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A model for sustainable management of shellfish polyculture in coastal bays

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Abstract

A multi-species model for shellfish polyculture in coastal embayments is presented, and an application of the model to a test site (Sanggou Bay, Northern China) used for large-scale longline cultivation of the Chinese scallop *Chlamys farreri*, the Pacific oyster *Crassostrea gigas* and the kelp *Laminaria japonica* is described.

The model integrates a bay-scale ecological simulation with individual-based modelling of scallops and oysters, and upscales the individual processes for the target species (scallops and oysters) by means of a multi-cohort population dynamics model. Human interaction with the target cohorts over a number of years is explicitly simulated. The model has been used to estimate the exploitation carrying capacity for scallops and oysters in the system, the harvest potential for different seeding and harvesting scenarios, and the impacts on the ecosystem of different polyculture management strategies.

Although an increase in seeding to 2 × and 15 × standard seeding for scallops and oysters respectively optimizes the yield of both, thus corresponding to the exploitation carrying capacity, the ratio of harvest/seed is lowered, which may make the fishery less attractive from an economic point of view.

Progressive increases in seeding lead to a collapse of the fishery: this occurs at >15 × standard seeding for scallops, and at >30 × for oysters. In parallel, there are profound modifications at the ecosystem level, which were studied by means of a mass balance carried out on the model. Under standard conditions, there is a net export of primary production from the bay to the Yellow Sea, but

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at 15–20× increase in seeding, the bay becomes a net phytoplankton importer, due to phytoplankton clearance by cultivated shellfish.

The model simulates a period of 6 years in about 2 min, and was shown to be a useful tool for polyculture management over multiannual periods; a development of the socioeconomic component will allow feedbacks between economic consequences of different cultivation scenarios and ecosystem responses to be explicitly considered. The application of this type of model may be of use in promoting a more holistic approach to shellfish aquaculture management.

Keywords: Polyculture; Scallop; Oyster; Model; Aquaculture management; China

1. Introduction

Shellfish and finfish aquaculture has grown rapidly over the last two decades (e.g. Rheault and Rice, 1995; FAO, 2001; Watson et al., 2001) and has been largely responsible for the worldwide increase in global aquatic production. During the first half of the 1990s, the annual contribution of cultivated shellfish and finfish to total marine production increased linearly from 11.7% to 18.5%. A large proportion of this growth is attributed to Far Eastern countries, particularly to China (Rana, 1997), although some of the latter data may be overestimated (Watson and Pauly, 2001). FAO (2001) estimates the total annual production of cultivated shellfish (in marine and brackish water) at about 5×10^6 metric tons, but other authors (e.g. Guo et al., 1999) indicate a 1996 yield of over 6×10^6 metric tons for China alone.

Shellfish cultivation is potentially one of the most sustainable forms of mariculture: it is largely extensive, requiring no artificial food input, since the animals obtain all their nutrition from phytoplankton, microphytobenthos and different types of organic detritus (e.g. Cranford and Grant, 1990; Grant, 1999; Scholten and Smaal, 1999; Hawkins et al., 2001). Nevertheless, the rapid growth of the industry has inevitably raised questions of carrying capacity and sustainability (e.g. Grant, 1999).

Cultivated bivalve filter feeders play a key role in many coastal ecosystems due to their high filtration capacity and culture density (Smaal et al., 2001). However, as more living biomass is accumulated, the proportion of primary production that is available for further growth in bivalve biomass declines (Dame and Prins, 1998), and factors such as increased biodeposition may contribute to significant environmental changes such as sediment anoxia (e.g. NRCA, 1998).

Carrying capacity concerns have gained visibility in two ways: (i) From the fishery perspective by the occurrence of decreased yields (e.g. for oyster culture in Marennes-Oléron Bay, see Raillard and Menesguen, 1994), and increased disease and mortality rates (e.g. Castro and Soares, 1995; Zhang, 2000); and (ii) From a more holistic ecosystem perspective of eutrophication (e.g. Folke and Kautsky, 1989; Fang et al., 1996a,b) or toxic algal effects (e.g. Matsuyama, 1999).

The concept of ecological carrying capacity is derived from the logistic growth curve in population ecology, defined as the maximum standing stock that can be supported by an ecosystem for a given time (Krebs, 1972; Kashiwai, 1995). For exploited ecosystems, this definition has been modified by Carver and Mallet (1990) as “the stock density at which production levels are maximized without negatively affecting growth rates''. Bacher et al. (1998) have further defined carrying capacity for shellfish culture as the standing stock at which the annual production of the marketable cohort is maximized. This will differ substantially from the *ecological* carrying capacity, and is termed the *exploitation* carrying capacity (Smaal et al., 1998).

The challenges to sustainable management of shellfish aquaculture are clearly interdisciplinary, involving an understanding of ecosystem processes, of the physiology and ecology of cultivated species and of cultivation practices. Furthermore, in some of the fastest developing aquaculture areas (e.g. Far Eastern countries such as China), there are traditional polyculture activities which may include combinations of shellfish, finfish and macroalgae (Scoggan et al., 1989; Fang et al., 1996b). Polyculture, which has a very reduced expression in Western aquaculture, is potentially more sustainable than monoculture, due to the reutilization of waste products of one species by another (Petrell et al., 1993; Chopin and Yarish, 1999).

Modelling has been used as an approach to examine environmental sustainability and to establish carrying capacity of shellfish aquaculture by different authors (e.g. Gerritsen et al., 1994; Raillard and Menesguen, 1994; Ferreira et al., 1998; Bacher et al., 1998; Chapelle et al., 2000; Gangnery et al., 2001; Grant and Bacher, 2001; Niquil et al., 2001), and is acknowledged as a powerful tool to support sustainable management (Gordon et al., 1996; Leung and El-Gayar, 1997). Many different types of models have been used, with a wide range of time and space scales, state variables and processes, and varying levels of detail. These models, together with many others [e.g. mussel ecophysiology models such as EMMY (Scholten and Smaal, 1998) or nitrogen cycling models (e.g. Lefebvre et al., 2001)] have provided a platform for integration of different processes. However, most carrying capacity models developed to date are usually monospecific, do not consider population structure, do not examine multi-year periods, and do not explicitly link to management issues such as changes in exploitation strategies.

The work presented herein aims to develop and apply an ecosystem model to simulate polyculture of scallops, oysters and kelp in a coastal bay. It integrates a bay-scale ecological model with individual-based modelling of scallops and oysters, and upscales the individual processes for the target species (scallops and oysters) by means of a multi-cohort population dynamics model.

The simulation was developed using an object-oriented approach, and has been called GAMBEY: *G*eneral *A*quaculture *M*odel for *B*ivalve *E*quilibrium *Y*ield. The model has the following objectives:

(i) Synthesize results from field observations and laboratory experiments into a coherent description of the key environmental variables and processes, polyculture activities and their interactions;
(ii) Estimate the carrying capacity for polyculture in a coastal embayment, considering interactions between cultivated species, explicitly targeting marketable cohorts, and fully integrating cultivation practices;
(iii) Examine bay-scale environmental effects of different culture strategies by using a mass balance approach;

(iv) Analyse different cultivation scenarios and provide new insights useful for aquaculture management.

The model was implemented for a test site (Sanggou bay, China) as part of a cooperative project between the European Union and China (INCO-DC), aimed at defining the carrying capacity for aquaculture in Chinese bays.

