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Trade-offs between shellfish aquaculture and benthic biodiversity: A modelling approach for sustainable management

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Abstract

This paper presents an ecosystem modelling approach aimed at improving shellfish aquaculture management by explicitly considering natural benthic biodiversity. This methodology uses a combination of benthic field survey data, sediment and bathymetric mapping, physiological models and dynamic ecosystem modelling. The Wild species Integration for Shellfish Ecoaquaculture (WISE) approach helps to understand the baseline food requirements for maintaining natural benthic biodiversity of suspension-feeding organisms, thus informing managers on potential upper thresholds for shellfish aquaculture. WISE was tested in four coastal systems in Europe and China, including bays, estuaries and sea loughs with widely differing aquaculture activities. In the European systems, where the aquaculture industry is developing, species diversity and abundance are much higher and suspension-feeding wild species play an important role in the consumption of food resources. Densities of wild individuals were estimated to be 13 ind m^{-2} in Sanggou Bay (total: 2×10^9), 33 ind m^{-2} in Xiangshan Gang (total: 122×10^9), 95 ind m^{-2} in Carlingford Lough (total: 4.62×10^9) and 175 ind m^{-2} in Loch Creran (total: 2.62×10^9). Total clearance rates by wild populations were calculated as 5% of the total volume d^{-1} in Sanggou Bay (75×10^6 m^3 d^{-1}), 11% d^{-1} in Xiangshan Gang (434×10^6 m^3 d^{-1}), 40% d^{-1} in Loch Creran (93 – 99×10^6 m^3 d^{-1}) and 45% d^{-1} in Carlingford Lough (170–250×10^6 m^3 d^{-1}). In relative terms, wild populations play a more important role than cultivated shellfish in clearing suspended particles from the European systems due to the much lower aquaculture activity. 56% and 76% of total primary production in Loch Creran and Carlingford Lough, respectively, are consumed annually by wild organisms, while less than 50% is consumed in Chinese systems (45% in Sanggou Bay and 2.9% in Xiangshan Gang). Integration of the WISE approach within broader ecological modelling illustrates some of the trade-offs between commercial aquaculture and the conservation of biodiversity, showing that rates of and capacities for shellfish culture are reduced when both wild and cultured suspension-feeding species are considered in relation to the available seston. When food resources are partitioned between wild and cultivated species, there is a decrease in individual length and weight (9 to 22% reduction in shell length and 24 to 52% reduction in total fresh weight for the Pacific oyster; reductions of 6% in length and 20% in weight for blue mussel; reductions of 4% in length and 13% in individual weight for bivalves in Xiangshan Gang), resulting in a lower aquaculture production (e.g. for Pacific oyster, a reduction of 12.5% in Carlingford Lough, 34% in Loch Creran and of 9% for bivalves in Xiangshan Gang).

Keywords: Ecoaquaculture; Sustainable shellfish aquaculture; Biodiversity; Conservation; Wild species; Resource partitioning; Coastal systems; Ecological modeling; GIS; China; Europe

1. Introduction

The decline in fisheries worldwide (e.g. Naylor et al., 2000; Neori et al., 2004; Pauly et al., 1998; Pauly et al., 2002; Troell

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et al., 2003) has been accompanied by an increased commercial interest in aquaculture to meet the demand for fishery products, which is estimated to grow by 50 million tons by 2015 (FAO, 2004). World aquaculture production has been increasing at about 7.2% per year, with China being the major contributor (FAO, 2004). In that country alone, there are an estimated 42×10^6 ha deemed suitable for mariculture, and national targets have been set for a 15% production increase by 2010 and a 30% increase by 2020 (Zhu, pers. com.).

Shellfish aquaculture appears to be a particular growth area (e.g. Howlett and Rayner, 2004), taking advantage of the natural processing by filter-feeders of the base of the food-chain. The quality of farmed shellfish, which are both sessile and rely on naturally supplied particulate organic matter (POM), is not affected by the textural and dietary issues which can occur in cultivated finfish such as salmon and sea bass. Furthermore, shellfish culture is generally extensive by nature (although high density cultivation such as seen in the Po delta lagoons may exist), and therefore poses fewer environmental problems with respect to accumulated surplus food debris, localised benthic organic enrichment and oxygen depletion (McKindsey et al., 2006). In fact, it frequently plays a role in top-down control of the food web (e.g. Newell, 2004), and may have a significant effect in reducing the expression of eutrophication symptoms, as exemplified for Chesapeake Bay by Cerco and Noel (2007) and for Jiaozhou Bay in China by Xiao et al. (in press). Nevertheless, though to a far lesser extent than finfish, bivalve culture can also have undesirable effects on the environment (Miron et al., 2005). Shellfish are at a lower position in the trophic chain and community changes can affect various trophic levels (Cranford et al., 2003), and in particular may adversely impact natural biodiversity (e.g. Read and Fernandes, 2003).

Environmental modifications in shellfish-growing areas have been extensively documented (Raillard and Ménesguen, 1994; Christensen et al., 2003; Kurlansky, 2007), but center mainly on the impacts of over-exploitation and pollution on the cultivated species themselves. With the prospective expansion of shellfish aquaculture in Europe and America, there has been an important literature focus on carrying capacity (over 500 articles in the last five years: SCIRUS, 2007), and an effort to define terms (e.g. Inglis et al., 2000, Nunes et al., 2003) and refine methodologies to develop accurate assessments (Ferreira et al., 2007a; Gibbs, 2007). This is partly driven by emerging legislation, including the proposed U.S. Offshore Aquaculture Act (NOAA, 2006) and the E.U. Common Aquaculture Policy, currently under preparation.

The sustainable management of shellfish aquaculture must address some key concepts related to carrying capacity, including the harmonious co-existence of cultivated bivalves and naturally occurring (henceforth wild) species. The latter are important for many reasons, including preservation of biodiversity (e.g. Worm et al., 2006), role in ecosystem structure, and conservation aspects. Shellfish aquaculture may result in changes in benthic community composition (Crawford et al., 2003), through a range of mechanisms, such as excessive partitioning of food resources (Newell, 2004), competition for space (Gibbs, 2004) and increased sediment deposition (La Rosa et al., 2002). These concerns are reflected in legislative instruments such as E.U. Directive 92/43/EEC (Habitats) or the E.U. Biodiversity Strategy (1998a), and are in broad terms covered by the United Nations Convention on the Law of the Sea (UNCLOS).

The existing literature on interactions between cultivated shellfish and wild benthic species focuses mainly on direct deposition effects, organic enrichment of soft sediments and near-field modifications to community composition (Gibbs, 2007). Very little work exists at a broader scale, i.e. addressing ecosystem-scale effects (e.g. Mckindsey et al., 2006), and there are to our knowledge no models for prediction of shellfish carrying capacity which explicitly account for the role of wild species in partitioning the available food, and therefore allow for these organisms to be included in scenarios of development of commercial aquaculture.

This paper presents a modelling approach for the incorporation of benthic wild species in ecosystem models designed for evaluation of sustainable carrying capacity for bivalve aquaculture. Our approach, which is termed *Wild species Integration for Sustainable Ecoaquaculture* (WISE), has been developed with the following three objectives:

1. To determine baseline food requirements for maintaining benthic biodiversity in a natural system;
2. To improve accuracy in modelling carrying capacity for shellfish aquaculture by partitioning the food resource, i.e. phytoplankton and other particulate organic matter, between wild species and cultivated shellfish;
3. To establish upper thresholds to ensure the maintenance of wild populations when considering shellfish aquaculture development scenarios.

2. Methodology

2.1. General approach

The WISE approach aims for integrated sustainable management, and thus considers both the physical and biological features of a given ecosystem, and applicable legislation and uses.

The methodology is developed in three sequential stages: (i) Wild species distribution and selection; (ii) Resource partitioning assessment; and (iii) Integration in ecosystem models. These are described below, with reference to the conceptual model illustrated in Fig. 1. The focus of this paper is on naturally occurring species of benthic shellfish, which compete with cultivated animals by filtering the common resource pool of particulate organic matter. The approach presented is however applicable to filter-feeders in a general sense.

2.1.1. Wild species distribution and selection

Physical and biological features of an ecosystem, such as bathymetry, characteristic sediment types for different species, location of biotopes, and benthic abundance and density are analysed by means of seabed mapping via Acoustic Ground Discrimination Systems (AGDS), benthic grab data, descriptive surveys using Remote Operated Vehicles, video observations or diver surveys.

