Assessment and comparison of the Marennes-Oléron Bay (France) and Carlingford Lough (Ireland) carrying capacity with ecosystem models

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Abstract

Based on the individual growth, food limitation, population renewal through seeding, and individual marketable size, a theoretical model of the cultured species population dynamics was used to assess the carrying capacity of an ecosystem. It gave a dome-shape curve relating the annual production and the standing stock under the assumption of individual growth limited by the available food in an ecosystem. It also showed the influence of mortality rate and marketable size on this curve and was introduced as a means to explore the global properties resulting from the interactions between the ecophysiology of the reared species and the environment at the ecosystem level.

In a second step, an ecosystem model was built to assess the carrying capacity of Marennes-Oléron bay, the most important shellfish culture site in France, with a standing stock of *Crassostrea gigas* around 100 000 tonnes fresh weight (FW) and an annual production of 30 000 tonnes FW. The ecosystem model focused on the oyster growth rate and considered the interaction between food availability, residence time of the water, oyster ecophysiology and number of individuals. It included a spatial discretization of the bay (box design) based on a hydrodynamic model, and the nitrogen or carbon cycling between phytoplankton, cultured oysters, and detritus. From simulations of the oyster growth with different seeding values, a curve relating the total annual production and the standing stock was obtained. This curve exhibited a dome shape with a maximum production corresponding to an optimum standing stock. The model predicted a maximum annual production of 45 000 tonnes FW for a standing stock around 115 000 tonnes FW. The prediction confirmed some results obtained empirically in the case of Marennes-Oléron bay and the results of the theoretical model. Results were compared with those obtained in Carlingford Lough (Ireland) using a similar ecosystem model. Carlingford Lough is a small intertidal bay where the same species is cultured at a reduced scale, with current biomass less than 500 tonnes FW. The model showed that the standing stock can be increased from 200 tonnes FW to approximately 1500 tonnes FW before any decrease of the production.

Introduction

Carrying capacity assessment is a major concern for the development of the shellfish aquaculture. The relationship between the production and standing stock of oysters in Marennes-Oléron Bay (France) is outlined by Héral (1993) who showed that the production is below a maximum value by using an empirical model based on mortality, growth, production and stock time series. Héral (1993) found that the maximum annual production of the Marennes-Oléron Bay lies around 40 000 tonnes fresh weight (FW) and that the production is more or less stable beyond 100 000 tonnes FW standing stock. These two values indicate the carrying capacity of the bay and it is assumed that it is driven by the food limitation. This is a restricted assessment of

the carrying capacity concept (for a review see Kashiwai, 1995), but it is appropriate for ecosystems supporting cultured filter-feeders where typical features such as food limitation, man-controlled seedings, rearing time and marketable weight have to be considered in the carrying capacity assessment.

In this context, understanding the link between the environmental conditions and the filter-feeder growth cannot be avoided. Dame (1993) emphasizes the coupling between transport of particles in coastal areas, ecophysiology and primary production as a way to understand the relationship between the filter-feeders and their environment. In his scheme, the food sources (phytoplankton, detritus) and the trophic interactions with the filter-feeders are the keys to the assessment of the filter-feeders growth and impact on the environment. Ecophysiological studies have been developing for the last 10 years and ecophysiology models have been published recently by Van Haren & Kooijman (1993), Smaal & Scholten (1997) on *Mytilus edulis*, Powell et al. (1992) on *Crassostrea virginica* and Raillard et al. (1993), Barillé et al. (1997) on *Crassostrea gigas*. These mechanistic models generally describe and quantify physiological processes which control the energy gain and loss, and result in the individual growth. The physiological processes are driven by temperature, food concentration (particulate organic matter, phytoplankton) and total suspended matter concentration (TPM) which includes organic and inorganic particles and acts on the ability of the individual to ingest or to reject a fraction of the available food as pseudofaeces. Not all the food can be used by the filter-feeders: a fraction is rejected without ingestion because of the high particle concentration. Another fraction of the ingested part is not assimilated (due to short gut passage time). Tidal currents, river flows or geographical situation of the filter-feeders may also result in a low percentage of food used by the filter-feeder populations. The food sources and their dynamics are, therefore, of primary interest in carrying capacity assessment. Most of the ecosystem models focusing on the food limited growth of the filter-feeders include a water transport and mixing submodel, primary production and ecophysiology submodels (Grant et al., 1993; Herman, 1993; Raillard & Ménesguen, 1994; Powell et al., 1994; Gerritsen et al., 1994). The other component often considered in such models deals with the filter-feeders population dynamics. Powell et al. (1992, 1994) use a simple equation based on individual growth rates, mortality and recruitment to represent the temporal variation of cohorts in harvested oyster populations. For the cultured species which are concerned by carrying capacity studies, the above description is still valid since the production is the product of the individual weights after a given amount of time (rearing time) and the number of survivals.

The main objectives of this paper are: (i) to translate the carrying capacity concept into mathematical terms which underlie the ecosystem modelling, (ii) to present the carrying capacity assessment of Marennes-Oléron Bay as an illustration of some of the modelling concepts mentioned above, and (iii) to highlight and interpret the differences in the carrying capacities of Marennes-Oléron Bay and Carlingford Lough which were studied in a similar way (Ferreira et al., this volume).

A theoretical model that is presented assumes food limitation at a global scale. Combined with the cultured population dynamics and some constraints due to the economic market, it lead to a predictable stock/production relationship. The key notion is, therefore, that there is a biological optimum standing stock, yielding a maximum production under some constraints due to the population dynamics and the culture practice. In the second part, the Marennes-Oléron Bay model is described and used to assess the carrying capacity. The results are then compared with the Carlingford Lough case and discussed.

The theoretical model

The consequence of the food limitation assumption is that the individual growth rate of the cultured species is a decreasing function of the stock of oysters, since the larger the stock, the lesser food is available for each individual. The following type of function was chosen for its simplicity in the calculations:

$$G = G_0 e^{-aS}, \tag{1}$$

where G is the annual individual growth rate (g yr^{-1}), G_0 is the maximum growth and S is the standing stock expressed in thousands of tonnes fresh weight (FW). Parameters were chosen to give plausible values (Figure 1). In this example, the maximum growth rate was equal to 40 gFW yr^{-1} and was divided by 2 for a standing stock equal to 100 000 tonnes FW to reflect the values typically found in the Marennes-Oléron Bay.

The population dynamics was described by the classical equation:

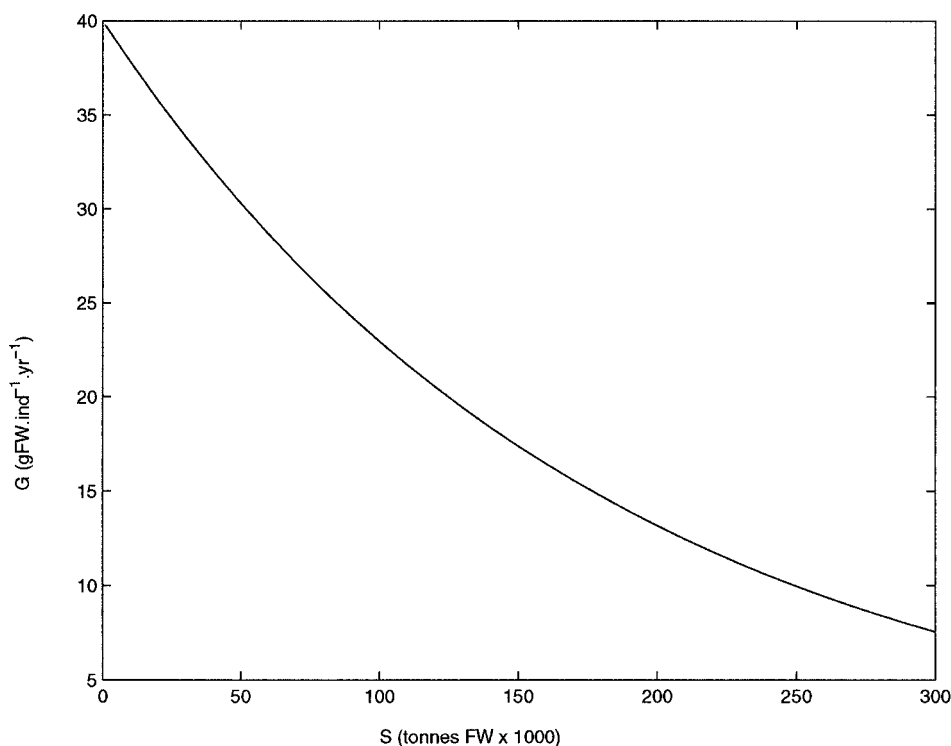$$\frac{\partial n}{\partial t} + G \frac{\partial n}{\partial w} = -m \cdot n, \tag{2}$$