2. Methods

2.1. Study area

The GAMBEY model was applied to Sanggou Bay (Fig. 1a), a 140-km^2 coastal embayment in northern China (37°01′–37°09′ N, 122°24′–122°35′ E), used for large-scale longline cultivation (Fig. 1b) of Chinese scallop (*Chlamys farreri*, about 60,000 tons yr^{-1}), Pacific oyster (*Crassostrea gigas*, about 13,000 tons yr^{-1}) and kelp (*Laminaria japonica*, 40,000 tons yr^{-1}). Exchange between the bay and the Yellow Sea is driven by a semi-diurnal tide (tidal range 2 m), across a broad (10 km) mouth. The average depth of the bay is 7.5 m (max. 15 m), and the water volume is about 1000×10^6 m^3 (Zhao et al., 1996). There are no major freshwater inflows. There is a local population of about 150,000 inhabitants, of which about 20% is involved in aquaculture, using a combination of polyculture and monoculture techniques. In 1994, over 30% of the total bay area was dedicated to aquaculture: 3300 ha for kelp, 1037 ha for scallop, and 391 ha for oysters (Zhao et al., 1996).

2.2. Available data and data analysis

Available data for Sanggou Bay include yearly campaigns conducted by the Yellow Sea Fisheries Research Institute (YSFRI) and the First Institute of Oceanography (FIO) in 1983–1984 (before the period of increased aquaculture), 1989–1990, 1993–1994, and 1999–2000, with samples for almost every month. The data include information on key physical, chemical and biological characteristics of the bay. Field observations and laboratory results were archived in the relational database BarcaWin2000™ (Ferreira et al., 1998). In total, about 50,000 records of historical and current data were stored, corresponding to 24,000 samples at 77 stations. The database was exploited to obtain boundary conditions and initial conditions for model state variables, to derive relationships for calibration and to extract validation data; GIS was used to obtain basic information about the system, such as morphological data, key nutrient ratios, and shellfish cultivation areas.

2.3. Model concept and implementation

A detailed ecological model was developed (Fig. 2), which includes physical exchanges with the ocean boundary, biogeochemical processes within the bay, individual growth and population dynamics of target species (scallops and oysters) and human exploitation

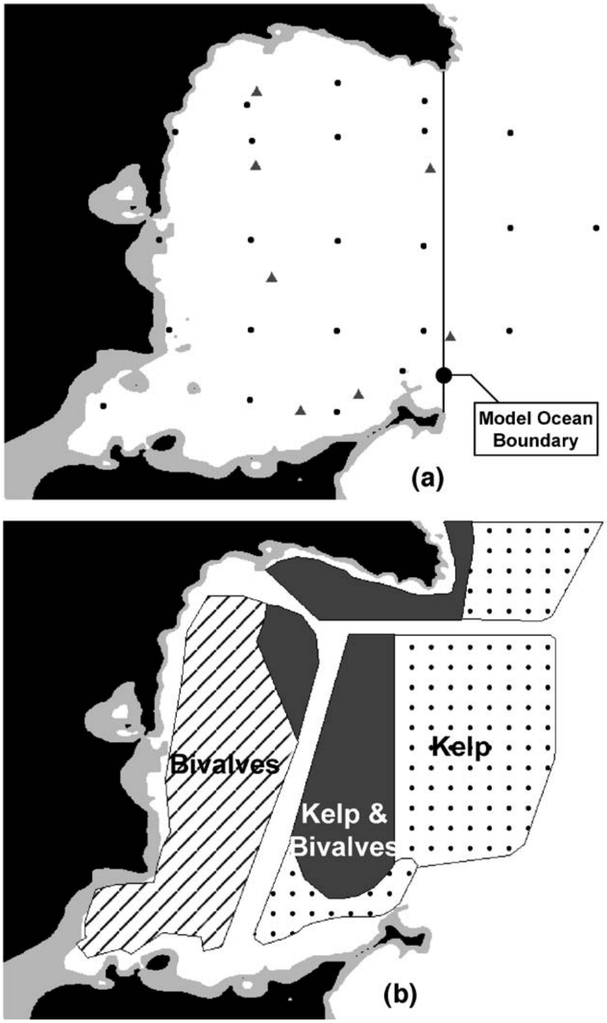

Fig. 1. (a) Sanggou Bay, showing sampling stations for the 1993–1994 (circles) and 1999–2000 (triangles) data sets. The black line shows the model ocean boundary; stations inside were used to characterize the system, external stations were used for ocean forcing; (b) aquaculture areas in the standard model.

(seeding and harvesting). The model is forced by light, temperature, man and exchanges of dissolved inorganic nitrogen (DIN), phytoplankton and suspended particulate matter (SPM) at the ocean boundary.

The spatial modelling domain for Sanggou Bay is limited on its western side by the coastline and on its eastern side by the ocean boundary. The model uses a quasi-one-dimensional approach: the system was considered spatially homogeneous internally but exchange of water and water properties at the ocean boundary are explicitly simulated.

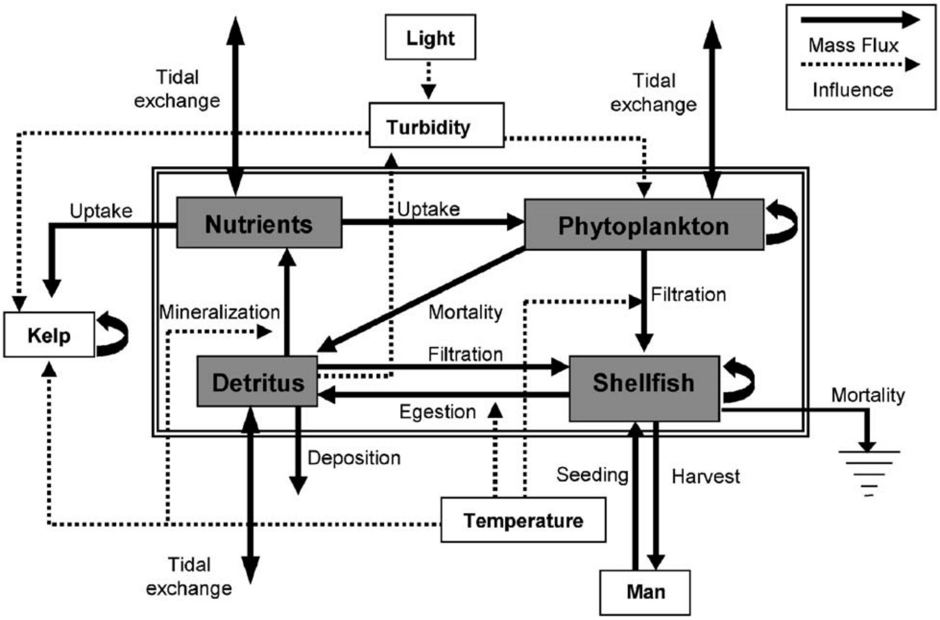

Fig. 2. Conceptual diagram of the Sanggou Bay ecological model.

2.3.1. *Forcing functions*

Photoperiod and light energy in Sanggou Bay were simulated using standard formulations (Brock, 1981) calibrated with field measurements for improved simulation of cloud cover (Gazeau, 2000). Water temperature was modelled by an empirical relationship fitted to the annual cycle.

Transport of water properties to and from the Yellow Sea plays an important role in Sanggou Bay, due to the large size of the bay's ocean boundary (Gazeau, 2000). Tidal exchange was used to force the water transport, with tidal height being generated using the Oceanus 2000™ software from harmonic equations (SHOM—Service Hydrographique et Océanographique de la Marine, 1984). Since no harmonic constants were available, the amplitude and phase of each periodical component was determined following Phillips (1998), using data from the 1983–1984 campaign. An empirical transport equation relating transport with differences in tidal heights was then determined (adapted from Gazeau, 2000), with residual flow corrections adjusted for spring and neap tides.

Kelp competes with phytoplankton for the assimilation of DIN, and is presently considered in the model as a forcing function. The growth of *L. japonica* is assumed to be only temperature dependent (Andersen and Nival, 1989; Petrell et al., 1993; Gazeau, 2000). Maximal growth rate was calibrated after Mao et al. (1993).

