Aquatic Ecology **31:** 361–378, 1998.

Trophic capacity of Carlingford Lough for oyster culture – analysis by ecological modelling

J.G. Ferreira[1], P. Duarte[2] and B. Ball[3]
[1]*Universidade Nova de Lisboa, Fac. Ciências e Tecnologia, DCEA, Quinta da Torre, 2825 Monte de Caparica, Portugal (web: http://tejo.dcea.fct.unl.pt);* [2]*Universidade Fernando Pessoa, Dep. de Ciências e Tecnologia, Praça 9 de Abril, 349, 4200 Porto, Portugal (E-mail: nop57746@mail.telepac.pt);* [3]*The Martin Ryan Marine Science Institute, University College Galway, Galway, Ireland (E-mail: brendan.ball@ucg.ie)*

Accepted 16 January 1998

Key words: carrying capacity, oyster culture, demographic modelling

Abstract

A one-dimensional ecosystem box model is presented for carrying capacity assessment. The model includes physical and biological processes. The physical processes are the transport of nutrients, suspended matter and phytoplankton through the system boundaries and between model boxes. The biological processes are primary production and oyster (*Crassostrea gigas*) population dynamics and physiology. The model was implemented using an object-oriented approach. The model was employed to estimate the carrying capacity of Carlingford Lough (Ireland) for oyster culture. In the Lough, low water temperatures prevent the oysters from reproducing. Therefore, recruitment is human-dependent. Small oyster spat is seeded every year during spring and harvested after the summer of the next year. During this period oysters reach commercially harvestable weight. The results obtained indicate that the carrying capacity of this system is approximately 0.45 g oysters (AFDW) m^{-3}, determined more by the availability of particulate matter than by phytoplankton. It is suggested that a five-fold increase in oyster seeding may optimise harvest yield.

Introduction

The carrying capacity may be defined as the stock density at which production levels are maximised without negatively affecting growth rates (Carver & Mallet, 1990). Due to the lack of proper management strategies bivalve cultivation often exceeds the carrying capacity of the environment, therefore reducing harvest yields and potentially compromising sustainability. The importance of modelling for carrying capacity assessment was discussed by Heral (1993); other authors (Bacher, 1989; Raillard & Ménesguen, 1994) assessed carrying capacity in a macrotidal shellfish system (Marennes-Oléron Bay in France), by means of an ecological model.

The previous authors used a physical and a biological sub-model. The physical sub-model simulated the transport of dissolved and particulate matter whereas the biological sub-model simulated the assimilation of the latter by an oyster population. The model of Bacher (1989) did not simulate primary productivity, assuming that the renewal of food by primary production is negligible when compared to the inputs by tidal currents at the ocean boundary. The oyster (*Crassostrea gigas*) population was the only biological variable explicitly simulated. The model of Raillard & Ménesguen (1994) simulated phytoplankton and zooplankton growth. The nitrogen cycle was also considered due to the role played by primary production. However, the deposition and resuspension of sediments within the model boxes were not considered.

The overall methodology in these models was identical. The ecosystem was assumed to be vertically homogeneous and divided into compartments (model boxes). Although the number and shape of the chosen compartments differed, in both cases the models were bidimensional and the size of the compartments was comparable to the tidal excursion (Bacher, 1989; Raillard & Ménesguen,1994).

In the present study the system was also divided into 'large' ecological boxes (see Figure 1) with the transport of particulate and dissolved substances between boxes calculated using an upwind 1-D transport scheme. However, instead of using the classical approach of dividing the model into a physical and a biological sub-model each with their state variables, an object-oriented approach was followed and the system divided in functional ecological units (objects), each with their state variables and forcing functions. For details regarding object-oriented programming (OOP) see, e.g., Schildt (1995). Sekine et al. (1991), Silvert (1993) and Ferreira (1995) discuss the utility and some applications of OOP in ecosystem modelling. The latter paper gives a detailed description of the programming approach used in the development of the present model (EcoWin). Some further details are given in the methods section.

The main objectives of the present work were the following:

- To simulate oyster growth in Carlingford Lough by means of an ecological model.
- To assess the carrying capacity of Carlingford Lough for the cultivation of the Pacific Oyster, and examine different management strategies for aquaculture.
- To perform a mass balance for nitrogen in the Lough, in order to understand the relative importance of physical and biological variables.
- To test and discuss the usefulness of the model against the results obtained.

The study area

Carlingford Lough is a small embayment on the Irish east coast, forming part of the border between the Republic of Ireland and Northern Ireland (Figure 1). It is 16.5 km long and 5.5 km wide at its widest point, with an area of approximately 40 km^2 and an average depth of 5 m. The mean tidal prism corresponds to about 50% of the mean Lough volume. It has important intertidal areas in the north and south margins that correspond to almost half of the total area. The main freshwater discharge is from the Newry (Clanrye) river, with a small flow rate that can vary from 1 m^3 s^{-1} in Summer to 9 m^3 s^{-1} in Winter (roughly 10^5–10^6 m^{3}d^{-1}).

In Carlingford Lough the oysters need approximately 1.5 years to reach a commercially valuable size, which was the period required in Marennes-Oléron when oyster culture was initiated, in clear contrast with the present 4-year period (Raillard & Ménesguen, 1994). There are several possible reasons to explain the differences in growth rates between both cultivation areas and these will be discussed below. However, the most obvious seems to be the difference in oyster density, since it was demonstrated by Bacher (1989) and confirmed by Raillard & Ménesguen (1994) that density correlates negatively with individual growth. In Marennes-Oléron Bay the oyster density in the boxes used for cultivation is approximately 6 individuals m^{-3} (calculated from Raillard & Ménesguen, 1994) whereas in Carlingford Lough it is over 100 times lower (approximately 0.05 individuals m^{-3}).

In Carlingford Lough the oyster recruitment is human-dependent. The oysters develop gametes but spawning does not occur, presumably because the temperature never reaches the required level. Oyster seeding takes place every year in the months of May and June – approximately 5 tonnes of spat. After two summers the oysters are harvested, by which time their biomass has increased to 300–400 tonnes. The oyster cultivation areas are located in boxes 2 and 3 (Figure 1). Although box 1 seems to have good conditions for oyster growth, bacterial contamination from domestic and cattle effluents prevents its use as a cultivation area.

Materials and methods

The modelling approach followed in the present study may be divided in four parts:

(1) Data loading and exploration for model calibration and validation by means of the database BarcaWin.

(2) Box definition with DifWin.

(3) Application of the hydrodynamic model for calculation of dispersion coefficients, and in order to refine box definition.

(4) Model development and simulations with EcoWin.

BarcaWin is a relational database that includes a program for file conversion between different formats, the data files, and database software for analysis and exploration of the data. The BarcaWin database is written in Turbo Pascal for Windows and C++, and uses the Borland Paradox Engine for all database-related functions. DifWin allows the interactive definition of the physical compartments in a box-model. The software is a tool allowing easy linkage between an ecological and a hydrodynamic model. It generates two

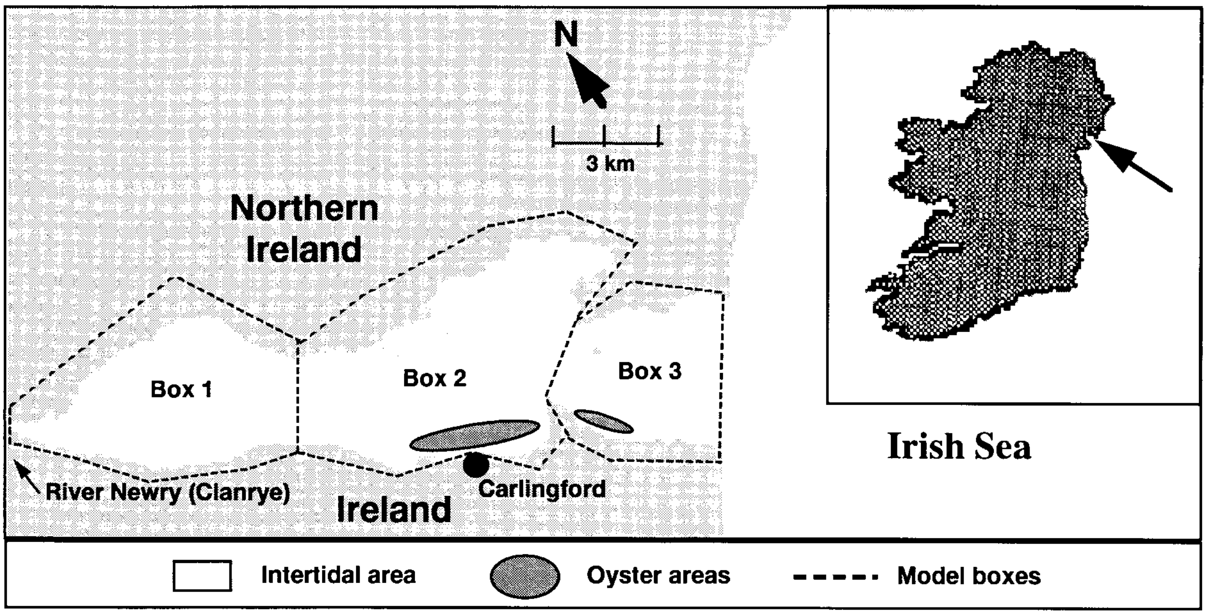

Figure 1. Carlingford Lough, showing the oyster cultivation areas and model boxes.

kinds of outputs: the compartment definition and its morphological parameters (areas and volumes). For further details see Vicente (1994). It uses as input the bathymetry files defined for hydrodynamic modelling, which typically have a resolution one to two orders of magnitude greater than the boxes used in ecological models. A digitised bathymetry for the system of interest must be obtained from existing charts or digital data. The definition of the compartments is made over the hydrodynamic model grid and the output generated consists of the identification of which hydrodynamic grid cells are contained in each ecological compartment. This information is used by the hydrodynamic model to calculate the dispersion coefficients between the ecological model boxes. The second kind of output, the compartment's morphological parameters, is used directly by the ecological model.

