Available online at www.sciencedirect.com

ScienceDirect

Aquaculture 275 (2008) 138–151

Aquaculture

www.elsevier.com/locate/aqua-online

Integrated assessment of ecosystem-scale carrying capacity in shellfish growing areas

J.G. Ferreira [a,*], A.J.S. Hawkins [b], P. Monteiro [c], H. Moore [d], M. Service [d], P.L. Pascoe [b], L. Ramos [e], A. Sequeira [a]

[a] *IMAR — Institute of Marine Research, Centre for Ocean and Environment, IMAR-DCEA, Fac. Ciencias e Tecnologia, Qta Torre, 2829-516 Monte de Caparica, Portugal*

[b] *Plymouth Marine Laboratory, The Hoe, Plymouth PL1 3DH, Devon, United Kingdom*

[c] *CSIR, PO Box 320. Stellenbosch 7599, South Africa*

[d] *Agri-Food and Biosciences Institute (AFBI), 18a Newforge Lane, Belfast, BT9 5PX, United Kingdom*

[e] *Ministério do Ambiente, Ordenamento do Território e Desenvolvimento Regional (MAOTDR), R. de O Século, 51, 1200-433, Lisboa, Portugal*

Received 22 September 2007; received in revised form 15 December 2007; accepted 17 December 2007

Abstract

This paper describes the development and application of an integrated framework for determination of sustainable carrying capacity in shellfish growing areas. This framework combines field data, experimental results and various types of models, ranging from individual shellfish growth models to broad-scale ecosystem models. The process by which we have integrated and coupled the various types of models is designed to capture the essential signal at each simulation scale, whilst allowing multi-year runs which provide results on cultivation of commercial species, nutrient and chlorophyll cycling, and other outputs of interest to decision-makers. The complete modelling framework enables integrated analyses of animal–environment interrelations affecting overall production at system-scales, according to different temporal and spatial scenarios, accounting for conservation aspects such as the presence of autochthonous wild species.

This framework was applied to three loughs in Northern Ireland; Carlingford (a transboundary system), Strangford and Belfast, to provide estimates of harvestable biomass over typical cultivation cycles of 2–3 years in both the blue mussel *Mytilus edulis* and the Pacific oyster *Crassostrea gigas*. The model accommodates different types of culture, whether subtidally on the bottom, suspended from rafts or intertidally on trestles.

Results predicted for Carlingford and Strangford are within ranges of landings reported by fisheries agencies. In Belfast lough, where 10,000 ton live weight are reported annually, our model framework provides stable results of 8700 ton after a 10 year model run. These models are shown to be useful for driving farm-scale simulations, which are of great interest to producers, and also for analyses of the consequences of changed environmental conditions or in the timing, distribution and/or composition of culture practice. Examples are presented that include (i) an analysis of the spatial redistribution of mussel culture, illustrating changes both to production and to the Average Physical Product; (ii) assessment of the differential effects of climate change on mussel and oyster production, indicating that oysters are significantly less impacted; and (iii) investigation of the consequences of including wild suspension-feeding species in the model framework, resulting in an expected reduction in the capacity for production of cultivated shellfish. These scenarios were produced to illustrate the uses of the modelling approach, and enable better-informed discussion between different stakeholders, towards sustainable aquaculture (ecoaquaculture).

Keywords: Shellfish aquaculture; Carrying capacity; Ecological model; Pacific oyster; Blue mussel; Sustainability; Ireland; Sea lough; EcoWin2000; ShellSIM; SMILE; Ecoaquaculture

1. Introduction

The assessment of environmentally sustainable carrying capacity for aquaculture in coastal areas poses a major challenge,

* Corresponding author. Fax: +44 20 7691 7827.
E-mail address: joao@hoomi.com (J.G. Ferreira).

0044-8486/$ - see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.aquaculture.2007.12.018

given the range of issues that must be taken into account (Inglis et al., 2000; ICES, 2005), the interactions between natural and social components, and the coupling between watershed and coastal zone (Whitall et al., 2007). Aquaculture is increasing in importance due to the overexploitation of marine resources (Naylor et al., 2000; Watson et al., 2001; Pauly et al., 2002; FAO, 2004), worsened by the progressive environmental degradation of many marine areas (Xiao et al., 2007). As a result, recommendations have been made to encourage nations to produce marine and estuarine species through cultivation.

However, these cultivation activities can themselves provoke environmental changes, which may in some cases be quite severe (Souchu et al., 2001; Read and Fernandes, 2003; Newell, 2004). Additionally, aquaculture is a subject of controversy in many countries, often involving local watermen, conservation agencies and non-governmental organisations (Crawford, 2003; Gibbs, 2004), and these conflicting viewpoints give rise to licensing concerns in many nations.

The acknowledgement of this paradox has led to discussions in different international fora, and to the presentation of guidelines designed to minimise negative impacts on the environment, and where appropriate to value aspects of aquaculture that may help to solve environmental problems.

Both the Oslo–Paris Convention (OSPAR), Bern Convention and Helsingfors Convention (HELCOM) include provisions in relation to aquaculture. In addition, the European Union is committed to principles of the Precautionary Approach, including guidelines for aquaculture in the FAO Code of Conduct for Responsible Fisheries, in which Article 9 covers Aquaculture Development, and other international initiatives such as the ICES Code of Practice on the Introductions and Transfers of Marine Organisms (ICES, 2005).

The Convention on Biological Diversity (CBD — http://www.biodiv.org) lists some potential results of aquaculture operations which can become a biodiversity concern through changes in the living conditions of other species:

- ❑ Seed collection for aquaculture purposes from sensitive habitats using destructive gear causes habitat destruction and/or alteration;
- ❑ Aquaculture takes up space, often very large areas, not only in bays and oceans, but also on nearby foreshore areas as a result of development of aquaculture infrastructures;
- ❑ Tidal marshes serve as important nursery grounds for populations of fish and shellfish and their destruction may cause species loss.

However, the CBD also recognizes that aquaculture may have positive effects on biodiversity:

- ❑ Reduction of predation pressure on commonly harvested aquatic species can help preserve biodiversity;
- ❑ Best site selection (including optimal flushing and dispersal of nutrients) may promote an increase of local and total productivity, especially in oligotrophic and mesotrophic systems, particularly when additional substrate heterogeneity, such as building of artificial reefs to soft bottom areas, is provided;
- ❑ Act as a mitigation process for biodiversity recovery — under controlled reproductive activity;
- ❑ Improve ecological status — e.g. macroalgal cultivation can remove significant amounts of nutrients from the surrounding waters and shellfish cultivation can extract both nutrients and contaminants from the water column;
- ❑ Provide the market with high quality farmed shellfish;

In the framework of the reform of the E.U. Common Fisheries Policy and in the development of the Common Aquaculture Policy, the European Commission recognised the importance of aquaculture and the necessity to develop a Strategy for the Sustainable Development of European Aquaculture. The Strategy sets out a wide range of policy principles on which the future development of aquaculture in the E.U. would be based, including the necessity to ensure that aquaculture becomes an environmentally sound activity. Similar initiatives are in preparation in the U.S., such as the proposed U.S. Offshore Aquaculture Act (NOAA, 2006).

To overexploit an area will have severe effects on the commercial productivity (Raillard & Ménesguen, 1994) and potentially also on ecosystem health, such that performance indicators are required to predict the ability of coastal environments to sustain bivalve culture (Gibbs, 2007). The concept of carrying capacity of an ecosystem for natural populations is derived from the logistic growth curve in population ecology, defined as the maximum standing stock that can be supported by a given ecosystem for a given time. Carrying capacity for shellfish culture has been further defined as the standing stock at which the annual production of the marketable cohort is maximized (Bacher et al., 1998; Smaal et al., 1998), which will differ substantially from the ecological carrying capacity. Inglis et al. (2000) and McKindsey et al. (2006) have defined sustainable carrying capacity for aquaculture according to four components, categorised according to physical, production, ecological and social aspects. These are themselves modulated by scaling, usually considered to be either system-scale (bay, estuary or sub-units thereof), or local scale (farm). As an example, social components might be analysed in terms of regional employment (system-scale), whereas farm siting might draw on space availability for competing uses (physical), food availability (production), and local biodiversity concerns (ecological).

It is important to assess the carrying capacity of an area prior to the establishment of large-scale shellfish cultivation, to ensure an adequate food supply for the anticipated production and to avoid or minimise any ecological impacts. For bivalve suspension feeders, the dominant factors determining the sustainable carrying capacity at the ecosystem-scale are primary production, detrital inputs and exchange with adjacent ecosystems (Gangnery et al., 2001; Nunes et al., 2003; Cerco and Noel, 2007). At the local scale, carrying capacity depends on physical constraints such as substrate, shelter and food transported by tidal currents, and density-dependent food depletion (Newell & Richardson, 2004; Ferreira et al., 2007a). Mortality is a critical factor, and high seed mortality due to sub-optimal seed deployment, particularly in bottom culture, is a key factor in reducing production yield and economic competitiveness (Newell, 1990).