2.3.2. *State variables*

2.3.2.1. Ecosystem model. The main equations for the bay-scale model state variables are given in Table 1, and the values for parameters are shown in Table 2. The model simulates

Table 1
Main model equations for bay-scale ecological model

Model equations	Comments
$(dB)/(dt) = B(p_{max}f(I)f(N) - r_b - e_b - m_b - c_sS - c_oO)$ B—Phytoplankton biomass [expressed as chlorophyll *a* (chl *a*)]; p_{max}—Phytoplankton maximum gross photosynthetic rate; $f(I)$—Steele's light intensity equation, vertically integrated; $f(N)$—Michaelis–Menten function for nutrient (N) limitation; r_b—Phytoplankton respiration rate; e_b—Phytoplankton exudation rate; m_b—Phytoplankton natural mortality; c_s and c_o—Scallop (S) and oyster (O) grazing rate.	
$(dN)/(dt) = \alpha B(e_b + m_b) + e_sS + e_oO - \alpha B(p_{max}f(I)f(N)) - f(K)$ N—Dissolved inorganic nitrogen; α—Conversion to nitrogen units; e_s and e_o—Scallop (S) and oyster (O) excretion; $f(K)$—Kelp production function.	Kelp production is calculated as a model forcing function.
$(dM)/(dt) = M(e_m - d_m) + f_sS + f_oO - Mp_sS - Mp_oO$ M—Suspended particulate matter (SPM); e_m—SPM resuspension rate; d_m—SPM deposition rate; f_s and f_o—Scallop (S) and oyster (O) faeces production; p_s and p_o—Scallop (S) and oyster (O) POM clearance rate.	Deposition is calculated as in Ferreira et al. (1998) by fractioning according to grain size and accounting for the effects of vertical turbulence, restricting deposition to a part of the tidal cycle.
$\mathrm{POM} = f(M)$ POM—Particulate organic matter; $f(M)$—Function of suspended particulate matter.	See Eq. (1) for details of POM calculation from SPM. POM is consumed by shellfish as part of the total SPM.
$(ds)/(dt) = g_sS - f_sS - m_sS$ $(dO)/(dt) = g_oO - f_oO - m_oO$ S—Scallops; O—Oysters; g_s and g_o—Scallop and oyster scope for growth (function of phytoplankton biomass and SPM, including the organic fraction, i.e., POM); m_s and m_o—shellfish (scallop and oyster) mortality rates.	Generic equations for shellfish growth (individual processes such as respiration or excretion not detailed). Individual models include simulation of different physiological processes, and are detailed in Raillard et al. (1993) for the Pacific oyster and Hawkins et al. (submitted for publication) for Chinese scallop. Scope for growth and mortality is combined in the population dynamics model.

Only sinks and sources are shown; exchange of relevant state variables across the ocean boundary is described in the text.

phytoplankton, SPM, DIN and light extinction in the water column as described in Ferreira et al. (1998). Only dissolved nitrogen is used as the limiting nutrient for phytoplankton production: Redfield ratios are below 16 for about 80% of observations. Particulate organic matter (POM), which is a key state variable for bivalve production in the model, is calculated from the SPM concentration using Eq. (1), empirically derived from Sanggou Bay field data.

$$\mathrm{POM} = \left[\frac{90.977}{\mathrm{SPM}} + 15.8\right] \times \frac{\mathrm{SPM}}{100} \qquad (1)$$

Table 2
Values of key parameters used in the model

Parameter	Meaning/observations	Value
Phytoplankton		
P_{max}	Maximum primary productivity	0.2 h^{-1}
I_{opt}	Optimum light intensity	300 W m^{-2}
k_s	Half-saturation constant for DIN uptake	1.5 μmol l^{-1}
m_b	Mortality rate	0.05 day^{-1}
Aquaculture		
Cultivation area	Oysters	391 ha
		2103 ha
	Scallop	3400 ha
		2347 ha
	Kelp	4400 ha
		2806 ha
Cultivation density	Oysters	59 ind. m^{-2}
	Scallop	59 ind. m^{-2}
	Kelp	12 ind. m^{-2}
Individual weight at seeding	Oysters	0.033 g TFW[a]
	Scallop	0.67 g TFW
		1.67 g TFW
	Kelp	1.2 g TFW
Seeding period	Oysters	15 April–15 May
	Scallop	15 April–15 May
		15 Oct.–15 Nov
	Kelp	1 Nov.–30 Dec.
Minimum individual weight at harvest	Oysters	40 g TFW
	Scallop	23 g TFW
		13 g TFW
	Kelp	200 g TFW
Harvest period	Oysters	15–30 Nov.[b]
		1 Mar.–31 May
	Scallop	1–30 Oct.[b]
		1–30 June
		1 June–30 July
	Kelp	1 May–30 June
m_o	Oyster mortality	0.1 yr^{-1}
m_s	Scallop mortality	0.2 yr^{-1}

Details of parameters for the individual oyster and scallop models as in Raillard et al. (1993) and Hawkins et al. (submitted for publication), respectively. Values in italic are modifications for the proposed aquaculture scenario.

[a] TFW: total fresh weight.

[b] Harvest periods are sequential, that is, first harvest takes place late in the year for animals of harvestable size followed by a second harvest in late Spring of the next year.

2.3.2.2. Shellfish models. Individual growth of oysters and scallops was simulated using two different mechanistic models: both relate physiological processes to external forcing, account for allometry, and provide feedback to ecosystem models through excretion of nutrients and elimination of particulates.

Pacific oyster scope for growth was modelled after Raillard et al. (1993). This model simulates filtration and ingestion of particulate matter, and digestion of phytoplankton and POM, and has previously been applied by different authors to Marennes-Oléron Bay (Raillard and Menesguen, 1994) and Carlingford Lough (Ferreira et al., 1998).

Growth for Chinese Scallop was simulated using a model developed by Hawkins et al. (submitted for publication) using experimental results from Sanggou Bay, which simulates feeding and rejection, post-filtration selection and ingestion separately for phytoplankton, organic detritus and inorganic particulate matter.

The individual oyster and scallop models were upscaled by the application of a population dynamics model (see e.g. Ferreira et al., 1998) to each species (Eq. (2)). Ten weight classes Table 2 were considered for oysters (0–100 g total fresh weight—TFW) and five for scallops (0–50 g TFW).

$$\frac{\mathrm{d}n(s,t)}{\mathrm{d}t} = -\frac{\mathrm{d}[n(s,t)\eta(s,t)]}{\mathrm{d}s} - \mu(s)n(s,t) \tag{2}$$

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

2.3.2.3. Human model. The human interaction with the cultivated bivalves is simulated by the introduction of a *Man* variable, which is responsible for seeding and harvesting for both scallops and oysters. The behaviour of this state variable was established heuristically by a collaborative definition of current cultivation practices and their variability. Key factors include:

(i) Seeding intensity and periods of seeding;
(ii) Transfer to growout areas and "cultivation" mortality;
(iii) Harvesting regime (which may conditionally occur several times a year depending on environmental conditions and growth rates), harvestable size, harvest effort and harvest yield.

Although this is not discussed in the present text, the model architecture (see below) easily scales to a detailed simulation of other aspects of *Man* behaviour, such as an analysis of manpower limitations to cultivation changes (e.g. limited increase of harvest pressure) and a cost–benefit analysis of different exploitation strategies.

2.3.3. Model architecture and operation

2.3.3.1. Architecture. A first cut at modelling was carried out using the visual simulation platform Powersim™, which provided an understanding of the key processes to be considered and initial results (Gazeau, 2000). Powersim was subsequently used throughout the development process for testing model components, such as the individual scallop growth simulation.

The GAMBEY model was built using EcoWin2000, an object-oriented (OOP) modelling platform (Ferreira, 1995) developed in C++. Current details are given at http://www.tejo.dcea.fct.unl.pt/ecowin/.