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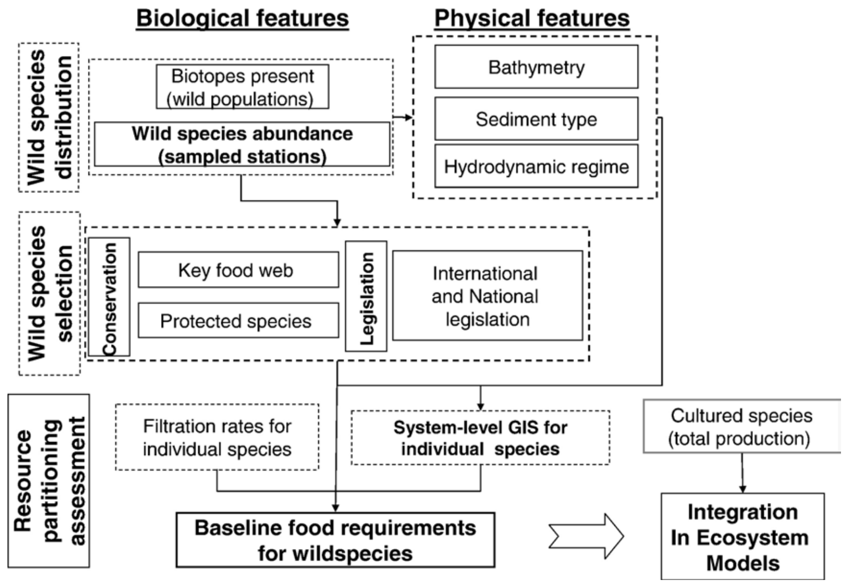

Fig. 1. Conceptual model of the WISE approach: Resource partitioning model for assessment of food availability and carrying capacity at the ecosystem / farm level. Dotted lines make reference to wild species distribution and selection stage of the methodology. Arrows represent the model sequential approach from the wild species distribution and selection to assess the resource partitioning between species and final integration in ecosystem models.

A considerable number of species usually emerges from survey data, but only a subset should be considered further, based both on the criteria detailed below (Fig. 1) and on practical aspects of application:

1. Keystone species, i.e. those which play a significant role in the flow of energy in an ecosystem, are fundamental components of the trophic web or are instrumental in buffering water quality, e.g. by exercising top-down control on chlorophyll concentrations;
2. Species of conservation interest, e.g. species in danger of extinction, those which are autochthonous and not easily found elsewhere, or reef-builders which provide a habitat for multiple species;
3. Species of economic interest. From an environmental economics standpoint, these include not only those with direct commercial importance, but all that provide important ecosystem goods and services (several of which are exemplified in the points above).

These species are selected using a dual approach, through: (i) the accumulated ecological and socio-economic knowledge available for a particular system; and (ii) applicable national and international legislation. Table 1 presents a review of relevant legislation concerning the marine environment, which aims to control the impacts of development and promote sustainable growth.

All spatial data are assimilated into a Geographic Information System (GIS) in order to generate bathymetry, sediment type and biotope/habitat surfaces. Quantitative data on wild species abundance are used to generate interpolated surfaces for each species. For our examples, an Inverse Distance Weight interpolation method was applied.

Information on typical habitat characteristics of each species is used to limit the interpolated results only to areas containing appropriate biotopes, sediment types and depths. Spatial statistical analysis is used to calculate the number of individuals of each species in the system.

The subset of species selected may form a large part of the overall species list, depending on the application of the criteria listed above. The overall abundance must be factored in so as to ensure that a reasonable approximation to the overall food requirement of wild species is simulated — this can be modelled in implicit form, by integrating the abundance of excluded species, considering a nominal average filtration rate, and including this bulk component as an extra GIS layer.

2.1.2. Resource partitioning assessment

The resource partitioning assessment aims to estimate the clearing/filtering capacity of the wild species selected in the previous stage as representative for a given ecosystem and determine the food availability for shellfish aquaculture development.

Total filtration by wild shellfish species is estimated using both the results of the spatial statistical analysis and appropriate filtration rates for each species present. When possible, minimal and maximal filtration rates are used in order to estimate a range for total filtration.

The volume cleared per day by the wild population is calculated by integrating the products of abundance and filtration rate for all species considered (Eq. (1)):

$$V_d = \sum_{i=1}^{n} (S_i F_i) \tag{1}$$

Where:

V_d Volume cleared per day (L d^{-1})
S_i Species i (of a total number n) expressed either in number of individuals or dry tissue weight (g_{dtw})
F_i Filtration rate for species i (L ind^{-1} d^{-1} or L g_{dtw} d^{-1})

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Table 1
Review of relevant legislation and policy instruments worldwide on the protection of the marine environment

Region	Title — Actions
Global	United Nations, 1982. US Doc. A/CONF.62/122 (UNCLOS) — Ensure that living resources in the EEZ is not endangered by over-exploitation
United States	Federal Water Pollution Control Act, 1972. USC 33 — Restore and maintain the chemical, physical and biological integrity of water
	The Coastal Zone Management Act, 1972. USC 16 — Develop and implement coastal zone management plans
	Harmful Algal Bloom and Hypoxia Research and Control Act, 1998 — combat the growing treat of HAB's
	NOAA, 2006 (Proposed Offshore Aquaculture Act) — Development of responsible marine aquaculture
Europe	EC, 1974. 94/156/EC (HELCOM) — Recommends criteria for the use of Best Available Techniques (BAT) and Best Environmental Practice (BEP)
	EC, 1976. 77/585/EEC (Barcelona Convention) — Mediterranean Action Plan (MAP)
	EC, 1992a. 98/249/EC (OSPAR) — Application of the precautionary and polluter pays principles
	EC, 1992b. 92/43/EEC (Habitats Directive) — Selection, designation and protection of Special Areas of Conservation (SAC's)
	EC, 1992c. COM/92/509 (Convention on Biological Diversity) — Conservation and sustainable use of biological diversity
	EC, 1998a. COM/98/0042 (Biodiversity Strategy) — Anticipate, prevent and attack causes of biodiversity loss or reduction
	EC, 1998b. COM/2002/539 (Marine Strategy) — Sustainable use of seas and conservation of marine ecosystems
	EC, 2000. 60/2000/EC (Water Framework Directive) — Programme of measures and River Basin Management Plans
Australia and New Zealand	Department of Conservation, 1994. ISBN: 0-478-01589-S— Sustainable management of natural and physical resources
	Commonwealth government's Coastal Policy, 1995 — Integrate government coastal management
	Commonwealth of Australia, 1998. ISBN: 0-642-54592-8 — coordination and consistency for marine planning and management
China	PRC laws on: Criminal (1979/03/14), Water (1988/01/21), Environmental Protection (1989/12/26), Animal Disease Prevention (1992/04/01), Entry-Exit Animal and Plant Quarantine (1992/04/01), Food Sanitation (1995/10/30), Prevention and Control of Water Pollution (1996/05/15), Marine Environmental Protection (2000/04/01), Fisheries (2000/10/31), Administration of Sea Areas (2002/01/01), Cleaner Production Promotion (2003/01/01), Environmental Impact Assessment (2003/09/01).
	Prescriptions of: Determining Fisheries Losses in Water Pollution (1996/10/08), Mollusc Produce Environment Sanitary Surveillance (1997/11/21) and Aquaculture Quality and Safety Administration (2003/09/01). Regulations on: Feeds and Feed Additives Administration (2001/ 11/29), Animal Drug Administration (2001/11/29).
	Standards on: Water Quality for Fisheries GB11607-89 (1990/03/01), Integrated Wastewater Discharge GB 8978-1996 (1998/01/01), Sea Water Quality GB 3097-1997 (1998/07/01), Environmental Quality for Surface Water GB 3838-2002 (2002/06/01), Discharge of Pollutants for Municipal Wastewater Treatment Plant GB 18918-2002 (2003/07/01). Criteria for Therapeutant Additives in Feeds (2001/07/01), Provisions for Marine Culture and Propagation Areas Monitoring (2002/04/01).

The time T (in days) required for wild shellfish species to clear the entire system is given by Eq. (2):

$$T = \frac{V}{V_d} \tag{2}$$

Where:

V System volume (L)
V_d Volume cleared (L d^{-1})

The food required for maintaining wild populations is calculated from Eqs. (3) and (4), which separately estimate both the living phytoplankton and detrital organic matter filtered daily, given that both components support shellfish growth, with associated dependencies that are explicitly modelled when accounting for cultured shellfish at larger scales (Hawkins et al., 2002; Ferreira et al., 2007a).

$$P_w = PV_d \tag{3}$$

$$D_w = DV_d \tag{4}$$

Where:

P_w Phytoplankton filtered per day (µg chl a d^{-1})
P Phytoplankton concentration (µg chl a L^{-1})
D_w Detrital POM filtered per day (mg d^{-1})
D Detrital POM concentration (mg L^{-1})

An identical approach can be taken for POM removal by cultivated shellfish, providing an indicator of the relative importance of both components (in this case P_c and D_c) in partitioning the food resource.