Carrying capacity modelling should include both ecosystem-scale and local-scale approaches. Estimation of the carrying capacity should take into account the functional role of shellfish beds as components of an ecosystem. This may be achieved if carrying capacity modelling is applied within the broader framework of decision support systems, where exploitation and conservation are evaluated. The Sustainable Mariculture in northern Irish Sea Lough Ecosystems (SMILE) project was commissioned in 2004 by the Department of Agriculture and Rural Development – Northern Ireland (DARD) to develop and apply a range of tools for decision-support in sustainable development of shellfish aquaculture, within the context of integrated coastal zone management (Ferreira et al., 2007b). Five loughs were studied in the project: Carlingford Lough, Strangford Lough, Belfast Lough, Larne Lough and Lough Foyle. These sea loughs are used for a variety of activities and one of them, Strangford Lough, is a Marine Nature Reserve, one of only three in the United Kingdom. All are subject to a range of conservation designations. Competing commercial activity comes from harbour developments, shipping and the use of the loughs as receiving bodies for waste water discharges. The work presented herein is a synthesis of the approach and results of SMILE, but focusing on the first three systems which were studied in greater detail. The main objectives of SMILE, as described in this paper are:

1. To establish functional models at the lough scale, simulating key environmental variables and processes, aquaculture activities and their interactions;
2. To evaluate the sustainable carrying capacity for aquaculture in the different loughs, considering interactions between cultivated species, targeting marketable cohorts, and fully integrating cultivation practices;
3. To examine the effects of overexploitation on key ecological variables;
4. To examine bay-scale environmental effects of different culture strategies.

2. Methods

The approach used in this work combines field data acquisition, experimental work on shellfish feeding behaviour, database and geographical information systems (GIS), and the implementation and coupling of various types of dynamic models. This methodology was applied to three sea loughs in northern Ireland: Carlingford, Strangford and Belfast.

2.1. Overview of the modelling process

The modelling approach may be interpreted as a series of steps (Fig. 1):

1. Development of fine-scale circulation models for the loughs and adjoining shelf waters;
2. Use of such models to provide a detailed description of the coastal-lough circulation, and to upscale processes in space and time for the development of ecological models;
3. Application of GIS and databases for the definition of larger boxes, where detailed ecological processes and shellfish growth will be simulated;
4. Development of models for individual growth of shellfish, capable of resolving different aspects of feeding behaviour, such as the use of phytoplankton and organic detritus;

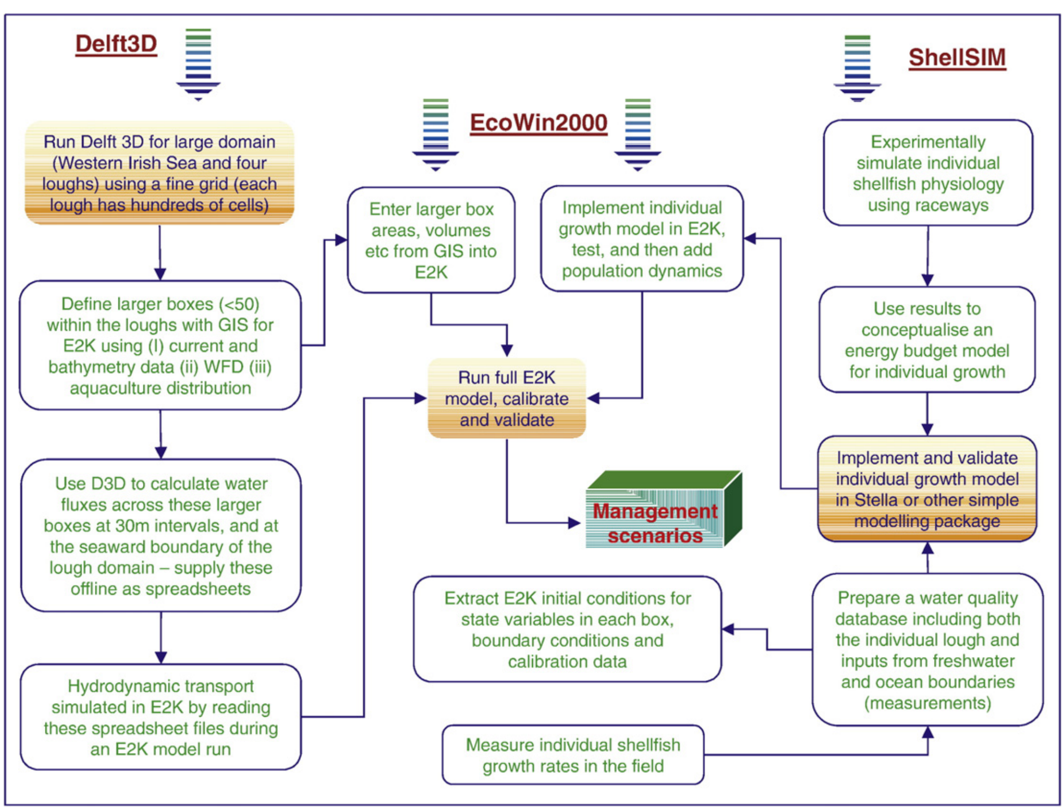

Fig. 1. General modelling framework used in SMILE.

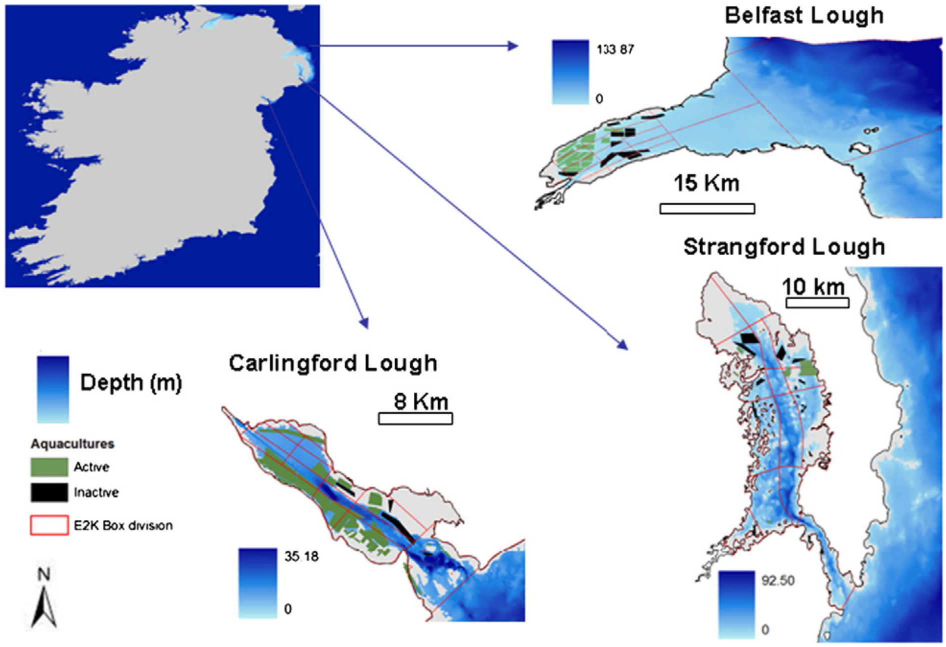

Fig. 2. Location of the three northern Irish sea lough ecosystems studied in the SMILE project.

5. Combination of the various components into ecological models which simulate processes over long periods, and thus allow predictions of multi-year system carrying capacity for sustainable shellfish aquaculture, in equilibrium with other ecosystem uses;

The names of the various models used are shown in Fig. 1.

2.2. Study area

The three sea loughs addressed in this paper are situated in northern Ireland (Fig. 2), have an aggregate area of 328 km^2 and drain a combined catchment of about 2100 km^2 (Table 1).

Belfast Lough is a shallow semi-enclosed bay, almost 96% of the area is subtidal. The main freshwater source is the River Lagan, which has a mean flow of 32 m^3 s^{-1}. Strangford Lough is a large marine lough which is connected to the Irish Sea by the Strangford narrows. It has a maximum depth of 66 m, a total area of approximately 150 km^2, and a volume of 1537×10^6 m^3. The main freshwater sources to Strangford Lough are the Comber River in the north-west and the Quoile River in the south-west. Carlingford Lough is the most southerly of the sea loughs. It is a shallow, well-mixed system with an average depth between 2 and 5 m and a deeper narrow channel along the centre of the lough. It is a cross-border system between Northern Ireland and the Republic of Ireland, with an area of about 50 km^2 (15 km in length from the mouth to Warrenpoint and 4 km at its widest point), and a volume of 460×10^6 m^3. The Newry River is its major freshwater source, with a small flow that can vary from 1 m^3 s^{-1} in summer to 9 m^3 s^{-1} in winter. The water residence time, estimated using the e-folding approach (e.g. Cuccoa and Umgiesserb, 2006) varies between 14 and 26 days. The main physical properties and cultivation data for these systems are shown in Table 1.

2.3. Field data

Data were collected through a series of surveys, carried out by DARD-NI, Queen's University Belfast and other institutes. The sampling stations occupied in each system included sites for spatial surveys, *in situ* moorings and shellfish growth trials. Over 185,000 records of data were loaded into the SMILE databases; including data for dissolved inorganic nitrogen (DIN), phosphate, chlorophyll *a* (chl *a*), total suspended particulate matter (TPM), particulate organic matter (POM) and dissolved oxygen.