Forcing functions and state variables correspond to model objects: these objects may be turned on and off, allowing, for example, a detailed analysis of the effects of resource partitioning between cultivated species. Key technical developments have been introduced in the present work: The simulation of individual processes and population dynamics for bivalve species has been implemented using multiple inheritance, which is a very flexible approach: It allows major changes to the simulation of individuals by the development of derived classes, full testing of responses at the individual level, and immediate upscaling to a population level when required by the creation of a common descendant, that is, a class which inherits the properties of both individual and population (Fig 3).

The second major change was the development of a "wrapper" class called TShellfishPolyculture, which manages two other objects, one for scallops and another for oysters. These are hidden from other objects in the model and are managed only by the wrapper class, which is exposed to all forcing functions and state variables. It provides the appropriate routing for communication required for harvesting and other processes, and although it presently wraps two bivalve species, can easily scale up to several more.

2.3.3.2. Coupling and operation. The individual bivalve growth models are forced by the ecosystem model, which in turn receives inputs of DIN and particulates from these. The individual simulations drive a population dynamics model, which combines allometric individual growth and population mortality to describe the migration of individuals between different cohorts (weight classes). The human object interacts with the appropriate cohorts of cultivated species, acting both as a source and a sink (Fig. 3).

The model contains three forcing function objects and seven state variable objects, corresponding to over 100 state variables. The standard model runs for a 6-year period with a time step of 1 h—a full run takes about 2 min, which makes multiple simulations practical. Cultivated bivalves begin to appear in the model in year 1, during the first seeding period, and harvesting only occurs from the second year onwards. The first years

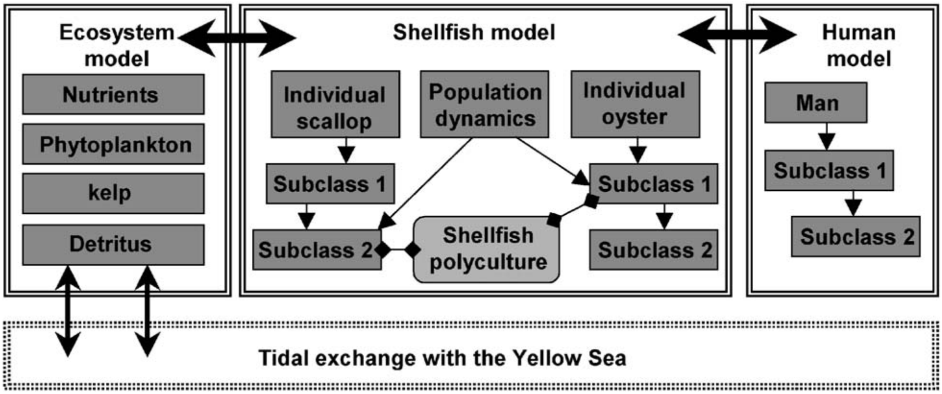

Fig. 3. Coupling between the different components of the GAMBEY model.

are therefore used to reach a steady state, and year 6 corresponds to stabilized conditions and is used for comparisons with observations.

The model was verified by comparison with field data, and through the construction of mass balances, and subsequently used to provide a description of stocks, energy flows between the different state variables, and to analyse development scenarios.

3. Calibration and validation

Model calibration was made using data from the 1993–94 campaign (D1 data set); the 1999–2000 data set (D2) was used for validation. Fig. 1a shows the location of sampling stations for both campaigns.

Boundary input of nutrients, SPM and phytoplankton were simulated operationally by the inflow of water with the concentrations measured in the ocean—these are the only parameters that were varied between calibration and validation.

The aquaculture conditions (Table 2) used were the same for both data sets, and were compiled both in collaborative meetings (Fang, pers. comm.; Zhu, pers. comm.) and from a number of historical sources (e.g. Fang et al., 1996a,b; Zhao et al., 1996). Aquaculture areas are depicted in Fig. 1b.

4. Results and discussion

The presentation and discussion of modelling results is divided into three different parts. Part I addresses the model description of the main variables simulated for Sanggou Bay. The general distribution of DIN, SPM and phytoplankton are examined for the D1 and D2 data sets, followed by a comparison of simulated and reported bivalve harvest data. The second part considers a new exploitation scenario for polyculture in Sanggou bay, defined collaboratively with local management authorities, and examines its consequences in terms of comparative yield and ecosystem impacts. The final part considers different seeding scenarios for oysters and scallops, and their effects on the system. These scenarios are used from a fishery management perspective to determine the exploitation carrying capacity for shellfish polyculture in the bay, and a mass balance approach is used to analyse environmental effects of increased cultivation at the bay scale.

4.1. Part I—Model description and general behaviour

4.1.1. Annual cycles for pelagic variables

The results for the year 6 (steady-state) simulations of DIN, chl *a* and SPM are shown in Fig. 4. The results for the calibration data set D1 (Fig. 4a–c) generally reflect the ranges and temporal variation of the observation means, although the Autumn DIN peak is poorly reproduced by the model. The causes of this peak are not well understood: they may be due to nutrient runoff (Gazeau, 2000) or to artificial nitrogen fertilizer enrichment of the bay during the period of kelp seeding—both these aspects are not considered by the model. Ammonium release from the sediment below shellfish culture areas (Baudinet et

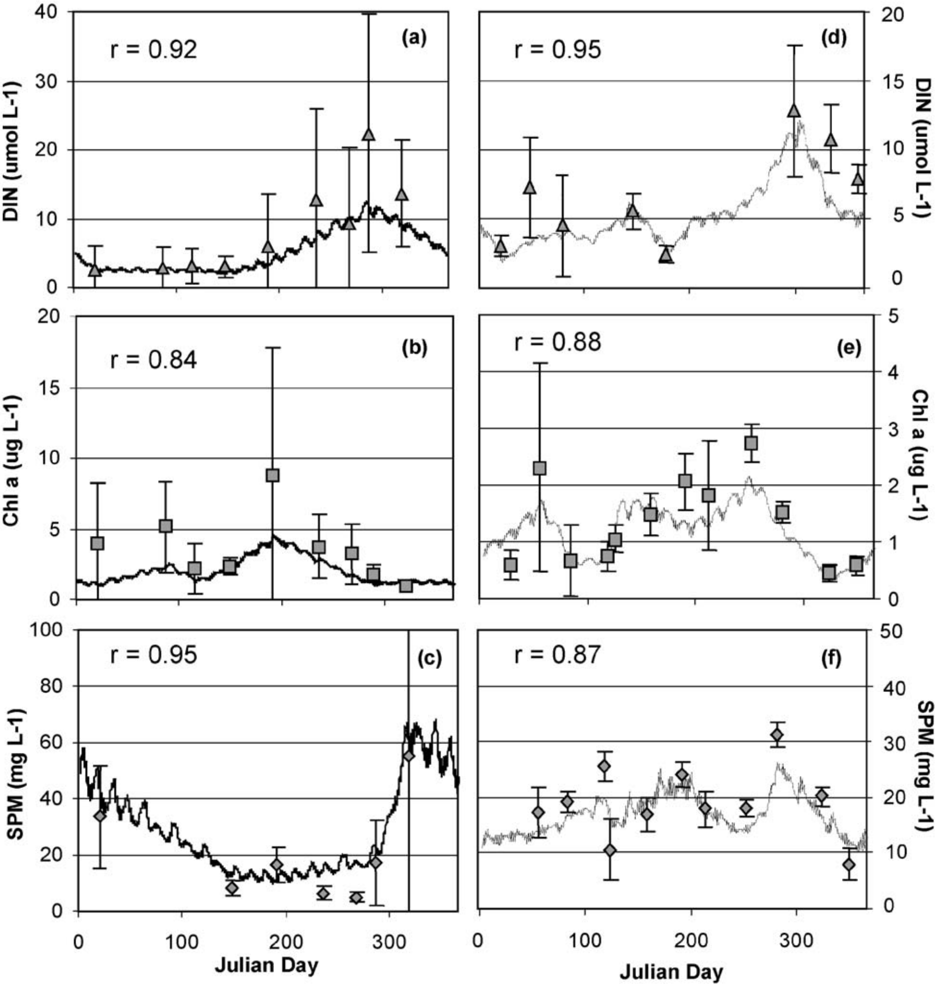

Fig. 4. Comparison of model values (lines) with measured values (points and error bars) for DIN, phytoplankton and SPM: (a) DIN 1993–1994; (b) Phytoplankton 1993–1994; (c) SPM 1993–1994; (d) DIN 1999–2000; (e) Phytoplankton 1999–2000; (f) SPM 1999–2000. Model parameters are identical for the 1993–1994 data set (D1—left) and 1999–2000 (D2—right) except for ocean forcing. Data sets were gathered for 12 consecutive months over both periods (1993–1994, 1999–2000).

al., 1990; Grant et al., 1995) is not considered to be important during this period: low water temperature leads to reduced mineralisation rates (Gazeau, 2000). The phytoplankton peaks in the first half of the year are also lower than the mean values for the data set, possibly due to the prior underestimation of DIN levels. Strongest variations occur when parameters inside the bay differ markedly from the ocean, which highlights the role of internal processes within the bay.