Although the use of ecological models is strongly recommended as the last stage of this methodology, if such a tool is not available, Eqs. (5) and (6) provide a simplified approach for determining an upper threshold τ for shellfish aquaculture. A mass balance may be written (Eq. (5)) for sources (left-hand side) and sinks of POM (right-hand side).

$$V(\phi P' + \varphi D) + L = \tau\left(\alpha_c P'_c + \beta_c D_c\right) + \sum_{i=1}^{n}\left(\alpha_i P'_w + \beta_i D_w\right) \tag{5}$$

Where:

ϕ Rate of autochtonous phytoplankton production (d^{-1})
P' Phytoplankton concentration (converted to mg L^{-1} for dimensional consistency with detrital POM)
φ Rate of autochtonous detritus supply (d^{-1})
L Net external loading of POM due to hydrodynamic exchange (mg d^{-1})
P'_w Phytoplankton filtered by wild species (converted to mg organic matter d^{-1} for dimensional consistency with detrital POM)

P'_C Phytoplankton filtered by cultivated species (converted to mg organic matter d^{-1} for dimensional consistency with detrital POM)

α and β Fraction of phytoplankton and detrital POM removed by wild and cultivated species. These coefficients are determined from the ratio of ingestion to filtration, i.e. correcting for rejection of faeces and pseudofaeces.

Eq. (5) may be rewritten as:

$$\tau = \frac{V(\phi P' + \varphi D) + L - \sum_{i=1}^{n} (\alpha_i P'_w + \beta_i D_w)}{(\alpha_c P'_c + \beta_c D_c)} \tag{6}$$

When $\tau = 1$ the average food resource remains unchanged, lower values of τ indicate that POM is being depleted in the system. The simplification shown in Eq. (6) is based on averages, and neglects the non-linearity inherent in the underlying ecological processes; it should therefore only be used for preliminary screening, and applied in a precautionary manner. Furthermore, although the decrease observed in τ with increased shellfish cultivation is an indicator of reduced sustainability, it does not allow stakeholders to analyse other consequences, such as the reduction in the Average Physical Product (APP) that accompanies excessive industry expansion.

2.1.3. Integration in ecosystem models

The final step is the integration with simulations of cultivated shellfish in the wider context of ecosystem modelling. Ecosystem models such as EcoWin2000 (Ferreira, 1995) may be used to dynamically simulate shellfish growth over a period of several years (Nunes et al., 2003; Ferreira et al., 2007a). Such models usually divide coastal systems into physical compartments (boxes) where biogeochemical processing is considered to be uniform, and which exchange pelagic state variables such as phytoplankton or detrital POM using a hydrodynamic module. Naturally occurring filter-feeders can be added to such models by superimposing the spatial box grid as a GIS layer on the (wild species filtration) GIS surfaces described above. We may therefore incorporate the natural removal of POM to reduce the food resource available to cultivated organisms.

EcoWin2000, which uses an object-oriented (OOP) approach, takes advantage of the polymorphism and multiple inheritance properties of OOP to simulate multiple shellfish species simultaneously. This approach, described by Nunes et al. (2003) for oysters and scallops, has been extended to include naturally occurring filter-feeders, and parameterised by defining a wild species abundance and filtration rate in each model box. The key difference is that in WISE the wild species are added to a model as forcing functions rather than state variables, such that growth is not being explicitly simulated, only their role in food removal. The boxes reflect differences in wild species composition, biotopes and abundance, as described previously, and provide appropriate spatial discrimination to reflect heterogenous estuarine and coastal benthic environments. An additional benefit from an ecological modelling standpoint is that the improved understanding of biotopes may be used as an additional criterion to define model boxes. Currently, for models such as EcoWin2000 these criteria include hydrodynamics, water quality, system uses and legislation such as the waterbody limits defined by EU Member States in compliance with Directive 60/2000/EC.

The simulation of wild species together with cultivated shellfish allows managers to evaluate the top-down pressure of both on the food resource, represented for instance as relative decrease in chlorophyll *a* (chl *a*) concentration, and the effects on shellfish production of maintaining wild communities. The use of this kind of model for mass balance analysis additionally allows an assessment of the relative roles of wild and cultivated populations in removing organic material produced in a waterbody.

The WISE methodology can be applied at the ecosystem scale (e.g. Ferreira et al., 2007a) or for a smaller area, such as an individual farm, using local depletion models such as FARM (Ferreira et al., 2007b). Ecological models such as these, which contemplate population dynamics of cultivated shellfish, provide additional leverage as management tools, since they will also provide information on changes to APP when expansion scenarios are considered.

2.2. Overview of case-study systems

Four case studies from Europe and China were selected to test this approach (Table 2 and Fig. 2).

The European systems, Loch Creran, (Western Scotland), and Carlingford Lough (a transboundary system in Eastern Ireland) are pristine environments with low to moderate aquaculture activities (Table 3).

The Chinese systems, Sanggou Bay in Northeast China and Xiangshan Gang near Ningbo City, help to illustrate why China is the major contributor to the world aquaculture production (FAO, 2004); Sanggou Bay is a coastal bay which annually produces an estimated 65 000 tons (total fresh weight) of shellfish, whereas the other Chinese system is an estuary with an annual production of about 38 000 tons. Although there are small areas in Europe which exhibit similarly high production, such as Sacca di Goro in Italy, where a clam production of over 15 000 tons takes place in an area of about 10 km^2, coastal embayments in China are systematically farmed in this way, resulting in an aggregate annual production of about eight million tons.

Table 2
Main physical characteristics of the four study sites

Physical characteristics	Sanggou Bay	Xiangshan Gang	Loch Creran	Carlingford Lough
Volume (10^6 m^3)	1486	3803	240	460
Surface area (km^2)	154 [a]	365	15	49
Maximum depth (m)	15	45	47	25
Mean temperature (°C)	12	24	10.5	11.5
Mean salinity	32	24	32.5	32.5
Catchment area (km^2)	600	1 478	164	274

[a] Interpolated area for the present study is 88 km^2.

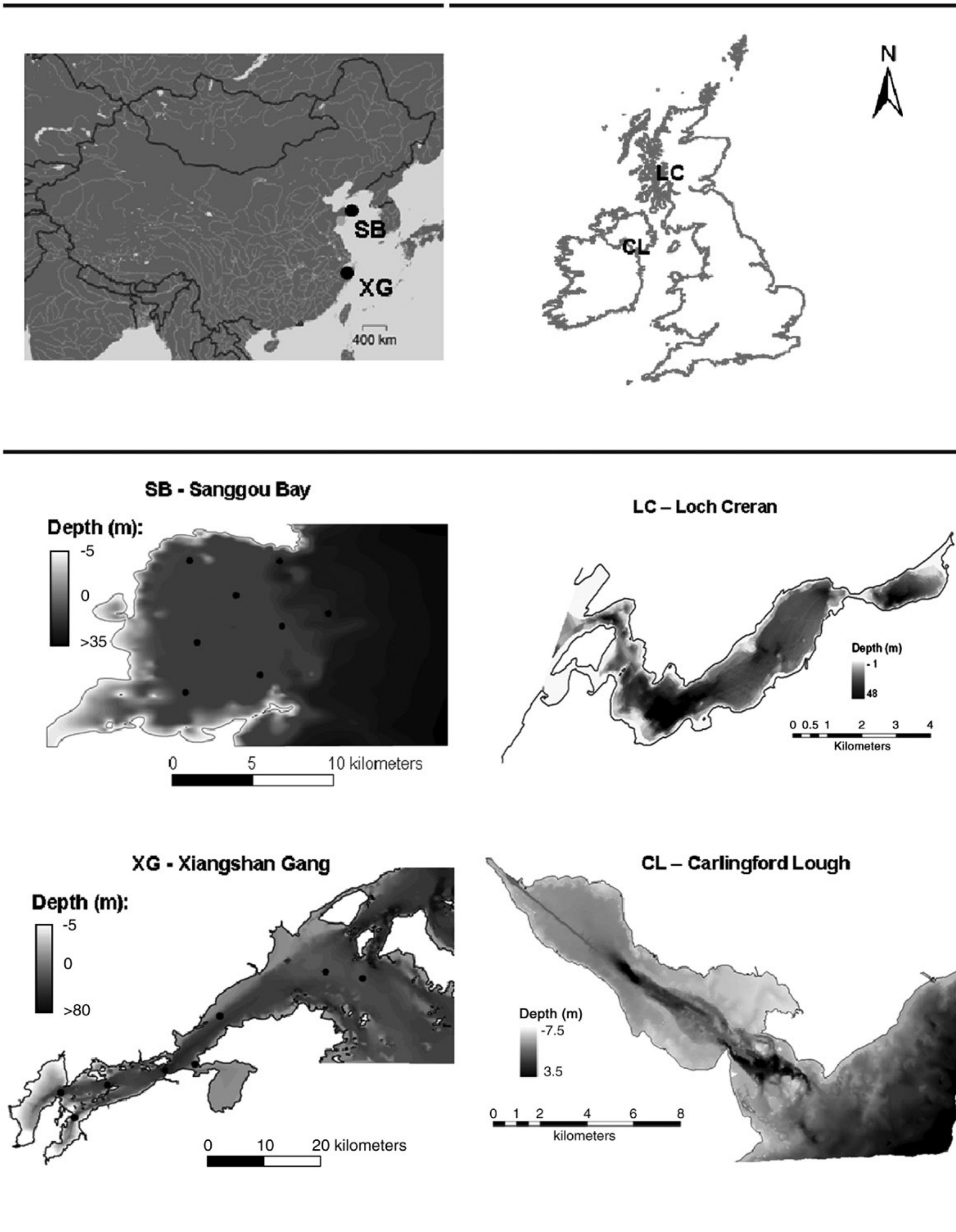

Fig. 2. Location and characteristics of the study sites. Chinese systems: SB — Sanggou Bay (Shandong Province), XB — Xiangshan Bay (Zhejiang Province) and European systems: LC — Loch Creran (Scotland) and CL — Carlingford Lough (Ireland). Black dots on the Chinese system maps indicate locations of sampling stations.

