.1	0.03	<0.05
		5	1.1	0.13	−194	86.0	0.39	<0.001
1999	Chlorophyll	2	1.3	0.13	−56	24.2	0.64	<0.001
		3	1.6	0.17	−157	29.3	0.56	<0.001
		5	3.1	0.50	−616	78.8	0.03	<0.05
	Detritus	2	0.6	0.05	265	28.9	0.75	<0.001
		3	0.4	0.05	363	29.3	0.51	<0.001
		5	1.9	0.31	−1148	192.8	0.06	<0.05

b and a are the slope and intercept of the RMA, respectively, and Conf. limit their confidence limits. R^2 is the Pearson variation and P is the P-value of the ANOVA analysis of the regressions.

Table 2. Sensitivity Test of Empirical Resuspension Parameterization

Year	Parameter	Parameter change (%)	Final value	Change in modelled detritus (%)
1998	Threshold	−10	4.5	+7.1
		+10	5.5	−3.2
	Resuspension rate	−10	135	−1.45
		+10	165	+1.45
1999	Threshold	−10	4.5	+8.55
		+10	5.5	−5.62
	Resuspension rate	−10	135	−1.72
		+10	165	+1.72

wind threshold and the rate of resuspension. In 1998, the variation of the threshold ±10% resulted in a maximum change of 7.1% in the detritus concentration within the bay (Table 2); in 1999, this change was 8.55%. The model was less sensitive to the change in the input rate of resuspended detritus. In 1998, the change of this factor ±10% provided a change in the detritus concentration within the bay of 1.45%, and only slightly higher in 1999, 1.72%.

Ecosystem-Level Effects

The extent of changes in seston due to mussel grazing may be quantified as the ratio of chlorophyll within the boxes compared to that at the boundary. Values of this ratio below 1 indicate depletion, and may be designated as a threshold for acceptable ecosystem-level effects. This ratio was calculated for 2 years and four mussel biomass scenarios (1, 2, 3 and 4 $\times$ 10^6 kg WW in the whole bay). The results of this ratio are shown for the north–south gradient in Figure 4A (1998) and 4B (1999). In 1998, the 1.0 $\times$ 10^6 kg WW scenario showed an enrichment of chlorophyll inside the bay compared with the boundary concentration, whereas higher mussel biomass showed depletion. For 2.0 $\times$ 10^6 kg WW, depletion was slight and only gradually accentuated moving to Boxes 3 and 5 in the interior of the bay. For the 3.0 and 4.0 $\times$ 10^6 kg WW scenarios, depletion was immediately more severe entering Box 2, but declining less thereafter in successive boxes. Results in 1999 had generally similar trajectories, but with important differences. The lowest biomass showed only marginal enrichment in Boxes 1 and 2, with gradual depletion thereafter. The next higher biomass class resulted in significant depletion in 1999 compared to a similar biomass in 1998. For 3.0 and 4.0 $\times$ 10^6 kg WW, patterns and levels of depletion were similar between years.

We used the natural variation of chlorophyll as a means of scaling the importance of depletion. A coefficient of variation of 27% was determined for all boxes and times, and this envelope is indicated in both figures. By this criterion in 1998, a cultured biomass of 1.0 and 2.0 $\times$ 10^6 kg WW produced acceptable grazing pressure in all boxes, that is, within system noise on phytoplankton, as did a biomass of 1.0 $\times$ 10^6 kg WW in 1999. Other biomass scenarios were not acceptable by this measure.

Mussel Production

Although mussel biomass was constant during the simulations and mussel growth was not determined, the accumulated input and output energy in the mussel compartment was calculated, their difference providing the net growth of the mussels in the bay. In describing mussel biomass through equation (4), we assume that seeding and the mortality process are (1) negligible in terms of biomass compared with the mussel net growth and (2) opposite in terms of effect such that net growth can be considered a measure of harvestable biomass. Therefore, the accumulated net growth can be used as a proxy of mussel production in the bay.