The phytoplankton mass balance closure (Table 3) indicates that the role of internal sinks and sources is essentially equal to that of boundary exchanges with the Yellow Sea.

Table 3
Mass balance for phytoplankton—standard model, year 6 (all values in gC m^{-2})

Boundary exchanges		Internal processes	
Inputs		*Sources*	
Input from Yellow Sea	109.54	Net primary production	32.62
Subtotal	109.54	Subtotal	32.62
Outputs		*Sinks*	
Export from bay	− 120.82	Phytoplankton mortality	− 15.33
Subtotal	− 120.82	Oyster phytoplankton uptake	− 1.48
		Scallop phytoplankton uptake	− 4.55
		Subtotal	− 21.35
Total	− 11.28	*Total*	11.26
	Total	0 gC m^{-2} yr^{-1}	
	Stock	24 mg chl *a* m^{-2}	

On a bulk basis, Δchl $a = -0.030$ µg chl a l^{-1} yr^{-1} in the model, providing additional evidence of model stability and dimensional consistency.

The phytoplankton flux at the ocean boundary is about three times the primary production, and under standard conditions, the bay is a net phytoplankton exporter. Field values for primary production were measured using ^{14}C (Sun et al., 1996; Zhang, pers. comm.), and corrected values per day give an annual net primary production of $\sum_{m=1}^{12} 30d_{\mathrm{m}} \cong 40$ gC m^{-2} yr^{-1}, where d_{m} is the measurement day for each month. In the model, annual phytoplankton net primary production (P) is estimated at about 33 gC m^{-2} yr^{-1} (Table 3) which is considered acceptable when compared to field observations, although both the field and model values seem lower than might be expected. By combining this with the mean biomass (B) simulated for the bay, a B/P ratio of 9.4 days is obtained, comparable to Delaware Bay and slightly above the bulk of systems reviewed by Dame and Prins (1998). The phytoplankton turnover in Sanggou Bay would thus appear to be similar to that of other shellfish cultivation areas such as Marennes-Oléron (Bacher et al., 1998). The behaviour of SPM is well reproduced by the model, although the high spatial variance of the December field data, which is difficult to interpret, provides no indications of model accuracy.

Fig. 4 also presents model results for the independent validation data set D2 from 1999–2000 (Fig. 4d–f); the only changes made to the model were in the ocean concentration of state variables. Observed and predicted DIN, chl *a* and SPM reproduce the patterns and observed ranges of variation over the annual cycle.

4.1.2. Shellfish cultivation and harvest

In the standard model, scallop aquaculture occupies an area about 10 times greater than that used for oysters. Individual scallop growth is shown in Fig. 5, for a period of 1 year. Seeding takes place in April–May, and harvesting occurs during October, thus avoiding the subsequent period of reduced growth.[1] Overall, the filtration of phytoplankton by scallop and oysters (from Table 3) is about 6.0 gC m^{-2} yr^{-1}, which is an order of

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[1] Since the growth curve is simulating a single individual, growing in parallel with the full population, there is no indication of mortality.

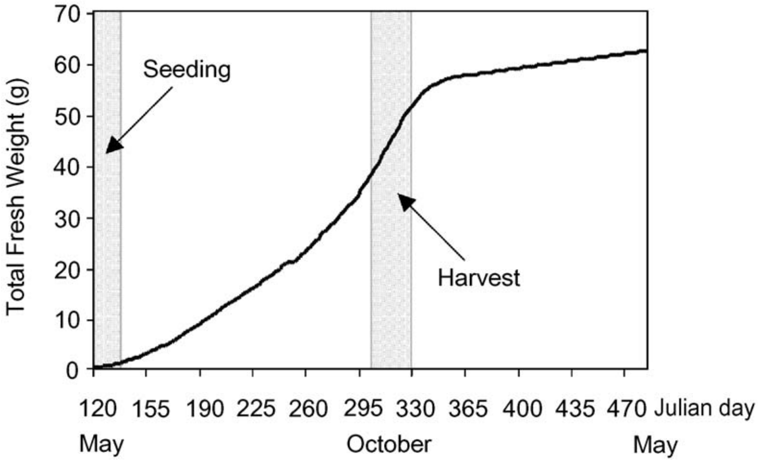

Fig. 5. Individual growth for the scallop *C. farreri* in the model, standard simulation for a 1-year-period beginning in May (TFW—total fresh weight including shell), showing seeding and harvest periods.

magnitude greater than model results for Carlingford Lough (Ferreira et al., 1998), where the annual oyster yield is only 300 TFW yr^{-1}, but about eight times lower than the filtration rate estimated by Bacher et al. (1998) for Marennes-Oléron Bay, an overexploited site.

Fig. 6 compares D1 (left) and D2 (right) year 6 model results for annual oyster and scallop harvests with existing data for Sanggou bay, both using official values given by government officials from Rongsheng City, Shandong Province, and the predicted harvest based on a consensus value estimated by Chinese fisheries scientists (Table 2).

Simulated values range between official and predicted values in both cases. Harvests in 1999–2000 (D2) are smaller than in 1993–1994 (D1), probably due to the lower

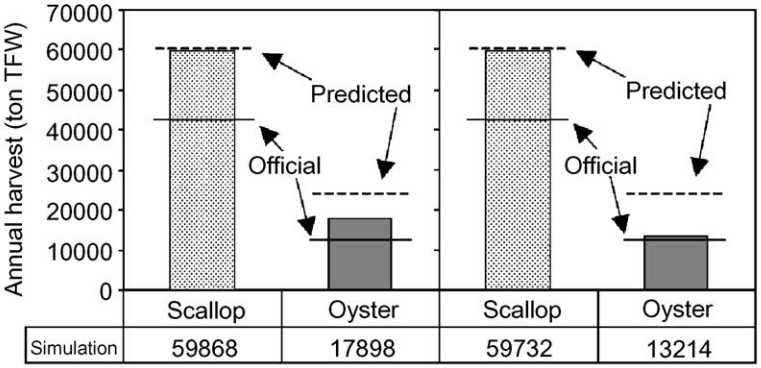

Fig. 6. Scallop and oyster harvest results from the model and comparison with official (lower dashed bar) and predicted (upper dashed bar) harvest values for 1993–1994 (a) and 1999–2000 (b).

phytoplankton concentration inside Sanggou bay; oysters appear to be more sensitive to this factor.

4.2. Part II—Polyculture development scenarios

The GAMBEY model explicitly simulates bivalve polyculture, and may therefore be applied to review different types of modifications to aquaculture practice. One such scenario, defined collaboratively for Sanggou Bay with local fisheries managers, has been analysed here. The key changes proposed lie in the cultivation areas (Table 2): oyster culture will increase at the expense of scallop culture. Other alterations include shifts in the seeding and harvesting periods for scallops, and changes to seed and harvest weights (Table 2).