The eutrophication status of the four case-study systems has been previously evaluated using the ASSETS method (Bricker et al., 2003) and can be found at http://www.eutro.org (NOAA/IMAR, 2007). All the systems except Xiangshan Gang are classified at high status, i.e. do not exhibit eutrophication problems. For the latter, which is attributed *Moderate* status, the main issue is related to the occurrence of harmful algal bloom (HAB) events, rather than chlorophyll *a* or dissolved oxygen related problems. HAB occurrence appears to be mainly driven by offshore advective episodes, common in the East China Sea (see e.g. Xiao et al., in press).

For the subset of naturally occurring benthic wild species (Table 4 and 5) specific filtration rates were only found for *Hiatella artica* and *Modiolus modiolus*.

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Table 3
Main cultivated species, tonnage and value for the study sites

	Cultivated species	Common name	Production (ton yr^{-1})	(€ value)
Sanggou Bay (Nunes et al., 2003)	*Crassostrea gigas*	Pacific oysters [a]	13 000	2 795 699
	Mytilus edulis	Blue mussel [a]	–	–
	Chlamys farreri	Chinese scallop [a]	44 000	33 118 280
	Haliotis discus	Abalone [a]	–	–
	Tapes philipinnarum	Manila clam [c]	–	–
	Total		57 000	35 913 979
Xiangshan Gang (2004/2005)	*Ostrea plicatula*	Chinese oyster [a, c]	34 320	4 390 668
	Tapes philipinnarum	Manila clam [c]	2 902	371 265
	Sinonvacula constricta	Razor clam [b, c]	920	766 858
	Tegillarca granosa	Ark shell [c]	917	162 054
	Total		39 059	5 691 106
Loch Creran (2003/2004)	*Mytilus edulis*	Blue mussel [d, e]	500	–
	Crassostrea gigas	Pacific oysters [a, e]	100	
	Total		600	–
Carlingford Lough (2004/2005)	*Mytilus edulis*	Blue mussel [f, g]	2 500	2 468 000
	Pecten maximus	King scallop [g]	–	–
	Crassostrea gigas	Pacific oysters [e]	320	332 200
	Ostrea edulis	Native oysters [e]	–	–
	Tapes philipinnarum	Manila clam [h]	–	–
	Mytilus edulis	Wild mussel dredging	1 000	–
	Total		3 820	2 800 200

Culture types are indicated in superscript: a—subtidal; b—pond; c—intertidal; d—bag (subtidal); e—trestles (intertidal); f—bottom (subtidal); g—suspended (subtidal); h—plots (intertidal).

The filtration rate of *H. arctica* was found to vary between 0.0055 and 0.0341 L ind^{-1} h^{-1} at 5 and 15 °C, respectively (Jørgensen et al., 1991). These values were used to estimate minimal and maximal filtration due to individuals of this species in Loch Creran, where temperatures range from 6 to 15 °C.

The filtration rate F for the horse mussel *M. modiolus* was determined after Willet et al. (1999) (Eq. (7)):

$$F = 0.929W^{0.74} \tag{7}$$

Where:

W Dry tissue weight (g)

The dry weight of *M. modiolus* was considered to vary between 2 and 4 g, since the fresh weight of this species varies from 18 to 39.8 g (Willet et al., 1999). The minimal and maximal filtration rates were calculated using 1.5 and 2.6 L ind^{-1} h^{-1}, both for Loch Creran and Carlingford Lough.

No filtration rates were available for the other species, thus an average filtration rate of 1.5 L ind^{-1} h^{-1} was used in all systems, based on ranges observed over seasons and life cycles in a variety of bivalve shellfish (Jørgensen, 1966; Bayne and Newell, 1983; Meyhöfer, 1985).

Species from the genus *Abra* (found in Loch Creran and Carlingford Lough) have the potential to be both deposit and filter-feeders, with those living in coarse sand being predominantly filter-feeders. Since *Abra alba* is usually present in mud substrates (Table 5), in this study it was not considered as a filter-feeder. Conversely, *Abra nitida* was taken into account to estimate total filtration, given that its typical habitat can be in

Table 4
Summary of field data on wild shellfish species and WISE model results for each study site

		Sanggou Bay	Xiangshan Gang		Loch Creran	Carlingford Lough
		ind m^{-2}	ind m^{-2}	g m^{-2}	ind m^{-2}	ind m^{-2}
Field data						
Year		2004	2001		1999	1994
Number of species found		4	7		18	18
Min–Max densities		10 – 80	5 – 120	0.15 – 18	10 – 820	5 – 3 500
Average densities		35	36	7.76	136	547
Most abundant species		*Macoma pretexta*	*Nassarius siquinjorensis*		*Corbula gibba* (Basket shell)	*Modiolus modiolus* (Horse mussel)
Model results						
Mean shellfish densities		13	33	6	175	95
Total wild shellfish ($\times 10^6$)		2 100	12 000	2 132 tons	2 600	4 600
Filtration by wild populations ($\times 10^6$ m^3 d^{-1})	Range	–	–	26 – 260	93 – 99	170 – 250
	Mean	75	434	140	–	–
Time to clear the system (days)	Range	–	–	15 – 150	2.4 – 2.6	1.8 – 2.8
	Mean	21	9	27	–	–

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Table 5
Major habitat characteristics of benthic wild species in Loch Creran[a], Carlingford Lough[b], Xiangshan Gang[c] and Sanggou Bay [d]

Species	Sediment type	Depth
Abra alba [a,b]	Inshore muddy sand or mud substrates	Low water-mark offshore to 70 m
Abra nitida [a,b]	Muddy sand and gravel	Lower shore to high depths
Circomphalus casina [a]	Coarse sand and shell gravel	Shallow sublittoral to the edge of the continental shelf
Corbula gibba [a] (Basket shell)	Muddy sand and gravel	–
Donax kiusiuensis [c] (Coquina shell)	Sand	Intertidal to 10 m
Dosinia exoleta [a]	Muddy or shell gravel	Lower shore to 100 m
Ennucula tenuis [c]	–	6 to 85 m
Hiatella arctica [a]	Soft rock and shells (holes, crevices or algal holdfasts)	Lower shore to 50 m
Macoma praetexta [d]	–	Lower shore to 50 m (Huang, 1994)
Modiolus modiolus [a,b] (Horse mussel)	Soft sediments; coarse grounds or attached to hard substrates	Lower shore to 280 m
Mya arenaria [a,b]	Sand, mud, sandy mud and sandy gravel	Burrows up to 50 cm
Mya truncata [a]	Mixed sand, sandy mud or gravel substrates	Lower shore to 70 m
Mysella bidentata [a,b]	Muddy sand or fine gravel	–
Nucula nitidosa [a]	Fine sand, sandy mud and silt	Offshore on bottom
Nucula nucleus [b]	Fine sand, sandy mud and silt	Bottom
Nucula turgida [b]	Fine sand, sandy mud and silt	Bottom
Phaxas pellucidus [a]	Fine mixed sand	Offshore to 100 m
Scapharca subcrenata (Half crenate Ark) [c]	Sandy mud (BISYOGAI, 1999)	Intertidal to 20 m (BISYOGAI, 1999)
Theora fragilis [d]	–	Offshore to 50 m (Huang, 1994)
Thyasira flexuosa [a,b]	Muddy sand or fine gravel	–
Yoldia similis [d]	–	Offshore to 30 m (Huang, 1994)

Data obtained from MARLIN (undated), unless otherwise indicated.

coarser sediments (Table 5). Shellfish species for which no habitat information was available were included as filter-feeders, for precautionary reasons.

In Xiangshan Gang, minimal and maximal filtration rates per unit of soft tissue weight (0.5 and 5 L g^{-1} h^{-1}, respectively) were used to estimate filtration, since biomass density data were available. To compare total filtration estimated using filtration rates per individual (1.5 L ind^{-1} h^{-1}) and per biomass, an average filtration rate per unit of soft tissue of 2.75 L g^{-1} h^{-1} was used.

To estimate how much food is removed, the removal efficiencies for each species need to be known. Since this information is not available for the majority of species, a mean removal efficiency of 95% was determined heuristically for all wild species.

Information on the habitat characteristics of each species was used to improve the interpolated surfaces. Where no information on habitat types was available, interpolation surfaces were created for the mud sediment area.