Figure 5 shows the annual mussel production in the bay in terms of kg WW and the production per kg WW of standing stock in the years 1998 and 1999, respectively. These curves provide a measure of carrying capacity in terms of yield versus stocking density curves. Results for total production in both years showed a similar trend, with a maximum production when the standing stock of mussels was around 5.0 $\times$ 10^6 kg WW. The absolute production was however different between years, and the differences were dependent on the standing stock biomass in the bay. In this way, at low mussel biomass in the bay, both years (1998 and 1999) resulted in similar production, 1.9 and 2.0 $\times$ 10^6 kg WW, respectively, with a standing stock of

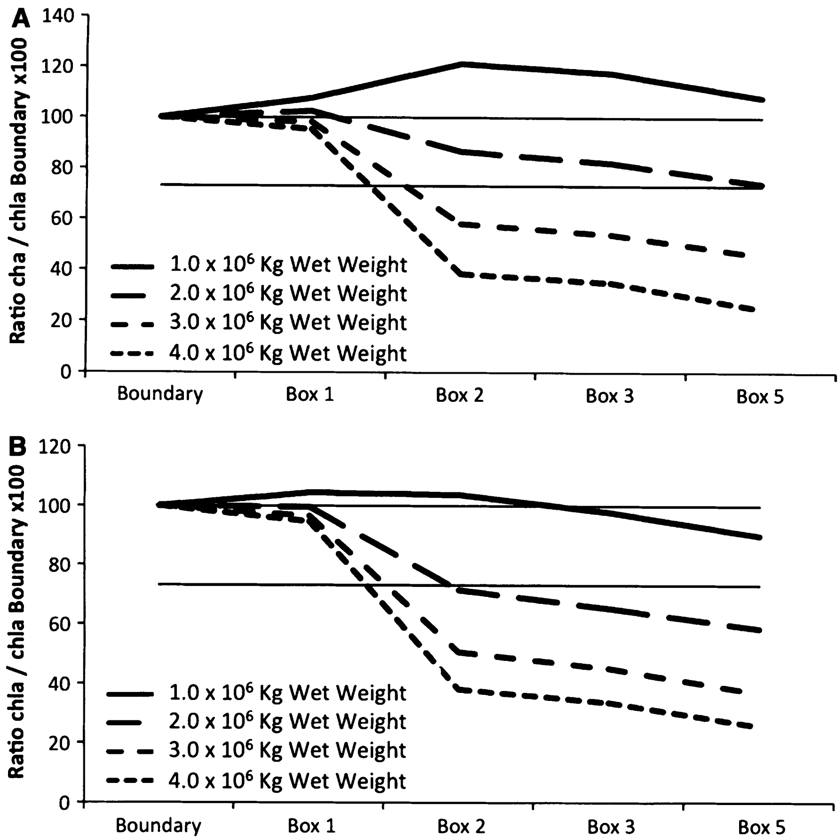

Figure 4. Ratio of chlorophyll within the boxes compared to that at the boundary in the north–south (Boundary–Box 5) gradient in four scenarios in terms of standing stock for 1998 (**A**) and 1999 (**B**). The *horizontal solid lines* represent the depletion/enrichment threshold (100%) and the confidence limit according to natural variation of chlorophyll (73%).

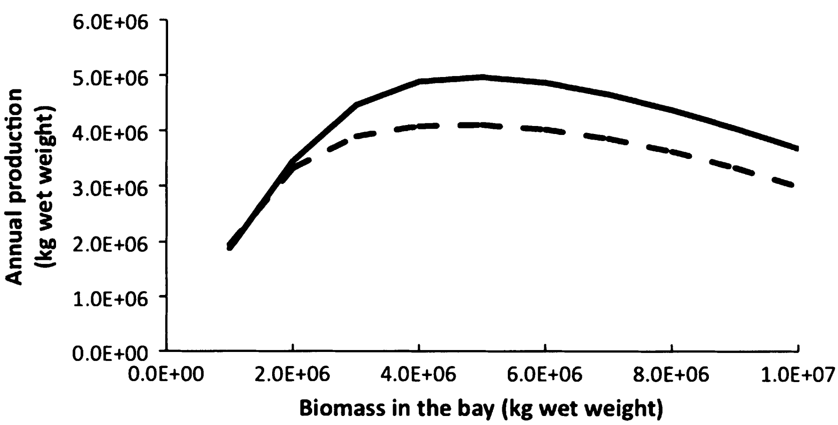

Figure 5. Mussel biomass annual production in different scenarios in terms of standing stock for 1998 (*solid line*) and 1999 (*dashed line*)

1.0×10^6 and 3.5 and 3.3×10^6 kg WW for both years when the standing stock was increased to 2.0×10^6 kg WW. From this standing stock biomass onwards the differences between both years increased sharply, showing a better yield in 1998 than in 1999 at all biomasses. The differences were larger in the 5.0×10^6 kg WW scenario, when the maximum mussel production was observed.

