Journal of Shellfish Research, Vol. 37, No. 3, 1–18, 2018.

ECOLOGICAL CARRYING CAPACITY FOR SHELLFISH AQUACULTURE—SUSTAINABILITY OF NATURALLY OCCURRING FILTER-FEEDERS AND CULTIVATED BIVALVES

JOAO G. FERREIRA,[1]* RICHARD A. CORNER,[2] HEATHER MOORE,[3] MATT SERVICE,[3] SUZANNE B. BRICKER[4] AND ROBERT RHEAULT[5]

[1]*Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa Quinta da Torre, 2829-516 Monte da Caparica, Portugal;* [2]*Longline Environment Ltd, 88 Wood Street, London EC2V 7RS, UK;* [3]*Coastal Science, Fisheries & Aquatic Ecosystems Branch, Agri-Food and Biosciences Institute, Newforge Lane, Belfast BT9 5PX, United Kingdom;* [4]*NOAA—National Ocean Service, NCCOS, 1305 East West Highway, Silver Spring, MD 20910;* [5]*East Coast Shellfish Growers Association, 1623 Whitesville Road, Toms River, NJ 08755*

ABSTRACT Carrying capacity models for aquaculture have increased in complexity over the last decades, partly because aquaculture growth, sustainability, and licensing are themselves extremely complex. Moreover, there is an asymmetric pattern to all these components, when considered from an international perspective, because of very different regulation and governance of the aquaculture sector in Asia, Europe, and America. Two case studies were used, from Long Island Sound in the United States, and Belfast Lough, in Europe, to examine the interactions between cultivated shellfish and other autochthonous benthic filter-feeders. The objective is to illustrate how such interactions can be incorporated in system-scale ecological models and analyzed from the perspective of ecological carrying capacity. Two different models are described, one based on equations that relate the filtration rate of the hard clam *Mercenaria mercenaria* to physiological and population factors and one based on a habitat-specific analysis of multiple species of benthic filter-feeders. Both types of models have relative advantages and challenges, and both were integrated in ecosystem modeling frameworks with substantial numbers of state variables representing physical and biogeochemical processes. These models were applied to (1) examine the relative role of the two components (cultivated and wild) in the filtration of particulate organic matter (both phytoplankton and organic detritus), (2) quantify the effect of wild species on harvest of cultivated organisms (eastern oyster and blue mussel), and (3) assess the role of organically extractive aquaculture and other filter-feeders on top–down control of eutrophication.

KEY WORDS: carrying capacity, shellfish, biodiversity, Belfast Lough, Long Island Sound

INTRODUCTION

Many nations in the developed world have enacted specific policies for aquaculture expansion to respond to challenges such as the decline in capture fisheries (FAO 2016). In Europe, the European Commission recently published its "Strategic Guidelines for the sustainable development of European Union (EU) aquaculture" (European Commission 2013) identifying the need to simplify and expedite licensing applications and to foster sustainable development through improved spatial planning, enhanced competitiveness, and shared best practices.

These guidelines state that aquaculture development must be balanced with improving the aquatic environment. European Union environmental policy for aquatic systems is enacted through instruments such as the Water Framework Directive (WFD; 60/2000/EC) and the Marine Strategy Framework Directive (MSFD; 56/2008/EC), and in compliance with the requirements of the Habitats Directive and Birds Directive. Member states are encouraged to contribute to sustainable aquaculture development to narrow the gap between EU production and consumption.

As an example, the Northern Ireland executive appointed an industry-led Agri-Food Strategy Board in 2012 to develop a Strategic Plan to chart the way forward for the agri-food sector. The Agri-Food Strategy Board consulted widely with stakeholders to inform the development of its strategy report, which outlines a number of recommendations to promote growth of the fish and aquaculture sector, with a target to grow turnover by 34% by 2020 (AFSB 2012).

In the United States, the National Aquaculture Act of 1980 (United States House of Representatives 20, 96th Congress 1980), the 2011 Department of Commerce (USDOC 2011), and National Oceanic and Atmospheric Administration aquaculture policies (NOAA 2011a), which include the National Shellfish Initiative (NOAA 2011b) and Aquaculture component of the National Ocean Policy (NOAA 2016) have similar aims, i.e., to increase shellfish cultivation and improve ecosystem health. The Shellfish Initiative exemplifies the goals of these acts—to increase populations of bivalve shellfish (oysters, clams, abalone, and mussels) in U.S. coastal waters through sustainable commercial production and restoration activities. The National Oceanic and Atmospheric Administration recognizes the broad suite of economic, social, and environmental benefits provided by shellfish, which include jobs and business opportunities, meeting the growing demand for seafood, habitat for important commercial, recreational, and endangered and threatened species, species recovery, cleaner water and nutrient removal, and shoreline protection. These programs also recognize the beneficial ecosystem services associated with large populations of shellfish (either cultured or wild) such as reduction in turbidity and improvements in water quality associated with filter feeding and the provision of structured habitat, which improves the productivity of juvenile finfish, crabs, and forage species.

---

*Corresponding author. E-mail: joao@hoomi.com

DOI: 10.2983/035.037.0300

In both the United Sates and EU, these policies are driven by considerations of food security, trade balance, and local employment—the EU currently imports 71% of its aquatic products (European Commission 2016). According to Tiller et al. (2013), 5 y ago, the United States imported 86% of its aquatic products, leading to an annual U.S. seafood trade deficit of 10 billion dollars; current data suggest that 91% (by value) is now imported, with an annual deficit presently standing at $11.2 billion (NOAA 2017).

As a consequence of this deficit, and projections of large increases in future global seafood demand (World Bank 2013), there is a need to increase production to meet local and global demands for food, while ensuring positive environmental impacts (Merino et al. 2012); increased bivalve culture is seen as an opportunity to achieve both.

The concept of carrying capacity for aquaculture has broadened over the last few decades to include ecological balance, social license, governance, and economic optimization (Smaal et al. 1998, McKindsey et al. 2006, Ferreira et al. 2008, Nunes et al. 2011) as multiple stakeholders engage in the discussion of sustainable expansion of shellfish and finfish farming in open waters.

These four pillars of carrying capacity are encapsulated in the Ecosystem Approach to Aquaculture (Soto et al. 2008), illustrated in Figure 1.

The multiple challenges for quantitative assessment of ecological balance have stimulated the development of tools to support decisions on species and site selection, stocking densities, and areal coverage (Ervik et al. 2008, Radiarta et al. 2008, Filgueira & Grant 2009, Byron & Costa-Pierce 2013).

For finfish culture in open water cages, the ecological component of the licensing process is often based on the assimilative capacity for organic loading to the sediment—similar thresholds exist in Canada (1 gC m^{-2} d^{-1}; Robinson personal communication) and Scotland (350 gC m^{-2} y^{-1}; Ross personal communication), and models are widely used to determine loading (e.g., Corner et al. 2006, Ferreira et al. 2014, Cubillo et al. 2016) and to analyze its impact on natural benthic biotopes (Cromey et al. 2002). From a regulatory perspective, the assessment has been developed into licensing criteria such as the Allowable Zone of Effect (Henderson & Davies 2000, Karakassis et al. 2013).

Bivalve shellfish present a more complex picture with respect to ecological carrying capacity, particularly when such species are nonindigenous, such as the Pacific oyster *Crassostrea gigas* and the Manila clam *Venerupis philippinarum*, both widely cultivated in Europe and the United States, or when indigenous species such as the blue mussel *Mytilus edulis* or the quahog *Mercenaria mercenaria* are cultivated on a large scale (e.g., Zhang et al. 2009, Silva et al. 2011).

In both cases, the cultivated species potentially threaten ecosystem balance, in particular with respect to other filter-feeding organisms. Apart from the serious issues of invasive species and aquatic diseases, this threat can be expressed in several ways:

(1) Bivalve aquaculture is organically extractive: native ''wild'' species and cultivated shellfish compete for phytoplankton and detrital organic matter available in the water column.
(2) Bivalve culture at high stocking density in suspended structures such as rafts or longlines may locally impact the bottom in a similar way to finfish cage culture. In extreme situations, bivalve culture (or even large populations of wild shellfish) may result in a net increase in organic matter *within* a system by increasing benthopelagic coupling and accelerating the deposition of particulate organic matter (POM) (Cranford et al. 2007), even though, in total budgetary terms, organically extractive aquaculture must lead to a net removal of POM.
(3) Bottom culture of bivalves, including geared culture in cages or trestles, may deprive naturally occurring species of habitat and, therefore, have an impact on conservation of natural biotopes (Sequeira et al. 2008). Mechanical harvest methods such as dredging may compound the problem although this disturbance is transitory (Stokesbury et al. 2011).