Figure 1. Theoretical curve relating the annual growth rate G (gFW ind^{-1} yr^{-1}) to the standing stock S (thousands of tonnes FW).

where $n(w, t)$ dw is the number of individuals having a weight between w and $w + dw$ at time t, and m is the annual mortality rate. In our theoretical case, we assumed that m and G were independent of weight and time. The previous equation simply states that the variation of $n(w, t)$ in time includes the loss of the individuals due to the mortality, the individuals leaving the weight class $w - dw$ and arriving in the weight class w at the rate G, and the individuals leaving the weight class w at the same rate. The population is increased by the arrival of new individuals (seeding), which was considered as a continuous input of individuals per year R having a null weight. The continuous seeding is the only way to control the stock level of the system since decreasing R results in a lower number of animals in each weight class. In the following, we considered only the case where R is constant. Consequently, the weight distribution of the population stabilizes, so that the population dynamics equation (2) can be simplified in:

$$G \frac{dn}{dw} = -m \cdot n, \tag{3}$$

where n is only a function of w.

Knowing that the number of individuals entering the population at each time step was equal to R, the distribution of individuals n in the weight class w was given by:

$$n = \frac{R}{G} e^{-(m/G)w}. \tag{4}$$

A major characteristic of the system is based on the cultivation specifications. The one considered here is related to the marketable weight that the animals must reach at the end of their growth period. This feature was quite crucial in the behaviour of our dynamical system and lead to define the variable T (yr) as the growth time for an animal. This variable depended on the total number of animals since the growth rate was a decreasing function of the stock. Our model, therefore, accounted for the time needed to reach a marketable weight w_m (gFW ind^{-1}). Assuming that the animals reaching the weight w_m were removed from the system, we calculated the total stock as the integral of the weight distribution between the weights 0 and w_m. First, because of the constant growth rate G, we wrote:

$$G \cdot T = w_m \tag{5}$$

which was derived from:

$$\frac{\mathrm{d}w}{\mathrm{d}t} = G.$$

The relationship between the growth time and the stock was then derived from the function $G = f(S)$ (see Equation (1)) when the marketable weight w_m equalled 80 gFW ind^{-1} (Figure 2). For the maximum growth rate, the growth time was, therefore, 3.5 years for a standing stock of 100 000 tonnes FW.

The total number of individuals is the integration of the number of individuals of each weight class:

$$N = \int_0^{w_m} n(w)\, \mathrm{d}w; \qquad (6)$$

Integrating the former equations yielded:

$$N = \frac{R}{m} \cdot \left(1 - e^{-(m/G)w_m}\right). \qquad (7)$$

In the case where $m = 0$, the total number was simply (see the development of the the previous formula in the vicinity of 0):

$$N = \frac{R}{G} w_m,$$

which means that the total number is equal to the number of individuals entering the system each year if the individual reaches the marketable weight within one year (i.e., $G = w_m$).

The standing stock is the integration of the weight of each weight class:

$$S = \int_0^{w_m} n(w)w\, \mathrm{d}w. \qquad (8)$$

Integrating by parts yielded:

$$S = R \cdot G \cdot \left[-\frac{1}{m}(Te^{-mT}) + \frac{1}{m^2}(1 - e^{-mT}) \right]. \qquad (9)$$

For the particular case where $m = 0$, a simple calculation showed that:

$$S = \frac{RGT^2}{2}.$$

Therefore, we had:

$$R = \frac{S}{G \cdot \left[-\frac{1}{m}(Te^{-mT}) + \frac{1}{m^2}(1 - e^{-mT}) \right]} \qquad (10)$$

and, in the case where $m = 0$:

$$R = \frac{2 \cdot S}{G \cdot T^2}.$$

The production P (tonnes FW yr^{-1}) was derived from the number of individuals reaching the final weight w_m:

$$P = R \cdot e^{-mT} w_m. \qquad (11)$$

Equations (10) and (11) were used to calculate the relationship between S and P for S varying between 10 000 and 300 000 tonnes FW, values of the mortality rate between 0 and 0.4 yr^{-1}, and a constant marketable weight $w_m = 80$ gFW ind^{-1} (Figure 3).

As an example, for a mortality rate equal to 0.1 yr^{-1}, the maximum production was obtained when the stock S equalled 154 000 tonnes FW and the production equalled 55 600 tonnes FW. The maximum of production equalled 66 200 tonnes FW and the corresponding stock was 180 000 tonnes FW when a zero mortality rate was considered. For an extreme value of the mortality rate of 0.4 yr^{-1}, the maximum of production decreased until 34 300 tonnes FW, and the optimum standing stock reached 111 000 tonnes FW. These results not only showed that the production exhibited a maximum value when the mortality rate was given, but also the sensitivity of the optimum values to the mortality rate.