The results shown in Figs. 7 and 8 compare the proposed scenario with the D2 standard simulation discussed above; A comparison of the total harvest (Fig. 7a) shows that total harvested shellfish biomass will increase by about 22000 TFW yr^{-1}. Since the area occupied by scallops is now about 70% of that used in the D2 simulation, the scallop harvest is reduced, and there is a clear shift toward oyster production, which will account for about 70% of the total tonnage.

The increase in total production will, however, reduce harvest efficiency (Fig. 7b) which will be lower for both oysters and scallops, due to a reduction in resource availability. This lowers the scope for growth of smaller weight classes, which conditions recruitment into the harvestable cohorts. The decrease is sharper for scallops due to changes in seed weight and reduction of minimum harvest weight—for oysters, these parameters are unchanged. Additionally, oyster mortality is parameterized as 50% of scallop mortality (Table 1). Fig. 7c shows that the harvest/seed ratio for scallops is reduced to 25% of the standard value.

The phytoplankton mass balance shown in Fig. 8 indicates that at the system scale, the increased phytoplankton uptake by shellfish in the proposed scenario will reduce net primary production (NPP) and the export of phytoplankton to the Yellow Sea. The 22000

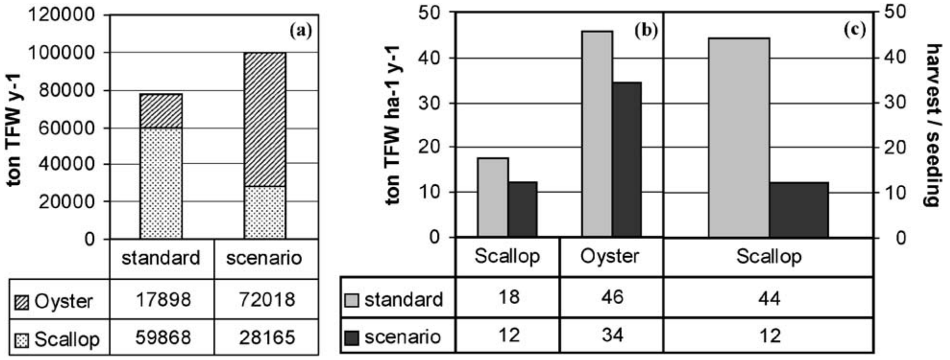

Fig. 7. Comparison between standard and proposed scenarios for polyculture in Sanggou Bay: (a) Overall harvest; (b) Harvest yield per hectare; (c) Harvest/seeding ratio for scallop.

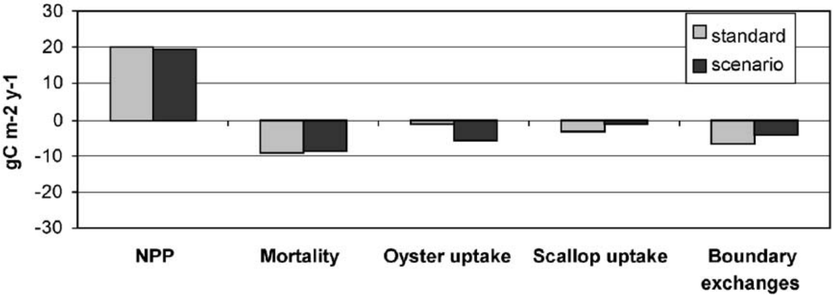

Fig. 8. Phytoplankton mass balance for 1999–2000 standard model and proposed polyculture scenario.

TFW yr^{-1} gain in annual shellfish yield will have to be examined in the light of several other factors:

(i) The relative value of the scallop and oyster fisheries;
(ii) The added costs of lower harvest/seed ratios and the reduction in yield per hectare;
(iii) The changes to ecosystem sustainability evidenced by the reduction in NPP.

The development of an economic component in the human "object" of the model will allow a more detailed evaluation of the best management strategy (Turner et al., 1998), by identifying the opportunity cost of different activities, as well as user costs and environmental impacts, with the support of the most adequate economic valuation methods.

4.3. Part III—Exploitation carrying capacity

To determine the exploitation carrying capacity for aquaculture of Sanggou bay, simulations were carried out where seeding density was changed, whilst retaining current areas for scallop and oysters. All simulations used the D1 calibration and the 1993/1994 data set for boundary conditions. The seeding density of both scallops and oysters was changed by multiplying the standard value by 0.5, 2, 5, 10, 15, 20, 25 and 30. Minimum harvestable weights are imposed by the model (Table 2) so that the carrying capacity always relates to the marketable cohort.

Fig. 9 shows the effects of this increase from the perspective of the fishery, both for harvested biomass (Fig. 9a) and the harvest/seed biomass ratio (Fig. 9b). Fig. 10 illustrates the consequences for the ecosystem, using phytoplankton as a descriptor, by examining alterations in its mass balance (Fig. 10a) and concentration (Fig. 10b).

4.3.1. Exploitation carrying capacity

The increased shellfish biomass is responsible for a progressive increase in the clearance of phytoplankton and POM, and generates major changes both for the fishery and for the system. The harvest yield for scallops (Fig. 9a) increases to a maximum at 5 × standard seeding, and diminishes thereafter. At 10 × seeding, the oyster harvest exceeds that of scallops; and at >15 ×, scallop harvesting can no longer take place. Oysters

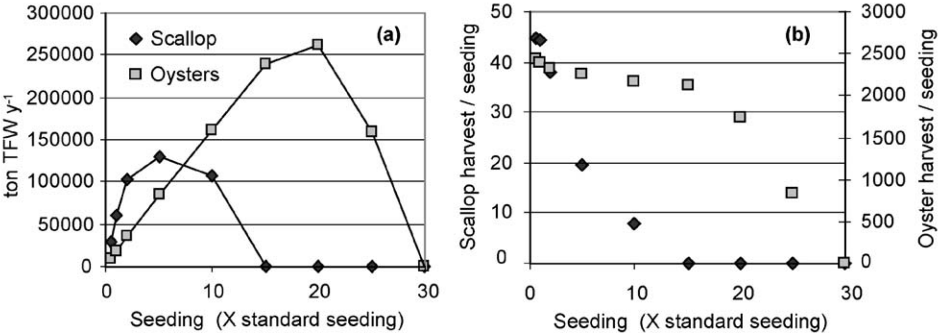

Fig. 9. Effects of increased seeding on harvesting (a) and harvest/seeding ratio (b) for scallop and oysters.

respond better to increased seeding, in part because the initial oyster biomass in the system is far lower. At about 20 × seeding, *C. gigas* harvest reaches a peak, falling rapidly as seeding increases. Fig. 9a shows that after a 2 × increase for scallops and a 15 × increase for oysters, the harvest increase is rather low, so these values are taken to be the exploitation carrying capacity for the two species (considered separately), with optimized cost–benefit between seeding and harvesting.

Moreover, if the combined culture is considered, a lower increase in oyster seeding would probably be appropriate to avoid depletion effects on the scallop yield. The response to overseeding in the Sanggou Bay model is similar to results for Carlingford Lough (Ferreira et al., 1998) and Marennes-Oléron Bay (Bacher et al., 1998). Although the maximum yield for scallops appears to be about half that for oysters, when expressed as TFW, the model considers an empirical conversion factor between soft tissue dry weight and TFW for scallops which is twice that of oysters. The maximum annual dry weight yield is therefore similar, corresponding to about 7500 tons of soft tissue dry weight, irrespective of the shellfish species considered.

Fig. 9b illustrates the economic implications of increased seeding for the two species, by considering the harvest/seed ratio. This ratio is reduced immediately for Chinese scallop, whilst remaining fairly stable for oysters until a seeding increase of about 15 ×.