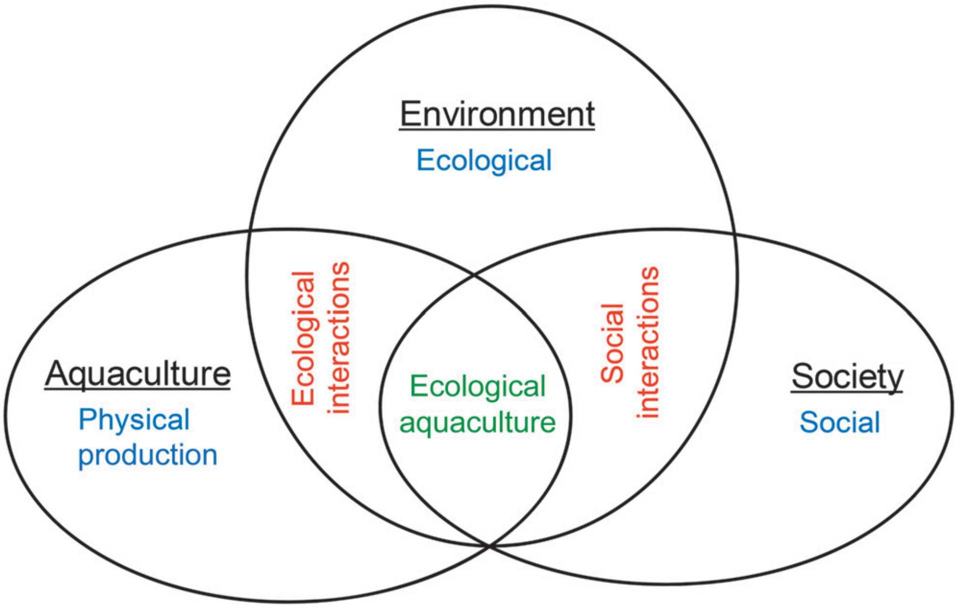

Figure 1. Harmonization of the four pillars (in blue) of carrying capacity to arrive at an ecosystem approach to aquaculture (in green).

(4) Bivalve culture is a net source of dissolved nutrients and can potentially lead to far-field (i.e., ecosystem-scale) eutrophication.

There is considerable discussion concerning these issues, all of which are broadly related to conservation—arguments on these topics are often emotionally charged and, therefore, a quantitative analysis of potential impacts may inform the decision-making process.

A number of mathematical models exist for the simulation of shellfish aquaculture in estuarine and coastal systems, with an emphasis on production (Raillard & Ménesguen 1994, Ferreira et al. 2008, Filgueira & Grant 2009) and, in some cases, also on environmental effects such as release of pseudofeces and feces (Ferreira et al. 2007, 2009) and on phytoplankton drawdown (Filgueira et al. 2014, 2015). Such models typically exhibit a set of common features, including (1) simulation of physiology at the individual level, (2) some form of integration to the population scale, and (3) a description of water and particle transport.

Only those models that address bivalve aquaculture at a system scale merit consideration in this context because both food depletion and habitat loss should be analyzed at an appropriate spatial dimension, to provide an assessment of overall ecosystem balance, and allow regulators to properly consider this element of licensing. Such models typically add the relevant biogeochemical compartments to the feature set above.

Although static approaches based on principles of ecosystem equilibrium have been previously used for an integrated analysis of carrying capacity (Byron et al. 2011a, 2011b) and make a more extensive use of food web analysis, the temporal and spatial elements necessary for detailed aquaculture management are not part of that approach.

Only Sequeira et al. (2008) have explicitly included a wild species component in dynamic, ecosystem-scale models focused on shellfish aquaculture, in an analysis for Loch Creran, Scotland, and Xianshang Gang, China.

This review illustrates how ecosystem models can be used to understand the role of wild species in an integrated assessment of carrying capacity and to optimize sustainable shellfish aquaculture production. The objectives of this work are as follows:

(1) to provide complementary examples of the application of mathematical models in habitat modeling;
(2) to evaluate the role of naturally occurring wild filter-feeders as competitors of cultivated organisms; and
(3) to advise managers and policy-makers on approaches for assessing environmentally sustainable and socially acceptable expansion of aquaculture.

MATERIALS AND METHODS

Overview

Two different approaches were reviewed for the assessment of the role of wild species in coastal areas used for shellfish cultivation. Both approaches were developed within an ecosystem model framework (EcoWin.NET, Ferreira 1995) that contains appropriate physical and biogeochemical processes, and a full implementation of growth and environmental effects of shellfish aquaculture (Ferreira et al. 2008, Bricker et al. 2018).

The first model was developed as part of the REServ Project for Long Island Sound (LIS), United States, where aquaculture of the eastern oyster *Crassostrea virginica* competes with harvest of the hard clam (quahog), *Mercenaria mercenaria*. Both species play an important role in top–down control of eutrophication through bioextraction of phytoplankton and organic detritus.

The second model, called *Total Ecosystem Approach to Sustainable Aquaculture in Northern Irish sea lough Ecosystems* (TEASMILE), was applied to Belfast Lough (BEL), Northern Ireland, which has an (historic) annual production of about 6,000 t of blue mussel (*Mytilus edulis*). The lough is regulated by a number of European Directives, and the main objectives of the model were to examine the role of different natural benthic biotopes in processing particulate organic material and to understand interspecific competition with cultivated mussels. Several MSFD quality descriptors (QD) are relevant to these questions, particularly QD1 Biodiversity (Cochrane et al. 2010), QD4 Food Webs (Rogers et al. 2010), QD5 Eutrophication (Ferreira et al. 2011), and QD6 Seafloor Integrity (Rice et al. 2012).

Long Island Sound Case Study

Site Description

Long Island Sound is a large estuary (3,259 km^2) located between Connecticut to the north and Long Island, NY, to the south (Fig. 2). Three major tributaries, the Connecticut, Thames, and Housatonic rivers, enter from the north, contributing 90% of the total freshwater to the Sound, with the Connecticut River alone accounting for about 70% of the total (Wolfe et al. 1991). F2

The watershed area is 12,773 km^2 and includes parts of Vermont, New Hampshire, Massachusetts, Connecticut, Rhode Island, and New York. It is highly developed, particularly in the areas including the New York metropolitan area as well as around Bridgeport and New Haven, two of Connecticut's largest cities. The watershed population in 2010 was about 8.93 million people, with nearly half the population living near the coast in New York and Connecticut (Bricker et al. 2018).

The Sound is connected to the Atlantic Ocean at its eastern end via Block Island Sound and connects to the East River and New York Harbor to the west. Average depth is about 20 m, with an average tidal range of about 2 m in the west and 1 m in the east, and water residence time is 2–3 mo. The mean salinity of LIS is 28 psu. Salinity at the eastern end of the Sound is 35 psu, i.e., full strength seawater, and the mean salinity in the western end is 23 psu, suggesting significant longitudinal mixing, although the East River discharge promotes stratification particularly during the spring runoff period (Bricker et al. 1997).