Other calculations also showed that the production was very sensitive to the marketable weight – since a larger marketable weight means that the animals should stay longer in the system. Results were obtained for the same range of standing stocks as before and for different values of the marketable weight – from 40 to 100 gFW ind^{-1} (not shown). For a mortality rate equal to 0.1 yr^{-1} and a marketable weight of 40 gFW ind^{-1}, the maximum production was then equal to 121 000 tonnes FW and the corresponding standing stock was 166 000 tonnes FW. Increasing the marketable weight up to 100 gFW ind^{-1} yielded a maximum of production of 42 700 tonnes FW and an optimum standing stock of 149 000 tonnes FW. This can be explained by the growth time which depended on the stock and, here, also on the marketable weight (Figure 4). For a marketable weight of 100 gFW ind^{-1}, the growth time reached 12 years at the optimum standing stock, which had the effect of a dramatic decrease in the number of animals surviving until the marketable weight was reached. Therefore, even if the marketable weight was twice as large as in the other case, the mortality was responsible for the decrease in the production. For low marketable
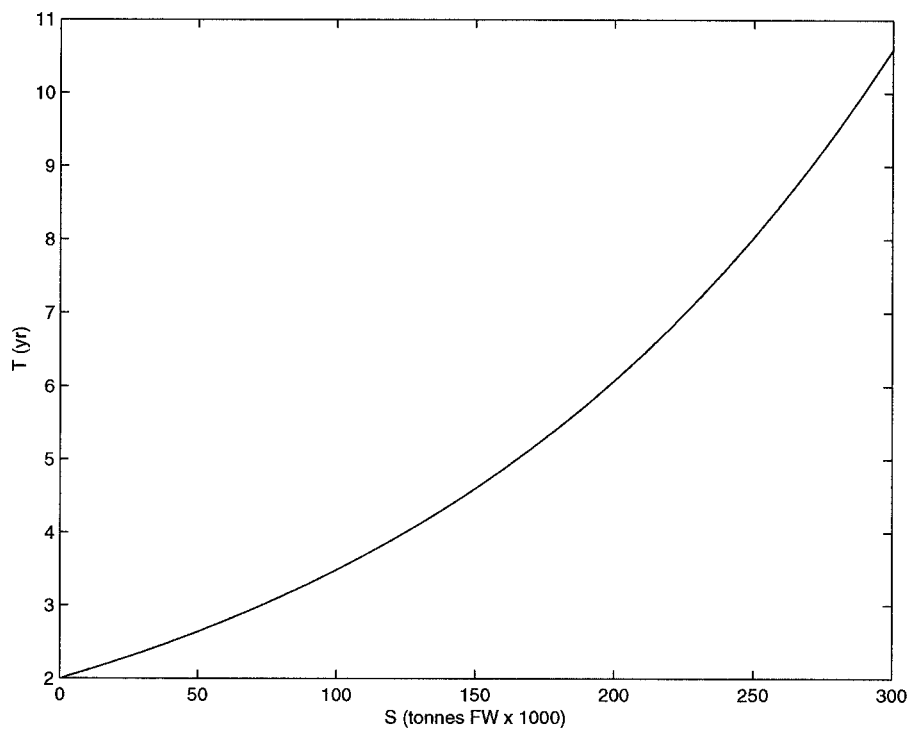
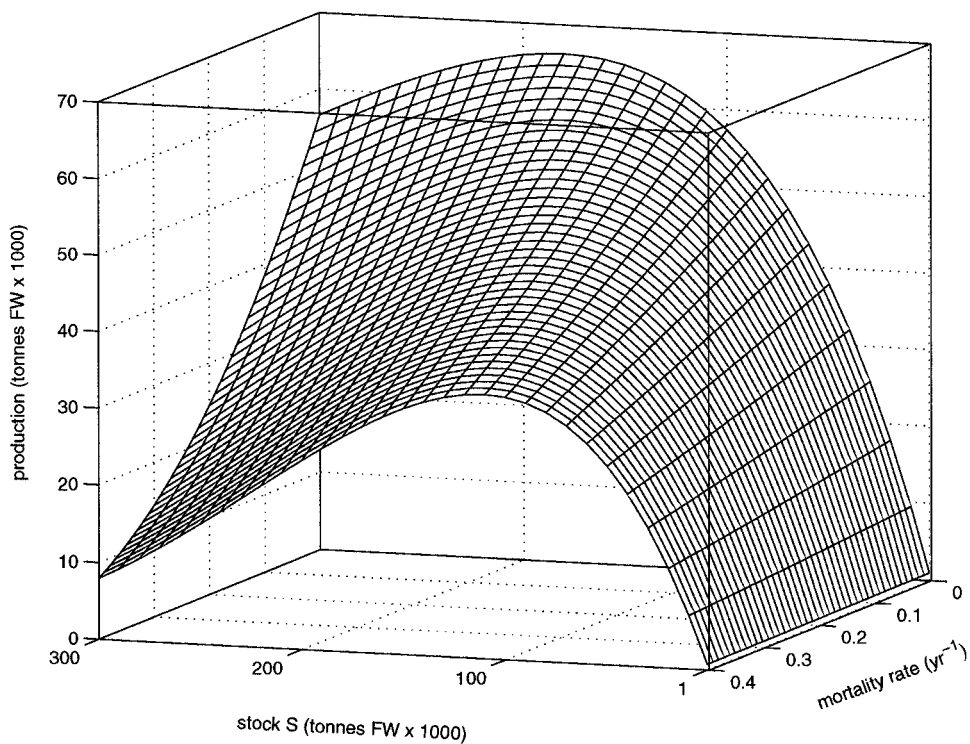*Figure 2*. Growth time T (years) as a function of the standing stock S (thousands of tonnes FW).

Figure 3. Production (thousands of tonnes FW) calculated with the theoretical model for different values of the annual mortality rate m – range 0–0.4 – and the standing stock S (thousands of tonnes FW).

weight – e.g., 40 gFW ind^{-1} – the growth time varied between 1 and 5 years (depending on the stock) and the loss of biomass due to the mortality was, therefore, less important. From an economic point of view, this does not mean that the benefits in the two extreme cases – e.g., low/large marketable weight – will support the same comparison, because a higher marketable weight yields a higher price. The economic response should also be considered to evaluate the optimum stock as well as the optimum marketable weight.

The theoretical model predicted the shape of the production and the standing stock functional relationship and its dependence on some key parameters related to the population dynamics, assuming that food was limiting the growth. In Marennes-Oléron bay and Carlingford Lough, this relationship was assessed by using an ecosystem model which computed the quantity of available food, its use by the filter-feeders and its effect on the growth in a more realistic but more complex way, as described below.

Marennes-Oléron Bay ecosystem model

Marennes-Oléron Bay (M.O.) is the most important oyster production area in France – with a stock around 100 000 tonnes FW and an annual production around 30 000 tonnes FW. It is a macrotidal ecosystem with important areas of tidal flats and high current velocities due to the tidal circulation. The water circulation has two main components: a residual tidal circulation which is responsible for the transit of the water masses from north of the bay towards the south, and water mixing during the tide at a typical length scale of a few kilometers. The residence time of the water in the part of the bay where oyster cultivation occurs, is short, less than 10 days. Transport and mixing are important physical factors which partly control the primary production and availability of food (detritus and phytoplankton) for the oysters. Also of major concern for the oyster growth is the high turbidity level, depending on the season, tidal level, bathymetry, currents and wind (Raillard et al., 1994). The turbidity acts on the primary production through light limitation and on oyster production as a food dilution factor. Concentrations of suspended sediment typically range from 50 to 200 mg l^{-1}. Primary production is controlled also by the nutrient inputs from the Charente river (Ravail-Legrand, 1993), whose flow generally varies between 10 m^3 s^{-1} in summer and 100 m^3 s^{-1} in spring, with extreme values up to 400 m^3 s^{-1}.

The nutrient inputs, mixing and transport by the currents, the turbidity level and the ecophysiology of the oysters are the main components of the box model developed by Raillard & Ménesguen (1994), which was adapted to address the issue of the carrying capacity assessment. These authors gave some clues on the carrying capacity of the bay through the sensitivity analysis of the oyster growth to the standing stock, using a spatial box model describing the nitrogen cycling between the dissolved phase, phytoplankton, detritus and cultured oysters (Figure 5). One of their conclusions was that the oyster population did not exert a strong control on the phytoplankton biomass because of the low residence time of the water. Due to turbidity, the planktonic primary production is not very high so that the bay can be characterized as a low production/high water turnover system. In these conditions, the carrying capacity is somehow inversely correlated to the water residence time: the food renewal is mainy due to the ability of the bay to very quickly transport the phytoplankton locally produced or imported. Even under these constraints however, the oyster growth is sensitive to the standing stock. This is why some more equations were added to the ecosystem model used by Raillard & Ménesguen (1994). Moreover, the box design was modified to include other parts of the bay (Figure 6) and the numerical code was rewritten to provide facilities to run simulations with different standing stock conditions. After some trials, the zooplankton compartment was removed from the model because of its very small influence on the phytoplankton dynamics compared with the oyster grazing. Since the core of the equations describing the nitrogen cycling did not change, the list of the equations is presented in Table 1 and the description will focus on the population dynamics equations introduced in the model.

The production model

The recruitment (seeding) was a discrete process which was defined as the input of a 0-age class through spat settlement at the beginning of each year. The oyster population was divided into 10 age classes represented by a number of individuals N having an average ash-free dry weight W and an average fresh weight FW (Table 1). The last-named variable was a new state variable in the model. The experimental studies have shown that the filter-feeders are sensitive to the variation in food and particulate matter (Barillé et al.,

Table 1. System of differential equations (from Raillard & Ménesguen, 1994). See also Figure 5

Nutrients (μmolN l^{-1}):

$$\frac{dNMIN_b}{dt} = -Pgrowth_b \cdot NPHY_b + Nremin \cdot NDET_b + \sum_{c=1}^{B} \frac{Q_{c,b}}{V_b} \cdot NMIN_c - \sum_{c=1}^{B} \frac{Q_{b,c}}{V_b} \cdot NMIN_b$$

Phytoplankton (μmolN $\cdot$ l^{-1}):

$$\frac{dNPHY_b}{dt} = Pgrowth_g \cdot NPHY_b - Pmort \cdot NPHY_b - Psed \cdot NPHY_b - Tingphy_b + \sum_{c=1}^{B} \frac{Q_{c,b}}{V_b} \cdot NPHY_c + \sum_{c=1}^{B} \frac{Q_{b,c}}{V_b} \cdot NPHY_b$$

Pelagic detritus (μmolN l^{-1}):

$$\frac{dNDET_b}{dt} = Pmort \cdot NPHY_b - Nremin \cdot NDET_b + Nresusp \cdot \frac{NBEN_b}{hwater_b} - \frac{Nsedim}{hwater_b} \cdot NDET_b + \sum_{c=1}^{B} \frac{Q_{c,b}}{V_b} \cdot NDET_c - \sum_{c=1}^{B} \frac{Q_{b,c}}{V_b} \cdot NDET_b$$