Discussion

In this study, a mussel aquaculture ecosystem was simulated over 2 years to consider forcing and variation in carrying capacity. The study is focused on the ecosystem-level properties and not on the mussel growth; therefore, it was assumed that mussel biomass remained constant over time. This assumption simplified the mussel submodel, especially from the point of view of population structure and processes carried out by the farmers, like seeding and harvesting. However, the mussel submodel interacted with the ecosystem such that the grazing uptake of C could be calculated, allowing the estimation of mussel production in the bay. One of the strong points of this study is the available data set, two time series in different years, 1998 and 1999. The ecological dynamics in the bay are dependent on the local processes and the characteristics of the far-field, so that boundary conditions influence the dynamics inside the bay. The information from two time series provides an ideal scenario for validation and groundtruthing, allowing a check on the robustness of the model in two different situations. Moreover, the data set contains information at three different locations, allowing spatial validation of the model relevant to managing strategies.

Groundtruthing of model results was based on chlorophyll and detritus values, using data from both years in three boxes. The results showed a very good agreement between model and observed values for both seston quantities, with major axis regressions explaining 60% of the variance for chlorophyll and 55% for detritus. The interannual variability in explained variance showed similar results in both years, 56% in 1998 and 62% in 1999. These spatial and temporal checks on model validity demonstrate that the differential equations and parameters of the ecosystem model provide reasonable predictions of ecological dynamics within the bay. Although the study by Waite and others (2005) provides mussel growth, the mussels were grown at the same density in different locations and therefore their results are not comparable with the modelled ones in which different densities were used in different boxes.

In general, the mussel compartment routes energy flow towards benthic food webs instead of the pelagic (Cloern 1982). The interaction between the mussel compartment and the sediment is governed by two main processes within the model. Mussels enhance sedimentation by repacking fine suspended material into larger biodeposits. This flux is controlled by the feces and pseudofeces production rate as well as physical variables like settling velocity, dissagregation rate and resuspension (Walker and Grant 2009). In contrast, sediment erosion and resuspension generate a flux of matter from the bottom to the pelagic environment. This process is controlled by the stability of sediment, which is affected by many factors such as biostabilization, porosity, organic content, grain size and bioturbation (Walker and Grant 2009), and in a shallow bay like Tracadie Bay, wind forcing is the dominant forcing agent on sediment resuspension (Lawson and others 2007). The sediment–water particle is difficult to parameterize, but we had direct measurements available from Tracadie Bay with which to work. The low sensitivity of the model to changes in the equation parameters and the good agreement between the modelled and observed values of detritus content suggest that the empirical equation can be used to characterize resuspension in Tracadie Bay.

Besides channelling energy flow towards the benthic community, mussels have been called "ecosystem engineers" (Jones and others 1994) due to their ability to alter environmental conditions, such as seston levels. In the particular case of phytoplankton, bivalves may also exert top-down regulation of primary production (Cloern 1982; Dame and Prins 1998). On the other hand, bivalves can accelerate the N cycle (Dame and others 1991), enhancing phytoplankton turnover and production (Prins and others 1995), and exerting bottom-up control of primary production. Given that phytoplankton constitute the base of marine food webs and that mussel populations are important in their control, carrying capacity has been expressed in terms of chlorophyll depletion. Previous studies of seston depletion have focused on small scales, usually the farm scale, and oriented the objectives towards bivalve growth (Campbell and Newell 1998), the relationship between density and growth (Pouvreau and others 2000; Bacher and others 2003) or sustainable standing stock (Ferreira and others 2007; Duarte and others 2008). Ferreira and others (2007) calculated the standing stock that maximizes the biomass production in a farm and subsequently, they applied the ASSETS methodology (Bricker and others 2003) to evaluate its effects with respect to eutrophication. Based on the raft production curves, Duarte and others (2008) observed that culture practices in Galician Rias are close to the carrying capacity at the farm scale; however, they suggest that any possible increase in mussel production should be considered at a broader spatial scale. In this way, Grant and others (2008) carried out a short-term study at the bay scale, in which seston depletion was modelled and followed by an intensive spatial groundtruthing.