Severe water quality degradation and critical habitat loss have resulted from a multitude of anthropogenic activities along its coastline (Latimer et al. 2014). Long Island Sound's large and highly developed watershed has resulted in high nutrient loading to the waterbody, primarily through atmospheric deposition, treated sewage discharge, and non-point runoff. Nitrogen loads increased dramatically over the last two centuries (Varekamp et al. 2014). Those loads, combined with strong summer thermal stratification in the western part of the Sound, make LIS susceptible to seasonal hypoxia, one of the main indicators of eutrophication impacts. The areal extent

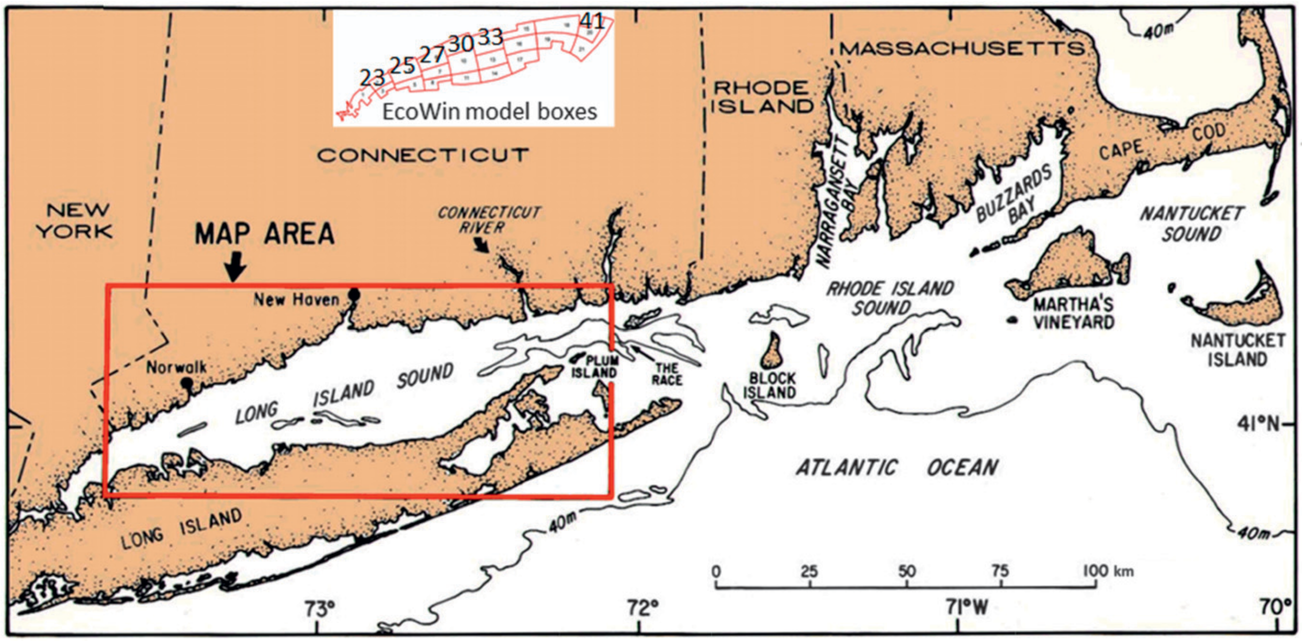

Figure 2. Map of LIS and surrounding areas (Knebel et al. 1998).

and duration of hypoxia have been tracked, with records showing the maximum area of hypoxia was about 1,000 km^2 in 1994 and the longest hypoxic event occurred in 2008 and lasted 79 days (CT DEEP 2013).

The shellfish industry in LIS is long-standing and well established. The industry harvests both eastern oyster (*Crassostrea virginica*) and hard clam (quahog; *Mercenaria mercenaria*) from shellfish grounds in the states of Connecticut and New York, and traditions are closely linked to notable clam and oyster harvests from the Sound (Fig. 3). Oysters are cultivated both on-bottom with no gear, which represents most of the current growing operations, and using gear (cages), which is a growing part of the industry.

LISS (2017) states, "In Connecticut, oysters and clams are harvested commercially by individuals and businesses that lease shellfish beds and shell fishermen can only harvest from their own leased beds. In New York, with the exception of one leased area inside a harbor, 'baymen' can harvest shellfish from any approved waters with the proper permits, including state waters in the open area of LIS."

In both states, oysters are cultivated, albeit mostly without gear at the present time, whereas the quahog harvest is more of a traditional fishery, particularly in New York, where any open areas can be harvested by multiple permit holders.

Data for Connecticut are not available after 2010 because of local governance challenges, but for the period (1990–2010) where data exist for both species, in both states, the aggregate value of the oyster industry peaked in 1992 at 40 million USD, subsequently declining to 5% of that value by 2006, mainly because of the impact of the protistan parasite *Haplosporidium nelsoni* (MSX). Oyster harvests began to rebound in 2006 (Fig. 3), in part because of efforts to restore and protect oyster habitats in Connecticut, and by 2010, were at 25% of the value in the early 1990s (data reworked from LISS 2017).

By contrast, the hard clam harvest has more than tripled between 1990 and 2010 (Fig. 3), in part because some lobster fishermen turned to clamming as lobster harvests declined and then closed completely.

Modeling Approach

The REServ Project (Bricker et al. 2018) used a combination of local- and system-scale circulation and aquaculture models, watershed models, field data, and experiments and laboratory experiments to evaluate the impacts of nutrient loading on water quality and shellfish aquaculture.

Quahogs (*Mercenaria mercenaria*) were not explicitly simulated, but their impact on the ecosystem was included in the EcoWin.NET ecosystem model (e.g., Nunes et al. 2011).

The effect of quahog growth was simulated through a mechanistic model of the drawdown of both phytoplankton and organic detritus, using the following approach:

(1) Four size classes were considered—littleneck, topneck, cherry, and chowder, and the mean live weight for each class was estimated for each (Rheault personal communication, Table 1). Total clam harvest value and volume were estimated based on historical trends (Fig. 3). Landings were extrapolated to 2012, based on interviews with growers and managers who projected a modest increase in landings over this period.

The conversion between live weight and length followed McKinney et al. (2004), by first converting the live weight to tissue wet weight and then tissue wet weight to length (Eqs. 1 and 2, Table 1).

$$W_f = 0.372 W_t^{0.97}. \qquad \text{Eq. 1}$$

$$L = 10^{\left[\log\left(\frac{W_f}{0.00005}\right)/3.09\right]}. \qquad \text{Eq. 2}$$

Here,

W_f: fresh tissue weight (g);
W_t: total fresh weight with shell (live weight, g); and
L: length (mm).

(2) For each class, a clearance rate was calculated based on length and on water temperature in each of the relevant model boxes for every model time step. Hibbert (1977) and Doering et al. (1986) provide equations relating clearance rate to these