Benthic detritus (mmolN m^{-2}):

$$\frac{dNNEN_b}{dt} = Nsedim \cdot NDET_b - Nresusp \cdot NVEN_b + (Tfecphy_b + Tfecdet_b) \cdot hwater_b$$

Mean oyster dry weight (g) for the age class i in the box b:

$$\frac{dW_b^i}{dt} = Wsfg_b^i - Spawn_b^i$$

Mean oyster fresh weight (g) for the age class i in the box b:

$$\frac{dFW_b^i}{dt} = FWsfg_b^i$$

Number of oysters in the box b and the age class i:

$$\frac{dNOYS_b^i}{dt} = -m_i \cdot NOYS_b^i$$

Mineral seston (mg $\cdot$ l^{-1}):

$$\frac{dSES_b}{dt} = \sum_{c=1}^{B} \frac{Q_{c,b}}{V_b} \cdot SES_c - \sum_{c=1}^{B} \frac{Q_{b,c}}{V_b} \cdot SES_b$$

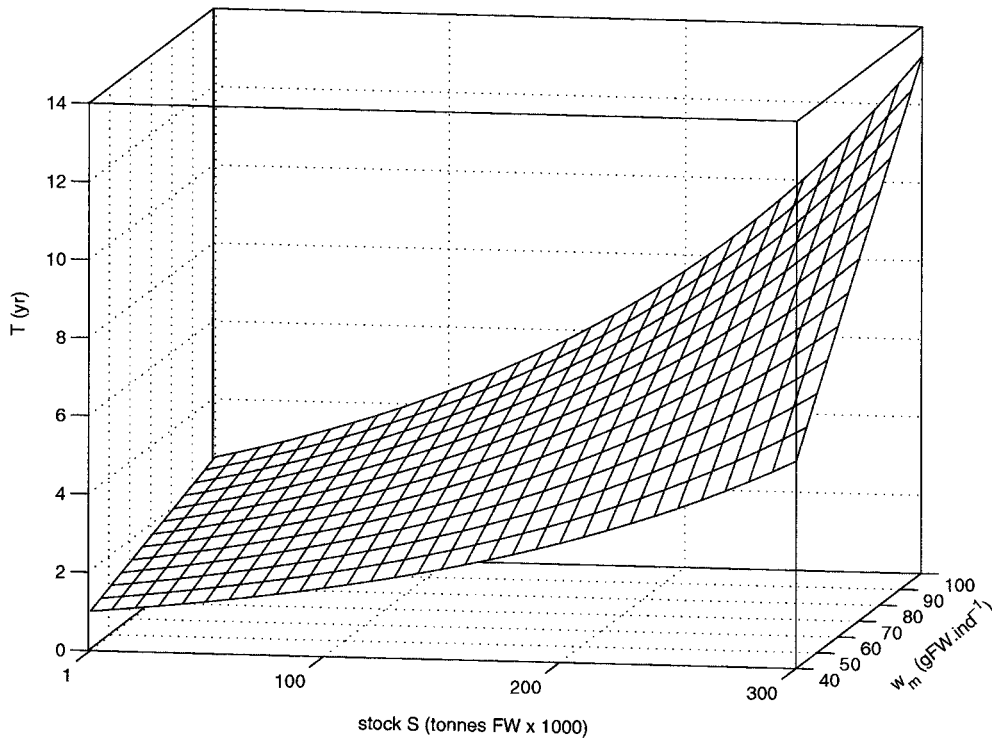| Notation	Parameter
$Pgrowth_b$	Phytoplankton growth rate (depending on the local characteristics of the box b)
$Pmort$	Phytoplankton mortality rate
$Psed$	Phytoplankton sedimentation rate
$Tingphy_b$	Phytoplankton ingestion by the oyster population
$Tingdet_b$	Detritus ingestion by the oyster population
$Tfecphy_b$	Phytoplankton egestion by the oyster population
$Tfecdet_b$	Detritus egestion by the oyster population
$Wsfg_b^i$	Individual oyster scope for growth (dry weight)
$FWsfg_b^i$	Individual oyster scope for growth (fresh weight)
$Spawn_b^i$	Individual oyster spawning
$Nremin$	Detritus mineralization
$Nsedim$	Detritus sedimentation rate
$Nresusp$	Detritus resuspension
$hwater_b$	Water height
m_i	Mortality rate for the age class i
B	Number of spatial boxes
$Q_{c,b}$	Flow from the box c to the box b
$Q_{b,c}$	Flow from the box b to the box c
V_b	Volume of the box b
X_b	State variable X in box b - X = NPHY, NDET, NMIN, SES, W, NBEN, NOYS

Figure 4. Growth time (years) related to the standing stock S (thousands of tonnes FW) and the marketable weight Wm – range 40 to 100 gFW ind^{-1}.

1993) and the responses are correlated to the dry weight (Bougrier et al., 1995). Because the marketable weight deals with the fresh weight and not the dry weight, we have to include this variable in the model. Some authors have established correlations between the size of the animal and the dry weight (Powell et al., 1992). In our case, however, it appeared that a relation between the total fresh weight (in which the shell weight has the major contribution) and the dry weight could not be fitted. High fluctuations of the dry weight within the year were generally masked by the more or less constant growth in total fresh weight. The variation of the total fresh weight was, therefore, based on three principles. Due to the importance of the shell weight, it was first assumed that the total fresh weight could not decrease. Second, the total fresh weight increase was a function of the energy budget when the budget was positive, i.e. only if the animal gained enough energy for its somatic growth. Third, a constraint on the total fresh weight was defined from the maximum total fresh weight an animal of a given dry weight might reach. These calculations involved the computation of the individual energy budget and we used the equations and parameters describing the oyster eco-

physiology as a function of detritus, phytoplankton, total suspended matter and temperature derived from Raillard & Ménesguen (1994).