A 2-D finite difference, vertically integrated hydrodynamic model with a 71m grid size was applied to the Lough. The definition of the ecological boxes was refined depending on the advective patterns obtained from the hydrodynamic model. Since the ecological model is tidally averaged, the hydrodynamic model was used to compute the dispersion coefficients for the large boxes. A complementary methodology was applied following the steady-state mean salinity approach described in Barretta & Ruardij (1988), taking advantage of the 1-D formulation of the ecological model. Both methods gave good agreement.

The EcoWin ecological model is written in C++, and is based on the object-oriented paradigm. The ecosystem is divided into objects that represent the different functional compartments in the model. The objects encapsulate attributes (variables) and methods (procedures and functions). Object properties are inherited by descendants, making it possible to establish object hierarchies which greatly improve code reusability and security, and the sensitivity of different compartments in the model may easily be tested by switching their objects on or off.

The objects defined for Carlingford Lough in the EcoWin shell are the following:
– Forcing functions.
– Advection-dispersion.
– Suspended particulate matter.
– Phytoplankton.
– Oysters.
– Man.

Forcing function objects

The model is forced by river flow, temperature and light. River flow is simulated by a flow object from an empirical relationship between time of the year and river flow, established with field data. Photoperiod and light intensity are calculated by a light object using standard formulations described in Brock (1981) and Portela & Neves (1994). Temperature is calculated by a temperature object from an empirical relationship between time of the year and water temperature.

Advection-dispersion object

For any physical compartment (box) in the model, the change of a property (e.g. dissolved substances) with time may be calculated by summing the total advective flows in/out of the box and the total dispersive flows in/out of the box, and adding a term representing non-conservative processes (internal sources and sinks). The sources and sinks for non-conservative substances are calculated by other objects (see below) but the fluxes of those substances between the different model boxes are calculated by the transport object.

Dissolved substances object

The dissolved substances object encapsulates the attributes and methods for all dissolved nutrients in the system. Ammonia, nitrite and nitrate are considered, as well as dissolved inorganic nitrogen (DIN: $NH_4^+ + NO_2^- + NO_3^-$). The concentration of DIN (and its component nutrient salts) is modified by nutrient removal by phytoplankton production, and nutrient addition by excretion by bivalves and phytoplankton mortality (Table 1) . The particulate organic detritus (non-living POM) is 'instantly' remineralized in the present model, with dissolved nutrients being returned by the relevant objects as ammonia. The nutrient object then carries out nitrification, which uses a fixed rate of oxidation of reduced forms of DIN.

Suspended particulate matter object

The suspended particulate matter (SPM) object is described in more detail due to the importance of the seston in the oyster growth in the Lough. It has three state variables for Carlingford. It is responsible for calculating the SPM concentration in each model box, for calculating the labile POC fraction of the SPM, and also for calculating values for the light extinction coefficient in each box. Suspended particulate matter is fractionated into seven classes: There are five size classes, and also two generic classes for extensibility, which are floatable materials and marine snow. Each class is characterised as follows:

- Settling velocity (m day^{-1}).
- Density (g cm^{-3}).
- Equivalent spherical diameter (ESD, mm).
- phi ($\log_2$ particle size in mm) (Wentworth scale).
- Percentage of organic matter (%).

Deposition of suspended matter

The deposition of suspended matter is calculated by the object's methods using the following approach: the suspended matter in the water column is fractionated into different size-classes, using Equation (1) (Stumm & Morgan, 1981).

$$n_d = \alpha d_p^{-b}, \tag{1}$$

where n_d: number of particles in a size-class per liter; α: coefficient related to the total SPM concentration in mg l^{-1}; d_p: particle diameter (μm); b: Empirical exponent.

The settling speed for each grain class is calculated according to Stokes' law. The density of the water-column is based on the current salinity and temperature values in each box. Particle settling is related to grain-size, and the size distribution is related (among other factors) to flocculation processes (implicitly considered in Equation (1)).

The sedimentation rate is calculated using the ratio between the settling speed (m day^{-1}) and the box depth, resulting in a decrease in SPM flux. As with all other variables, this is integrated at the end of each time-step to provide the new value for the state-variable (Table 1).

Parameterization of deposition coefficients

The coefficients used in equation 1 were parameterized by taking the value for b as 4 (Stumm & Morgan, 1981), considering that an equal volume of particles was distributed in each logarithmic size interval. α was empirically adjusted so that the sum of the particle mass per unit volume in each size-fraction was equal to pre-defined concentrations in the range 1–300 mg l^{-1}.

Effect of turbulence

The effect of turbulence in preventing the settling of suspended matter is simulated by the introduction of an empirical coefficient, which effectively reduces the downward flux of suspended matter. The coefficient

Table 1. Main model equations and corresponding processes. These equations consider the sources and sinks for each model box. The transport equation calculates mass transfer between model boxes. Parameter values were taken from the literature (e.g. Jørgensen et al., 1991) and tuned to calibrate the model

Suspended particulate matter (mg l^{-1})		(5)
$\frac{\partial Spm}{\partial t} = Spmd_s - \textit{Resuspension}$		
d_s	Suspended matter deposition rate	Calculated from particle-size distributions and Stokes' law (see text)
Dissolved mineral nitrogen (μmol l^{-1})		(6)
$\frac{\partial N}{\partial t} = Phytp_{pN} + Oyse_0$		
P_{pN}	Phytoplankton gross photosynthetic rate calculated by eq. 14 and converted to nitrogen units.	
Phytoplankton (μg Chla l^{-1})		(7)
$\frac{\partial Phyt}{\partial t} = Phyt(p_p - e_p - r_p - m_p - gOys)$ Carbon to Chlorophyll		
P_p	Phytoplankton gross photosynthetic rate	h^{-1} (Eq. (14))
e_p	Phytoplankton exudation rate	0.3 of p_p
r_p	Phytoplankton respiration rate	0.3 of p_p
m_p	Phytoplankton mortality	0.002 h^{-1}
gOys	Oyster grazing pressure	h^{-1}
CarbonToChlorophyll	Conversion factor	0.03
Oysters		
Oyster number for each class		(8)
$\frac{\partial Oys_s}{\partial t} = \frac{n^t_{s-\Delta s}\eta^t_{s-\Delta s} - n^t_s\eta^t_s}{\Delta s} - \mu^t_s n^t_s$		(see text)
η	Individual oyster scope for growth	As in Raillard (1991) and Raillard & Ménesguen (1994)
m_s	Oyster mortality of the sth class	(See text)
Fresh weight to ash free dry weight		0.05
In the first class recruitment must also be added to eq. 8		
For classes where oyster weight is above 65 g (FW) harvest may also occur, in which case it must be subtracted from Equation (8).		

used is 0.8, which effectively means that deposition may only occur during a small part of the tidal cycle, i.e. on or about high and low water slack. This has been validated by tests with a hydrodynamic model.

Resuspension

Resuspension depends on the shear-stress at the sediment-water interface, and on the nature and compaction of the sediment. Based on the studies carried out on the benthos, and on results from the existing database on the nature of the sediment in the different model boxes, a different sediment resuspension rate was used for each box in the model.

Extinction coefficient

The light extinction coefficient k is estimated empirically, using an empirical relationship between SPM concentration in the water column and k values, obtained from measured data. The equation used for this is the following:

$$k = \frac{1.7}{\exp(2.034)} e^{0.723\ln(\mathrm{SPM}))}, \tag{2}$$

where k: light extinction coefficient (m^{-1}); SPM: suspended particulate matter (mg l^{-1}).

Particulate organic carbon

The proportion of SPM which is made up of particulate organic carbon is estimated to vary between 0.03 and 0.05 from field data gathered in Carlingford Lough.

Phytoplankton object

Primary production is estimated from light intensity, delivered by the respective forcing function object, and nutrient data, delivered by the dissolved substances object. If this object is not activated by the user then primary production is calculated solely as a function of light. The light function is taken from Steele (1962), integrated over depth, and the nutrient limitation is calculated by a Michaelis-Menten function (Table 2). Only nitrogen limitation is used, because an analysis of the Redfield ratio for dissolved nutrients indicates that nitrogen is the limiting factor.