In the Chinese systems no habitat information, sediment or biotope maps were available for wild shellfish species. Consequently, the interpolation surfaces for Xiangshan Gang were generated for the mud sediment area (entire ecosystem). For Sanggou Bay only the area for which there are quantitative data on wild shellfish abundance was considered, with no restrictions applied to the interpolation. Consequently, the accuracy of the GIS analysis for these two systems is reduced, which may lead to an overestimation of wild species abundance. This is nevertheless precautionary, since our aim is to contribute to the accurate definition of thresholds for sustainable commercial shellfish aquaculture.

The application of ecological models with and without naturally occurring filter-feeders was implemented for the four systems. This was done by integrating WISE into EcoWin2000 models, which have been described in general terms above, and reported in detail by Nunes et al. (2003) and Ferreira et al. (2007a).

If an appropriate ecological model is unavailable, the food removed by cultivated species may be accounted for by using nominal filtration rates. As an example, a filtration rate of 250 L ind^{-1} d^{-1} may be used for the Pacific oyster (*Crassostrea gigas*), and 16 L ind^{-1} d^{-1} for blue mussel (*Mytilus edulis*). The food removed and assimilated by these species may be calculated using the same approach as for wild species. To estimate the total number of cultivated animals, aquaculture production may be divided by mean individual weight at harvest. This would typically be 80–100 g for Pacific oyster and about 20 g for mussels.

3. Results and discussion

3.1. Wild species distribution and selection

3.1.1. Biotopes and sediment distribution

The biotope map for Loch Creran (Fig. 3) shows that sea pens and burrowing macrofauna occupy the mud sediment area, whilst aggregations of the red tube worm *Serpula vermicularis* are present in the shells and mud areas. Horse mussel (*M. modiolus*) beds can be found in the upper basin of the loch (Fig. 3).

Loch Creran sediments (Fig. 3) consist predominantly of fine mud except at the mouth and narrows where, due to stronger currents, the sediments are mainly cobbles (Black et al., 2000) and around the margins of the loch where shell and mud sediments occur.

Species abundance data for Loch Creran were available for the 5 sampling stations shown in Fig. 3. The basket shell (*Corbula gibba*) was found to be most abundant — 820 ind m^{-2} (Table 4). *M. modiolus* was also found to be present at high densities — 175 ind m^{-2}.

In Carlingford Lough, sediments vary gradually from coarse sand to mud from the entrance of the lough towards the Newry (Clanrye) river, and in the central part sediments are very irregular but dominated by

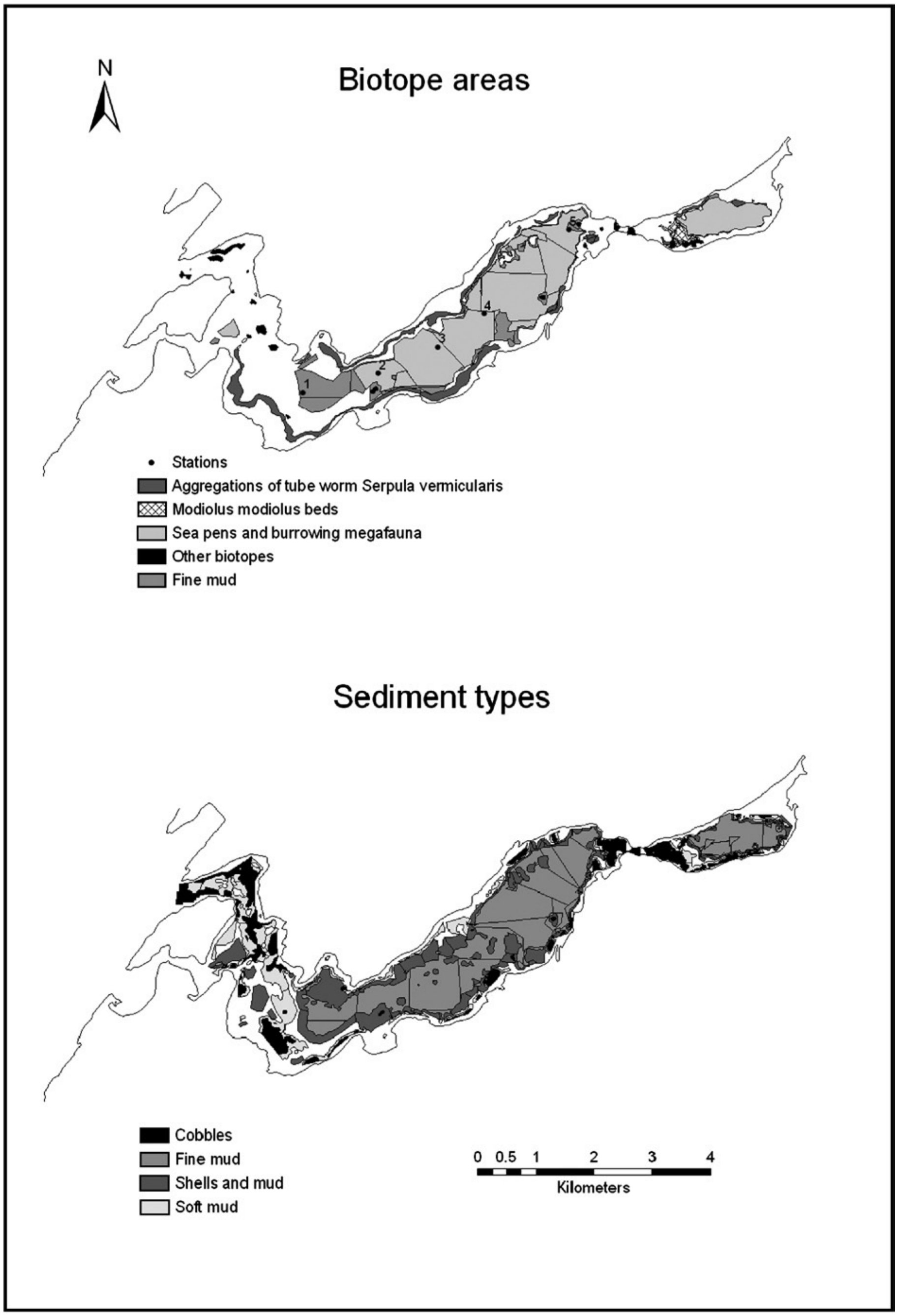

Fig. 3. Biotope and sediment maps and location of stations for species abundance data (1 to 5) for Loch Creran (Black et al., 2000).

sand (Fig. 4). Extensive beds of the sea-pen (*Virgularia mirabilis*) are present in the upper parts of the lough as shown in the habitat map (Fig. 4).

The most abundant species sampled was the horse mussel — a total of 3500 ind m^{-2} (Table 4).

The physical features analysed in the Chinese systems were limited by lack of data to the bathymetry and the sediments for Xiangshan Gang, which are a variable mixture of fine sand and mud. Species abundance data were available in these systems for the sampling stations shown in Fig. 2. A small variety of wild shellfish species were found to be present (Table 4). The most abundant species were *Macoma pretexta* (80 ind m^{-2}) in Sanggou Bay and *Nassarius siquinjorensis* (120 ind m^{-2}; 18 g m^{-2}) in Xiangshan Gang.

Table 5 provides a review of the habitat characteristics for each wild shellfish species found at the four study sites.

These species can be found from the intertidal zone to variable depths and within a range of fine to coarse sediments, but the majority is usually present in muddy sediments.

In the European study sites, where aquaculture is still in expansion, there is higher number of wild species (18 species — Table 4), with estimated average densities of 175 ind m^{-2} in Loch Creran and 95 ind m^{-2} in Carlingford Lough (Table 4). In the two Chinese systems, where shellfish aquaculture is very substantial, biodiversity was much lower and average densities were estimated to be 13 ind m^{-2} in Sanggou Bay (interpolation for only 60% of the total area, due to data availability) and 33 ind m^{-2} in Xiangshan Gang (Table 4).

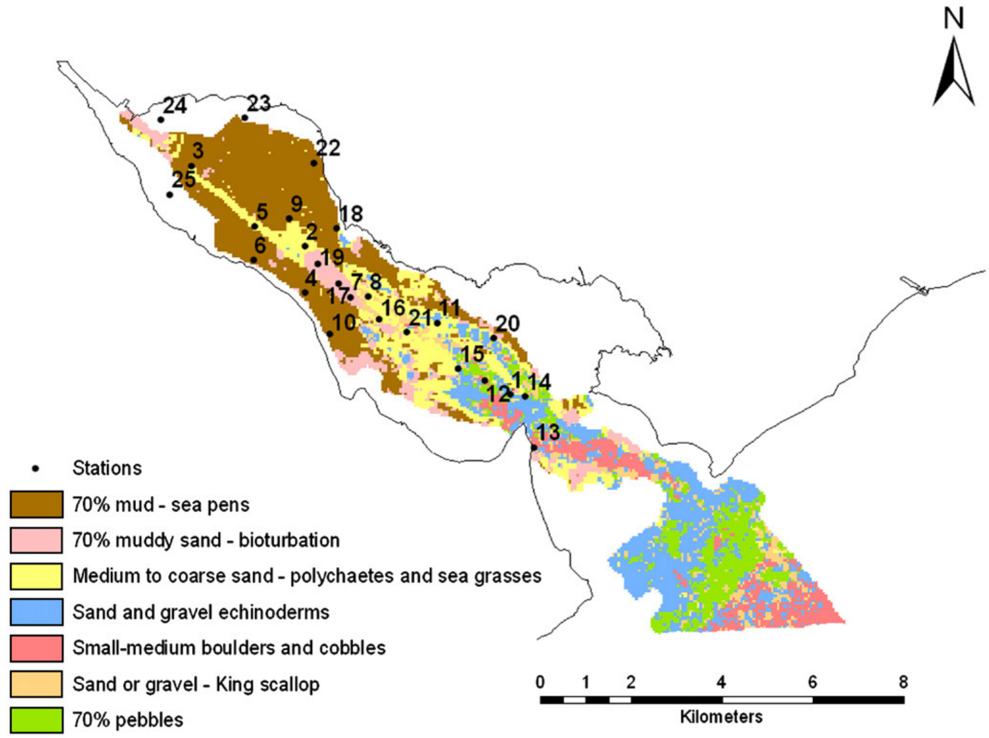

Fig. 4. Carlingford Lough habitats map and location of stations for species abundance data (1 to 25) (Ferreira et al., 2007a).