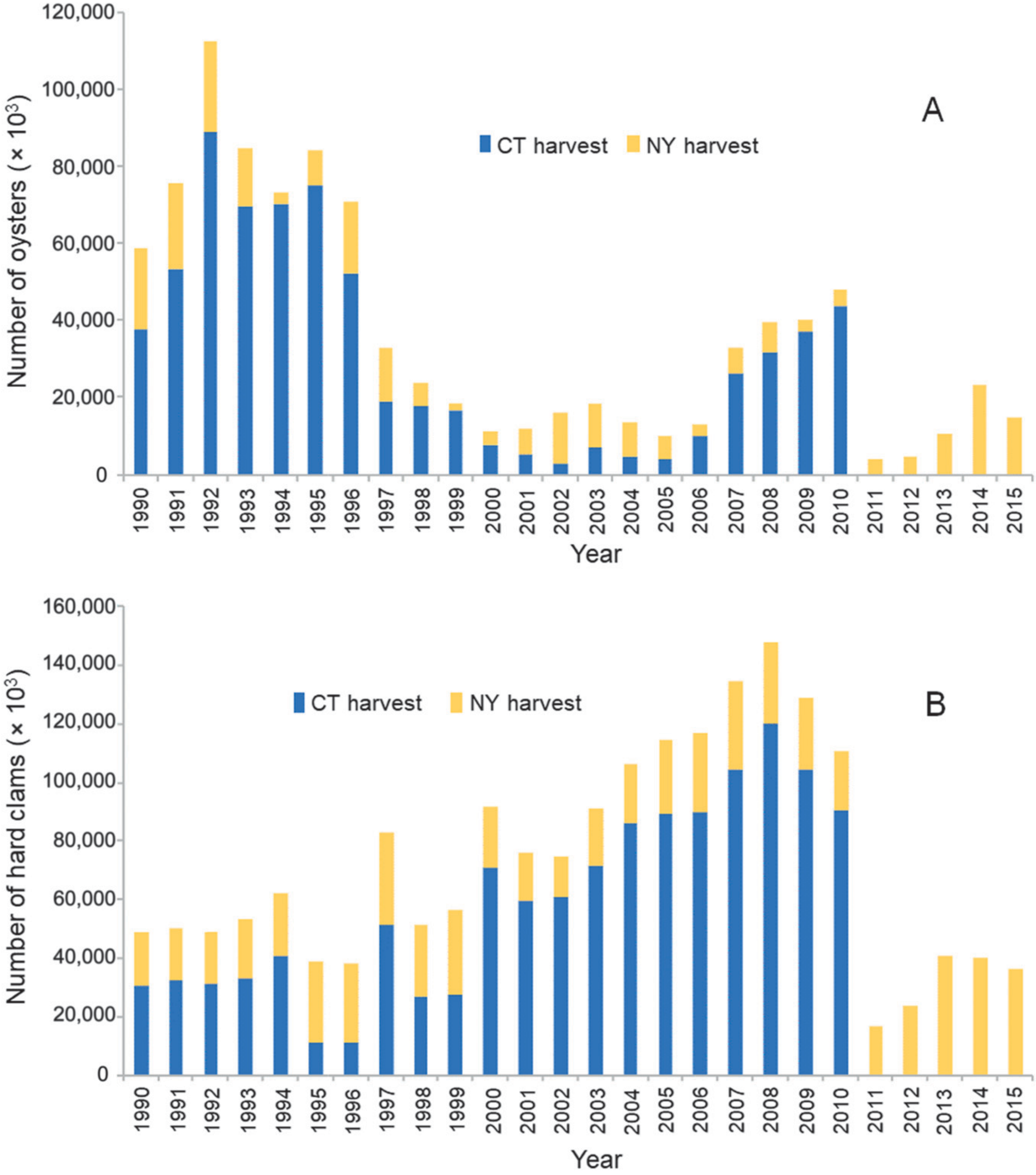

Figure 3. Harvest of (upper panel, A) oysters (*Crassostrea virginica*) and (lower panel, B) quahogs (*Mercenaria mercenaria*) in LIS, 1990 to 2015. Recent Connecticut landings data are not available but New York clam harvest declined from 2007 to 2011.

parameters–the latter formulation was chosen, which gives slightly higher clearance rates and, therefore, has a slightly greater effect on food limitation for oysters (Eq. 3).

$$CR = L^{0.96}T^{0.95}. \qquad \text{Eq. 3}$$

Here,

CR: clearance rate (ml ind.$^{-1}$ min^{-1});
L: length (cm); and
T: temperature (°C).

(3) The culture practice component described in Bricker et al. (2018) provides the abundance (ind. m^{-2}) of quahogs in LIS but not the frequency distribution of the different size classes. Data from Fegley (2001) were

TABLE 1.

Morphometric data for the hard clam *Mercenaria mercenaria*.

Size class	Live weight (g)	Tissue wet weight (g)	Length (mm)
Littlenecks	51.6	17.1	61.7
Tops	93.2	30.2	74.3
Cherries	147.5	47.2	85.9
Chowders	246.2	77.7	100.8

T2 used to derive the distribution shown in Table 2, and the dataset was refined to obtain an approximate match to the four size classes in Table 1; on that basis, the proportions were estimated as 15% littlenecks, 20% topnecks, 35% cherries, and 30% chowders. This confirms the results of the determination of ratios of size classes based on historical trends (Rheault personal communication) and allowed to define the relative landings for the various size classes by using the typical size distribution of quahogs (Table 2).

(4) The clearance rate determined for each size class at each model time step was scaled to an overall clearance based on abundance, proportion of that size class, and habitat area within "quahog boxes." The overall volume cleared was integrated for the four size classes and was used to determine the chlorophyll and organic detritus (i.e., POM) removed at every model time step.

The model assumes a fixed proportion of the four size classes throughout the year, which is incorrect, but nevertheless, considerably better than using only a constant weight and clearance rate for that weight. The aggregate clearance rate varies between 0.5 and 3.2 L ind.$^{-1}$ h^{-1}, where one "individual" is a composite of the proportion of each size class and its clearance rate at a particular water temperature.

The quahog population model was included in the EcoWin.NET simulation framework, and the model was used to establish the role of this species in modulating eastern oyster growth, and in top–down control of chlorophyll, to evaluate its contribution to mitigation of eutrophication symptoms.

Belfast Lough Case Study

Site Description

F4 Belfast Lough (Fig. 4) is a natural tidal sea lough situated on the northeast coast of Northern Ireland, adjacent to the city of Belfast. It is a designated Natura 2000 and RAMSAR site, associated with intertidal mudflat zones used by internationally important wading birds in the inner part of the lough.

In the outer part of the lough, the RAMSAR boundary is coincident with a Special Protected Area and a Site of Special Scientific Interest. Bottom culture of mussels in BEL began in 1989, and the lough is one of the larger production areas of bottom-grown mussels in Northern Ireland (Ferreira et al. 2008). In recent years, production of bottom-grown mussels varied between 5,177 t (2010) to 3,458 t (2012). Mussel seed is dredged from seed beds in the Irish Sea during periods of the year when seed beds are declared open by the Irish and Northern Irish Governments. The seed is relayed on licensed mussel growing sites and on-grown until the mussels reach market size, whereupon the mussels are harvested by dredging (Fig. 5). F5

TABLE 2.

Frequency distribution of shell length in *Mercenaria mercenaria* from eastern LIS (data from Malinowski, in Fegley 2001).

Length (mm)	%	Wet tissue weight (g)	Total wet weight (g)
55	5	11.9	35.7
65	10	20.0	60.8
75	20	31.1	95.9
85	35	45.8	142.9
95	25	64.6	203.6
105	5	88.0	280.1

Modeling Approach

An overview of the main steps and rationale for the development of the BEL benthic biodiversity model is shown in Table 3. T3

The inclusion of wild species within the model required an assessment of habitat types and associated fauna.

Definition of habitat types. Under the MSFD, EU member states were required to present maps of coastal habitat types listed in the Habitats and Birds Directives and by international conventions (e.g., on OSPAR, HELCOM, and UNEP-MAP lists). The habitat types used for this work are those applied under the MSFD. A total of eight MSFD habitat types were identified in BEL in areas where data were available; these habitats were present in variable proportions within each model box. To limit the variables added to the model, these were reduced to four broader sediment types. Habitat codes derived for the MSFD are often similar in typology but differentiated on the basis of characteristic flora, which is not required by the model used herein. MSFD sediment categories were reclassified into four substrate classes: *medium boulder*, *medium sand*, *muddy sand*, and *mud*.

Benthic filter-feeders were separated into two classes:

(1) Class 1: generic noncommercial wild species, which are relevant for biodiversity modeling, resource partitioning with commercial species, and top–down control of primary production.

(2) Class 2: bespoke commercially valuable wild species (blue mussel and the cockle *Cerastoderma edule*), which not only contribute to biodiversity but also a proportion of which additionally constitute a potential source of income and compete with cultivated blue mussels in the lough.

Model conceptualization. The EcoWin.NET model was extended to include wild species, split between Class 1 and Class 2.

The updated model incorporated subclasses of sediment types that could be apportioned to the various spatial boxes in the model, with their associated species. For an analysis of drawdown of food by benthic species, new variables were added to the lower boxes only (box numbers 22–42, Figure 4), although the upper boxes are affected by the interrelationships among all model boxes (Ferreira et al. 2008).