The DIN and phosphate data were used to determine the limiting nutrient for phytoplankton production in each lough. This type of information is critical to the modelling process. Belfast Lough and Strangford Lough appear to be nitrogen limited, but in Carlingford Lough the nitrogen to phosphate ratio only falls below the Redfield ratio in summer.

2.4. Fine scale models

The Delft3D-FLOW hydrodynamic model was used to simulate the tidal, wind and ocean currents in the study area. This fine-grid model (Fig. 3) provides a detailed description of the circulation for a part of the Irish Sea and the three loughs, and represents both the local conditions in each lough and the processes responsible for water exchange among the different loughs and with the Irish Sea as a whole.

This model was combined with the Delft3D-WAQ model to simulate circulation and phytoplankton productivity for periods of up to a year, and used

Table 1
Physical characteristics and shellfish cultivation data for the three loughs

System	Carlingford Lough	Strangford Lough	Belfast Lough	Total
Volume ($\times 10^6$ m^3) [a]	460	1537	1548	3545
Area (km^2) [b]	49	149	130	328
Maximum depth (m) [b]	35	59	22	–
Catchment (km^2)	474	772	900	2146
Temperature (°C)	3–20	2–19	2–21	–
Mean salinity	32.5	33	28	–
River flow (m^3 s^{-1})	1–9	3.5	32	–
Water residence time (d) [b]	14–26	4–28	10–20	–
Mussel culture (ha)	867.5	5.9	952.6	1826
Oyster culture (ha)	197.8	23.5	–	221
Total shellfish culture (ha)	1065.3	29.4	952.6	2047
Percentage occupied by shellfish culture (%)	21.7	0.2	7.3	

[a] Volumes, areas and depths calculated at High Water using GIS.
[b] All residence times calculated using Delft3D.

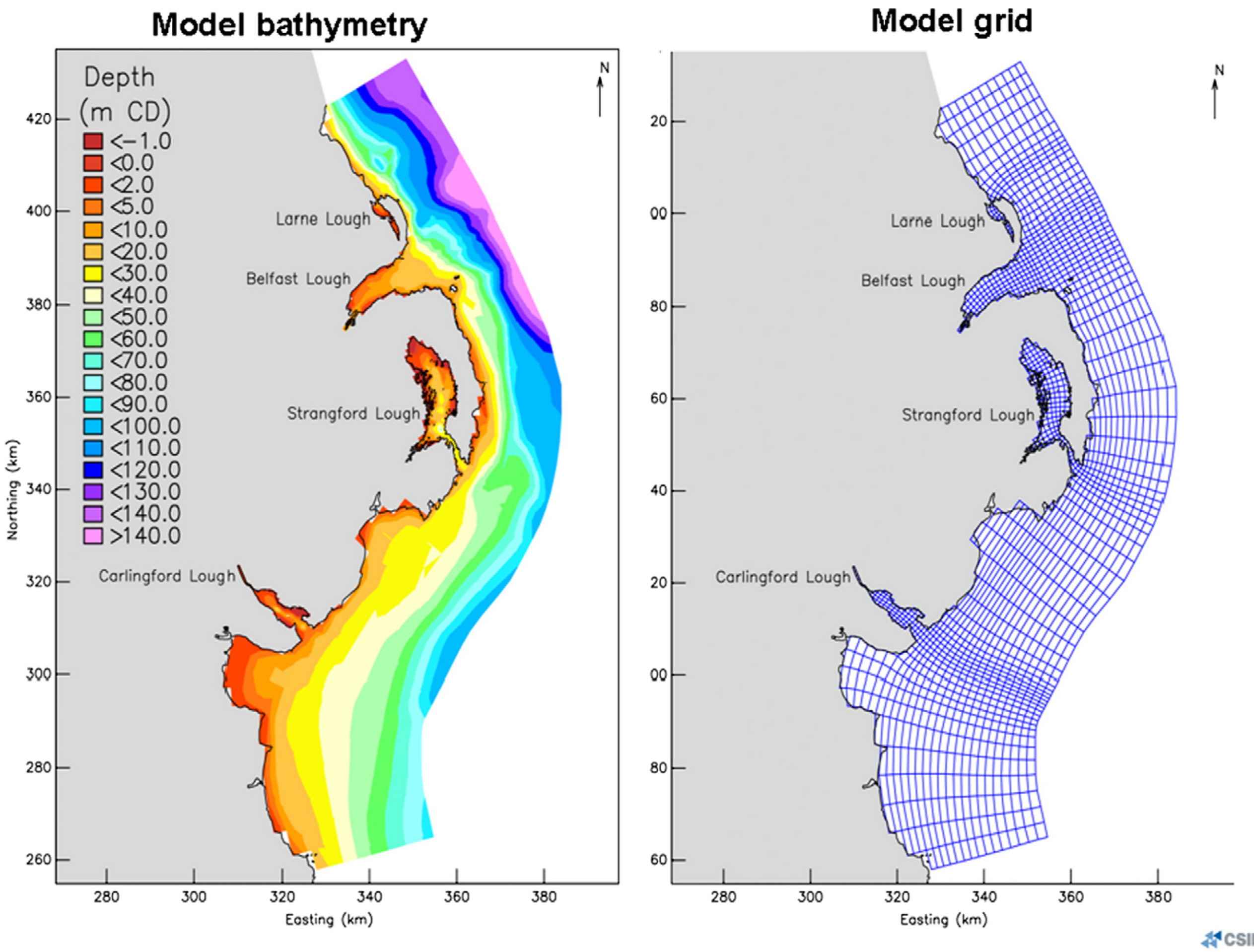

Fig. 3. Delft3D model bathymetry and grid. Note the very dense grid inside the loughs, comprising hundreds of cells and 8 sigma layers.

to generate aggregated water exchange and boundary conditions for each of the loughs, for use in broader scale ecological models. Delft3D-WAQ is capable of integrating the complexity of dynamic variability linked to physics with the core processes that govern the biogeochemistry, but does not include higher levels of the marine ecosystem (e.g. zooplankton, shellfish, fish) that are explicitly addressed by the EcoWin2000 ecological model.

2.5. Box definitions

Hydrodynamic models use a fine grid to simulate the water circulation patterns at the coast-lough scale for periods of up to one year. To simulate processes at the ecosystem-scale, a coarser grid of boxes needs to be defined, since these models are usually run for multi-year periods and simulate multiple variables such as nutrients, phytoplankton, detritus, and cultivated shellfish. These larger boxes were defined using a multi-criteria approach (see e.g. Câmara et al., 1987), resulting in different sets which were superimposed to arrive at a final schema. Five different criteria were used:

1. Morphology, analysed by GIS. The larger boxes are assumed to be homogeneous in these models, so an analysis of the morphology provides a first division, to ensure that deep channels and shallow areas are classified as distinct zones;
2. Water circulation patterns, through hydrodynamic modelling and density stratification, by comparing surface and bottom densities, calculated using salinity and temperature data available for each system in the BarcaWin2000 database;
3. Distribution of water quality parameters, including nutrients and chl *a*, obtained from field survey data;
4. Aquaculture farm locations and other uses of the loughs. Insofar as possible, the aquaculture areas were grouped into boxes rather than cutting across box limits;
5. Policy divisions such as the boundaries of water bodies from the E.U. Water Framework Directive (WFD — European Commission, 2000).

On the basis of these criteria, Belfast Lough was divided into 42 boxes, Strangford Lough into 34 boxes, and Carlingford Lough into 38 boxes. Although there does not appear to be significant vertical stratification, the systems were nevertheless modelled at the broader scale using two vertical layers, to reflect differences in food supply to shellfish in the upper and lower water column.

2.6. Modelling of feeding, metabolism and growth of cultured species

To account for the complexity of both positive and negative feedbacks between bivalve shellfish and their environments, there is a need for dynamic simulations that use mathematical equations to define functional inter-relationships between the component processes. There are two main challenges in modelling these interactions. Firstly, to identify the environmental variables, and in particular the components of available food, with significant effects on shellfish physiology. Secondly, to resolve the main interrelations, not only between environmental variables and physiology, but also between separate physiological processes, towards a common model structure that may be calibrated with a different standard set of parameters according to species and/or location.

Towards addressing these challenges, we have based our simulations upon the functional dependencies whereby environmental drivers influence shellfish physiology, including functional interrelations between the component processes of growth, drawing upon established physiological principles of energy balance.

Those various functional interrelations have been integrated within a generic dynamic model structure (ShellSIM) which simulates feeding, metabolism and growth, building upon that described for the Chinese scallop (Hawkins et al., 2002). ShellSIM has been calibrated and validated for the blue mussel *Mytilus edulis*, Pacific oyster *Crassostrea gigas* and other suspension-feeding bivalve species at contrasting sites throughout Europe (Hawkins et al., in preparation) (http://www.shellsim.com/index.html).

The environmental drivers used as forcing functions in ShellSIM are Chl *a*, POM, TPM, salinity and temperature. Compared with previous simulations of shellfish physiology, novel elements of ShellSIM include correcting for a significant and variable error in the measurement of TPM and POM, based upon water that is bound to minerals, and which has historically been mistaken for POM following ashing at high temperatures. In addition, ShellSIM resolves rapid regulatory adjustments in the relative processing of living chlorophyll-rich phytoplankton organics, non-phytoplankton organics and the remaining inorganic matter during both differential retention on the gill and selective pre-ingestive rejection within pseudofaeces.