It may happen that the food limitation is so strong that the annual growth rate (in dry weight) is null or negative, even if the spring growth is still observed. In such a case, the total fresh weight growth was limited by the previous constraint, which may even prevent the animal from reaching the marketable weight after several years in the bay. This constraint was derived from data on dry weight and fresh weight (Deslous-Paoli & Héral, 1988). For one given dry weight, the maximum fresh weight was defined as the value under which 90% of the observations were found. It was, therefore, necessary to divide the observations into dry weight classes and to calculate the distribution of the fresh weights for each class. A logistic model was fitted to the data coming from the analysis of the dry weight/fresh weight values distribution. Approximately 1500 values were used to estimate the upper value of the fresh weight for a given dry weight. Given this maximum, the fresh weight increased as a function of the energy budget calculated for the dry weight. Though the fresh weight gain may be important, the
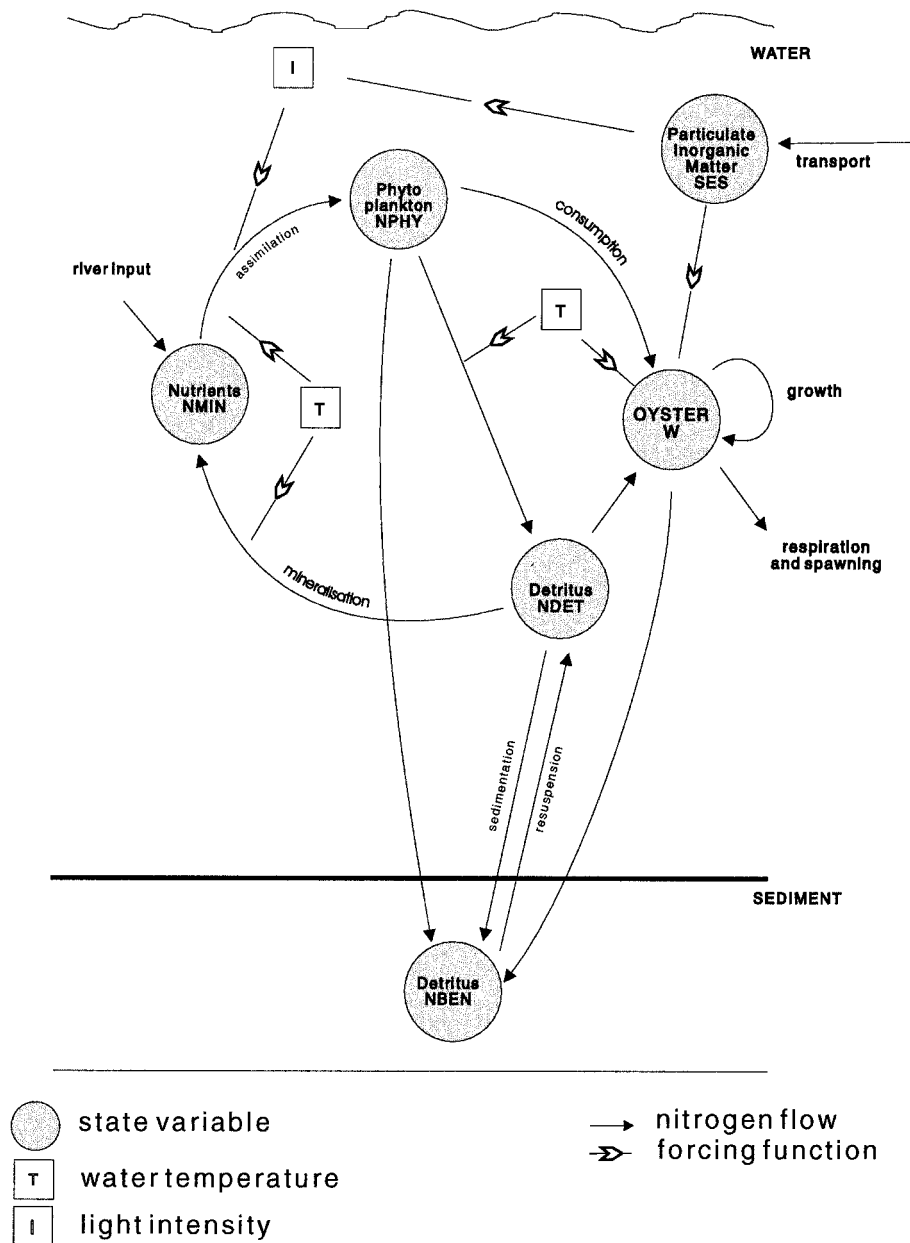
Figure 5. Conceptual scheme of the nitrogen cycling in one spatial box. State variables are represented by circles and processes (nitrogen flows) by arrows (see Table 1 for the equations).

energy used for this growth is generally very low due to the low organic content of the shell which is the major component of the fresh weight. It is, therefore, important to note that the fraction of energy devoted to the fresh weight growth was not taken into account in the equation of the dry weight variation (Raillard & Ménesguen, 1994).

In the model, this calculation was achieved at each time step for each age class in all the boxes containing oysters. The population dynamics was described very simply. Neither the import of oysters from other bays nor the transportation of oysters within different locations within the bay were considered. It was assumed that the seeding took place at the beginning of the year
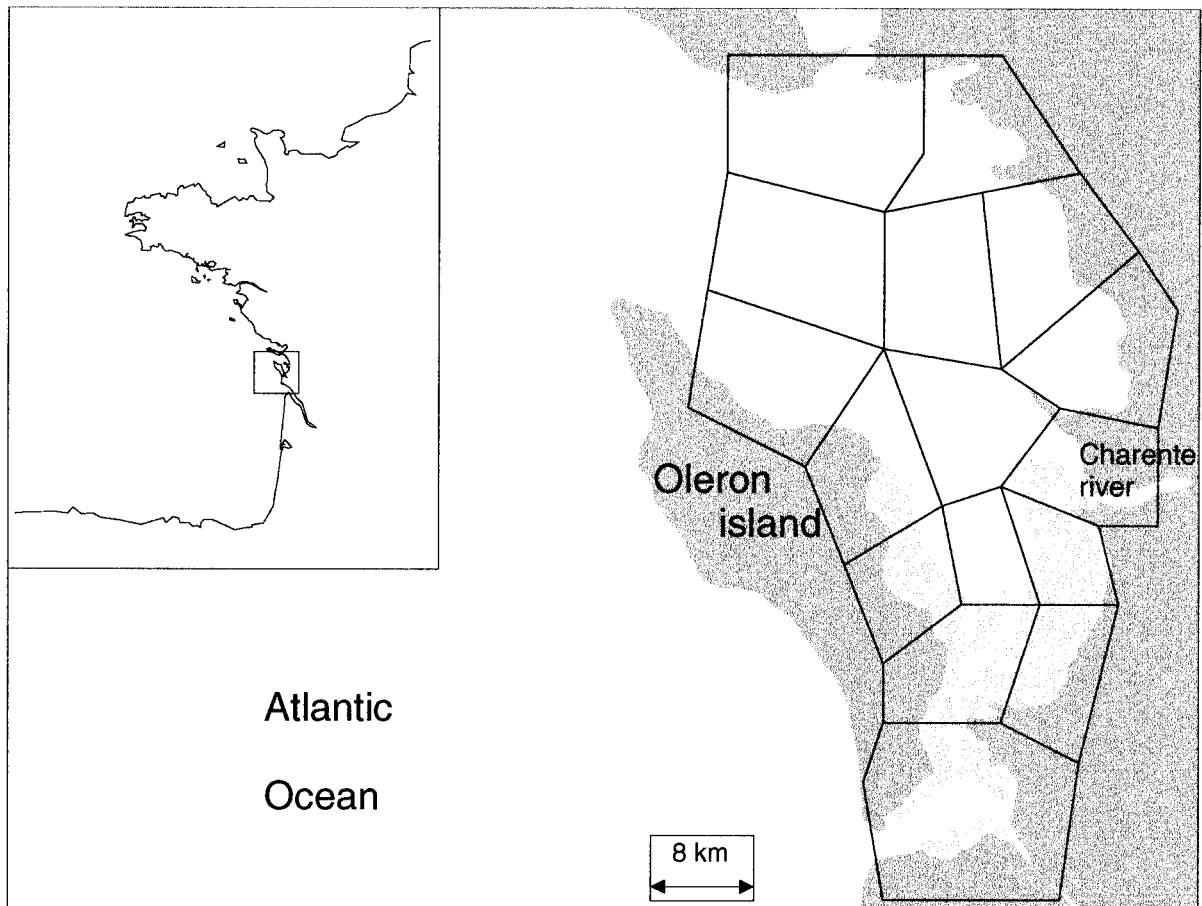
Figure 6. Spatial box scheme in the Marennes-Oléron (M.O.) model.

and that the oysters remained in the same place until they reached the marketable weight. Since the commercialization of the oysters generally occurs at the end of the year, a test was performed to decide whether or not one age class in a given box would be removed from the bay at the end of one simulated year. If not, the age class was increased by one, the number of oysters in the new age class decreased the next year with the same mortality rate, and the individual growth – in dry weight and fresh weight – was simulated for one more year. Each age class in each box had, therefore, its own dynamics and the model had to be run to simulate several years before the system became stable, i.e. simulated growth curves for each age class in each box did not change from one year to the other. Since the growth performance varied between the boxes, the growth time also differed and some age class could stay longer than others.

There were two major differences with the theoretical approach. First the mortality rate was not constant but depended on the age of the animal. Similarly, the individual growth rate depended on the individual weight – allometric functions usually describe the ecophysiological functions of the animal. Following the available information, the mortality rate equalled 0.3 yr^{-1} for the first age class, and 0.1 yr^{-1} for the others and the marketable size was equal to 80 gFW.