Two new objects or classes (*sensu* object-oriented programming) were added to the SMILE model framework

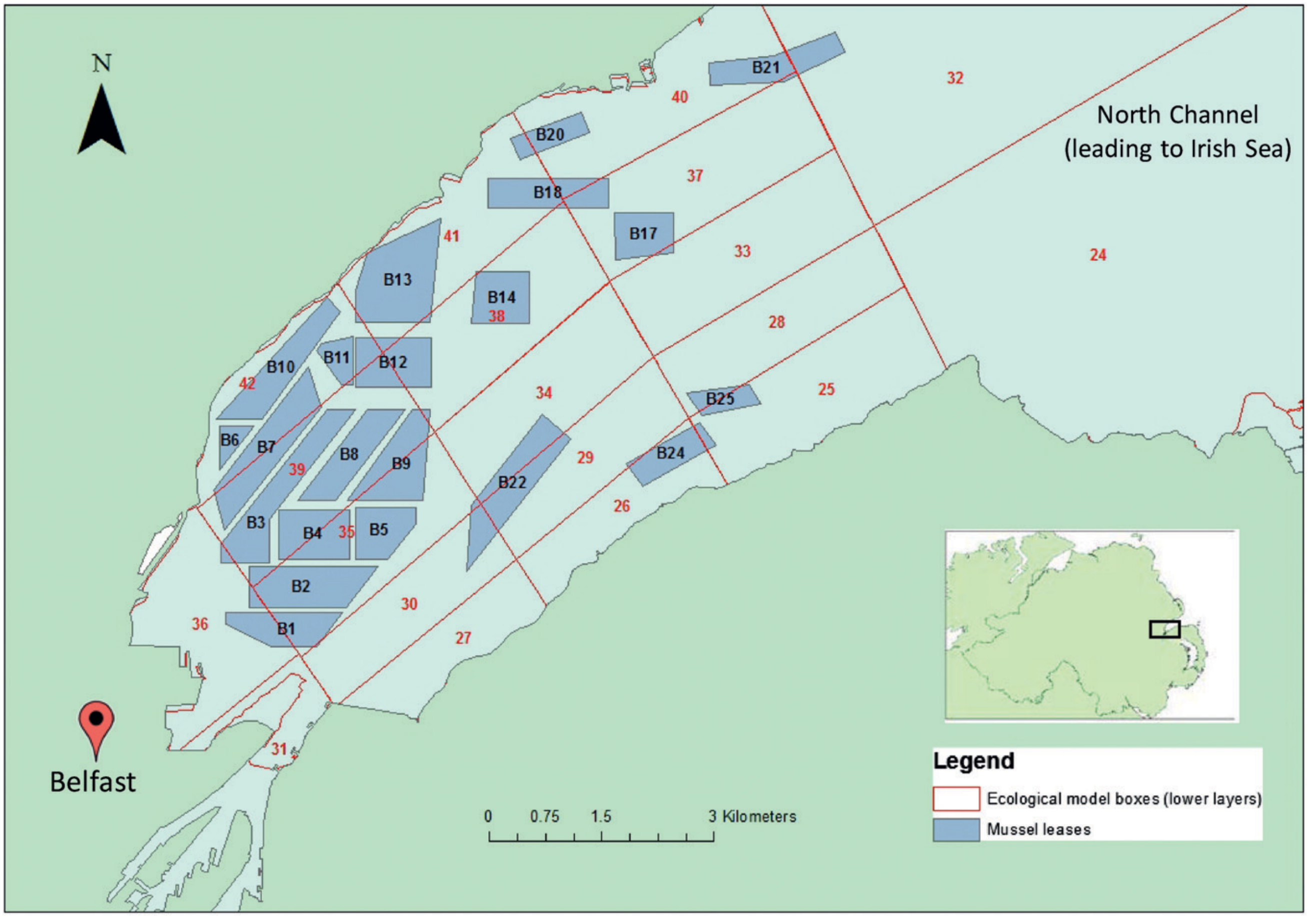

Figure 4. Map of BEL, showing licensed aquaculture sites B1 to B25, and lower layer model boxes numbered 22–42. Corresponding upper layer model boxes (1–21) are not shown.

(Ferreira et al. 2008), one to handle the new collection of wild species and another as a wrapper to handle multiple cultivated and wild species. For Class 1, the variables habitat area, abundance, biomass density, and filtration rate were added to four substrate classes: *medium boulder*, *medium sand*, *muddy sand*, and *mud*. For Class 2 (i.e., the commercially valuable wild species), the same variables were defined for mussels and for cockles under each of the defined subclasses, resulting in the creation of a further eight variables. Overall, 24 new variables were added to the EcoWin modeling framework.

All these variables were implemented as forcing functions, with the distinction that Class 1 integrates a set of various species, and the collective effect of these species on food availability for aquaculture is determined according to substrate. For Class 2, by allowing commercially important wild species to be simulated separately, model users can explore management-defined scenarios, both by changing values of variables at the box level and by switching classes on or off.

Class 1: species, habitats, and model parameterization. Benthic species data are often limited, not least because collection takes place for a specific reason, rather than to provide a generalized picture of whole ecosystems. In 2009, 33 $\times$ 0.1 m^2 grab samples were taken at various stations in BEL, mostly associated with aquaculture sites; these data were used herein as the basis of the benthic species composition and abundance dataset for Class I, noncommercial wild species. One hundred and ninety-two species were identified, though not all were present in each grab. Abundance per grab sample was standardized to abundance per square meter.

Polychaete worms dominated in terms of the species diversity (e.g., *Nepthys hombergii* and *Anaitides mucosa*), and a range of bivalves (e.g., *Abra alba* and *Mysella bidentata*), crustaceans, including crabs (e.g., *Liocarcinus* sp.) and amphipods such as *Ampelisca* sp. and *Caprella* sp., oligochaetes (e.g., *Tubificoides* sp.), and echinoderms (e.g., *Amphipholis* sp.) were also present. All species were typical of muddy and sandy coastal environments in the United Kingdom. These organisms include predators, subsurface and surface deposit feeders, grazers, and suspension and filter-feeders. Only the latter (collectively called "filtering wild species"), however, affect drawdown of POM from the water column, and the focus on wild species in the TEASMILE model was placed on these (Table 4). T4

An analysis of the benthic community and underlying habitat types was conducted using the Community Analysis Package (Pisces Conservation Ltd). Species composition was subject to a double square root transformation to minimize the

Figure 5. Mussel dredge used to harvest bottom-grown *Mytilus edulis*.

effect of outliers before the routines TWINSPAN (two-way indicator species analysis) and DECORANA (detrended correspondence analysis) were applied. This allowed species grouping and station clusters to be identified. Average similarity cluster analysis was undertaken using a Euclidean distance F6 matrix. Five species clusters (Fig. 6) were identified, four related to the four combined sediment types and one could not be placed with any degree of confidence in a particular sediment type. Thus, grab samples labeled Group 1b in Figure 6 were excluded from the analysis.

The number of filtering wild species present ranged between 12.6% and 19.2% of the total number of species present within each subclass, and represented between 6.4% and 56.4% of the T5 total abundance of all species within each subclass (Table 5). Thus, although filtering wild species were relatively small in number, they represented a reasonable proportion of the total abundance recorded in most of the sediment types, which impacts the extent to which wild species affect POM removal within each of the model boxes.

Class 1 inputs to each lower layer model box for each subclass of sediment type were

(1) spatial area (m^2) of each sediment type;
(2) abundance of wild filtering species (ind. m^{-2}); and
(3) average filtration rate for wild filtering species as a group (L ind.$^{-1}$ h^{-1}), based on calculations of abundance and species-specific filtration rate.

Spatial area of the sediment types within each of the EcoWin.NET lower layer boxes were estimated from the percentages identified in Table 5 multiplied by the total area of each box. As an example, box 29 has a total area of 2,826,441 m^2 and 12.3% of this is sand (i.e., habitat group 1a) equating to an area of sand of 348,807 m^2. Group 1c (medium boulder) was 36.4% or 1,030,028 m^2, Group 2a (mud) was 28.4% or 801,918 m^2, and Group 2b (muddy sand) was 17.8% or 503,707 m^2. Similar calculations were made for all the boxes.

There is a paucity of data available on filtering capacity for noncommercial species, and filtration rates vary throughout the life cycle, depending on water temperature, seston availability, and species-specific allometry, typically related to ash-free dry weight (e.g., Cranford et al. 2011). Class 1 consisted of bivalve species and one species of polychaete worm, *Melinna palmata*. Filtration rates applied in the model were based on whole life averages, and where no data were available, the filtration rate was selected based on similarity of morphological characteristics of species with existing data.

No filtration rate data were available for larger species of bivalve (*Mya truncata*, *Phaxas pellucidus*, and *Parvicardium scabrum*), so the rate applied for mussels and cockles (0.5 L ind.$^{-1}$ h^{-1}), the Class 2 species (Denis et al. 1999, Okumuş et al. 2002), was used. There are no published filtration rates for *Lucinoma borealis*, *Chamelea striatula*, *Tapes rhimboides*, and *Spisula* sp., so the rate applied (0.12 L ind.$^{-1}$ h^{-1}) was based on *Tellina* sp. (Wilson 1990) because of similarity in shape, shell thickness, and overall size. For all other species of bivalve with no available data, a filtration rate of 0.1 L ind.$^{-1}$ h^{-1} was used, taking into account their smaller relative size, compared with those species previously listed.