Seston depletion is a direct measure of food availability; therefore, an integrative assessment of the depletion in the whole bay can provide a useful tool for carrying capacity evaluation. Due to its importance in marine food webs, chlorophyll is a tempting ecosystem-level variable to use for carrying capacity. It has however been difficult to calibrate this variable relative to system health or requirements. To remove its subjectivity from the application, we have scaled it to the natural variation in chlorophyll as an assessment of the noise within the system. Preservation of food webs is an important tenet of ecosystem-based management (EBM, Crowder and Norse 2008). The placement of shellfish farming within the context of EBM is an important advance in aquaculture management, an approach also employed by Ferreira and others (2007) as mentioned above.

Using this criterion, we were able to show differences between two years, especially in the scenarios that are close to the estimated standing stock of Tracadie Bay, between 1 and 2 $\times$ 10^6 kg WW of mussels. The higher depletion observed in 1999 would suggest that the boundary conditions are less suitable for growing mussels than the conditions observed during 1998, a result confirmed by the Tracadie growth studies of Waite and others (2005). In fact, if we inserted the chlorophyll ratio observed in 1998 for the 1 $\times$ 10^6 kg scenario into the 1999 conditions, the standing stock would need to be reduced by 40%, reaching a biomass of 0.6 $\times$ 10^6 kg. In other words, this result implies that the bay during 1999 would suffer a deviation from natural conditions 40% higher than in 1998. This result highlights the finding that there is not a single stocking density that can be designated as the carrying capacity for a given location. A stocking density suitable for a single year may not be so for other years; our study is the first to examine this temporal scale of carrying capacity. The results of the 1 $\times$ 10^6 kg scenario are in very good agreement with the pattern observed by Grant and others (2008) and show the maximum concentration of phytoplankton residing in the middle of the bay, decreasing towards the mouth and the head. The authors suggest that this pattern is caused by the influence of the Winter River, which supplies a nutrients source, enhancing the primary production in Box 4.

In terms of biomass production, the results are in good agreement with the estimation of Dowd (2005), who predicted a production of mussel biomass of 3 $\times$ 10^6 kg WW with a standing stock of 2 $\times$ 10^6 kg WW. With the same standing stock of mussels, the predicted production in this study is 3.5 and 3.3 $\times$ 10^6 Kg WW for 1998 and 1999, respectively. Figure 5 shows that the yield per unit of stocked kilogram decreases sharply with an increase in the standing stock biomass. Nevertheless, the annual production can be enhanced to 5.0 and 4.0 $\times$ 10^6 kg WW for 1998 and 1999, respectively, when the standing stock is 5.0 $\times$ 10^6 kg WW. This suggests that the aquaculture output of the bay could be maximized by increasing the standing stock biomass. However, the decrease in the ratio between the chlorophyll in each box and in the far-field when standing stock is above 1.0 $\times$ 10^6 kg WW suggests that pressure on the ecosystem would be substantial, compromising ecosystem health by this criterion. A continued increase in stocked biomass would surpass the asymptote of these production–biomass curves and lead to a decreased yield due to food limitation, as suggested by the downward trends in Figure 5.