With this set of parameters, a simulation with a standard value of the standing stock and a cultivation time of 3 years was first carried out to calculate the fresh weight of one age class during 3 years in order to check the relevance of the model outputs. The individual fresh weight was compared with the observed values that were collected between 1979 and 1981 (Deslous-Paoli & Héral, 1988). Second, the model was run with different annual seedings which yielded different standing stocks. Several simulations were,

therefore, performed with different seeding intensities and the model output was used to compute the annual production versus the stock at the equilibrium situation – e.g., the model simulated 10 years with the same forcing functions (temperature, light, seeding) and boundary conditions. The rearing time is the time needed for an oyster to reach the marketable size – as in the theoretical model. The relationship between stock and production was expressed in various ways. Since the output of the model typically represents time series of individual ash-free dry weight (AFDW or W for short), individual total weight – or fresh weight (FW) – and number of individuals for each age class in six different boxes, the results were summarized and standardised to enable comparisons between different systems. First the results were summed or averaged over the spatial boxes. The rearing time, for instance, was averaged over the boxes with a weight equal to the number of oysters in the last age class in this box. As previously mentioned, the stock was dependent on the seeding. Therefore the stock was calculated from the number of oysters in the different age classes and boxes at the end of the year. The production was expressed in total FW, total AFDW or as a fraction of the stock. In all cases, the production was based on the number and mass of oysters removed from the bay at the end of the year – e.g., when the individual fresh weight was greater or equal to the marketable size (80 gFW).

Results

In the standard simulation, there was a good agreement between the predicted and observed values during the 3 years (Figure 7), although the ash-free dry weight was underestimated in the second and third year (not shown). Due to the structure of the ecophysiology model, there was no impact of the fresh weight growth on the dry weigh (see above).

The production/stock relationship ($P = f(S)$) was derived from several simulations (Figure 8a). After a linear increase of the production from 5000 to 45 000 tonnes FW, the production stabilized at 45 000 tonnes FW for standing stocks above 115 000 tonnes FW, and eventually decreased for standing stocks greater than 270 000 tonnes FW. The mortality rate was responsible for the dome shape of the $P = f(S)$ relationship. Increasing the rearing time, because of the food limitation resulting from the overstocking, resulted in a decreasing production due to the decreasing number of individuals reaching the marketable size. The rear-

ing time (in months) was averaged over the boxes and plotted versus the standing stock (Figure 8b). It had an exponential type shape - the first values were about 2 years, the last one was almost 10 years for a stock equal to 400 000 tonnes FW. The rearing time corresponding to the maximum production (45 000 tonnes FW) and the standing stock 115 000 tonnes FW was equal to 40 months.

Figure 8c depicts the decrease of the annual growth rate as a function of the density (equal to the total number of oysters divided by the volume of water in boxes containing cultured areas). Because individual performances are better described with the dry weight, the growth rate G (yr^{-1}) was calculated from the ash-free dry weight increase per gram during one year. It is a standardized way to express the carrying capacity of a bay since the scale effect of the system was removed. The maximum annual weight increase in one year was equal to 0.5 when the oyster density was very low – around 0.1 ind m^{-3}. It decreased to 0.05 with a density equal to 1.5 ind m^{-3}.

The M.O. model confirmed the general trend in the relationship between the production and the standing stock obtained by Héral (1993) with an empirical model based on mortality, growth, production, and stock time series. However, the empirical model does not predict any decrease of the production, opposite to the ecosystem model which predicted a maximum production of 45 000 tonnes FW for a standing stock around 115 000 tonnes FW and a rearing time of 3–4 years. In the latter, annual production decreased for high stocks due to the combination of mortality rates and increasing rearing times.

Comparison of Marennes-Oléron Bay and Carlingford Lough carrying capacity and discussion

It is interesting to compare the Marennes-Oléron (M.O.) carrying capacity with the carrying capacity of Carlingford Lough (C.L.), which was also assessed with an ecosystem model (Ferreira et al., this volume). In Carlingford Lough, the oysters need about 1.5 years to reach a commercially valuable size, the period required in Marennes-Oléron when oyster culture was initiated, in clear contrast with the present 4-year period (Raillard & Ménesguen, 1994). The methodology of the Carlingford Lough and the Marennes-Oléron models was very similar. Both models were based on the coupling between physical and biological processes at
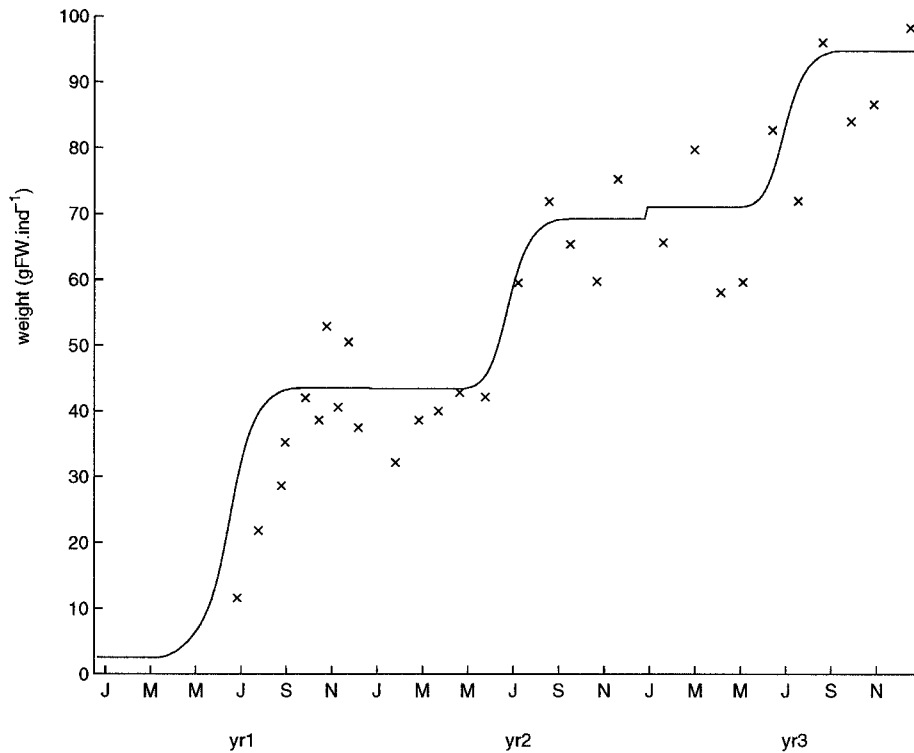
Figure 7. Simulation of the fresh weight (gFW ind^{-1}) during three years with the M.O. model and comparison with a time series of observations in the center of the bay.

the scale of spatial boxes of several kilometers length. The major differences were related to the population dynamics of the cultured oyster. The C. L. model used 40 weight classes instead of 10 age classes. Instead of computing the growth of different age classes (see above), the C.L. model used a discretized formulation of the continuous equation representing the variation of the population abundance in size and time – see for instance the equation used to build the theoretical model at the beginning of this paper. It was, therefore, designed to give more clues than the M.O. model on the growth and size variability among the population. Another difference between the two models was related to the relationship between the fresh and the dry weights. In the C.L. case, a fixed ratio was used because the oysters did not lose weight through gamete release. In the M.O. model, it was necessary to describe the oyster growth with 2 different variables – fresh weight and dry weight – to account for the dry weight decrease due to food depletion and spawning.

The production, standing stock, rearing time, mean growth rate and densities were simulated as in the M.O. case to assess the carrying capacity of the bay, with a marketable weight of 80 gFW. The marketable weight differs from that used in Ferreira et al. (this volume). The total standing stock varied between 200 and 3000 tonnes FW and the related annual production between 10 and 1400 tonnes FW (Figure 9a). The production was maximum for a standing stock around 1200 tonnes FW. It dramatically decreased for greater stocks and, for stocks over 3000, the production was less than 10 tonnes FW. The rearing time was positively correlated to the standing stock (Figure 9b). It varied from 17 months to 45 months, with a steep slope from 18 to 40 months as the production collapsed. Another clue to the decline of the production for high standing stocks is shown by the mean annual growth rate G (yr^{-1}) plotted against the density (Figure 9c). Growth rate values greater than one were obtained for biomasses lower than 0.2 ind m^{-3} and became lower than 0.5 for densities over 0.5 ind m^{-3}. The increase in the rearing time was negatively correlated to the growth rate (compare Figures 9b and 9c). Therefore, increasing the seeding yielded a dramatic decrease of the growth rate and resulted in an increased rearing time required to reach marketable size.