The object also calculates exudation and respiration. In the literature, estimates of dissolved organic carbon (DOC) losses are highly variable. Values ranging from almost zero to 90% of carbon fixed are given by different authors (see Jørgensen et al., 1991). There is also variability in the literature concerning the factors affecting DOC loss. Some authors refer increased losses with poor growth conditions (e.g., Ittekot et al., 1981), and others have found greater DOC exudation at high productivity rates. In this model exudation is computed as a fixed fraction of gross production (0.1). Phytoplankton respiration is calibrated to remove a constant proportion of the fixed carbon, thus converting the phytoplankton gross primary production (GPP) into net primary production (NPP). This has been defined as 0.3, based on a range of values for algal respiration and primary production given by Jørgensen et al. (1991).

Crassostrea gigas object

Due to the economic importance of this species, there are already some models developed to simulate its growth (Bacher, 1989; Bacher et al., 1991; Raillard, 1991; Raillard & Ménesguen, 1994). In the present work the simulation of oyster growth is carried out at two levels – the physiological level and the population level using a physiological and a demographic model. The demographic model is based on a series of weight classes. Oyster recruitment and harvest are man-controlled. At the physiological level the model equations and parameters are those used earlier by Raillard (1991) and Raillard & Ménesguen (1994). Excretion rates are those reported in Bernard (1974). Scope for growth is calculated by subtracting respiration and excretion from assimilation, as described by the previous authors. The demographic model is based on a conservation equation for the number of individuals:

$$\frac{\partial n(s,t)}{\partial t} = -\frac{\partial[n(s,t)\eta(s,t)}{\partial s} - \mu((s)n(s,t), \quad (3)$$

where, n: number of individuals of weight s; η: scope for growth (g day^{-1}); μ – mortality (day^{-1}).

Equations of this type have been used in demographic models for many years (see Sinko & Streifer, 1967; Sinko & Streifer, 1969, Streifer, 1974). Equation (3) was discretized following a upwind integration scheme that seems to be the most appropriate in transport problems (in the present case it is transport of individuals between weight classes) (Press et al., 1995):

$$n_s^{t+\Delta t} = \left(\frac{n^t_{s-\Delta s}\eta^t_{s-\Delta s} - n^t_s\eta^t_s}{\Delta s} - \mu^t_s n^t_s\right) \times$$
$$\times \Delta t + n^t_s \quad (4)$$

Δs: class amplitude.

In this equation the population is discretized in size/weight classes and s refers to the weight of each class. The scope for growth calculated at the physiological level is then used in (4) to calculate transitions of individuals between weight classes. A total of forty size classes between 0.65 g (FW) and 97.75 g (FW) were used. The class amplitude was 2.5 g (FW). The choice of classes was made after running the model with various numbers of classes until the model solution became stable taking always into consideration the Courant condition. The first class corresponds to the juvenile oysters seeded in the Lough.

At every time step the biomass of the different classes is calculated as the product of the number of individuals they contain and the class weight. Seeding, natural mortality and harvesting mortality are calculated and added/subtracted to the numbers and biomass of each class. Natural mortality was determined experimentally in Carlingford Lough for oysters of various sizes (Douglas, 1992).

Man object

This object allows the simulation of different management strategies. Seeding and harvesting are carried out according to normal rates (Standard simulation) or to

Table 2. Rate equations for the biological processes and parameter values. Parameter values taken from the literature (e.g. Jørgensen et al., 1991) and tuned to calibrate the model

Phytoplankton		
$P_p = P_{\text{max}}\frac{e}{k_{\text{depth}}}(e^{-I/I_{\text{opt}}} - e^{(-i_{\text{sup}}/I_{\text{opt}})})s(N)$		(9)
$f(N) = \frac{n_{\text{lim}}}{K_n + n_{\text{lim}}}$		(10)
P_{max}	Maximum photosynthesis	0.02 h^{-1}
I	Light intensity at box depth	Calculated – μ E m^{-2} s^{-1}
I_{sup}	Surface light intensity	Calculated – μ E m^{-2} s^{-1}
I_{opt}	Optimum light intensity	400 μ E m^{-2} s^{-1}
$f(N)$	Nutrient limitation	Calculated
n_{lim}	Nutrient concentration	μmol N l^{-1} (delivered by the dissolved substances object)
K_n	Half-saturation constant for limiting nutrient	1.19 μmol N l^{-1}
Oysters	All equations and parameters as in Raillard (1991) and Ralillard & Ménesguen (1994)	

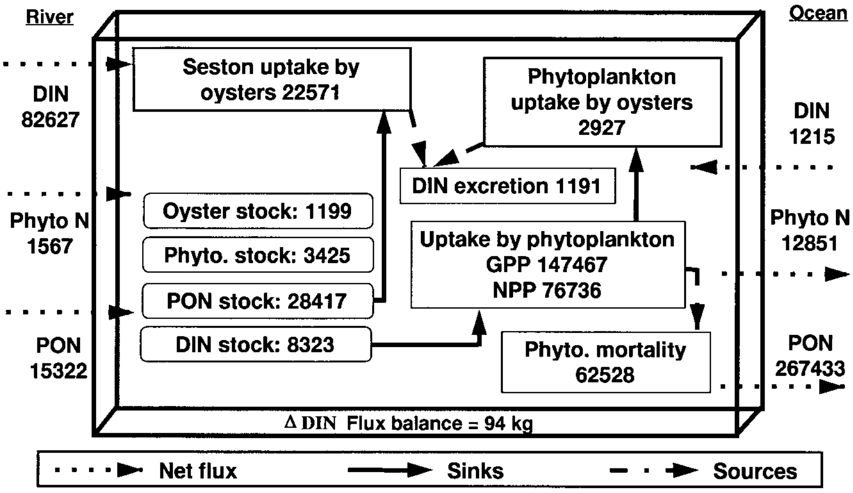

Figure 2. Standard simulation. General scheme of stocks (rounded rectangles), fluxes (rectangles), sources and sinks of nitrogen in the model (all values in kg N yr^{-1}).

different rates to estimate the carrying capacity of the Lough. Normal seeding rates correspond to an average of 0.08 tons of oysters per day during May and June. Harvest is carried out during autumn and in the model a constant rate of 4.6 tons per day is used. Whenever necessary a higher rate is assumed in order to remove all the commercial sized oysters before the end of the year. The model calibration and validation has been described elsewhere (Ball et al., 1994), showing results for measured data and simulations of pelagic state variables and oysters. The model runs were performed for a simulation period of four years, using a time step of two hours. EcoWin has variables to save the inputs and outputs to the objects calculated at every time step. It also allows the storage of boundary fluxes due to advection and dispersion of pelagic state variables. It is thus possible to use the model to compute integrated production, average standing stocks and mass budgets for all state variables.