2.6.1. ShellSIM calibration and validation

To calibrate ShellSIM, experimental measures of dynamic physiological responses were undertaken using local field facilities in blue mussel and Pacific oyster from the three loughs. Measures included clearance rate, particle retention efficiency, filtration rate, rejection rate, ingestion rate, absorption efficiency, absorption rate and total deposition rate over feeding conditions that spanned full normal ranges of food quantities and qualities (Ferreira et al., 2007b).

Outputs from ShellSIM have been successfully validated using monthly field measures of environmental drivers and shellfish growth for both *M. edulis* and *C. gigas* in each lough where these species are currently cultured. When run with a separate single standard set of parameters for each species, optimized upon the basis of all calibrations undertaken to date, ShellSIM effectively (±20%) simulates dynamic responses in physiology and growth to natural environmental changes observed over normal culture cycles in each lough (Ferreira et al., 2007b).

2.7. Ecosystem models

EcoWin2000 (E2K) is an ecological model that provides a platform for integration of the various other models, and adds functionality of its own. This object-oriented model has been developed over the last 15 years (Ferreira, 1995; Nunes et al., 2003; Nobre et al., 2005; Simas and Ferreira, 2007) and although it can be used to run short-term simulations, in the past five years it has mainly been used to run multi-year models.

EcoWin2000 typically divides coastal systems into (less than one hundred) boxes, which may be structured in one, two or three dimensions, and performs simulations at the system-scale, using water exchanges across box faces and system boundaries, which are upscaled from detailed hydrodynamic models. The mass flows across these faces must consider both directions, since EcoWin2000 uses longer integration periods (typically 30 m to 2 h) and therefore one timestep can include a current inversion (Fig. 4).

This model is not an appropriate tool for looking at effects at the farm-scale, for which other tools such as the Farm Aquaculture Resource Management (FARM™ — http://www.farmscale.org) model may be used (Ferreira et al., 2007a) — these are tailored to smaller scale processes, and may be driven by measured data or by outputs of models such as Delft3D, COHERENS or EcoWin2000.

The full EcoWin2000 model for this study runs with eight different objects, containing a total of 20 forcing functions and 88 state variables. These state variables simulate the relevant biogeochemistry of the three systems, and provide the appropriate drivers for the ShellSIM individual growth formulations. Growth provided by ShellSIM is used to drive population models (e.g. Simas and Ferreira, 2007), which simulate the demography of the species of interest in order to allow the harvesting of only the marketable cohort(s) (Eq. (1)).

$$\frac{\partial n(s,t)}{\partial t} = -\frac{\partial[n(s,t)g(s,t)]}{\partial s} - \mu[(s)n(s,t)] \tag{1}$$

where t, time; s, weight class; n, number of animals; g, scope for growth (growth rate); μ, mortality.

Previous models have used a constant Δs (in the discretised form of the equation); in the present models the weight classes have variable amplitude, with narrower amplitudes for the smaller animals. In a typical setup for *M. edulis*, the initial cultivation weight might be of the order of 0.5 g total fresh weight (TFW), therefore a 1 g amplitude is appropriate. For harvestable classes in the range 15–25 g TFW, four 3 g classes will suffice. The "Man" object in the model, responsible for seeding and harvesting shellfish, has been completely recoded to allow for the seeding and harvesting of multiple species, considering different individual weights at seeding, variable seed densities in model boxes and variable seeding periods, together with identical flexibility for harvesting practices (see e.g. Gangnery et al., 2004 for a similar approach for monoculture). Our updated approach enables the calculation of the Average Physical Product (APP) and allows decision-makers to set harvesting rates to match a particular APP management target. Determination of the Total Physical Product (TPP),

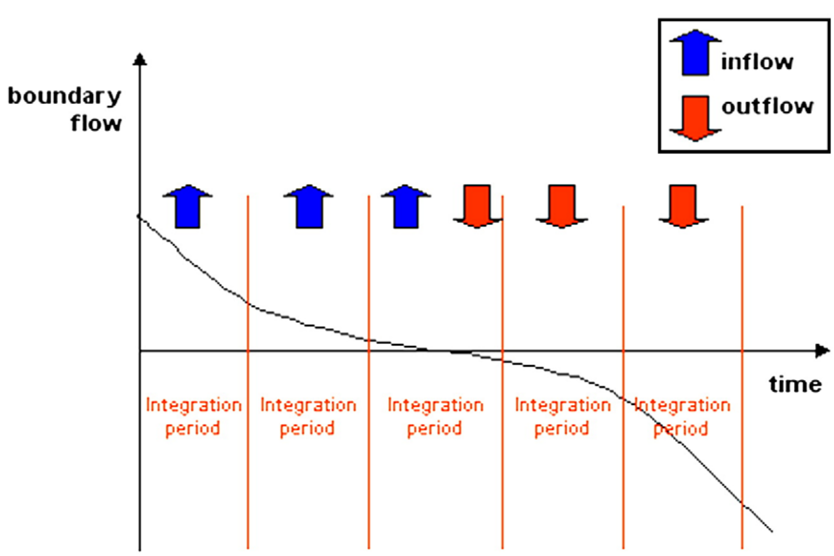

Fig. 4. Flow integration for EcoWin2000, illustrating the need for bidirectional flows (courtesy J.P. Nunes).

APP and Marginal Physical Product (MPP) for a range of seeding densities and/or cultivation areas allows managers to determine optimal levels of cultivation with respect to potential profit (e.g. Ferreira et al., 2007a). This is one element of a trilogy which additionally includes environmental and social components (see e.g. Inglis et al., 2000), and which should form the backbone in decision-making on development and licensing of coastal and offshore shellfish aquaculture.

The EcoWin2000 large-scale ecosystem models are designed to run for multiple years, necessarily simplifying some of the finer-scale system behaviour, whilst permitting the capture of event-scale phenomena such as tidal and seasonal variability. The commercial production of shellfish in northern Ireland generally occurs over a three year period, and for bottom culture, "crop rotation" is widely practised, with only some parts of the licensed areas seeded annually.

An EcoWin2000 model run will produce the first harvest (of the part of the overall area seeded in the first year) over the fourth year, and begin to yield results for the overall culture only in the sixth year. Over that period, some animals will remain unharvested. Consequently, the model needs to be run for a relatively long period of about 10 years in order to give consistently stable harvesting results. For these reasons, the EcoWin2000 code has been optimised to be extremely fast. A ten-year simulation for Carlingford Lough, with about 175,000 timesteps, considering 38 boxes and 88 state variables, including 10 weight classes for oysters and mussels, takes about 20 m. This is already an acceptable run time, as research progresses towards integrating this type of ecological simulation with socio-economic models running for 10–25 year periods.

2.7.1. Assessment of the ecological significance of wild species

Evaluation of ecoaquaculture should take into account the food availability for wild populations of grazers and filter feeders, including wild bivalve stocks. An ecosystem modelling approach based on the application of Geographical Information Systems (GIS) was developed and tested in Carlingford Lough, and is fully described in Sequeira et al. (in press). The limitations to this approach are the availability of appropriate benthic survey and sediment mapping data, together with experimental measures of filtration rates of key wild species.

2.7.2. EcoWin2000 validation

With the objective of simulating individual shellfish growth and total production at the population scale in the three loughs, the models were initialised with nutrient and growth driver inputs specific for each system, drawing on data archived in the BarcaWin2000 databases or on outputs of other models. Boundary conditions for the river and ocean end-members were set following the results from the WAQ–D3D model and river sampling stations where appropriate.

Wherever possible, the values for parameters were taken from local studies. For the individual shellfish models, parameters were measured through experimental trials, which provided data on filtration rates, ingestion rates and many other parameters. An identical approach was taken for the system-scale modelling, with respect to primary production parameters such as optimal light climate and nutrient uptake. Some parameters such as ressuspension were taken from the detailed Delf3D hydrodynamic model.

The ecological model outputs for each box were validated against field data to check if conditions for shellfish growth were being appropriately simulated. Example results from a few boxes from the Strangford Lough model are shown in Fig. 5.

An assessment of goodness of fit of model outputs to measured data was carried out following Oreskes et al. (1994), providing scores ranging from good to fair. This evaluation was carried out for environmental drivers and for shellfish individual growth models, but no validation of this kind is possible with respect to shellfish harvest yields, where models are limited to comparisons with landings data.

3. Results and discussion

3.1. Shellfish distribution and culture practice

Most revenue sources from shellfish culture in the three loughs are derived from blue mussels (*M. edulis*) and Pacific oysters (*C. gigas*), with contributions from European oysters (*Ostrea edulis*) and King scallops (*Pecten maximus*). Table 2 summarises the details of culture practice in the three loughs. In general, one third of the cultivation areas are seeded every year, and culture periods from seeding to harvestable size vary between 18 and 33 months. The total value of aquaculture production is around 2.5 million pounds (about 4 million euro) per annum.

In addition, about 50 ton of native oysters (*O. edulis*) are produced per year in Strangford Lough. Wild mussel dredging is an important source of shellfish products in Carlingford Lough, corresponding to about 1000 ton per year.