Table 2. Comparison between some characteristics of Carlingford Lough and Marennes-Oléron bay. Flows and biomass estimations were derived from the standard simulation with the current oyster standing stocks and averaged on one year. Flows were converted to gN m^{-2} yr^{-1} to enable comparisons between the 2 systems

Phytoplankton	Carlingford Lough	Marennes-Oléron
input I (gN m^{-2} yr^{-1})	0.04	11.6
primary production P (gN m^{-2} yr^{-1})	1.94	15.8
filtration rate F (gN m^{-2} yr^{-1})	0.07	7.14
biomass B (gN m^{-2})	0.087	0.42
B/P (d)	16.4	12.2
B/I (d)	96	9.7
B/F (d)	454	21.5
F/T (%)	4	30

Nutrients	Carlingford Lough	Marennes-Oléron
input I (gN m^{-2} yr^{-1})	2.09	143
biomass B (gN m^{-2})	0.52	4.1
B/I (d)	91	10.5

Notations: *input* I is the annual phytoplankton or nutrients input from rivers and ocean, *filtration rate* F is the food consumption by the oyster population, T is the throughflow (input + production), B/I, B/P, B/F are time constants computed to compare the time scales for the primary production, the filtration and the transport.

The models revealed that C.L. and M.O. differed in their properties. Though the curves for the two had similar shapes, the rearing time was about 3 times higher in M.O. than in C.L. (Figures 8 and 9). Also the densities differed. The density value corresponding to the current standing stock lay around 0.5 ind m^{-3} in M.O., compared with 0.1 ind m^{-3} in C.L. Similarly, the current growth rate was three times higher in C.L. than in M.O. Besides theses differences between the standardized production and stock values, the scales differed. The current M.O. standing stock was approximately 200 times higher than the C.L. stock. Because of the differences in the growth rates and rearing times – that may be seen as a difference in the efficiency of the system from the aquaculture point of view – the production was only 40 times higher in M.O. than in C.L.

From the outputs of the models, time scales have been calculated through the integration over time and over the spatial boxes of the phytoplankton nitrogen concentration and primary production for a standard simulation with current oyster standing stock (Ferreira et al., this volume; Bacher, unpublished). Water flows through the boxes, clearance rate of the oyster population and box volumes computations were also carried out to estimate the water turnover rate and the clearance time of the oysters (Table 2). These calculations were performed on the boxes containing oysters or concerned by the impact of the oysters (e.g. in M.O. only the boxes in the southern part of the bay were considered). The primary production was 6 times higher in M.O. than in C.L. Also the phytoplankton input (from river and ocean) was much higher in M.O. Phytoplankton inputs explain why the mean phytoplankton biomass was 0.087 gN m^{-2} in C.L. and 5 times higher in M.O. though the 2 ecosystems had comparable turnover rates (see the phytoplankton B/P ratio in Table 2). The summation of the 2 previous flows is referred as the phytoplankton throughflow T. The ratio between the filtration rate F and the throughflow T gave the fraction of the total phytoplankton input consumed by the filter feeders. Expressed as a percentage, this ratio was equal to 4% in C.L. and 30% in M.O. Despite this markedly higher rate for M.O., the standing stock was 2 orders of magnitude greater in M.O. than in C.L. Increasing the stock in C.L. will rapidly decrease the food concentration and consequently the primary production, resulting in a high F/T value. The difference in the carrying capacity is thus essentially explained by the difference in flows through the two ecosystems. M.O. has for instance very striking features related to the short time constants – e.g. the turnover, residence and filtration times lie between 10 and 22 d (Table 2).
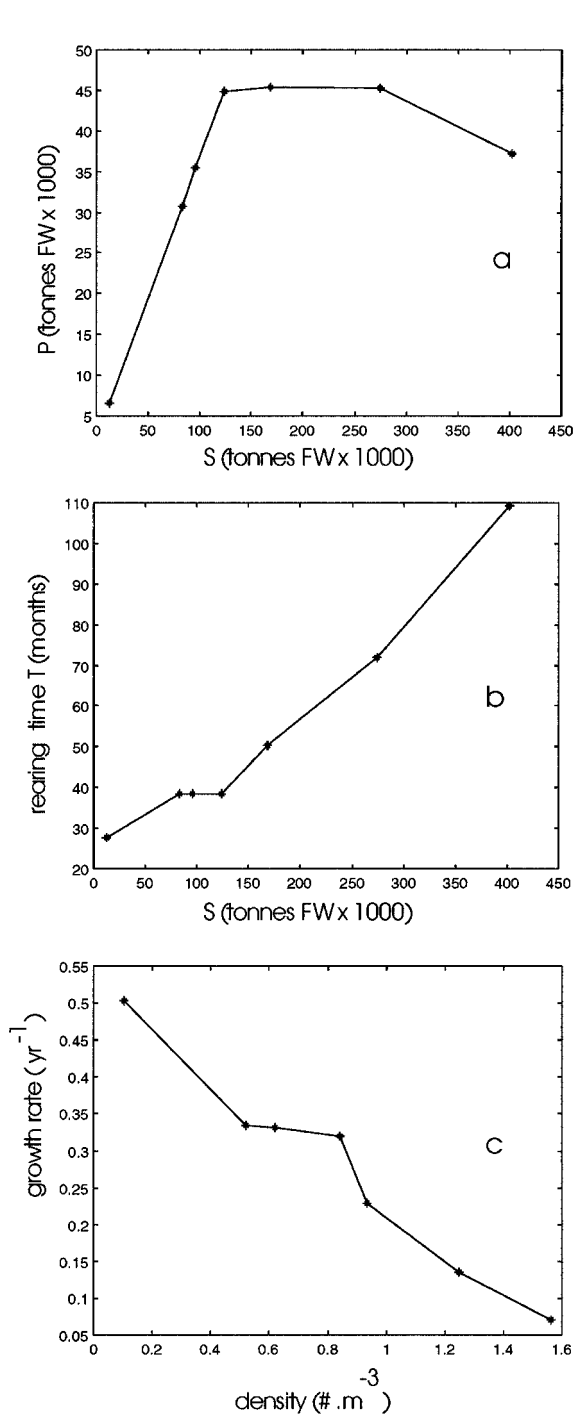
Figure 8. Different outputs of the model highlighting the carrying capacity of the bay. (a) Annual fresh weight production (thousands of tonnes FW) versus fresh weight standing stock (thousands of tonnes FW). (b) Mean rearing time (months) versus seeding (tonnes FW). (c) Growth rate (yr^{-1}) versus density (ind m^{-3}).
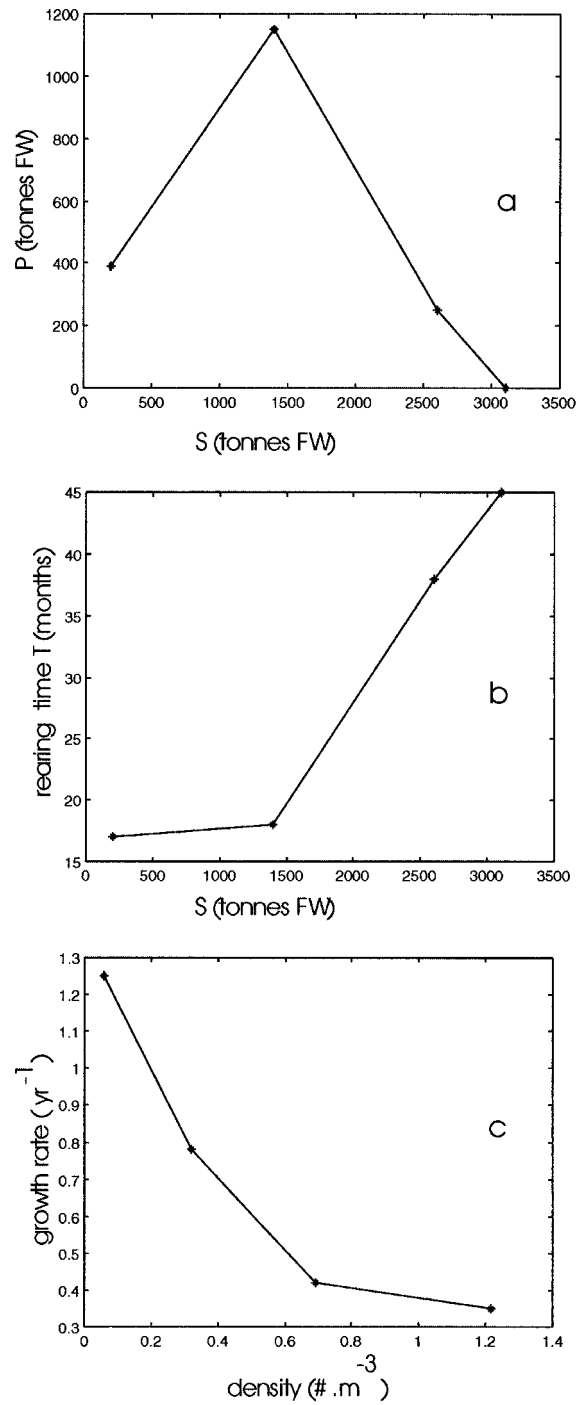
Figure 9. Model simulation results to test the effect of the standing stock and the seeding on the oyster production and time to reach an harvestable size in Carlingford Lough (same as Figure 8 for Marennes-Oléron). (a) Annual fresh weight production (tonnes FW) versus fresh weight standing stock (tonnes FW). (b) Mean rearing time (months) versus seeding (tonnes FW). (c) Growth rate (yr^{-1}) versus density (ind m^{-3}).