In conclusion, our approach of using a constant biomass to force grazing pressure in a bay wide ecosystem model of carrying capacity has been effective in assessing system-level impacts on seston fields. In addition, continually increasing biomass forcing leads to estimates of maximal production benefit as a function of stocking density. Thus, a single model is useful in predicting farm yield in the context of sustainable aquaculture assessed with an ecosystem health criterion. The available time series for two different years and three different locations constitutes an ideal situation for groundtruthing, allowing spatial validation of the model and checking its robustness as a function of changing boundary conditions. Specifically, the use of two time series showed the importance of the inter-annual variability in carrying capacity, a unique application compared to most studies of this kind. The model indicates that conditions observed during 1999 are more sensitive to grazing pressure from aquaculture than those observed during 1998. This result is important from a management perspective because it emphasizes application of a precautionary policy and prediction in regulation of aquaculture activity in the bay. The use of different boundary conditions based on expected trends provides the capability for exploring future scenarios and planning for suitable standing stock biomass. For instance, modifying temperature time series according to different climate change scenarios would allow the adjustment of the standing stock biomass to the new situation in order to maintain sustainable culture. The success of prospective analysis will depend on the veracity of the estimated boundary conditions. In this study, the retrospective analysis showed that although the bay could yield greater mussel biomass production, stress on the environment would lead the ecosystem outside of its natural range of variation. Despite the spatial simplicity employed in the present model, it provides substantial management capability as well as an ecosystem-oriented approach to shellfish aquaculture.

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REFERENCES

Bacher C, Duarte P, Ferreira JG, Héral M, Raillard O. 1998. Assessment and comparison of the Marennes-Oléron Bay (France) and Carlingford Lough (Ireland) Carrying Capacity with ecosystem models. Aquatic Ecol 31:379–94.

Bacher C, Grant J, Hawkins A, Fang J, Zhu P, Duarte P. 2003. Modeling the effect of food depletion on scallop growth in Sungo Bay (China). Aquat Living Resour 16:10–24.

Bricker SB, Ferreira JG, Simas T. 2003. An integrated methodology for assessment of estuarine trophic status. Ecol Model 169:39–60.

Campbell DE, Newell CR. 1998. MUSMOD, a production model for bottom culture of the blue mussel, *Mytilus edulis* L. J Exp Mar Biol Ecol 219:171–203.

Carver CEA, Mallet AL. 1990. Estimating carrying capacity of a coastal inlet for mussel culture. Aquaculture 88:39–53.

Chapelle A, Menesguen A, Deslous-Paoli JM, Souchu P, Mazouni N, Vaquer A, Millet B. 2000. Modelling nitrogen, primary production and oxygen in a Mediterranean lagoon. Impact of oysters farming and inputs from the watershed. Ecol Model 127:161–81.

Cloern JE. 1982. Does the benthos control phytoplankton biomass in southern San Francisco Bay? Mar Ecol Prog Ser 9:191–202.

Cranford PJ, Strain PM, Dowd M, Hargrave BT, Grant J, Archambault MC. 2007. Influence of mussel aquaculture on nitrogen dynamics in a nutrient enriched coastal embayment. Mar Ecol Prog Ser 347:61–78.

Crowder L, Norse E. 2008. Essential ecological insights for marine ecosystem-based management and marine spatial planning. Mar Policy 32:772–8.

Dame RF, Dankers N, Prins T, Jongsma H, Smaal A. 1991. The influence of mussel beds on nutrients in the West Wadden Sea and Eastern Scheldt estuaries. Estuaries 14:130–8.

Dame RF, Prins TC. 1998. Bivalve carrying capacity in coastal ecosystems. Aquatic Ecol 31:409–21.

Dowd M. 1997. On predicting the growth of cultured bivalves. Ecol Model 104:113–31.

Dowd M. 2003. Seston dynamics in a tidal inlet with shellfish aquaculture: a model study using tracer equations. Estuar Coast Shelf Sci 57:523–37.

Dowd M. 2005. A bio-physical coastal ecosystem model for assessing environmental effects of marine bivalve aquaculture. Ecol Model 183:323–46.

Dowd M, Page FH, Losier R, McCurdy P, Budgen G. 2001. Physical oceanography of Tracadie Bay, PEI: analysis of sea level, current, wind and drifter data. Canadian Technical Report of Fisheries and Aquatic Sciences 2347

Duarte P. 2003. A review of current methods in the estimation of environmental carrying capacity for bivalve culture in Europe. In: Yu H, Bermas N, Eds. Determining environmental carrying capacity of coastal and marine areas: progress, constraints and future options. PEMSEA Workshop Proceedings No. 11. p 37–51

Duarte O, Labarta U, Fernández-Reiriz MJ. 2008. Modelling local food depletion effects in mussel rafts of Galician Rias. Aquaculture 274:300–12.