No species-specific data were available for *Melinna palmata*, so the filtration rate applied was based on Dubois et al. (2009), who showed that filtration rates of the reef-building polychaete *Sabellaria alveolata* varied depending on the concentration of phytoplankton and detrital POM, but retained an average filtration rate of 0.002 L m^{-1} h^{-1}, about 0.012 L ind.$^{-1}$ h^{-1}, based on the average size of this species.

TABLE 3.

Data treatment and model development for simulating benthic biodiversity.

Step	Approach	Rationale	Output
1	Collate benthic grab data by species and abundance, analyze by means of clustering software	Identify potential areas for wild species based on four sediment classes	Dendrogram of species clusters associated with the underlying sediment/habitat maps
2	Select most representative species with respect to mean abundance. Around 10 species were chosen for each sediment category	Obtain an appropriate subset of wild species for incorporation in EcoWin.NET	List of species and abundances per m^2
3	Determine typical filtration rates for selected species, using literature data	Calculate drawdown of food resources (phytoplankton and organic detritus) per unit area for each species in the subset	Filtration per species per unit area, scaled on the basis of mean abundance to provide overall filtration for species subsets and the four sediment types
4	Identify areas for the selected sediment types in each EcoWin.NET box using GIS	Calculate percentage areal coverage for each sediment type for each model box	Tabulated aggregate filtration data per sediment type per box, scaled to box area for input into the model
5	Correction for unclassified areas per EcoWin.NET box. These areas were broken down into two types (1) intertidal (unsampled); (2) other types of sediment. These will be handled as follows: Type 1 areas used bespoke filtration rates for blue mussels and cockles. Type 2 areas are calculated by heuristically assigning sediment types to one of the four classified types (Step 1)	Full accounting for all the benthic fauna, including intertidal and subtidal areas	Updated table from Step 4 with a minimum percentage areal coverage per EcoWin.NET box to be agreed
6	Addition of wild species data to EcoWin	Incorporation of natural benthic fauna to partition the food resources available to cultivated organisms and determine role in top–down control of primary production	Updated EcoWin.NET model input file

Mean filtration rate (MFR, Table 6) for each subclass of sediment type was calculated using Eq. 4.

$$MFR = \frac{\Sigma(S_c S_f)}{n}, \qquad \text{Eq. 4}$$

where S_c is the abundance of a specific species s within each subclass, S_f is the species-specific filtration rate, and n is the total abundance of all Class 1 species present in the sediment subclass.

Class 2: species, habitats, and model parameterization. Class 2 are commercially valuable but noncultivated species, which in BEL are blue mussels and cockles, with a total estimated *potential* annual harvest of 800 and 1,500 t, respectively. For both species, stocks are present only in a few EcoWin.NET boxes, typically associated with intertidal areas in the inner part of the lough. Mussels are found on the north shore, in model boxes 40–42, and on the south shore in boxes 25 and 26 (Fig. 4), and cockle populations are present on the south shore only, covering boxes 27 and 30. At present, mussel harvest (gathering) in intertidal areas is forbidden.

Estimates of mussel wild stock on the northern shores of BEL were obtained from an intertidal habitat mapping survey carried out in 2012 (unpublished). The average number of mussels in each bed was 800 ind. m^{-2}, but limited to only 0.8%, 1.3%, and 2.0% of boxes 40, 41, and 42, respectively. On the southern shore, an estimate of mussel coverage was made using GIS and evaluated as 5% of the area in both boxes. The model considers homogeneous properties within a box, so the density scaled to the entire box was used for model initialization.

Cockle densities were calculated from the maximum biomass (1,500 t y^{-1}), partitioned equally between the two boxes where the species is present (25 and 26). This gives a total tonnage per box of 854 and 846 t, respectively, or 314 g m^{-2}. Average weight at harvest was assumed to be 25 g, which gives an average abundance of 12.6 ind. m^{-2}. The management policy for the cockle population considers that only about one-third of the stock, i.e., 600 t was considered harvestable. This was further divided into three components: 200 t for fishery, 200 t for birds, to satisfy the requirements of the EU Habitats Directive, and 200 t as an environmental allocation. The maximum biomass used herein is a theoretical value designed to inform potential drawdown of POM and cannot be used to inform fishery effort.

Model Recalibration and Validation

The addition to the BEL model of a further component that partitions the food resources affected the existing calibration. It was anticipated that there would be a reduction in phytoplankton (indicated by the chlorophyll *a* concentration) and detrital POM and, thus, the yield of cultivated mussels would also be reduced.

The BEL SMILE model (see Ferreira et al. 2008) was recalibrated to provide an appropriate representation of the

TABLE 4.

Species composition, abundance, individual filtration rates, and total filtration rates for benthic filter-feeding wild species, grouped by habitat.

Species	Abundance	Filtration rate (L ind.$^{-1}$ h^{-1})	Total filtration rate (L species^{-1} h^{-1})
1A: sand			
Melinna palmata	1,973	0.01	9.87
Phoronis spp.	226	0.01	1.13
Mysella bidentata	177	0.10	17.70
Thyasira flexuosa	121	0.10	12.10
Abra alba	105	0.10	10.50
Parvicardium scabrum	83	0.50	41.50
Nucula nucleus	77	0.10	7.70
Abra nitida	38	0.10	3.80
Corbula gibba	16	0.10	1.60
Phaxas pellucidus	12	0.50	6.00
Mya truncata	12	0.50	6.00
Spisula sp. juv	8	0.12	0.96
Spisula subtruncata	8	0.12	0.96
Tapes rhomboides	8	0.12	0.96
Chamelea striatula	6	0.12	0.72
Thracia convexa	6	0.10	0.60
1A: totals	2,876	–	122.10
1A: average filtration rate (L ind.$^{-1}$ h^{-1})	–	–	0.042
1C: medium boulder			
Mysella bidentata	445	0.10	44.50
Abra alba	110	0.10	11.00
Nucula nucleus	90	0.10	9.00
Parvicardium scabrum	75	0.50	37.50
Tapes rhomboides	30	0.12	3.60
Lucinoma borealis	25	0.12	3.00
Mya truncata	10	0.50	5.00
Chamelea striatula	5	0.12	0.60
1C: totals	790	–	114.20
1C: average filtration rate (L ind.$^{-1}$ h^{-1})	–	–	0.145
2A: mud			
Melinna palmata	37	0.01	0.19
Abra alba	23	0.10	2.25
Abra nitida	14	0.10	1.38
Mysella bidentata	8	0.10	0.75
Lucinoma borealis	4	0.12	0.46
Parvicardium scabrum	4	0.50	1.90
Goodallia triangularis	1	0.10	0.13
Chamelea striatula	1	0.12	0.16
2A: totals	91	–	7.21
2A: average filtration rate (L ind.$^{-1}$ h^{-1})	–	–	0.079
2B: muddy sand			
Abra alba	30	0.10	3.00
Abra nitida	20	0.10	2.00
Nucula nucleus	9	0.10	0.90
Corbula gibba	8	0.10	0.80
Mya truncata	5	0.50	2.50
Mysella bidentata	4	0.10	0.40
Parvicardium scabrum	3	0.50	1.50
Thyasira flexuosa	1	0.10	0.10
Chamelea striatula	1	0.12	0.12
2B: totals	81	–	11.32
2B: average filtration rate (L ind.$^{-1}$ h^{-1})	–	–	0.140

main ecosystem variables against which validation is possible against measured time series, i.e., dissolved nutrients, phytoplankton, and to some extent total POM.

This recalibration was carried out by adjusting parameters and boundary conditions. The intent was to change as few parameters as possible, by as little as possible, while keeping model outputs consistent both with measured data and with the previous SMILE model. After the addition of the full set of wild species, the simulated yield of cultivated mussels decreased by about 30% because of the lower food supply.