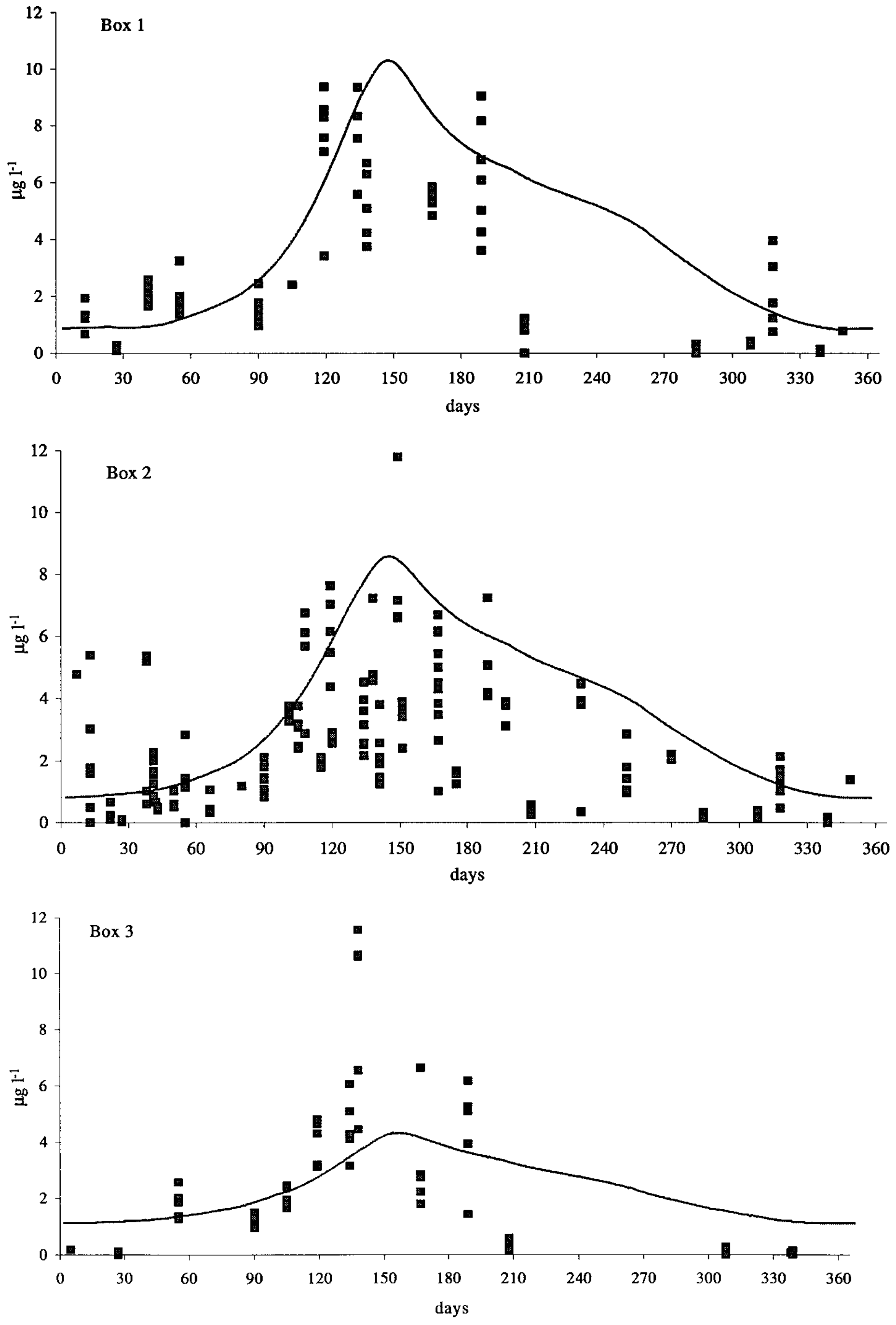

Figure 3. Standard simulation. Predicted and simulated phytoplankton biomass in model boxes 1, 2 and 3 (μg Chlorophyll l^{-1}).

Results and discussion

Six model simulations were carried out in order to assess the carrying capacity of Carlingford Lough for oyster culture and its sensitivity to different nutrient loads. The standard simulation represents the present situation in the Lough, both regarding nutrient loads and oyster standing stocks. The next three simulations

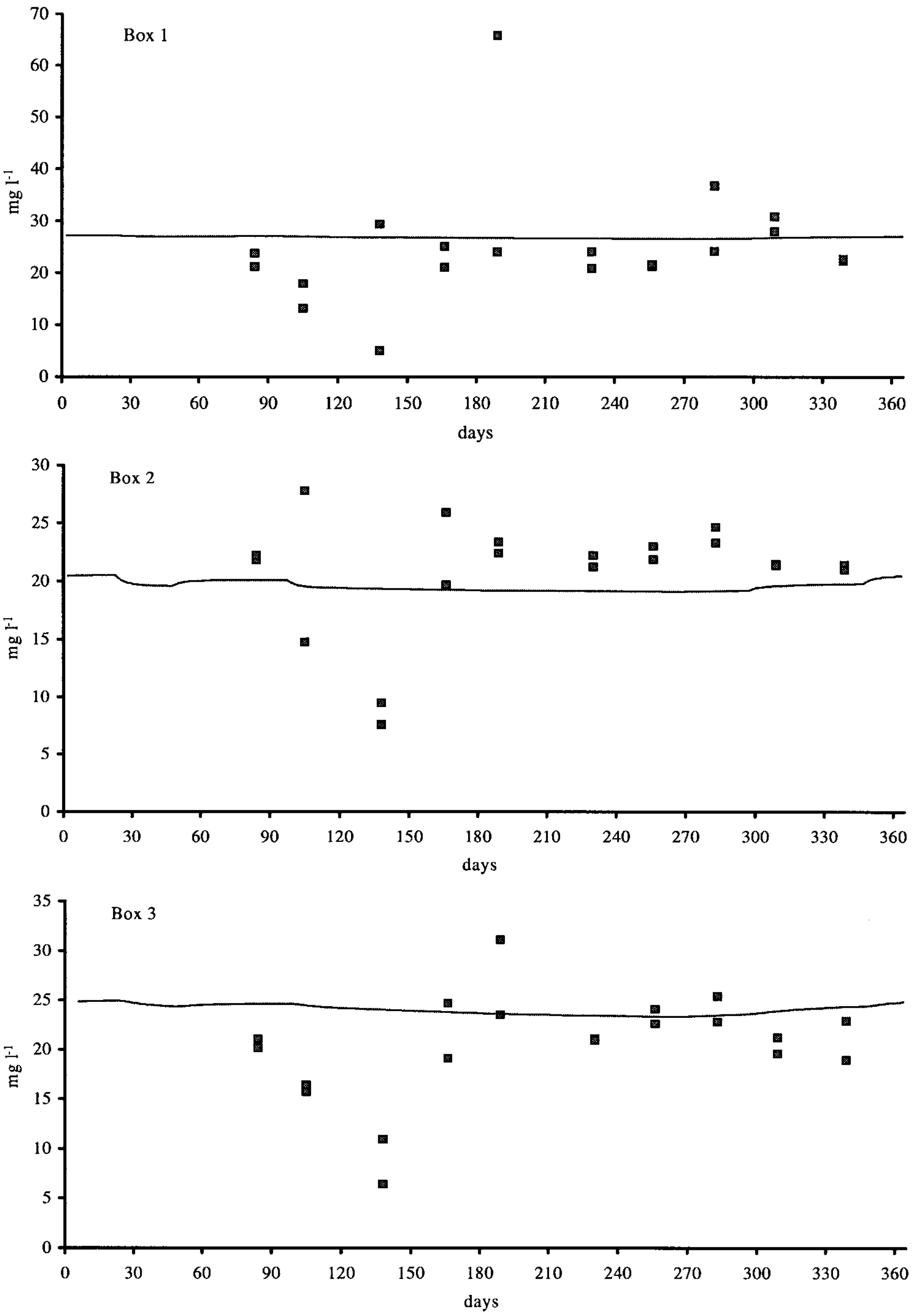

Figure 4. Standard simulation. Predicted and simulated suspended matter (mg l^{-1}) in model boxes 1, 2 and 3.

were carried out to test the effects of seeding increase of small oyster spat by 5, 10 and 20 times the actual rate. In the last two simulations the nitrogen loads were changed by −50% and +100%, keeping everything else as in the standard simulation. In all simulations the man object interacts with the oyster object through seeding and harvest of large (> 65 g FW) oysters.

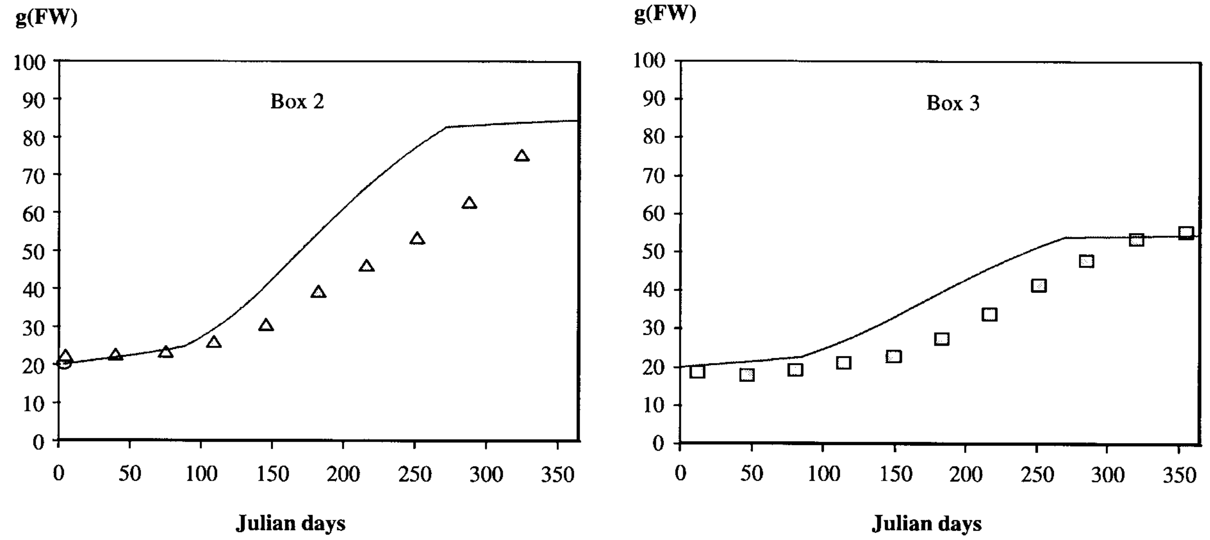

Figure 5. Standard simulation. Growth simulation of an oyster with 20 g (FW) at the beginning of the year. Triangles and squares refer to measurements obtained in box 2 and 3, respectively (Douglas, 1992).