Duarte P, Meneses R, Hawkins AJS, Zhu M, Fang J, Grant J. 2003. Mathematical modelling to assess the carrying capacity for multi-species culture within coastal waters. Ecol Model 168:109–43.

Ferreira J, Duarte P, Ball B. 1998. Trophic capacity of Carlingford Lough for aquaculture—analysis by ecological modelling. Aquatic Ecol 31:361–79.

Ferreira J, Hawkins AJS, Bricker SB. 2007. Management of productivity, environmental effects and profitability of shellfish aquaculture—the Farm Aquaculture Resource Management (FARM) model. Aquaculture 264:160–74.

Grant J, Bacher C, Cranford PJ, Guyondet T, Carreau M. 2008. A spatially explicit ecosystem model of seston depletion in dense mussel culture. J Mar Syst 73:1555–68.

Grant J, Cranford P, Hargrave B, Carreau M, Schofield B, Armsworthy S, Burdett-Coutts V, Ibarra D. 2005. A model of aquaculture biodeposition for multiple estuaries and field validation at blue mussel (*Mytilus edulis*) culture sites in eastern Canada. Can J Fish Aquat Sci 62:1271–85.

Grant J, Curran KJ, Guyondet TL, Tita G, Bacher C, Koutitonsky V, Dowd M. 2007. A box model of carrying capacity for suspended mussel aquaculture in Lagune de la Grande-Entrée, iles-de-la-Madeleine, Québec. Ecol Model 200:193–206.

Grant J, Dowd M, Thompson K, Emerson C, Hatcher A. 1993. Perspectives on field studies and related biological models of bivalve growth. In: Dame R, Ed. Bivalve filter feeders and marine ecosystem processes. New York: Springer-Verlag. p 371–420.

Grant J, Hatcher A, Scott DB, Pocklington P, Schafer CT, Honig C. 1995. A multidisciplinary approach to evaluating benthic impacts of shellfish aquaculture. Estuaries 18:124–44.

Héral M. 1993. Why carrying capacity models are useful tools for management of bivalve molluscs culture. In: Dame R, Ed. Bivalve filter-feeders in estuarine and coastal ecosystems. New York: Springer-Verlag. p 455–77.

Kremer J, Nixon SW. 1978. A coastal marine ecosystem: simulation and analysis. New York: Springer-Verlag.

Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. Oikos 69:373–86.

Lawson SE, Wiberg PL, McGlathery KJ, Fugate DC. 2007. Wind-driven sediment suspension controls light availability in a shallow coastal lagoon. Estuar Coast 30(1):102–12.

Odum HT, Odum EC. 2000. Modeling for all scales. An introduction to system simulation. San Diego: Academic Press.

Pastres R, Solidoro C, Cossarini G, Melaku Canu D, Dejak C. 2001. Managing the rearing of *Tapes philippinarum* in the lagoon of Venice: a decision support system. Ecol Model 138:231–45.

Pouvreau S, Bacher C, Heral M. 2000. Ecophysiological model of growth and reproduction of the black pearl oyster, *Pinctada margaritifera*: potential applications for pearl farming in French Polynesia. Aquaculture 186:117–44.

Prins TC, Escaravage V, Smaal AC, Peters JCH. 1995. Nutrient cycling and phytoplankton dynamics in relation to mussel grazing in a mesocosm experiment. Ophelia 41:289–315.

Raillard O, Ménesguen A. 1994. An ecosystem model for the estimating the carrying capacity of a macrotidal shellfish system. Mar Ecol Prog Ser 115:117–30.

Smaal A, Stralen M, Schuiling E. 2001. The interaction between shellfish culture and ecosystem processes. Can J Fish Aquat Sci 58:991–1002.

Waite L, Grant J, Davidson J. 2005. Bay-scale spatial growth variation of mussels *Mytilus edulis* in suspended culture, Prince Edward Island, Canada. Mar Ecol Progr Ser 297:157–67.

Walker TR, Grant J. 2009. Quantifying erosion rates and stability of bottom sediments at mussel aquaculture sites in Prince Edward Island. J Mar Syst 75:46–55.

Zar JH. 1984. Biostatistical analysis. NJ: Prentice-Hall.