The interpolation surfaces show that wild shellfish species are not equally distributed within each system. Interspecific differences in spatial distribution are recognised, resulting from the types of sediment, water depths and biotopes. This differential distribution is shown in Fig. 5 for four different species in Loch Creran.

The spatial distribution for the total wild shellfish in each system was computed in GIS and is illustrated in Fig. 6.

The different spatial distributions suggest that food requirements vary both temporally (e.g. in spring blooms or winter periods) and spatially. Where wild species are present in large numbers more phytoplankton and detrital POM are required and less competition for food can be imposed through shellfish aquaculture.

3.1.2. Conservation and legislative aspects

Loch Creran is of great marine biological interest due to its tidal rapids and reefs of horse mussel and red tube worm (Scottish Executive, 1999). These reef-building species filter organic particles from the water column, although in the present study only shellfish

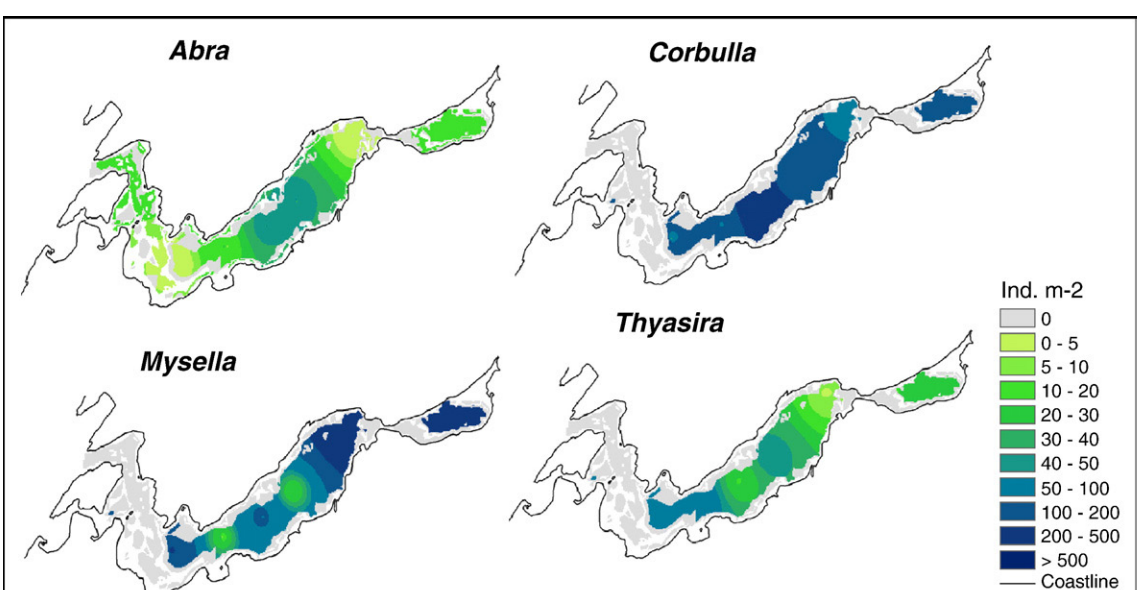

Fig. 5. Spatial distribution of four different species in Loch Creran (total estimated wild individuals are 167, 954, 818 and 105 million for *Abra nitida*, *Corbula gibba*, *Mysella bidentata* and *Thyasira flexuosa* respectively).

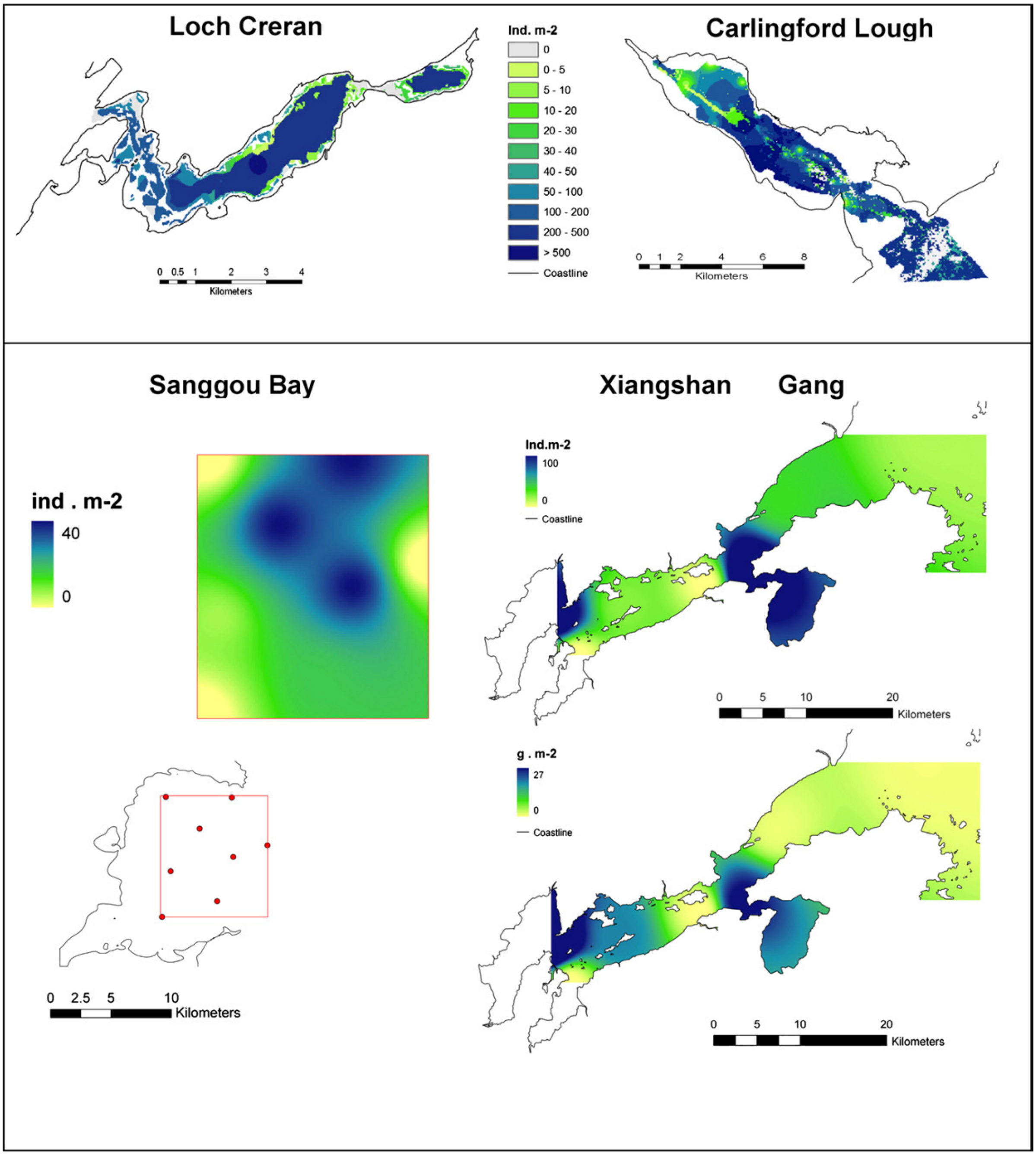

Fig. 6. GIS interpolations showing spatial distribution of the total shellfish species found in the European systems: Loch Creran (2.6×10^9 ind) and Carlingford Lough (4.6×10^9 ind) and for the Chinese systems: Sanggou Bay (2.1×10^9 ind) and Xiangshan Gang (12×10^9 ind).

filter-feeders were considered. The loch is considered a Special Area of Conservation (SAC) under the Habitats Directive for its "biogenic reefs". These are unique within the UK (JNCC, undated), and have been declining due to unknown causes (UK Biodiversity Group, 1999) which constitutes an additional concern with respect to sustainable growth of shellfish aquaculture.