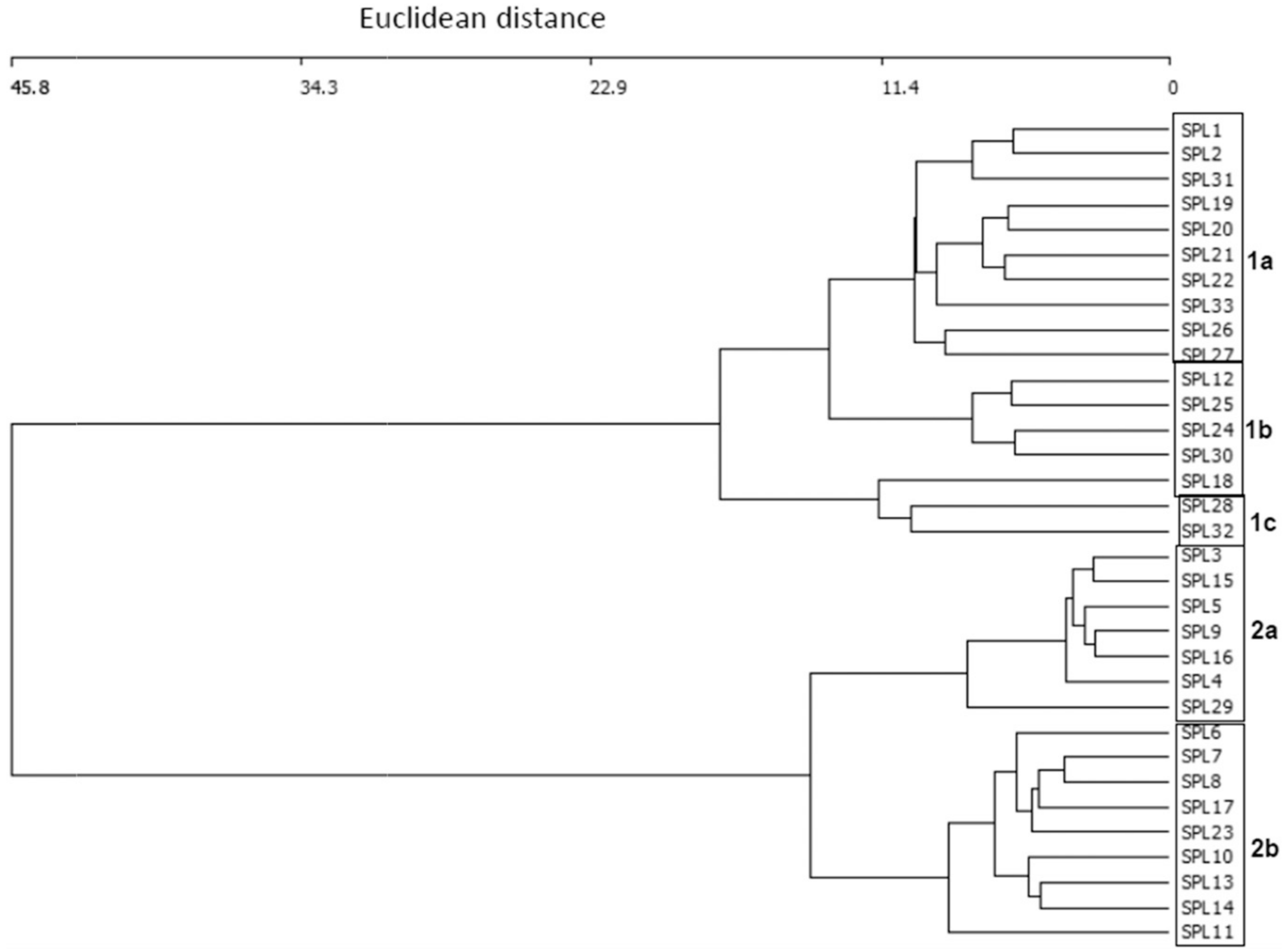

Figure 6. Dendrogram showing the similarity between benthic grab species composition and habitat type. The more similar the samples are the closer they are presented so that distinct groupings can be determined as a single group [blue boxes—Groups 1a: medium sand, 1b: excluded from analysis (see text for explanation), 1c: medium boulder, 2a: mud, and 2b: muddy sand]. Data supplied by AFBI.

Natural mortality of phytoplankton was reduced to account for this change, given its initial parameterization would overcompensate for nonnatural mortality effects that were not in the model. In addition, the flux of POM across the seaward boundary on the flood tide was slightly increased, enhancing the food supply to cultivated mussels (and the wild species now simulated).

The model was validated first against phytoplankton and nutrient time-series within BEL, and finally on reported landings of cultivated mussels.

RESULTS AND DISCUSSION

Different types of outcomes are obtained for each reported case study, and collectively they exemplify the kind of information that can be supplied to decision-makers required to make decisions on ecological carrying capacity. This section is structured thematically, and combines outcomes from both case studies when appropriate, to illustrate specific points.

Filtration by Benthic Wild Species

LIS and BEL both have a significant component of benthic secondary production associated with native species; in BEL, the wild species filtration was partitioned into both (potentially) commercial (blue mussels and cockles) and noncommercial species, whereas in LIS, only the hard clam was considered.

Table 7 shows the consolidated outputs for BEL, based on a model run with the blue mussel aquaculture enabled, and outputs for Year 9 of a decadal run. Because wild species growth is not simulated, only the removal of organic matter based on average filtration rates for each habitat type (scaled to abundance), and on the food (phytoplankton and detritus) available, can be obtained. This provides the gross mass balance rather than net removal, and corresponds to more than 50 kt C y^{-1}, and about 8 kt N y^{-1}. Based on well-established ecological efficiency (Ryther 1969) calculations (0.1–0.2; the lower limit was used for precautionary reasons), this corresponds to an annual net removal of about 5 kt C y^{-1} and 0.8 kt N y^{-1}. These values can be converted into population equivalents (PEQ) and are estimated to be about 250,000 PEQ (in 2015, Belfast City had a population of 334,000).

If a nitrogen removal cost of 12.4 USD kg^{-1} is considered, as estimated by Lindahl et al. (2005) for 47 small stabilization ponds (lagoons) in Sweden, then the equivalent ecosystem service provided can be valued at 10.1 million USD or about 9 M€.

TABLE 5.

Abundance (ind. m^{-2}) of filtering wild species distributed by habitat type in each EcoWin.NET model box.

EcoWin.NET box	1A sand wild species abundance (m^{-2})	1C medium boulder wild species abundance (m^{-2})	2A mud wild species abundance (m^{-2})	2B muddy sand wild species abundance (m^{-2})
22	0	0	0	0
23	0	10	0	1
24	81	433	0	191
25	127	39	11	127
26	0	18	1	325
27	0	0	0	0
28	280	284	4	166
29	248	101	11	272
30	5	77	0	228
31	0	0	0	0
32	19	452	0	223
33	196	453	0	148
34	394	119	4	196
35	6	43	5	798
36	0	0	1	1
37	125	430	6	188
38	346	94	21	26
39	5	4	43	157
40	2	99	6	143
41	26	32	21	137
42	0	0	15	34

Similar budget calculations were made for quahogs in LIS T8 (Table 8). The net nutrient removal by hard clams in LIS is estimated to be 1.8 kt C y^{-1} and 0.3 kt N y^{-1}. The corresponding ecosystem service is equivalent to 85,000 PEQ, with a valuation of 3.5 million USD (3.1 M€). For both BEL and LIS, the cost equivalent is a minimal estimate, based on nutrient removal costs for point sources. Ferreira and Bricker (2016) reviewed costs for different treatment options, which can exceed the values above by at least one order of magnitude, if nutrient loading is from diffuse sources.

Bricker et al. (2018) simulated three scenarios for spatial extent of the quahog fishery in LIS, all of which consider areas in excess of the standard model results in Table 8, so the estimates presented herein can be considered a baseline.

Carrying Capacity of Cultivated Species

Phytoplankton and organic detritus are food resources partitioned between cultivated shellfish and wild filter-feeders and, therefore, biomass and production of each group will depend on stocking density and food availability. In LIS, both eastern oysters and quahogs are harvested, but the EcoWin.NET model only simulates oyster harvest, just as in BEL, only cultivated blue mussels are harvested within the model, although there is a small wild cockle fishery. T9

TABLE 6.

Mean filtration rate of wild species calculated for each habitat type.