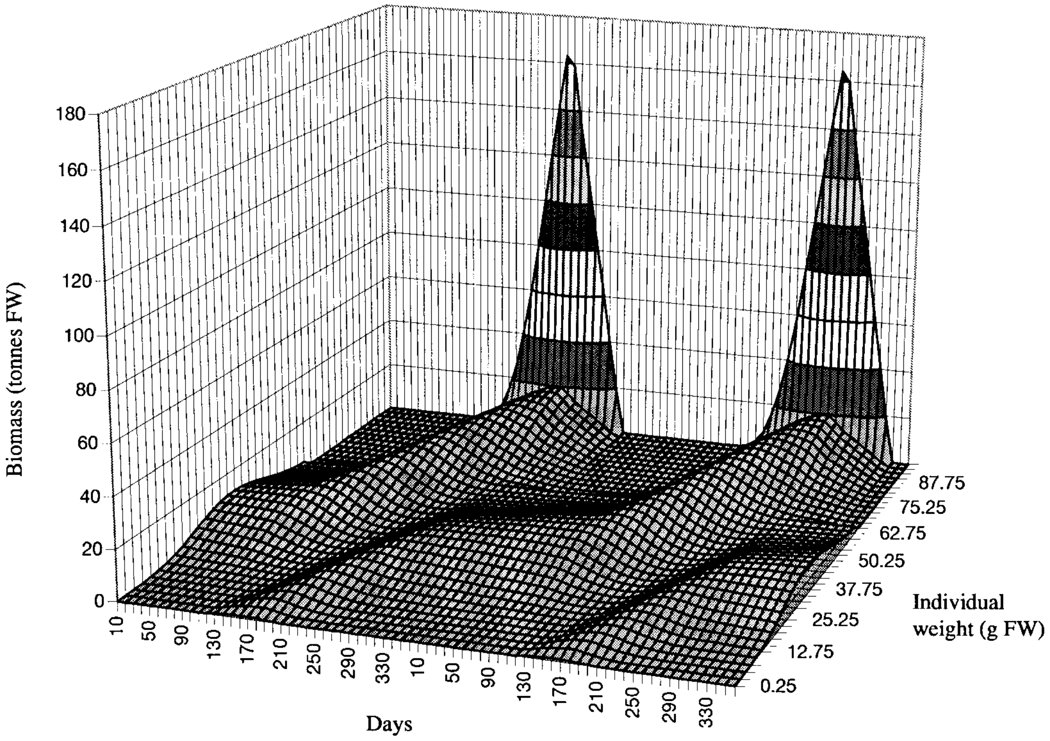

Figure 6. Standard simulation. Oyster biomass in box 2 as a function of time and individual weight. The drop in the biomass of large oysters at the end of each year corresponds to harvest.

Seeding is simulated during May and harvest between the beginning of fall and the end of the year.

In Figures 3 and 4 predicted and simulated chlorophyll and suspended matter concentrations are shown. Because the observed data has a significant scatter, it

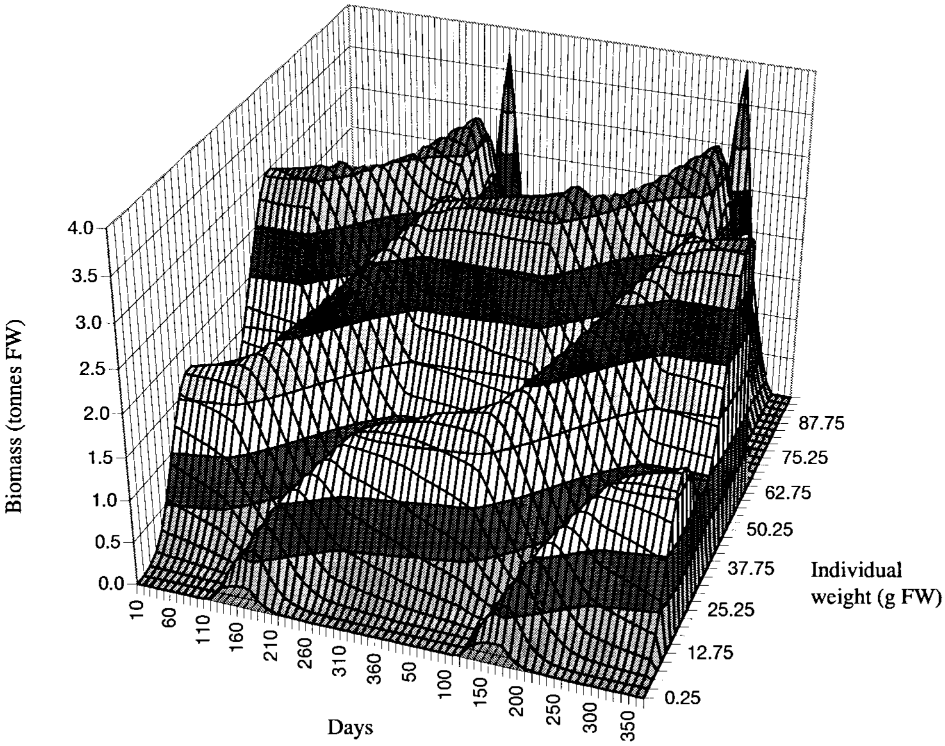

Figure 7. Standard simulation. Oyster biomass in box 3 as a function of time and individual weight. The drop in the biomass of large oysters at the end of each year corresponds to harvest.

is very difficult to judge the quality of the model results. However, the simulated values are well within the range of observed data. There is a chlorophyll peak at the end of spring or beginning of summer. This peak results from a combination of high light intensities with nitrogen concentrations ranging from 10 to 20 μmol N l^{-1} (Ball et al., 1994). Observed data on suspended matter do not follow any particular pattern. The model results show average values that are close to those observed in the Lough (between 20 and 30 mg l^{-1}).

Mass balances

The execution of a mass balance is very useful both for model analysis and in analysing the ecosystem being modelled:

- The role of physical (advection-dispersion) and biological processes within each box may be determined, i.e. the role of internal processes may be compared with the throughput of material.
- It allows an assessment of the relative importance of the different biological state variables within each box.
- Residence times may be calculated for different model variables, allowing an analysis of turnover of water relative to other variables such as DIN or phytoplankton.
- Inaccuracies in the mass balance closure are an effective indicator of problems with the model, leading to improvements in the formulation. These are not always obvious in graphical output of results, where errors may cancel each other out.

The mass balance for dissolved inorganic nitrogen (DIN), phytoplankton and particulate organic nitrogen (PON) is presented in Tables 3, 4 and 5. The results were obtained for the standard simulation, and are normalised per unit of surface area to allow a comparison with other systems.

The mass balances are presented separately for physical inputs and outputs and biological sources and sinks. The Lough imports dissolved nitrogen both from riverine sources and from the Irish Sea (Table 3). The DIN is converted to particulate N by the phytoplankton, some of which is exported to the Irish Sea (0.29 g N m^{-2} yr^{-1}) (Table 4). Internal sources of DIN in the model are natural phytoplankton mortality and DIN

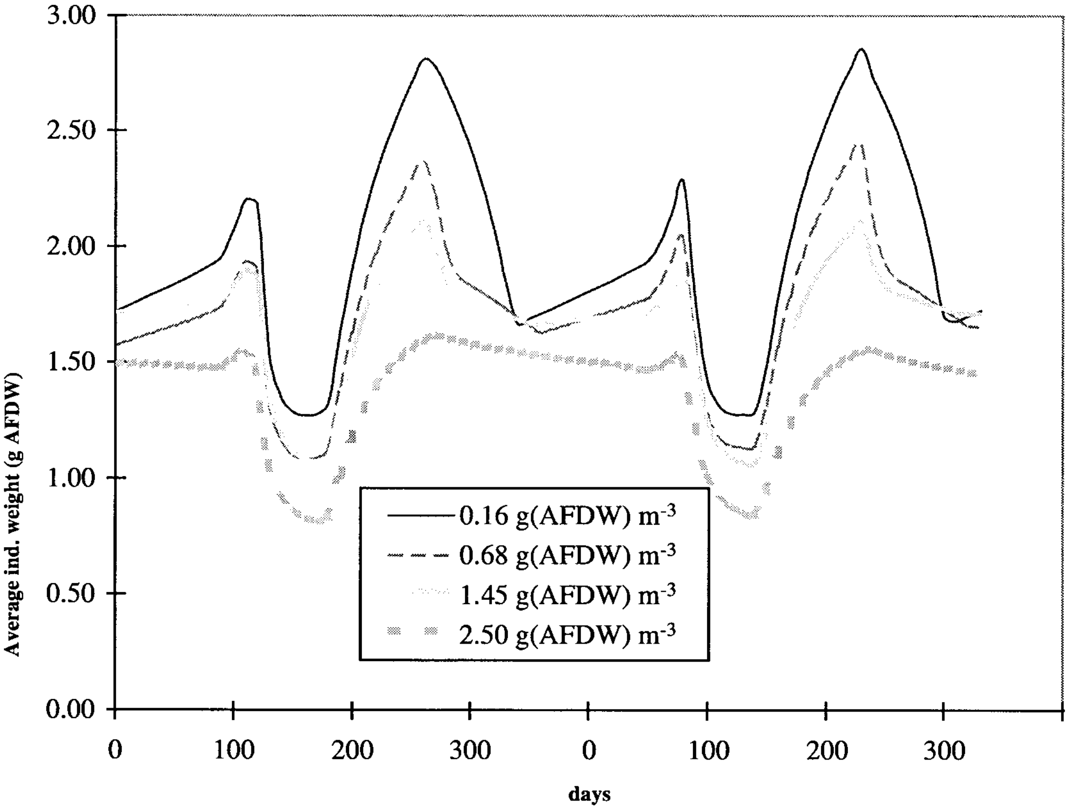

Figure 8. Average individual weight of the oyster population as a function of time and under different average standing stocks in box 2 (see text for explanation).