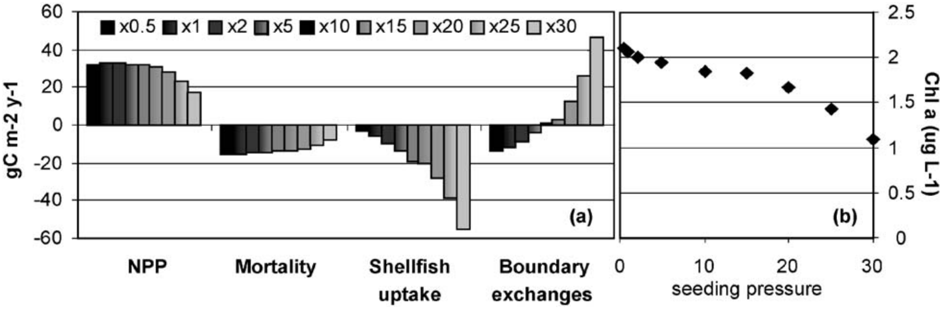

Fig. 10. Effects of increased seeding on phytoplankton mass balance (a) and concentration (b).

Competition for an increasingly limited food supply causes a reduction in the scope for growth of the lower weight classes, thus lowering recruitment into the marketable cohorts. Therefore, from a management point of view, a lower exploitation carrying capacity than indicated above should be considered, since the reduction of the harvest/seed ratio implies a lowering of culture efficiency, which negatively affects the profit structure of polyculture. As in the prior scenario analysis, the need for incorporating a socioeconomic model explicitly in the simulation is clearly identified (Turner et al., 1998).

4.3.2. Ecosystem impacts

The changes in the phytoplankton mass balance (Fig. 10a) illustrate the consequences of overseeding at the ecosystem level. Increased seeding causes a progressively sharper decrease in net primary production (Fig. 10a) and in phytoplankton biomass (Fig. 10b). Contrary to Chesapeake Bay, the longline cultivation practice in this system means that vertical stratification and "flank" mixing constraints on bivalve exposure to phytoplankton (Gerritsen et al., 1994) are of reduced importance.

As shellfish uptake increases, phytoplankton outwelling to the Yellow Sea decreases; Between 15 × and 20 × increase in seeding, the bay becomes a net phytoplankton importer. Increases in cultivation intensity within the bay will therefore lead to potential modifications in food availability (and possibly fisheries) for the adjacent ocean area.

5. Conclusions

The simulation approach presented herein strives to fulfill the general objective of combining available data and understanding (sensu Holling, 1978) to estimate the exploitation carrying capacity for a polyculture system: an appropriate level of disaggregation was chosen, following the recommendations of Gordon et al. (1996) regarding biogeochemical modelling.

From the point of view of process descriptions at a system scale, it is not clear that an increase in spatial disaggregation necessarily improves overall accuracy (e.g. Uncles and Peterson, 1995) and, in keeping with the general objective of supporting decision-making at the bay-scale for a multi-year period, the description of circulation within the bay was not considered. Consequently, other tools must be used for management decisions regarding the optimum location for farms, based on aspects such as local food availability, depletion or flow modification effects (see e.g. Gangnery et al., 2001; Grant and Bacher, 2001). Furthermore, the data gathered on aquaculture of Sanggou Bay did not permit a full validation of the model and future applications should include a better description of culture practice.

The GAMBEY model combines a detailed representation of individual shellfish growth with demographic aspects, allowing the interaction with the human component to target harvestable cohorts, and focussing on the examination of multi-year development scenarios. It is also clearly oriented toward further coupling with socioeconomics, which acts on a timescale of several years. Future developments aim to incorporate the social component not just as a driving force on the model, but as a state variable where feedback effects of exploitation strategies will be quantified in terms of employment, profitability structure of the fishery, and the valuation of natural capital (Turner et al., 1998).

This model may be used to examine the effects of differential seeding and harvest strategies for several species, and to account for limitations in the human capacity to increase harvesting pressure. It may also be extended without difficulty to include a greater variety of cultivated species, taking advantage of its object-oriented architecture, and is easily applied to other coastal systems.

The last decade has seen the appearance of many different models applied to mariculture, accompanied by strong developments in the coupling of processes on widely varying scales (e.g. shellfish feeding behaviour and the phytoplankton annual cycle). What is as yet incipient is the application of such models for management: this is partly due to the lack of integration of stakeholders in shellfish aquaculture systems. Arguably, modelling is currently the best tool for achieving this integration, enabling a paradigm shift toward a more holistic form of management.

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References

Andersen, V., Nival, P., 1989. Modelling of phytoplankton population dynamics in an enclosed water column. J. Mar. Biol. Assoc. U. K. 69, 625–646.

Bacher, C., Duarte, P., Ferreira, J.G., Héral, M., Raillard, O., 1998. Assessment and comparison of the Marennes-Oléron Bay (France) and Carlingford Lough (Ireland) carrying capacity with ecosystem models. Aquat. Ecol. 31 (4), 379–394.

Baudinet, D., Alliot, E., Berland, B., Grenz, C., Plante-Cuny, M.-R., Plante, R., Salen-Picard, C., 1990. Incidence of mussel culture on biogeochemical fluxes at the sediment water interface. Hydrobiologia 207, 187–196.

Brock, T.D., 1981. Calculating solar radiation for ecological studies. Ecol. Modell. 14, 1–9.

Carver, C.E.A., Mallet, A.L., 1990. Estimating the carrying capacity of a coastal inlet for mussel culture. Aquaculture 88, 39–53.

Castro, C.A., Soares, S.J., 1995. Proceedings of the Symposium on the Potential for Development of Aquaculture in Massachusetts, 15–17 February 1995, Chatham/Edgartown/Dartmouth, MA. NOAA Technical Memorandum NMFS-NE-109. http://www.nefsc.nmfs.gov/nefsc/publications/tm/tm109/tm109.pdf.

Chapelle, A., Ménesguen, A., Deslous-Paoli, J.-M., Souchu, P., Mazouni, N., Vaquer, A., Millet, B., 2000. Modelling nitrogen, primary production and oxygen in a Mediterranean lagoon. Impact of oysters farming and inputs from the watershed. Ecol. Modell. 127, 161–181.

Chopin, T., Yarish, C., 1999. Seaweeds must be a significant component of aquaculture for an integrated ecosystem approach. Bull. Aquacult. Assoc. Can. 99, 35–37.

Cranford, P.J., Grant, J., 1990. Particle clearance and absorption of phytoplankton and detritus by the sea scallop *Plactopecten magellanicus* (Gmelin). J. Exp. Mar. Biol. Ecol. 137, 105–121.

Dame, R.F., Prins, T.C., 1998. Bivalve carrying capacity in coastal ecosystems. Aquat. Ecol. 31, 409–421.

Fang, J.G., Kuang, S., Sun, H., Sun, Y., Zhou, S., Song, Y., Cui, Y., Zhao, J., Yang, Q., Li, F., Grant, J., Emerson, C., Zhang, A., Wang, X., Tang, T., 1996a. Study on the carrying capacity of Sanggou bay for the culture of scallop *Chlamys farreri*. Mar. Fish. Res. 17 (2), 21–31.

Fang, J.G., Sun, H.-L., Yan, J.-P., Kuang, S.-H., Li, F., Newkirk, G., Grant, J., 1996b. Polyculture of scallop *Chlamys farreri* and kelp *Laminaria japonica* in Sungo bay. Chin. J. Oceanol. Limnol. 14 (4), 322–329.

FAO, 2001. The State of World Fisheries and Aquaculture (SOFIA). Food and Agriculture Organization of the United Nations, Rome.

Ferreira, J.G., 1995. EcoWin—an object-oriented ecological model for aquatic ecosystems. Ecol. Modell. 79, 21–34.

Ferreira, J.G., Duarte, P., Ball, B., 1998. Trophic capacity of Carlingford Lough for oyster culture—analysis by ecological modelling. Aquat. Ecol. 31, 361–378.

Folke, C., Kautsky, N., 1989. The role of ecosystems for a sustainable development of aquaculture. Ambio 18, 234–243.