Carlingford Lough is considered a Special Protection Area (SPA) under Directive 79/409/EEC (Birds Directive) due to its important feeding areas, in particular significant mud-flats and salt marshes. In these areas, aquaculture development may impact competition for space and for food between the cultivated species and the wild shellfish species consumed by birds.

In China several laws, regulations, prescriptions and standards were found to be applicable (Table 1). Specifically to the study sites referred here, Sanggou Bay was established as a conservation area for its valuable marine species (both cultured and wild) in 1987 by the Oceanic and Fisheries Bureau of Rongcheng City; however no further specific actions or updated information was available for this system. In Xiangshan Bay, several protection measures and legal dispositions were established by Ningbo Municipal City, listing species of economic interest (such as oysters and clams) as protected, establishing minimum sizes for harvest, prohibiting use of antibiotics, etc. Furthermore, the Huangdun Bay area (at the head of Xiangshan Gang) has been regulated as a protected area for natural restocking of juveniles of Manila clam.

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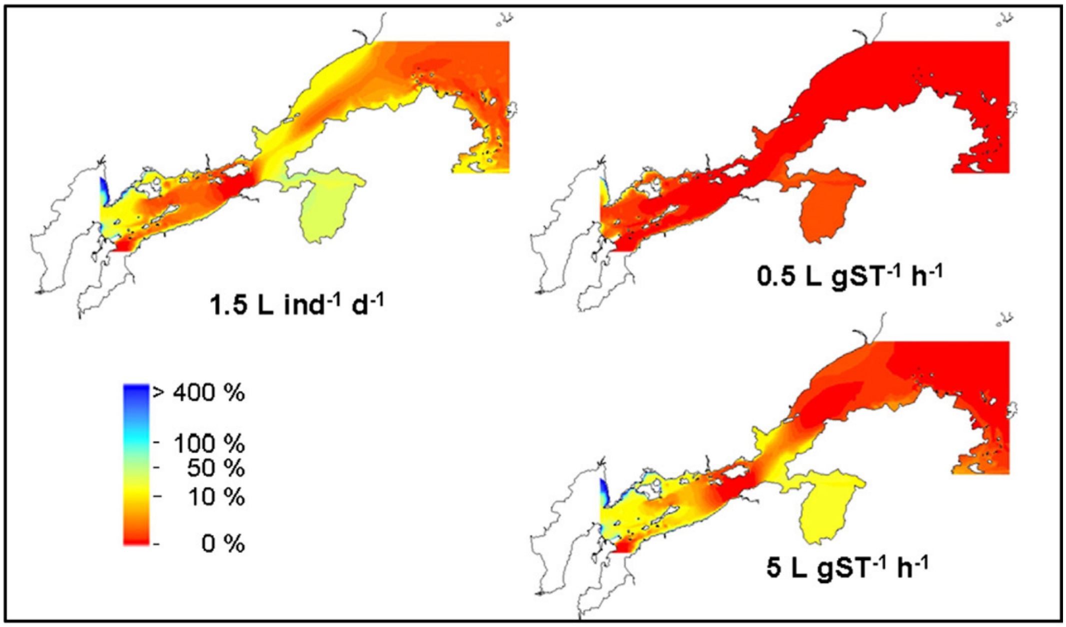

Fig. 7. Differences in clearance rates in Xiangshan Gang due to the differential spatial distribution of wild species and water depths. Surfaces were created based on the different filtration rates applied to this system (ST: soft tissue).

China is also part of the United Nations Convention on the Law of the Sea — UNCLOS, which stipulates that living resources in the Exclusive Economic Zone should not be endangered by overexploitation.

3.2. Resource partitioning assessment and ecosystem modelling

Total clearance rates by wild populations (Table 4) were calculated as 5% of the total volume d^{-1} in Sanggou Bay (75×10^6 m^3 d^{-1}), 11% d^{-1} in Xiangshan Gang (434×10^6 m^3 d^{-1}), 40% d^{-1} in Loch Creran (93 – 99×10^6 m^3 d^{-1}) and 45% d^{-1} in Carlingford Lough (170 – 250×10^6 m^3 d^{-1}). In relative terms, wild populations play a more important role in clearing suspended particles from the European systems due to the much lower aquaculture activity.

The total filtration rate in Xiangshan Gang was also estimated using an average filtration rate per unit biomass (Fig. 7). The time needed to clear the ecosystem was estimated to be about 27 days — much longer than the time estimated using individual filtration rates (about 9 d, see

Table 6
Sources and sinks of POM calculated for the four systems (values normalised per unit area in brackets, where applicable)

	Sanggou Bay	Xiangshan Gang	Loch Creran	Carlingford Lough (SMILE[a] model)	Carlingford Lough (early 1990's)
Average concentrations					
Chl *a* (µg l^{-1})	1.7	5.7 (median)	0.8	2.5	2.5
Detrital POM (mg l^{-1})	4.2	15.4	1.5	2.5	2.5
Sources of POM					
NPP (ton C yr^{-1}) (gC m^{-2} yr^{-1})	5024 (32.6)	399 900 (500)	272 (18.6)	2850 (56)	907 (17)
Sinks of POM					
Food uptake by wild species					
Phytoplankton (ton C yr^{-1}) (gC m^{-2} yr^{-1})	2250 (14.6)	11 600 (230)	152 (39)	81.4 (1.7)	690 (13.5)
Percentage NPP uptake	45%	2.9%	56%	2.9%	76%
Detrital POM (ton yr^{-1}) (g m^{-2} yr^{-1})	114 000 (740)	1670 (35)	38 758 (2657)	1708 (33.4)	38 061 (745)
Food uptake by cultivated species					
Blue mussel: phyto. (ton C yr^{-1}) (gC m^{-2} yr^{-1})	–	–	1.5 (0.101)	200 (3.92)	35.7 (0.7)
Blue mussel: POM (ton yr^{-1}) (g m^{-2} yr^{-1})	–	–	1473 (101)	201 000 (4 072)	35 691 (698)
Pacific oyster: phyto. (ton C yr^{-1}) (gC m^{-2} yr^{-1})	228 (1.48)	–	1.4 (0.097)	6.6 (0.13)	2.2 (0.04)
Pacific oyster: POM (ton yr^{-1}) (g m^{-2} yr^{-1})	161 500 (1049)	–	1447 (99.2)	6650 (130)	2211 (43.3)
Other: phyto. (ton C yr^{-1}) (gC m^{-2} yr^{-1})	701 (4.55)	–	–	–	–
Other: POM (ton yr^{-1}) (g m^{-2} yr^{-1})	15 247 (99)	–	–	–	–
Chinese oyster[b]: phyto. (ton C yr^{-1}) (gC m^{-2} yr^{-1})	–	1340 (45)	–	–	–
Chinese oyster[b]: POM (ton yr^{-1}) (g m^{-2} yr^{-1})	–	1380 (46)	–	–	–
Percentage NPP uptake	18.5%	0.34%	1.07%	7.25%	4.2%

[a] SMILE — Sustainable Mariculture in northern Irish Sea Lough Ecosystems (Ferreira et al., 2007a).
[b] Includes other cultivated shellfish species of lesser importance (see Table 3).

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Table 7
Percentage reduction in aquaculture production and animal size due to the inclusion of benthic wild filter-feeders in the EcoWin2000 carrying capacity model

Ecosystem	Cultivated species	Production (Harvested)	Shell length	Total fresh weight
Loch Creran	Pacific oyster	−34%	−21.5%	−52%
Carlingford Lough	Blue mussel	−19%	−5.8%	−20%
	Pacific oyster	−12.5%	−9.2%	−24%
Xiangshan Gang	Chinese oyster [a]	−9%	−4.3%	−13%

[a] Includes other cultivated shellfish species of lesser importance (see Table 3).

Table 4). This may suggest that the average filtration rate per individual used for the species in the Chinese systems is overestimated; this rate varies allometrically, and the wild species found in Chinese systems are thought to be generally smaller than those found in the European ones. For precautionary reasons, the higher of the two values was used in subsequent calculations, including the application of the ecosystem model.

Results of the integration of the WISE model in broader ecosystem models can be seen in Table 6, which shows food uptake by wild species, i.e. the natural baseline food requirements, together with food uptake by cultivated species in each system.

The food consumed by naturally occurring shellfish species in Loch Creran was estimated to be 152 tons of phytoplankton carbon per year (56% of net primary production — NPP) and about 39×10^3 tons of detrital POM per year. Wild species in Loch Creran are shown to be consuming more than half of the available net primary production.

In Carlingford Lough, these numbers currently correspond to about 81 ton C yr^{-1} (3% of NPP) and 1.7×10^3 ton yr^{-1} of detrital POM. The numbers of wild individuals were initially estimated based on surveys from 1994, but our simulations have considered a substantial reduction, given that present aquaculture production values are markedly higher than at that time (Ferreira et al., 1998). If the original benthic distribution data for surveys in the early ’90s are used, wild species account for 76% removal of NPP. For comparison, Table 7 shows simulation results both for the 1990’s benthos data and for a more realistic set of present conditions. An updated benthic survey is a key management requirement in order to improve confidence in models simulating the partitioning of food resources.