The reported mortalities are particularly high for mussel bottom culture, largely because of the methods used for distribution and spreading of seed. An accurate evaluation of both mortality and cultivation areas is critical for the success of the type of simulations described herein, since these are model forcing functions. As an example, if we consider a seed weight of 1 g TFW and a harvest weight of 10 g TFW, a 1 ha area seeded with a mussel density of 100 animals per m^2 will yield a 10 ton harvest at zero mortality (APP = 10) but only a 3 ton harvest at 70% mortality. Consequently, models are severely constrained by these inputs, and as long as the food available within the simulated growth period allows the animals to reach harvestable weight, these results will not vary.[1] In many studies of this nature in which the authors have been involved, it has become clear that the difficulties in obtaining an appropriate description of cultivation practice, essential for accurate modelling, are grossly underestimated, and we now consider this an early stage, high priority activity for successful carrying capacity assessment.

3.2. Shellfish individual growth

Fig. 6 illustrates growth and environmental impacts predicted by ShellSIM for *C. gigas* during a typical culture cycle in Carlingford Lough, having been deployed as seed of 24 mm shell length in April (Julian Day 96) and harvested at 57 mm shell length in January the following year (Day 375).

Simulations illustrate the significant cumulative environmental impacts resulting from each individual oyster, which include about 9 m^3 of water cleared of particles >2 µm diameter, 50 g of dry biodeposits, 0.5 l of dissolved oxygen consumed and 30 mg of nitrogen excreted. These simulations have been successfully validated using monthly field measures of environmental drivers and shellfish growth for both *M. edulis* and *C. gigas* in each lough where these species are currently cultured.

Comparisons of simulated and observed growth in SMILE and other projects indicate that ShellSIM is an effective common model structure that may be calibrated according to species and/or location, successfully simulating growth across a broad range of shellfish types cultured in a diverse set of locations under varying culture scenarios and/or practices (http://www.shellsim.com/index.html). Model outputs confirm that ShellSIM, when run with a separate single standard set of parameters for each species, optimised upon the basis of all calibrations undertaken to date, can effectively (±20%) simulate dynamic responses in physiology and growth to natural environmental changes experienced by *M. edulis* and *C. gigas* at contrasting sites and under different culture practices throughout Europe and Asia. There is potential for greater accuracy (±5%) upon site-specific calibration. On a single-site basis, ShellSIM has additionally been calibrated and validated for the Chinese scallop *Chlamys farreri*, Mediterranean mussel *Mytilus*

[1] This is a simplified example, because in a model the mortality rate is calculated at each timestep. Nevertheless the general principle applies.

galloprovincialis, Manila clam *Tapes philippinarum*, blood clam *Tegillarca granosa*, Chinese oyster *Ostrea plicatula* and razor clam *Sinonvacula constricta* (http://www.shellsim.com/index.html).

3.3. Carrying capacity modelling

The ShellSIM individual growth model was implemented and tested within the EcoWin2000 platform. Individual growth in weight and length were simulated for one mussel and one oyster in each model box where cultivation occurs. With the addition of population dynamics to the individual model, shellfish stocks over multi-year periods can be estimated. As the shellfish culture cycle in all the loughs occurs over a three year period, the ecological model for each system needs to run for at least 6 years to produce stable results. Results for individual growth and harvestable biomass (>15 g TFW for mussels and >70 g TFW for oysters) are shown in Fig. 7 for Carlingford Lough.

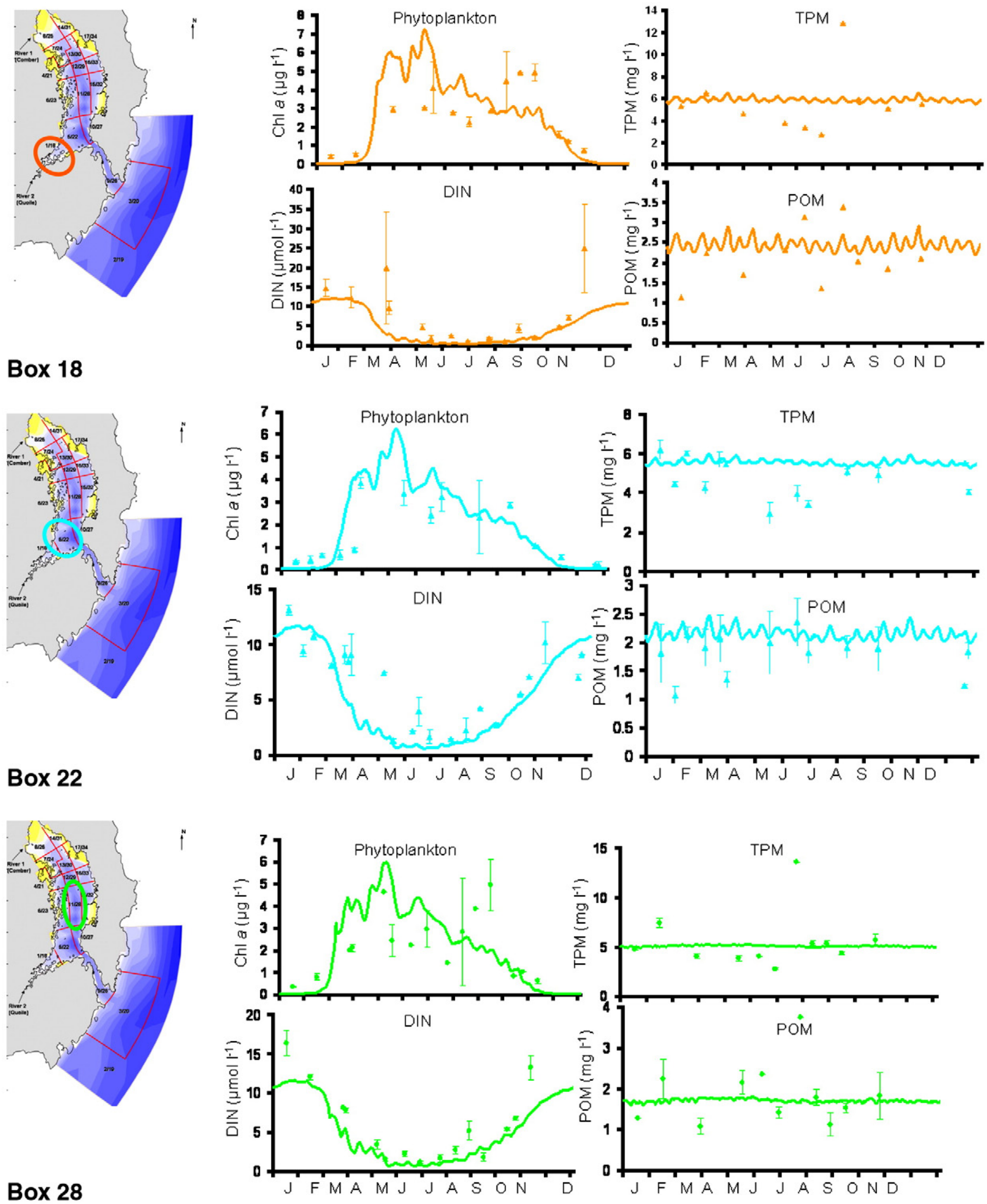

Fig. 5. Validation of shellfish growth drivers simulated by the EcoWin2000 model for Strangford Lough.

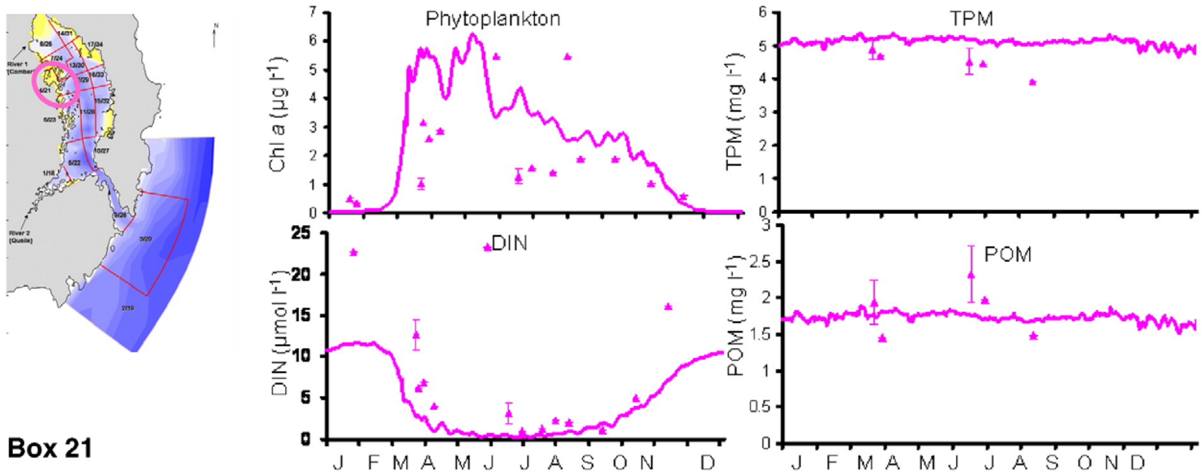

Fig. 5 (*continued*).