Gangnery, A., Bacher, C., Buestel, D., 2001. Assessing the production and the impact of cultivated oysters in the Thau lagoon (Mediterranee, France) with a population dynamics model. Can. J. Fish. Aquat. Sci. 58, 1–9.

Gazeau, F., 2000. An ecosystem model applied to an aquaculture site: Sanggou Bay (China). DEA Thesis, University of Liège/Universidade Nova de Lisboa.

Gerritsen, J., Holland, A.F., Irvine, D.E., 1994. Suspension-feeding bivalves and the fate of primary production: an estuarine model applied to Chesapeake Bay. Estuaries 17 (2), 403–416.

Gordon Jr., D.C., Boudreau, P.R., Mann, K.H., Ong, J.E., Silvert, W.L., Smith, S.V., Wattayakorn, G., Wulff, F., Yanagi, T., 1996. LOICZ biogeochemical modelling guidelines. LOICZ/R and S/95-5,vi + 96 pp. LOICZ, Texel, Netherlands.

Grant, J., 1999. Ecological constraints on the sustainability of bivalve aquaculture. In: Svennevig, N., Reinertsen, H., New, M. (Eds.), Sustainable Aquaculture: Food for the Future? Proceedings of the Second International Symposium on Sustainable Aquaculture. Balkema, Rotterdam, pp. 85–96.

Grant, J., Bacher, C., 2001. A numerical model of flow modification induced by suspended aquaculture in a Chinese bay. Can. J. Fish. Aquat. Sci. 58 (5), 1003–1011.

Grant, J., Hatcher, A., Scott, D.B., Pocklington, P., Schafer, C.T., Winters, G.V., 1995. A multidisciplinary approach to evaluating impacts of shellfish aquaculture on benthic communities. Estuaries 18, 124–144.

Guo, X.M., Ford, S.E., Zhang, F.S., 1999. Molluscan aquaculture in China. J. Shellfish Res. 18 (1), 19–31.

Hawkins, A.J.S., Fang, J.G., Pascoe, P.L., Zhang, J.H., Zhang, X.L., Zhu, M.Y., 2001. Modelling short-term responsive adjustments in particle clearance rate among bivalve suspension-feeders: separate unimodal effects of seston volume and composition in the scallop *Chlamys farreri*. J. Exp. Mar. Biol. Ecol. 262, 61–73.

Hawkins, A.J.S., Duarte, P., Fang, J.G., Pascoe, P.L., Zhang, J.H., Zhang, X.L., Zhu, M.Y., 2002. A functional simulation of responsive filter-feeding and growth in bivalve shellfish, configured and validated for the scallop *Chlamys farreri* during culture in China. J. Exp. Mar. Biol. Ecol. (in press).

Holling, C.S. (Ed.), 1978. Adaptive Environmental Assessment and Management. Wiley, Chichester.

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

Krebs, J., 1972. Ecology—The Experimental Analysis of Distribution and Abundance. Harper & Row, New York, 694 pp.

Lefebvre, S., Bacher, C., Meuret, A., Hussenot, J., 2001. Modelling nitrogen cycling in a mariculture ecosystem as a tool to evaluate its outflow. Estuarine Coastal Shelf. Sci. 52, 305–325.

Leung, P., El-Gayar, O.F., 1997. The role of modelling in the managing and planning of sustainable aquaculture. In: Bardach, J.E. (Ed.), Sustainable Aquaculture. Wiley, New York, pp. 87–101.

Mao, X.-H., Zhu, M.-Y., Yang, X.-L., 1993. The photosynthesis and productivity of benthic macrophytes in Sanggou bay. Acta Ecol. Sin. 13 (1), 25–29.

Matsuyama, Y., 1999. Harmful Effect of Dinoflagellate *Heterocapsa circularisquama* on Shellfish Aquaculture in Japan. http://www.ss.jircas.affrc.go.jp/engpage/.

Niquil, N., Pouvreau, S., Sakka, A., Legendre, L., Addessi, L., Le Borgne, R., Charpy, L., Delesalle, B., 2001. Trophic web and carrying capacity in a pearl oyster farming lagoon (Takapoto, French Polynesia). Aquat. Living Resour. 14, 165–175.

NRCA, 1998. Mariculture draft policy and regulation. Natural Resources Conservation Authority, Coastal Zone Management Division. http://www.nrca.org/CZM/Mariculture/.

Petrell, R.J., Mazhari Tabrisi, K., Harrison, P.J., Druehl, L.D., 1993. Mathematical model of *Laminaria* production near a British Columbian salmon sea cage farm. J. Appl. Phycol. 5, 1–14.

Phillips, T., 1998. Harmonic Analysis and Prediction of Tides. http://www.math.sunysb.edu/~tony/tides/harmonic.html.

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

Raillard, O., Deslous-Paoli, J.M., Héral, M., Razet, D., 1993. Modélization du comportement nutritionnel de *Crassostrea gigas* dans le bassin de Marennes-Oléron. Oceanol. Acta 16, 73–82.

Rana, K.J., 1997. Global Overview of Production and Production Trends: Trends in Global Production, 1984–1995. http://www.fao.org/docrep/003/w7499e/w7499e05.htm.

Rheault, R.B., Rice, M.A., 1995. Transient gear shellfish aquaculture. World Aquat. 26 (1), 26–31.

Scholten, H., Smaal, A.C., 1998. Responses of *Mytilus edulis* L. to varying food concentrations: testing EMMY, and ecophysiological model. J. Exp. Mar. Biol. Ecol. 219, 217–239.

Scholten, H., Smaal, A.C., 1999. The ecophysiological response of mussels (*Mytilus edulis*) in mesocosms to a range of inorganic nutrient loads: simulations with the model EMMY. Aquat. Ecol. 33, 83–100.

Scoggan, J., Zhimeng, Z., Feijiu, W., 1989. Integrated farming—polyculture. Culture of kelp (*Laminaria japonica*) in China. UNDP/FAO Regional Seafarming Project RAS/86/024, pp. 125–137.

SHOM—Service Hydrographique et Océanographique de la Marine, 1984. Table des Marées des Grands Ports du Monde. France, 186 pp.

Smaal, A.C., Prins, T.C., Dankers, N., Ball, B., 1998. Minimum requirements for modelling bivalve carrying capacity. Aquat. Ecol. 31, 423–428.

Smaal, A., Stralen, M.V., Schuiling, E., 2001. The interaction between shellfish culture and ecosystem processes. Can. J. Fish. Aquat. Sci. 58 (5), 991–1002.

Sun, Y., Song, Y., Cui, Y., Fang, J., Sun, H., Yang, Q., Yin, L., 1996. Primary productivity and the affecting factors in Sanggou bay. Mar. Fish. Res. 17 (2), 31–40.

Turner, R.K., Adger, W.N., Lorenzoni, I., 1998. Towards Integrated Modelling and Analysis in Coastal Zones: Principles and Practices LOICZ Reports and studies No. 11, iv + 122 pp. LOICZ IPO, Texel, Netherlands.

Uncles, R.J., Peterson, D.H., 1995. A computer model of long-term salinity in S. Francisco Bay: sensitivity to mixing and inflows. Environ. Int. 21 (5), 647–656.

Watson, R., Pauly, D., 2001. Systematic distortions in world fisheries catch trends. Nature 414, 534–536.

Watson, R., Pang, L., Pauly, D., 2001. The Marine Fisheries of China: Development and Reported Catches. Fisheries Centre Research Report 9(2). Univ. British Colombia, Canada.

Zhang, G., 2000. CEBN workshop on aquaculture biotechnology, Guangzhou, China, 16–19 January 2000. http://www.ebnic.org/aquacult/agenofaqua.htm.

Zhao, J., Zhou, S., Sun, Y., Fang, J., 1996. Research on Sanggou bay aquaculture hydro-environment. Mar. Fish. Res. 17 (2), 68–79.