The box model is the best which can be presently achieved. However, it does not take into account all the complexity and variability of the system and should be improved. In the M.O. case for instance, the complexity is related to the interaction between the physical and the biological processes. Some ecophysiological processes (gametogenesis, local density-dependence effect, mortality), still not studied, may influence the response of the oyster to environmental forcing. The mixing of the water is responsible for the resuspension of organic and inorganic matter, which both affect the oyster growth. These factors are difficult to account, having a typical time scale of hours and a spatial scale of a hundred meters (Raillard et al., 1994). As for the biology, only recently some attempts have been made to incorporate gametogenesis and some related processes (Barillé et al., 1997; Soletchnick et al., 1997). Food limitation due to local density-dependence effects (Butman et al., 1994) was not considered here, assuming that the food depletion was related to the oyster consumption at the scale of the bay. However, mortality rates should increase at high stocking densities due to local conditions (Fréchette et al., 1996). For very high standing stocks, overestimated production could result from not accounting for mortality.

Conclusion

The interactions between biological processes (primary production, oyster growth) and physical process (transport and mixing) were successfully modelled to assess the carrying capacity of Carlingford Lough (C.L.) and Marennes-Oléron Bay (M.O). The first site has a very low density of cultured oysters and the second one is overstocked. Experimental data and modelling tools were developed to simulate the growth of cultured molluscs as a function of the available food – phytoplankton, organic matter and inorganic particulate matter. The relation between the annual production and the total stock was assessed by simulating different scenarios. The definition of the carrying capacity was then derived in different ways from the odelling results. Therefore, the modelling methodology proved to be powerful. The model predicted the optimum standing stock in C.L. and M.O. In C.L. the production increased while the standing stock increased from 200 tonnes FW to approximately 1500 tonnes FW. The production decreased for higher standing stocks. In M.O., the model predicted a maximum production of 45 000 tonnes FW for a standing stock around 115 000 tonnes

FW and a rearing time of 3–4 years. The difference in the carrying capacity of the two systems was essentially explained by the difference in biological and physical flows derived from the models outputs.

The interactions between the oyster ecophysiology, the population dynamics and the food production were summarized in the theoretical model. This model demonstrated the dome-shaped curve of the production/stock relationship and its sensitivity to ecological parameters (e.g. mortality rate) and economic constraint (e.g. the marketable weight).

References

Barillé L, Prou J, Héral M and Bougrier S (1993) No influence of food quality but ration-dependent retention efficiencies in the Japanese oyster *Crassostrea gigas*. J Exp Mar Biol Ecol 171: 91–106

Barillé L, Héral M and Barillé-Boyer AL (1997) Modélisation de l'écophysiologie de l'huitre *Crassostrea gigas* dans un environnement estuarien. Aquat Living Resour 10: 31–48 Bougrier S, Geairon P, Deslous-Paoli JM, Bacher C and Jonquieres G (1995) Allometric relationships and effects of temperature on clearance and oxygen consumption rates of *Crassostrea gigas* (Thunberg). Aquaculture 134: 143–154

Butman CA, Frechette M, Geyer WR and Starczak VR (1994) Flume experiments on food supply to the blue mussel *Mytilus edulis* L. as a function of boundary-layer flow. Limnol Oceananogr 39: 1755–1768

Dame R. F. (Ed.) (1993) Bivalve filter feeders in estuarine and coastal ecosystem processes. Springer-Verlag, Berlin, 579 pp

Deslous-Paoli JM and Héral M (1988) Biochemical composition and energy value of *Crassostrea gigas* (Thunberg) cultured in the bay of Marennes-Oléron. Aquat Living Resour 1: 239–249

Ferreira JG, Duarte P and Ball B (1998) Trophic capacity of Carlingford Lough for oyster culture – analysis by ecological modelling. Aquat Ecol 31: 361–378.

Fréchette M, Bergeron P and Gagnon P (1996) On the use of self-thinning relationships in stocking experiments. Aquaculture 145: 91–112

Gerritsen J, Holland AF and Irvine DE (1994) Suspension-feeding bivalves and the fate of primary production: an estuarine model applied to Chesapeake Bay. Estuaries 17: 403–416

Grant J, Dowd M, Thompson K, Emerson C and Hatcher A (1993) Perspectives on field studies and related biological models of bivalve growth and carrying capacity. In: Dame RF (ed.) Bivalve filter feeders in estuarine and coastal ecosystem processes (pp. 371–420) Springer-Verlag, Berlin

Héral M (1993) Why carrying capacity models are useful tools for management of bivalve molluscs culture. In: Dame RF (ed.) Bivalve filter feeders in estuarine and coastal ecosystem processes (pp. 465–477) Springer-Verlag, Berlin Herman PMJ (1993) A set of models to investigate the role of benthic suspension feeders in estuarine ecosystems. In: Dame RF (ed.) Bivalve filter feeders in estuarine and coastal ecosystem processes (pp. 421–454) Springer-Verlag, Berlin

Kashiwai M (1995) History of carrying capacity concept as an index of ecosystem productivity (Review). Bull Hokkaido Natl Fish Res Inst 59: 81–101

Powell EN, Hofmann EE, Klinck JM and Ray SM (1992) Modeling oyster populations. I. A commentary on filtration rate. Is faster always better? J Shellfish Res 11: 387–398

Powell EN, Klinck JM, Hofman EE and Ray SM (1994) Modeling oyster populations. IV: rates of mortality, population crashes and management. Fish Bull 92: 347–373

Raillard O, Deslous-Paoli JM, Héral M and Razet D (1993) Modélisation du comportement nutritionnel et de la croissance de l'huitre japonaise *Crassostrea gigas*. Oceanol Acta 16: 73–82

Raillard O and Ménesguen A (1994) An ecosystem model for estimating the carrying capacity of a macrotidal shellfish system. Mar Ecol Prog Ser 115: 117–130

Raillard O, Le Hir P and Lazure P (1994) Transport de sédiments fins dans le bassin de Marennes-Oléron: mise en place d'un modèle mathématique. La Houille Blanche 4: 63–71

Ravail-Legrand B (1993) Incidences du débit de la Charente sur la capactié biotique du bassin ostréicole de Marennes-Oléron. Thèse de Doctorat, Univ. Nantes, 171 pp

Smaal AC and Scholten H (1997) An ecophysiological model of the mussel *Mytilus edulis* (EMMY). In: Smaal A.C. Food supply and demand of bivalve suspension feeders in a tidal system. PhD thesis State University Groningen: 147–190

Soletchnick P, Razet D, Geairon P, Faury N and Goulletquer P (1997) Ecophysiologie de la maturation sexuelle et de la ponte de l'huitre creuse *Crassostrea gigas*. Réponses métaboliques (respiration) et alimentaires (filtration, absorption) en fonction des différents stades de maturation. Aquat Living resour 10: 179–186

Van Haren RJF and Kooijman SALM (1993) Application of a dynamic energy budget model to Mytilus edulis (L.). Neth J Sea Res 31: 119–133