An estimate of total production for both mussels and oysters in each system was made by running the standard models (Table 3). Predictions are as a rule slightly lower than the harvest data recorded by the DARD-NI Fisheries Division, Loughs Agency and BIM. At the shellfish population level, the only way of validating this kind of model is through comparison with fisheries data. Models can be tuned to provide an exact match to such data, although there is arguably little value in that approach, not least because data on landings are themselves often a less than adequate proxy for total production.

Variations in culture practice, with respect to size of seed deployed and adults harvested, cultivation periods, areas and densities, as well as uncertainties with respect to mortality, all affect model results. Since the models adequately reproduce individual growth, it is probable that a combination of these factors plays a part in explaining the differences observed. The model APP results (Table 3) also differ among systems, with higher values reflecting cultivation using rafts and trestles, and lower ones associated with bottom culture. On the basis of reported mortalities, the model provides an APP of 4 for mussel bottom leases in Belfast Lough, although the industry often quotes a ratio of about 1, suggesting that profit is only on the price differential between inputs and outputs, rather than incorporating a biomass multiple. Improved seeding practices (Newell & Richardson, 2004; Ferreira et al., 2007b) will significantly contribute to the reduction of mortality, leading to higher yields and a more profitable business structure.

3.4. Management scenarios

Models such as the ones developed for Carlingford, Strangford and Belfast loughs allow managers to examine the potential outcomes of different development options without the social consequences of experimental implementation. Changes in (i) culture practice e.g. by altering species distributions, mortality rates or seeding densities; (ii) local environmental factors, e.g. river basin management to modify nutrient discharges, or global climate change e.g. in water temperature

Table 2
Culture practice, production and value for *Mytilus edulis* and *Crassostrea gigas* in the three loughs

Lough	Carlingford Lough [a]		Strangford Lough [b]		Belfast Lough [c]	Total	
Species	Mussels	Oysters	Mussels	Oysters	Mussels	Mussels	Oysters
Seeding							
Weight (g)	0.5	0.8	0.1	0.8	0.6	–	–
Length (mm)	10–15	12–16	2	13	20	–	–
Period	May–Sep	May–Jun	Mar–May	Apr–Jun	Jun–Aug	–	–
Harvesting							
Weight (g)	12	60–70	13	115	13	–	–
Length (mm)	60–65	75	53	114	55–65	–	–
Period	Jan–Feb	Jan–Mar	Dec–Feb	Jan–Feb	Oct–Jan	–	–
Growing time (months)	18–24	33	24	26	30	–	–
Mortality (%)	>70	<2	<20	10–15	70	–	–
Crop rotation	1/3	1/3	1/3	1/3	1/3	–	–
Aquaculture type	Bottom culture Submerged rafts	Trestles	Submerged rafts	Trestles	Bottom culture	–	–
Production (ton) [a]	2500	320	2	272 *50*	10,000	12,502	592 *50*
Value (GBP) [d]	1617331	217697	Unknown	601596 102800	Unknown	1617331	*819293* *102800*

[a] Production values for Carlingford Lough combine data for Northern Ireland (NI) and the Republic of Ireland (ROI) for 2004 (source Loughs Agency).
[b] Oyster production and revenue values for 2002 are from Roberts et al. (2004). Mussel production values are for 2003 (source: DARD Fisheries Division).
[c] Production values for Belfast Lough are for 2003 (source: DARD Fisheries Division).
[d] For oyster columns, where applicable — upper number: Pacific oyster *Crassostrea gigas*, lower number (in italics): native oyster *Ostrea edulis*.

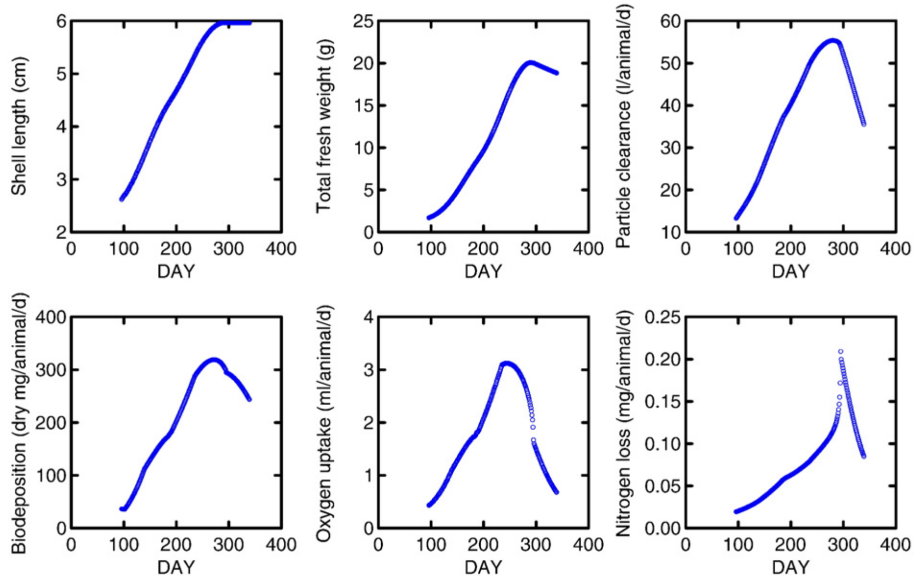

Fig. 6. Growth and environmental impacts predicted by ShellSIM for Pacific oysters during a typical culture cycle in Carlingford Lough.

or sea level rise; and (iii) protected areas or distribution of wild species of conservation interest; are all examples of scenarios which may be analysed with this type of approach. As an illustration, Table 4, Figs. 8 and 9 show the results for three different types of scenarios:

3.4.1. Changes in culture distribution

The first scenario was tested for Belfast Lough, where aquaculture already occupies a significant percentage of the entire system. Since there are several licensed sites in this lough which are presently inactive, the EcoWin2000 model was run considering that some of these aquaculture leases had become active. The aquaculture areas within box 29 were considered to be active in this scenario and seeding densities were set to be same as for the rest of the lough. The results obtained per box can be seen in Table 4, and a comparison between the standard model and the scenario can be made for seeded and harvested biomass, APP and mussel individual weight. The model suggests that additional cultivation at these sites is of some value from a system perspective. The APP is about average for the lough, and the added mussel production for that box affects (to a small degree) the production in all the other model boxes, resulting in an overall increase in harvest, but which is accompanied by a marginal decrease in both APP and individual weight of mussels in most boxes which are presently cultivated.

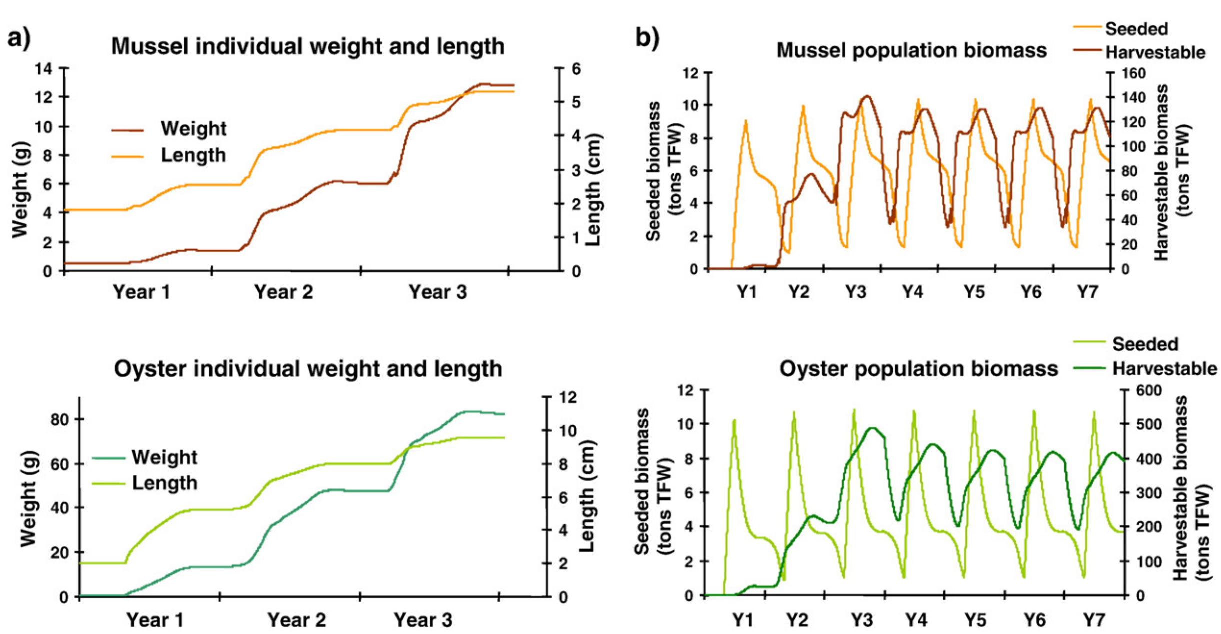

Fig. 7. Results of simulations in Carlingford Lough: a) mussel and Pacific oyster growth in weight (g) and length (cm) during one culture cycle and b) mussel population biomass as total fresh weight (TFW) of seed and harvestable weights in two model boxes.