Wild species in Sanggou Bay remove 2 250 ton of phytoplankton C yr^{-1} and 114×10^3 ton detrital POM yr^{-1}, and 11 600 ton phytoplankton C yr^{-1} and 1670 ton detrital POM yr^{-1} in Xiangshan Gang. These quantities correspond to 45% of net primary production in Sanggou Bay and 2.9% in Xiangshan Gang. The spatial variability in removal of phytoplankton and organic detritus is illustrated for Xiangshan Gang in Fig. 8.

Table 6 shows that in Loch Creran, a pristine site where aquaculture is still potentially expanding, the contribution of wild species to food removal from the system is highly significant compared to the food removed by cultivated species. In Sanggou Bay (where shellfish aquaculture production is substantial) the percentage of NPP uptake by cultivated species is the highest out of all the systems, and in Xiangshan Gang both values are low, probably due to the lower filtration rates of the Chinese Oyster *Ostrea plicatula* and the prevalence of fish cage culture in the bay, which constitutes an additional supply of organic detritus, since this is an area where integrated multi-trophic aquaculture is common practice.

Aquaculture production accounting for the maintenance of wild species in the systems was also estimated using EcoWin2000 model (Table 7). For Loch Creran, simulation results yield a total production of

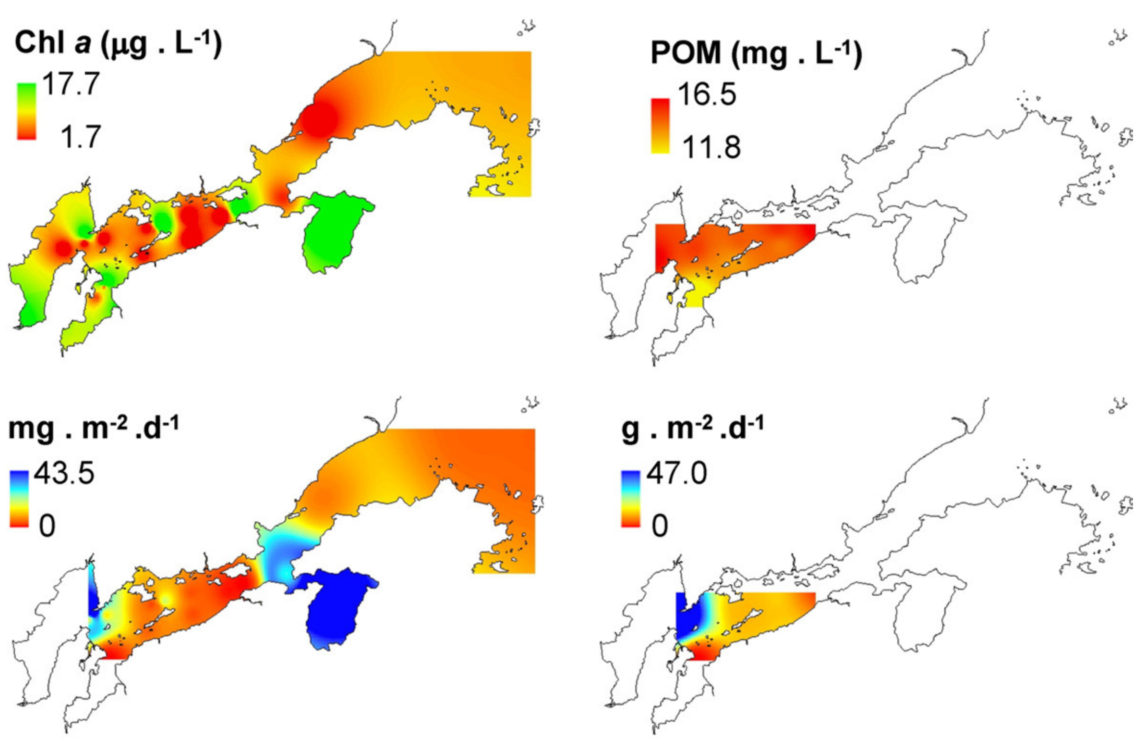

Fig. 8. Chl *a* and detrital POM availability in the water column and differential food clearance by wild species in Xiangshan Gang, according to the number of wild species present in the different areas.

146 tons of oysters, with mean individual (total fresh) weight of 48 g and mean shell length of 7.9 cm, when wild species are not considered. When these are added to the simulation, the total production in the Loch was reduced by 34% to a total of 96 tons of oysters, with lower shell lengths (6.2 cm; 21.5% reduction) and weights (23 g; 52% reduction).

In Carlingford Lough, where the cultivation of Pacific oysters and blue mussels is simulated, an identical pattern was observed. Oyster production decreased 12.5% from 320 to 280 tons, shell length decreased 9.2% from 9.8 to 8.9 cm and total fresh weight decreased 24% from 82.1 to 62.4 g, while mussel production decreased 19% from 1600 to 1300 tons, shell length from 5.2 to 4.9 cm (5.8% reduction) and total fresh weight decreased 20% from 11.5 to 9.2 g.

In Xiangshan Gang the simulated biomass of the cultivated species when wild species were considered was 38 564 tons, with mean individual (total fresh) weight of 29 g and mean shell length of 6.3 cm. This represents a small reduction of 9% in the production and a corresponding reduction of 4.3% and 13% of individual length and weight, respectively.

These results suggest that in systems where shellfish aquaculture is expanding, but nevertheless still at a sustainable stage, the food required for maintaining natural communities may constitute a significant cap on production. Scenarios of increased seeding density and/or spatial occupation for shellfish culture reveal that the APP decreases more sharply when wild species are included in the model, and in some locations in Carlingford Lough, when the 1990's benthic species abundances were considered, the growth of cultivated animals was not sufficient to classify such areas as viable for aquaculture. This type of simulation approach may thus also be used to develop maps prior to the development of cultivation areas, which provide management information on the trade-offs between natural and cultivated species, suggesting where both can co-exist harmoniously and provide appropriate business incentives, and where competition for food will mean that shellfish aquaculture development may have a significant opportunity cost with respect to other management options.

4. Conclusions

The approach described in this paper is a significant step towards improved assessment of ecological carrying capacity (*sensu* Gibbs, 2007) for shellfish growing areas. It was first applied in the Sustainable Mariculture in northern Irish Sea Lough Ecosystems (SMILE) project (Ferreira et al., 2007a), addressing the oversight concerns expressed by environmental and conservation stakeholders.

Presently there are a number of limitations to WISE, which should be considered in future developments:

- ❑ Only benthic filter-feeding shellfish are simulated. Other groups such as polychaetes and cnidaria are candidates for inclusion, given their role in competing with cultivated shellfish for the same food resource;
- ❑ There is no specific accounting for the role of pelagic organisms in competition for food resources, although models such as EcoWin2000 typically simulate zooplankton production; for this reason, WISE will not be extended to incorporate the pelagic component, which must in any case be addressed differently, since the GIS approach used for sessile benthic species is not applicable;
- ❑ Improvements in baseline data. Experimental measurements are required on filtration/clearance rates of key wild species; these rates exhibit both intraspecific (e.g. allometric and seasonal) and interspecific variability. For population estimates, robust species abundance data and a good habitat map can be of great help in improving interpolation surfaces and GIS analysis;
- ❑ Wild species are considered in the ecological model as forcing functions, i.e. their role in limiting food available to cultivated animals is simulated, but their own growth reduction due to competition from aquaculture is not simulated. Ongoing development of models for species such as the horse mussel *M. modiolus* are designed to address this shortcoming. Explicit simulation of individual growth for key wild species (see e.g. Ferreira et al., 2007a) will allow their incorporation in population dynamics models, which explicitly account for feedbacks between the cultivated and natural populations.

The integration of WISE in ecosystem models is particularly valuable when, as is the case in EcoWin2000, the demography of cultivated shellfish is simulated. The effect of wild species in the model is typically a reduction in scope for growth of cultivated animals, and population dynamics models driven by individual growth reflect this in a reduction in yields of the marketable cohort(s). APP values fall, and the seeding density at which profit is maximized will be lower (see Ferreira et al., 2007b for an example of profit maximization using marginal analysis).

The demand for cultivated shellfish in the U.S., where shellfish aquaculture production is two orders of magnitude lower than in Europe, substantially outstrips supply. However Europe is already also a net importer (MacAllister Elliott and Partners, 1999). Given the constraints on large-scale development of aquaculture, including substantial differences in cost structure, shellfish farmers in the western world cannot hope to compete with their eastern counterparts on volume. The future of shellfish aquaculture in the west lies in comparatively low-volume production of high-quality branded shellfish, returning a premium by selling to niche markets. This strategy, which might be termed ecoaquaculture, reflects a number of concerns, including the quality of raw materials, conservation aspects and preservation of natural capital, resulting in a well-integrated industry and highly competitive products. The development of approaches such as WISE, and the integration of these into ecological models used in decision-support, aims to go some way towards making these aspirations a success.

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