Table 3. Standard simulation. Mass balance for DIN in Carlingford Lough (all fluxes in g N m^{-2} yr^{-1})

Advection-dispersion		Internal processes	
Inputs		Sources	
Upstream	2.09	Phyto. mortality	1.58
Irish Sea	0.03	Oyster excretion	0.03
Sub-total	2.12	Sub-total	1.61
Outputs		Sinks	
Downstream	–	Gross primary prod.	−3.73
Sub-total	0	Sub-total	−3.73
Total	2.12	*Total*	−2.12
	Total	0 g m^{-2} y^{-1}	
	Stock	0.52 gN m^{-2}	

excretion by the oysters. The natural mortality and filtration by oysters of the phytoplankton are living particulate N sinks in the model (Table 4).

The PON mass balance (Table 5) shows that PON is exported from the Lough to the Irish Sea, and that the oyster filtration of seston is approximately one order of magnitude greater than that of phytoplankton.

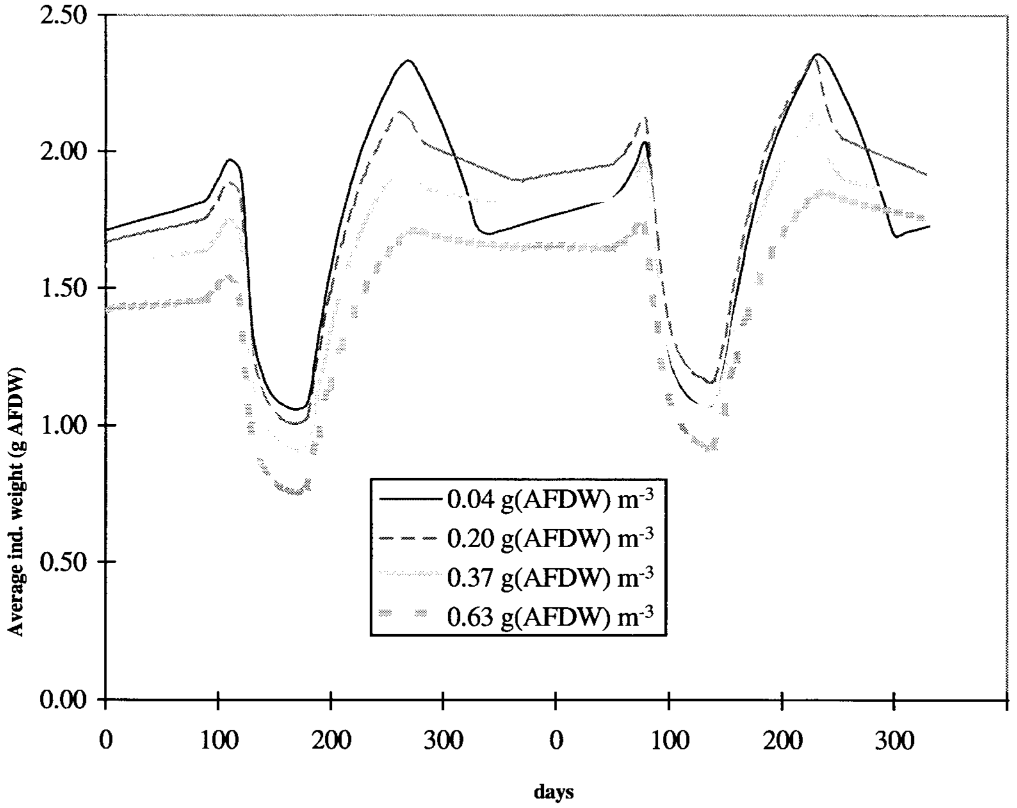

Figure 9. Average individual weight of the oyster population as a function of time and under different average standing stocks in box 3 (see text for explanation).

Table 4. Standard simulation. Mass balance for phytoplankton in Carlingford Lough (all fluxes in gN m^{-2} yr^{-1})

Advection-dispersion		Internal processes	
Inputs		Sources	
Upstream	0.04	Net primary prod.	1.94
Sub-total	0.04	Sub-total	1.94
Outputs		Sinks	
Downstream	−0.33	Natural mortality	−1.58
Sub-total	−0.33	Oyster filtering	−0.07
		Sub-total	−1.65
Total	−0.29		
		Total	0.29
	Total	0 g m^{-2} y^{-1}	
	Stock	0.087 gN m^{-2}	

Although the sediment resuspension exceeds deposition, it corresponds only to a negligible net resuspension of a layer 4 × 10^{-7} mm thick (sediment density of 2600 kg m^{-3}).

From Figure 2 it can be seen that the upstream nitrogen input is largely in the form of DIN, and that the largest internal sink of DIN is phytoplankton production. Phytoplankton biomass turnover is equal to 22.4 yr^{-1}, which is in the range indicated by oth-

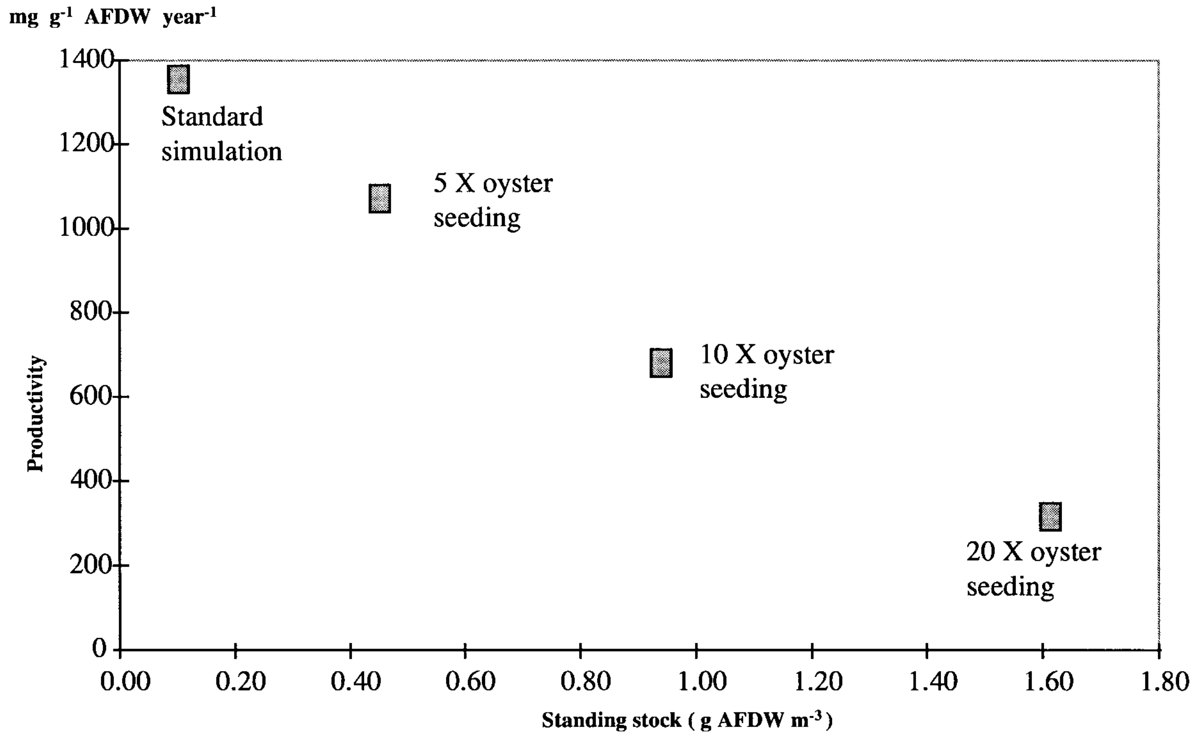

Figure 10. Oyster productivity as a function of average standing stock.

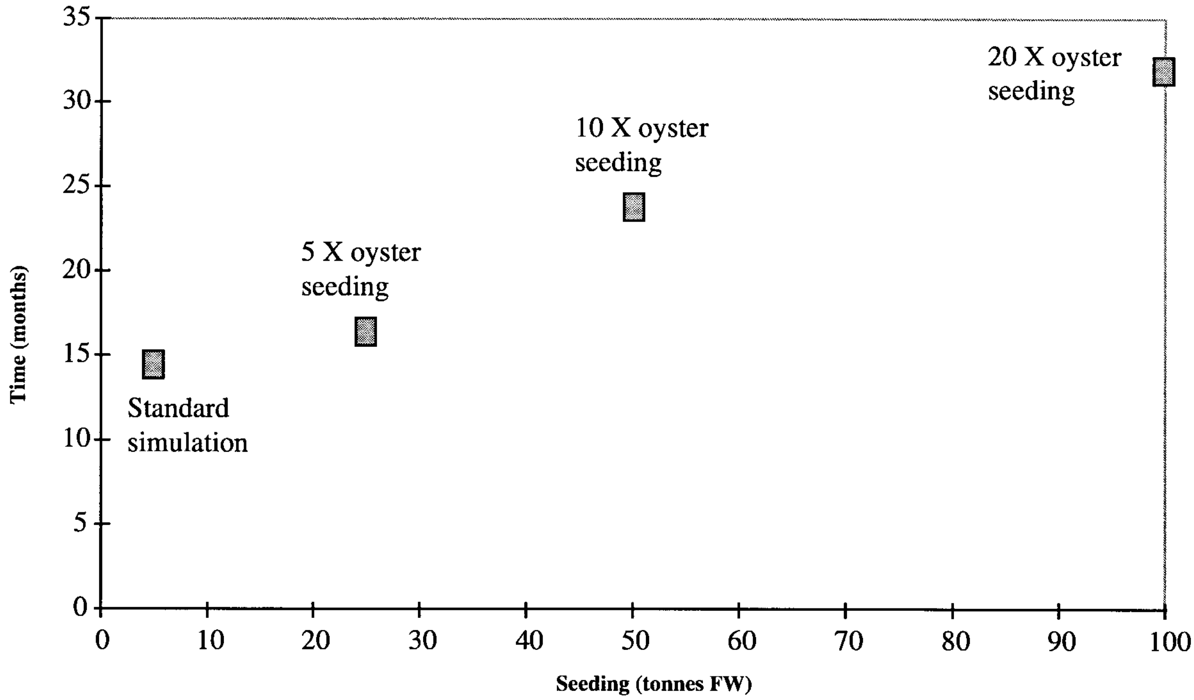

Figure 11. Time to reach a harvestable size as a function of seeding.