Table 3
Production data for the three loughs and comparison with simulations from EcoWin2000[a]

		Carlingford Lough	Strangford Lough	Belfast Lough	Total
Production records (ton)	Blue mussel	1500 to 3000	2.4	10,000	11,500
	Pacific oyster	365 to 868	260	–	635
Model simulation (ton)	Blue mussel	1870	14	8682	10,566
	Pacific oyster	800	255	–	1055
APP	Blue mussel	3.8 (NI)*	13.8	4	–
	Pacific oyster	12.5 (NI)*	7.15	–	–

[a] The production records shown were provided by DARD Fisheries Division for Strangford and Belfast Loughs and by the Loughs Agency and BIM for Carlingford Lough.

3.4.2. Global climate change

We examined the potential effects of global climate change by considering an increase in water temperature of 1 °C and 4 °C for Strangford Lough (Fig. 8). The one degree increase scenario was proposed by DARD Fisheries; the higher increase of 4 °C is the maximum increase, by the year 2100, predicted by the UN Intergovernmental Panel on Climate Change, in its February 2007 report. From these results it can be seen that an increase in water temperature would lead to a reduction in aquaculture productivity and a decrease in both the mean weight and mean length of individuals. These decreases would have a dramatic effect on the blue mussel and lesser consequences for the Pacific oyster population. An increase of 1 °C in the water temperature would lead to a reduction of about 50% in mussel production and less than 8% in Pacific oyster production, and an increase of 4 °C would result in a reduction of 70% in mussel production and less than 8% in Pacific oyster production. Climate change will also affect nutrient inputs due to modifications in the hydrological regime and land use of the catchment. The application of catchment models, as was done for Lough Foyle with the Soil and Water Assessment Tool — SWAT (Ferreira et al., 2007b) may be used for a more detailed analysis of the consequences to aquaculture of global change or of modifications in management practices. Marinov et al. (2007) applied a similar approach, using SWAT to simulate the catchment loading for Sacca di Goro, Italy, and a 3D biogeochemical model to simulate clam farming in the lagoon, and provide a detailed scenario analysis considering e.g. changes in macroalgal bloom patterns and climatic variability. The main difference from the present work lies in the modelling approach within the lagoon, where the circulation, biogeochemistry and shellfish growth were all processed within the same model, corresponding to model runs with a duration of one day (Marinov et al., 2007). By contrast, our approach has been to combine different scales for the various processes, allowing us to capture the relevant signal at each scale and optimise performance to permit models for large systems such as Belfast Lough (the volume of which is about 40 times that of Sacca di Goro) to run for a ten-year period in about 15 m. This allows managers to quickly examine long-term simulations, and helps build a bridge to socio-economic models.

3.4.3. Conservation and biodiversity

The final scenario (Fig. 9) considers cultivated shellfish production in Carlingford Lough, with and without the inclusion of wild species in the model. Considering the average number of wild species individuals existing per unit area, the EcoWin2000 model predicts that production values for cultivated species would be reduced, together with individual length and weight. This type of simulation may help different stakeholders to establish consensus thresholds for cultivation, whilst taking into account the protection of natural ecosystem biodiversity, and may contribute to inform risk assessment of shellfish farming (e.g. Crawford, 2003).

4. Conclusions

Ecosystem-scale assessment of carrying capacity for shellfish aquaculture is a necessary pre-requisite to local (farm-scale) analysis. Work carried out in the SMILE project, and described here in detail for three loughs, represents one approach to address this requirement. A key finding from our work has been that the combination of models running at widely varying time and space

Table 4
Belfast Lough model results for an increase in seeding area for Box 29 (Ferreira, 2007b)

Box	Seeded		Harvested		APP		Individual weight	
	Standard	Scenario	Standard	Scenario	Standard	Scenario	Standard	Scenario
29	None	264	None	1534	None	4.6	None	14
35	426	No change	2607	2565	5	4.8	15.4	15
36	6	No change	48	48	6	6.1	20.2	20
37	37	No change	148	147	3	3	8.4	8.3
38	193	No change	975	966	4	3.9	11.6	11.5
39	599	No change	2261	2209	3	2.9	10.3	10.2
40	19	No change	100	100	4	4.1	11.4	11.4
41	293	No change	1642	1645	4	4.4	13.3	13.3
42	313	No change	900	872	2	2.2	9.4	9.3
Total/average	1886	2150	8682	10085	4	4	–	–

Results of the standard model are shown for comparison.

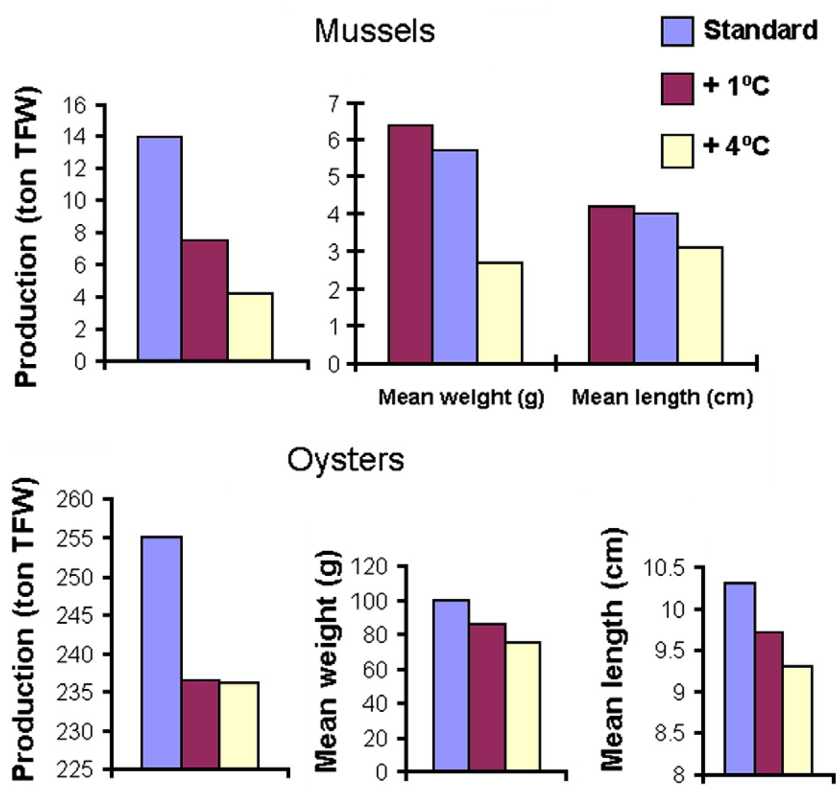

Fig. 8. Results for the Strangford standard model and two scenarios considering an increase in water temperature of 1 °C and 4 °C.

scales is at the core of a successful analysis. Using a range of models is a requirement for scaling, but the models also act as co-validators of each other, lending confidence to the outcomes. The outputs from multi-year models are not only useful in themselves, as highlighted previously, but serve to drive farm-scale models and other screening models of various types, which are of interest to both the farmer and regulator. The possibility of operating coarser scale models, such as the EcoWin2000 implementations described in this work, allows users to deal with manageable amounts of data and acceptable run-times. This trade-off between multiple-year simulation and spatial complexity, whilst preserving acceptable levels of accuracy, is essential in building a bridge with microeconomic models, which require simulations at the decadal scale.

Future developments of simulation approaches must include the linkage of both the natural and social sciences, if possible with explicit feedbacks. This will allow changes in pricing linked to production, supply and demand, to be reflected in the attractiveness of commercial shellfish cultivation, and provide indicators on employment and other aspects of social welfare. Additionally, by factoring in the non-use value of ecosystems, with respect e.g. to the valuation of biodiversity, a more complete mass balance of the effective gains to society may be computed. A holistic assessment of aquaculture on the basis of people, planet and profit, as has been applied elsewhere (e.g. Verbooma et al., 2006) should become central to studies of sustainable carrying capacity. This concept, sometimes termed the triple bottom line, is a goal that is at present challenged by the application of fragmented

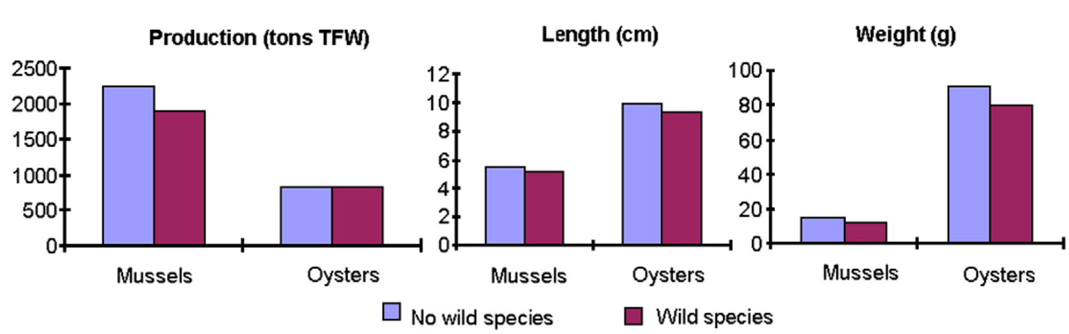

Fig. 9. Scenario showing aquaculture production in Carlingford Lough with and without resource partitioning.

approaches. The work we have described in the framework of SMILE allows managers to examine the consequences of development for biodiversity, conservation and habitat protection (Sequeira et al., in press), water quality (Lindahl et al., 2005; Ferreira et al., 2007a) and yield, including profit maximisation through the use of marginal analysis (Jolly & Clonts, 1993). This approach may be summarised as ecoaquaculture (Sequeira et al., in press), i.e. a practical implementation of the triple bottom line concept to sustainability in aquaculture.

Ongoing research on the integration of basin-scale models such as SWAT, which will allow for the effects of changes in land use agricultural practice to be explicitly simulated in this framework, provides a link to the drivers and pressures of nutrient loading to the coastal zone. The explicit connection with economic models, including incorporation of dynamic feedbacks, is also an area where exciting developments are expected in the near future. The challenge of bringing the various components of the People–Planet–Profit equation together as a holistic indicator of sustainable carrying capacity in shellfish growing areas appears both achievable and appropriate for integrated coastal management.

Acknowledgements

Financial support from DARD-NI for the execution of the SMILE project is gratefully acknowledged. The authors wish to thank all the members of the SMILE team, the shellfish growers in Northern Ireland and Ireland, and Bord Iascaigh Mhara (BIM).

References

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.

Câmara, A.S., Silva, M.C., Ramos, L., Ferreira, J.G., 1987. TEJO1 — an interactive program for the division of estuaries into homogeneous areas. Water Sci. Technol. 19, 43–51.

Cerco, C.F., Noel, M.R., 2007. Can oyster restoration reverse cultural eutrophication in Chesapeake Bay? Estuar. Coast. 30 (2), 331–343.

Crawford, C., 2003. Qualitative risk assessment of the effects of shellfish farming on the environment in Tasmania, Australia. Ocean Coast. Manag. 46, 47–58.

Cuccoa, A., Umgiesserb, G., 2006. Modeling the Venice Lagoon residence time. Ecol. Model. 193 (1–2), 34–51.

European Commission, 2000. Directive 2000/60/EC of the European Parliament and of the council of 23 October 2000 establishing a framework for Community actions in the field of water policy. Off. J. Eur. Communities L327, 1 (22.12.2000).

FAO, 2004. The State of the World Fisheries and Aquaculture. Food and Agricultural Organization of the United Nations.

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

Ferreira, J.G., Hawkins, A.J.S., Bricker, S.B., 2007a. Management of productivity, environmental effects and profitability of shellfish aquaculture — the Farm Aquaculture Resource Management (FARM) model. Aquaculture 264, 160–174.

Ferreira, J.G., Hawkins, A.J.S., Monteiro, P., Service, M., Moore, H., Edwards, A., Gowen, R., Lourenço, P., Mellor, A., Nunes, J.P., Pascoe, P.L., Ramos, L., Sequeira, A., Simas, T., Strong, J., 2007b. SMILE — Sustainable Mariculture in northern Irish Lough Ecosystems – Assessment of Carrying Capacity for Environmentally Sustainable Shellfish Culture in Carlingford Lough, Strangford Lough, Belfast Lough, Larne Lough and Lough Foyle. IMAR – Institute of Marine Research. 97 pp.

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

Gangnery, A., Bacher, C., Buestel, D., 2004. Modelling oyster population dynamics in a Mediterranean coastal lagoon (Thau, France): sensitivity of marketable production to environmental conditions. Aquaculture 230, 323–347.

Gibbs, M.T., 2004. Interactions between bivalve shellfish farms and fishery resources. Aquaculture 240 (1–4), 267–296.

Gibbs, M.T., 2007. Sustainability performance indicators for suspended bivalve aquaculture activities. Ecol. Indicat. 7, 94–107.

Hawkins, A.J.S., Duarte, P., Fang, J.G., Pascoe, P.L., Zhang, J.H., Zhang, X.L., Zhu, M.Y., 2002. A functional model of responsive suspension-feeding and growth in bivalve shellfish, configured and validated for the scallop *Chlamys farreri* during culture in China. J. Exp. Mar. Biol. Ecol. 281 (1–2), 13–40.

Hawkins, A.J.S., Pascoe, P.L., Parry, H., in preparation. A generic model structure for the dynamic simulation of feeding, metabolism and growth in suspension-feeding bivalve shellfish (ShellSIM): calibrated and validated for both *Mytilus edulis* and *Crassostrea gigas* cultured at contrasting sites throughout Europe.

ICES, 2005. European Union Legal Framework — "Report of the Working Group on Environmental Interaction of Mariculture, 11–15 April, Ottawa, Canada. ICES WGEIM Report 2005".

Inglis, G.J., Hayden, B.J., Ross, A.H., 2000. An overview of factors affecting the carrying capacity of coastal embayments for mussel culture. NIWA Client Report CHC00/69, Christchurch, New Zealand.

Jolly, C.M., Clonts, H.A., 1993. Economics of Aquaculture. Food Products Press, p. 319 pp.

Lindahl, O., Hart, R., Hernroth, B., Kollberg, S., Loo, L., Olrog, L., Rehnstam-Holm, A., 2005. Improving marine water quality by mussel farming: a profitable solution for Swedish Society. Ambio 34 (2), 131–138.

Marinov, D., Galbiati, L., Giordani, G., Viaroli, P., Norro, A., Bencivelli, S., Zaldívar, J.M., 2007. An integrated modelling approach for the management of clam farming in coastal lagoons. Aquaculture 269, 306–320.

McKindsey, C.W., Thetmeyer, H., Landry, T., Silvert, W., 2006. Review of recent carrying capacity models for bivalve culture and recommendations for research and management. Aquaculture 261 (2), 451–462.

National Oceanic and Atmospheric Administration, 2006. National Offshore Aquaculture Act. Available: http://www.nmfs.noaa.gov/mediacenter/aquaculture/docs/03_National%20Offshore%20Aquaculture%20Act%20FINAL.pdf.

Naylor, R.L., Goldburg, R.J., Primavera, J.H., Kautsky, N., Beveridge, M.C.M., Clay, J., Folke, C., Lubchenco, J., Mooney, H., Troell, M., 2000. Effect of aquaculture on world fish supplies. Nature 405, 1017–1024.

Newell, C.R., 1990. The effects of mussel (*Mytilus edulis*, Linnaeus, 1758) position in seeded bottom patches on growth at subtidal lease sites in Maine. J. Shellfish Res. 9, 113–118.

Newell, C.R., Richardson, J.R., 2004. Shellfish carrying capacity and site optimisation. Aquac. Irel. 115, 15–19.

Newell, R.I.E., 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. J. Shellfish Res. 23 (1), 51–61.

Nobre, A.M., Ferreira, J.G., Newton, A., Simas, T., Icely, J.D., Neves, R., 2005. Management of coastal eutrophication: integration of field data, ecosystem-scale simulations and screening models. J. Mar. Syst. 56 (3/4), 375–390.

Nunes, J.P., Ferreira, J.G., Gazeau, F., Lencart-Silva, J., Zhang, X.L., Zhu, M.Y., Fang, J.G., 2003. A model for sustainable management of shellfish polyculture in coastal bays. Aquaculture 219 (1–4), 257–277.

Oreskes, N., Shrader-Frechette, K., Belitz, K., 1994. Verification, validation, and confirmation of numerical models in the earth sciences. Science 263, 641–646.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., Zeller, D., 2002. Towards sustainability in world fisheries. Nature 418, 689–695.

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.

Read, P., Fernandes, T.F., 2003. Management of environmental impacts of marine aquaculture in Europe. Aquaculture 226 (1–4), 139–163.

Roberts, D., Davies, C., Mitchell, A., Moore, H., Picton, B., Portig, A., Preston, J., Service, M., Smyth, D., Strong, D., Vize, S., 2004. Strangford Lough Ecologicall Change Investigation (SLECI). Report to Environment and Heritage Service by the University, Belfast.

Sequeira, A.S., Ferreira, J.G., Hawkins, A.J., Nobre, A., Lourenço, P., Zhang, X.L., Yan, X. in press. Trade-offs between shellfish aquaculture and natural biodiversity: a modelling approach for sustainable management. Aquaculture.

Simas, T.C., Ferreira, J.G., 2007. Nutrient enrichment and the role of salt marshes in the Tagus estuary (Portugal). Estuar. Coast. Shelf Sci. 75, 393–407.

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

Souchu, P., Vaquer, A., Collos, Y., Landrein, S., Deslous-Paoli, J.M., Bibent, B., 2001. Influence of shellfish farming activities on the biogeochemical composition of the water column in Thau lagoon. Mar. Ecol., Prog. Ser. 218, 141–152.

Verbooma, J., Alkemadeb, R., Klijna, J., Metzgerc, M.J., Reijnena, R., 2006. Combining biodiversity modeling with political and economic development scenarios for 25 EU countries. Ecol. Econ. 62 (2), 267–276.

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.

Whitall, D., Bricker, S.B., Ferreira, J.G., Nobre, A.M., Simas, T., Silva, M.C., 2007. Assessment of Eutrophication in Estuaries: Pressure–State–Response and Nitrogen Source Apportionment. Environ. Manage. 40, 678–690.

Xiao, Y., Ferreira, J.G., Bricker, S.B., Nunes, J.P., Zhu, M., Zhang, X., 2007. Trophic Assessment in Chinese Coastal Systems— Review of methodologies and application to the Changjiang (Yangtze) Estuary and Jiaozhou Bay. Estuar. Coast. 30 (6), 1–18.