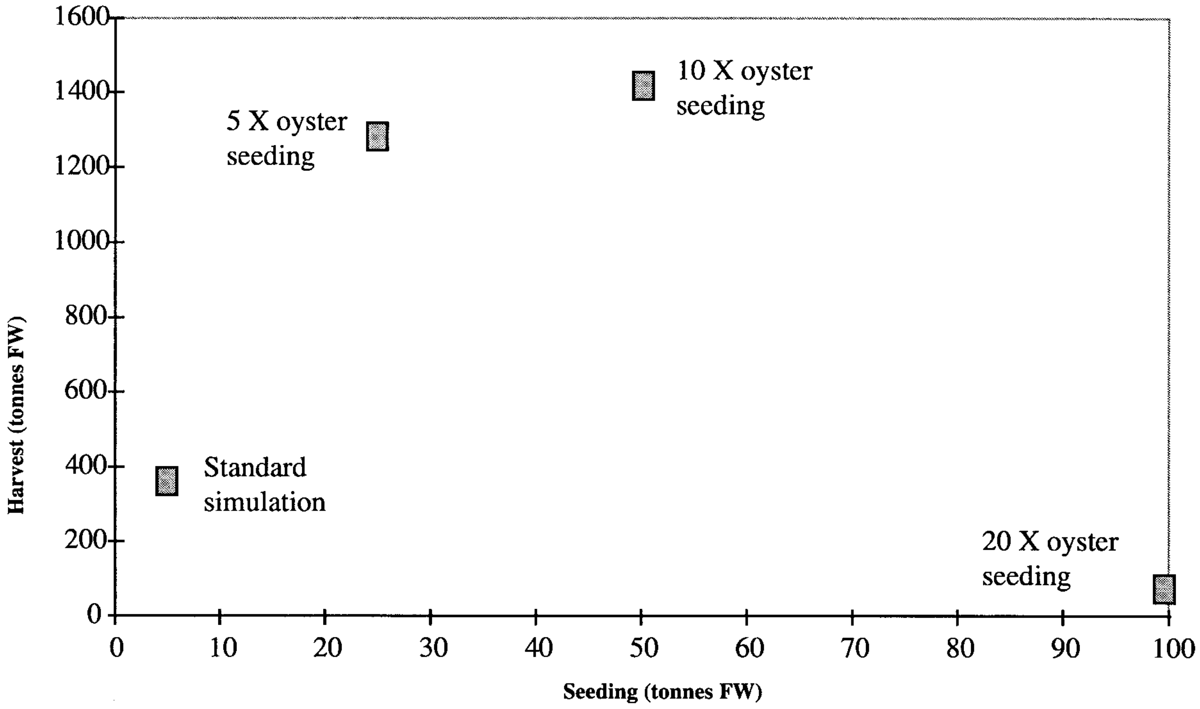

Figure 12. Oyster harvest as a function of seeding after the time necessary for the oysters to reach an harvestable size (see text).

Table 5. Standard simulation. Mass balance for PON in Carlingford Lough (all fluxes in gN m^{-2} yr^{-1})

Advection-dispersion		Internal processes	
Inputs		Sources	
Upstream	0.39	Resuspension	16.55
Sub-total	0.39	Sub-total	16.55
Outputs		Sinks	
Downstream	−6.77	Deposition	−9.61
Sub-total	−6.77	Oyster filtering	−0.57
		Sub-total	−10.18
Total	−6.38		
		Total	6.37
	Total	0.01 g m^{-2} y^{-1}	
	Stock	0.72 gN m^{-2}	

er authors (e.g., Valiela, 1995). The oysters excrete about 5% of their nitrogen uptake, and the nitrogen removal due to them is relatively small compared to the upstream inputs. The relation of biological inputs to physical inputs shows that for DIN mass flux, physical processes are more important, whereas for phytoplankton, biological processes dominate. As regards outputs, biological processes are far more important than physical ones, both for DIN and phytoplankton. This contrasts with other ecosystems (e.g., Grillot & Ferreira, 1996), where the exchange of material across the system boundaries plays a greater role than internal recycling. Tables 3, 4 and 5 and Figure 2 show that the influence of the oysters in the processes of phytoplankton and particulate matter sinking and as a dissolved nitrogen source is negligible.

Oyster growth and production

In Figure 5 oyster growth predicted by the model and measured in field experiments are shown. The experimental data are described in Douglas (1992). The model results tend to overestimate oyster growth in box 2. Since the same set of parameters is used to simulate the oyster growth both in box 2 and 3, any parameter tuning to improve box 2 results would tend to underestimate oyster growth and production in box 3 beyond reasonable levels. Additionally, it was not possible to decrease oyster growth in box 2 and box 3, and at the same time maintain the total biomass production within the normal levels (ca. 400 tonnes year^{-1}).

The oysters in Carlingford Lough do not exhibit any diminishing trends in their individual weight over the annual cycle (Figure 5). This is because they do not reproduce and therefore do not lose weight through gamete emission as in Marennes-Oléron Bay (Bacher, 1989). The losses through respiration, the smaller amount of organic seston and the lower temperatures prevent any significant growth during winter. Growth in box 2 is higher than in box 3 due to higher phytoplankton concentrations in the former (Figure 3).

In Figures 6 and 7 the biomass dynamics of the forty oyster weight classes is shown for a period of two years. Three cohorts can be observed in Figure 6 and four in Figure 7. The beginning of a cohort is located between days 120 and 180 (May and June) when seeding takes place. The growth of the cohort may be followed to the right of Figures 6 and 7. The growth acceleration is clearly seen during spring and summer. After day 265 there is a sudden decrease in the biomass of the large oysters due to harvest. All oysters above 65 g (FW) are harvested. By following the cohort from seeding to harvest it is possible to estimate the number of months it takes for the oysters to reach a commercial size – between about 12 months in box 2 and 17 months in box 3. The sharp peaks observed in Figure 6 indicate a greater biomass concentration in the largest oysters in excess of that observed in box 3. The model predicts a 325 tonnes (FW) harvest in box 2 and 42 tonnes (FW) in box 3 after two summers. Both results are well within the real values (Douglas, pers. comm.).

The next figures synthesise results obtained with model simulations of different seeding rates. In Figures 8 and 9 the average individual weight of the oysters is plotted against time for different average standing stocks in box 2 and 3. These standing stocks resulted from different seeding rates as explained earlier. All lines follow a similar pattern with a decreasing trend after seeding, when a large number of small spat is introduced in the Lough and after harvest, when the largest oysters are removed from the system. It is clearly seen that the larger the standing stock the smaller tends to be the average individual weight. This negative relationship suggests intraspecific competition for food at higher than normal standing stocks.

The maximum value for oyster productivity was obtained for the standard simulation corresponding to 1370 mg g^{-1} year^{-1} (Figure 10). These values were averaged for both boxes. It is clearly seen that oyster productivity declines sharply as standing stock increases. The time taken to reach a harvestable size increases very fast with seeding (Figure 11). When seeding is increased to 10 times its normal value, the time to reach an harvestable size is more than two years. In this hypothetical scenario the oysters seeded during the spring of one year would not grow fast enough to be harvested after the summer of the next year as is presently the case in Carlingford Lough. It is important to note that the present model simulates cohorts based on weight rather than on age. The time needed to reach an harvestable size was determined graphically following the cohorts since their seeding. It is theoretically possible that animals of different ages appear in the same weight class. This may happen with two cohorts born in different years when the first one had to survive through a period of poor growth conditions. In the present case this did not happen because the model forcing did not differ from one year to the next. An important improvement in the demographic model would be the implementation of a age-weight equation as described in Sinko & Streifer (1967). This would give the model more flexibility and utility in management terms.

Harvest can be maximised by increasing the actual seeding rates approximately 5 times (Figure 12). Above these values the increase in harvest is very small and according to the previous results the oysters will take much more time to reach a harvestable size. These results suggest a maximum sustainable yield around 1300 tons of commercial sized oysters per year. The simulations with seeding increased 10 and 20 times produced a average oyster density of about 0.92 and 1.6 individuals m^{-3}. These values are still well below the 6 individuals m^{-3} of Marennes-Oléron Bay (Raillard & Ménesguen, 1994) but growth depression is apparent. The differences between both systems may be at least in part due to the higher productivity in Marennes-oléron bay (see paper in this volume).

In all model simulations oyster mortality was calculated solely as a function of individual weight using the experimental results described in Douglas (1992). According to Raillard & Ménesguen (1994) oyster mortality tends to increase with oyster density. If this dependence was included in the model the differences between the simulations would be even more pronounced.

The sensitivity of the model to changing nitrogen loads was not very noticeable in terms of oyster production . The model predicted that a decrease of 50% in the nitrogen load leads to an oyster productivity of 1340 mg g^{-1} yr^{-1} whereas a 100% increase leads to a productivity of 1390 mg g^{-1} yr^{-1}. These values are very close to those obtained under the standard simulation (1370 mg g^{-1} yr^{-1}). This may be explained because oyster growth in Carlingford Lough depends more on particulate matter, rather than on phytoplankton biomass.

A possible weakness of the model is in the way scope for growth is calculated, because the equations use constant parameters over the all simulation period. However, as discussed by Bayne (1993) these parameters change as a result of physiological and morphological adaptation of the filter-feeders at various time-scales. An important step in model refinement would be the description of oyster feeding based on principles of optimality (Willows, 1992). It is important to note that the usage of average exchange coefficients between model compartments implies that part of the system dynamics, namely that resulting from the tide excursion, is lost. Considering the non-linearities between the biological processes and the environmental conditions it is likely that these averaging procedures may lead to some distortion of the results.

Conclusions

Carrying capacity models are necessary to predict responses of bivalve growth rate in relation to different management strategies (Heral, 1993). Carlingford Lough is an example of a system where bivalve cultivation is still below the level where oyster growth begins to be inhibited by stock density. Furthermore, since the oysters are not able to reproduce within the Lough due to low water temperatures, it is easier to control the population. According to the model results it seems likely that a five-fold increase in seeding would maximise oyster production in the Lough, allowing harvest to grow from the present 300–400 tonnes to a level of 1300 tonnes $year^{-1}$ without significantly affecting the oyster growth rate. Further increases in seeding do not seem to lead to very significant increases in large oysters. Therefore, according to the definition of carrying capacity quoted previously, it may be stated that the carrying capacity of Carlingford Lough is approximately 0.44 g (AFDW) m^{-3} (see Figure 10) or 0.26 oysters m^{-3}.

In its present form, the model allows a fast and easy simulation of different seeding and harvesting strategies, with direct access to all model parameters and results. The model predictions generally show a reasonable agreement with observed data, making it a useful tool for carrying capacity assessment. However, the small number of model boxes may cause some bias on the results. The main oyster cultivation areas in box 3 are located very close to the boundary between box 2 and 3. For this reason it is likely that in this area the environmental conditions may be closer to those of box 2 than predicted by the model. This could help to reduce the differences in predicted oyster growth in boxes 2 and 3 (Figure 5).

The usage of a demographic model proved to be useful in obtaining a detailed description of the biomass dynamics of the studied species. When the objective is to optimise a sustainable yield, it is important to know the harvestable and non-harvestable classes and the rate at which the population recovers from the harvest (Usher, 1966). Although the usage of the demographic model significantly increases the computing time, the coupling between the physiological and the demographic processes seem to be the best solution to simulate biomass dynamics of a exploitable resource. This coupling allowed the advantages of the general dynamic population models and analytical models (*sensu* Heral, 1993) to be synthesised in one model.

The combination of the three key components of, a large-scale coupled physical-ecological model, detailed physiological modelling of the target species, and the demographic aspects which are fundamental to aid decision-making for management purposes, appears to be generally applicable to carrying capacity assessment for bivalve species. This modelling approach further benefits from the object-oriented methodology used – it allows for easy development of the code to incorporate more species, and the preprocessing tools employed make it straightforward to apply the same model to different estuarine and coastal ecosystems.

Acknowledgements

This work was supported by EU FAR project AQ-2-516 'Development of an Ecological Model for Mollusc Rearing Areas in Ireland and Greece' and by EU Concerted Action AIR3-CT94-2219 'Trophic capacity of coastal zones for rearing oysters, mussels and cockles'. The authors wish to thank two anonymous referees for helpful suggestions.

References

Bacher C (1989) Capacité trophique du bassin de Marennes-Oléron: couplage d'un modèle de transport particulaire et d'un modéle de croissance de l'huître *Crassostrea gigas*. Aquat Living Resour 2: 199–214

Bacher C, Héral M, Deslous-Paoli and Razet D (1991) Modèle énergétique uniboite de la croissance des huîtres (*Crassostrea gigas*) dans le bassin de Marennes-Oléron. Can J Fish Aquat Sci 48: 391–404

Ball B, Ferreira JG and Keegan B (1994) Development of a model to determine the trophic capacity of mollusc rearing areas in Ireland and Greece. Final Report to the CEC for project FAR-AQ2516

Baretta J and Ruardij P (eds) (1988) Tidal flat estuaries. Simulation and analysis of the Ems Estuary. Springer-Verlag, Berlin

Bayne BL (1993) Feeding physiology of bivalves: Time dependence and compensation for changes in food availability. In: RF Dame (ed.). Bivalve filter feeders in estuarine and coastal ecossystem processes. (pp. 1–24) Springer-Verlag, Berlin

Bernard FR (1974) Annual biodeposition and gross energy budget of mature pacific oysters, *Crassostrea gigas*. J. Fish Res Bd Can. 31: 185–190

Brock TD (1981) Calculating solar radiation for ecological studies. Ecol Modelling 14: 1–9

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

Douglas DJ (1992) Environment and Mariculture (A study of Carlingford Lough). Ryland Research Ltd., Ireland

Ferreira JG (1995) EcoWin – An Object-oriented Ecological Model for Aquatic Ecosystems. Ecol. Modelling 79: 21–34

Grillot N and Ferreira JG (1996). Ecological model of the Cala do Norte of the Tagus Estuary. ECOTEJO, Rel. A-8403-06-96-UNL, Ed. DCEA/FCT, New University of Lisbon

Heral M (1993) Why carrying capacity models are useful tools for management of bivalve molluscs culture. In: R.F. Dame (ed.). Bivalve filter feeders in estuarine and coastal ecossystem processes. (pp. 455–477) Springer-Verlag, Berlin

Ittekot V, Brockmann U, Michaelis W and Degens ET (1981) Dissolved, free and combined carbon hydrates during a phytoplankton bloom in the Northern North Sea. Mar Ecol Progr Ser 4: 259–305

Jørgensen SE, Nielsen S and Jørgensen L (1991) Handbook of Ecological Parameters and Ecotoxicology. Elsevier, Amsterdam

Portela LI and Neves R (1994) Modelling temperature distribution in the shallow Tejo estuary. In: Tsakiris & Santos (ed). Advances in Water Resources Technology and Management. (pp. 457–463) Balkema, Rotterdam

Press WH, Teukolsky SA, Vetterling WT and Flannery BP (1995) Numerical recipes in C – The art of scientific computing. Cambridge University Press, Cambridge

Raillard O (1991) Etude des interactions entre les processus physiques et biologiques intervenant dans la production de l'huître japonaise *Crassostrea gigas* du bassin de Marennes-Oléron: essais de modélisation. Thèse doct. Océanographie, Univ. Paris VI

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

Schildt H (1995) C++, the complete reference, 2nd. Edition. Osborne

Sekine M, Nakanishi H, Ukita M and Murakami S (1991) A shallow-sea ecological model using an object-oriented programming language. Ecol Modelling 57: 221–236

Silvert W (1993) Object-oriented ecosystem modelling. Ecol Modelling 68: 91–118

Sinko JW and Streifer W (1967) A new model for age-size structure of a population. Ecology 48: 910–918

Sinko JW and Streifer W (1969). Applying models incorporating age-size structure of a population to *Daphnia*. Ecology 50: 608–615

Steele JH (1962) Environmental control of photosynthesis in the sea. Limnol Oceanogr 7: 137–150

Streifer W (1974) Realistic models in population biology. Adv Ecol Res 8: 199–266

Stumm W and Morgan J. (1981) Aquatic Chemistry, 2nd. Edition. Wiley-Interscience

Usher MB (1966) A matrix approach to the management of renewable resources, with special reference to selection forests. J Appl Ecol 3: 355–367

Valiela I (1995) Marine ecological processes, 2nd Edition. Springer-Verlag

Vicente P (1994) DifWin: A package for the definition of compartments and calculation of dispersion coefficients in box models – Application to the Carlingford Lough. In: Proceedings of the First International Conference on Hydroinformatics, Delft, The Netherlands, 717–721

Willows RI (1992). Optimal digestive investment: A model for filter-feeders experiencing variable diets. Limnol Oceanogr 37: 829–847