Habitat type	Mean filtration rate (L $ind.^{-1}$ h^{-1})
Sand: Group 1A	0.042
Medium boulder: Group 1C	0.145
Mud: Group 2A	0.079
Muddy sand: Group 2B	0.140

Table 9 shows the change in oyster harvest in LIS in the presence and absence of quahogs. In box 23, there is a slight decrease in oyster harvest if no quahogs are present, and in the remaining boxes, the absence of quahogs enhances oyster yields. As a rule, yield of cultivated species in a box would be expected to increase in the absence of wild species, but the opposite can be observed for a number of reasons, including greater food availability due to lower production in adjacent boxes. Overall, the enhancement of oyster harvest in LIS is positive but minimal (1.4%) because the system is well below production carrying capacity, and these two species are not food-limited at current stocking densities. It is worth noting that Bricker et al. (2018) identified substantial uncertainty in the data for effective use of leases, stocking densities, and natural mortality. The usefulness of models of this kind depends strongly on effective stakeholder engagement because farmers are the only group able to supply an accurate description of culture practice—this is often a surprisingly difficult part of the modeling process (Ferreira et al. 2008).

Belfast Lough shows a much clearer pattern when mussel production with and without wild filter-feeding species is analyzed (Table 10). T10

This is partly because stocking densities are higher for both cultivated and wild components and partly because there is a more limited food availability: the percentile 90 for chlorophyll in all cultivated boxes is 2.5 μg L^{-1} in BEL (Model Year 9, standard run), compared with a P_{90} of 11.1 μg L^{-1} in LIS (Model Year 9, standard run). Field data for chlorophyll in the western part of LIS, spanning a period of 20 y (1996–2016; LISS 2017), give an even higher P_{90} of 15.8 μg L^{-1}.

TABLE 7.

Mass balance for nutrient and chlorophyll uptake by wild species in BEL for Model Year 9 from a 10-y run.

Box	Phytoplankton carbon (kg C y^{-1})	Phytoplankton chlorophyll (kg Chl y^{-1})	Detrital carbon (kg C y^{-1})	Detrital POM (kg DW y^{-1})	Gross carbon removal (kg C y^{-1})	Gross nitrogen removal (kg N y^{-1})	Net carbon removal (kg C y^{-1})	Net nitrogen removal (kg N y^{-1})	Net PEQ (PEQ)
23	269	8	74,763	196,746	75,032	11,672	7,503	1,167	354
24	241,411	6,897	23,134,446	60,880,122	23,375,857	3,636,244	2,337,586	363,624	110,189
25	13,606	389	541,166	1,424,121	554,772	86,298	55,477	8,630	2,615
26	38,549	1,101	798,953	2,102,509	837,502	130,278	83,750	13,028	3,948
28	21,231	607	866,758	2,280,942	887,989	138,132	88,799	13,813	4,186
29	24,275	694	546,984	1,439,431	571,259	88,863	57,126	8,886	2,693
30	17,542	501	268,605	706,855	286,146	44,512	28,615	4,451	1,349
31	0.10	0.00	1.79	4.71	1.89	0.29	0.19	0.03	0.01
32	171,008	4,886	18,573,583	48,877,849	18,744,591	2,915,825	1,874,459	291,583	88,358
33	37,630	1,075	1,623,371	4,272,030	1,661,001	258,378	166,100	25,838	7,830
34	22,769	651	586,376	1,543,095	609,146	94,756	60,915	9,476	2,871
35	118,052	3,373	2,392,042	6,294,847	2,510,094	390,459	251,009	39,046	11,832
36	1.64	0.05	26.79	70.50	28.42	4.42	2.84	0.44	0.13
37	38,992	1,114	1,588,999	4,181,575	1,627,990	253,243	162,799	25,324	7,674
38	11,476	328	306,053	805,404	317,530	49,394	31,753	4,939	1,497
39	5,890	168	137,292	361,296	143,182	22,273	14,318	2,227	675
40	17,713	506	471,903	1,241,850	489,616	76,162	48,962	7,616	2,308
41	18,688	534	379,017	997,412	397,704	61,865	39,770	6,187	1,875
42	14,773	422	292,278	769,151	307,051	47,763	30,705	4,776	1,447
Total	813,876	23,254	52,582,617	138,375,309	52,582,617	8,179,518	5,258,262	817,952	247,864

Wild species include both noncommercial (Class 1) and commercial (Class 2). Conversion coefficients: C:Chl = 35; C:POM = 0.38; PEQ:N = 3.3; ecological efficiency for conversion of gross to net nutrient removal: 0.1; see Figure 4 for model box locations.

If all the cultivated model boxes are considered, i.e., the lough as a whole, the effect of wild species on blue mussel harvest is extremely significant—there is an increase of 136% in mussel yields if wild species are not active. As in LIS, the relative gain varies among boxes, and is related to spatial variation in stocking density of cultivated and wild components, and to food availability: the lowest multiple is 42% enhancement in box 36, located at the head of the lough (Fig. 4), compared with 441% in box 42 in the northwestern part of the system.

The relative yields with and without wild species are illustrated in Figure 7, drawn using log scale because of the considerable differences in yield among boxes. In BEL, the total change in harvestable biomass is about 5,800 t y^{-1} live weight.

Local-scale models used to predict aquaculture yields and/or environmental effects (e.g., Cromey et al. 2002, Stigebrandt et al. 2004, Silva et al. 2011, Cubillo et al. 2016) do not account for resource partitioning, whereas ecosystem-scale models must do so to be correctly calibrated for yield. As a rule, however, they do so implicitly, by compensating factors such as natural mortality of phytoplankton and/or of the cultivated species themselves (e.g., Gangnery et al. 2004, Filgueira et al. 2014). Because autochthonous benthic filter-feeders perform a similar ecosystem function to cultivated bivalves, with respect to drawdown of primary symptoms of eutrophication (*sensu* Bricker et al. 2003), they contribute to short-circuiting the organic decomposition cycle; if instead a model increases natural mortality of phytoplankton, there are potential

TABLE 8.

Mass balance for nutrient and chlorophyll uptake by wild species in LIS for Model Year 9 from a 10-y run

Box	Phytoplankton carbon (kg C y^{-1})	Phytoplankton chlorophyll (kg Chl y^{-1})	Detrital carbon (kg C y^{-1})	Detrital POM (kg DW y^{-1})	Gross carbon removal (kg C y^{-1})	Gross nitrogen removal (kg N y^{-1})	Net carbon removal (kg C y^{-1})	Net nitrogen removal (kg N y^{-1})	Net PEQ (PEQ)
23	1,350,176	38,576	2,106,117	800,324	2,150,500	334,522	215,050	33,452	10,137
25	2,637,374	75,354	4,850,563	1,843,214	4,480,588	696,980	448,059	69,698	21,121
27	2,553,272	72,951	5,834,938	2,217,277	4,770,549	742,085	477,055	74,209	22,487
30	2,647,982	75,657	7,550,944	2,869,359	5,517,341	858,253	551,734	85,825	26,008
33	302,086	8,631	1,214,292	461,431	763,516	118,769	76,352	11,877	3,599
41	62,579	1,788	465,500	176,890	239,470	37,251	23,947	3,725	1,129
Total	9,553,469	272,956	22,022,355	8,368,495	17,921,964	2,787,861	1,792,196	278,786	84,481

Wild species include only quahogs; Conversion coefficients as in Table 7; see Figure 2 for model box locations.

TABLE 9.

Oyster harvest in LIS for Model Year 9 with and without quahogs.

Scenario	Box 23	Box 25	Box 27	Box 30	Box 33	Box 41	Total
Standard model (t y^{-1})	630.34	24,012.66	299.72	4,372.37	296.09	1,177.59	30,788.78
No quahogs (t y^{-1})	626.93	24,245.93	307.83	4,551.87	303.43	1,189.84	31,225.82
Difference (t y^{-1})	3.42	–233.26	–8.11	–179.50	–7.34	–12.25	–437.04
Percentage change	–0.54	0.97	2.70	4.11	2.48	1.04	1.42

implications for the subsequent modeling of diagenesis and oxygen balance.

The difference in cultivated shellfish production simulated for BEL provides an indication *per se* of ecological carrying capacity, as discussed by Sequeira et al. (2008), by setting an upper boundary for cultured shellfish stock, to allow a healthy and diverse natural benthic community to flourish. Knowledge of these aspects is essential to support managers in implementing some of the MSFD QD, in particular, those that address biodiversity, food webs, and sea floor integrity.

Mitigation of Eutrophication

Aspects of eutrophication abatement are touched on in the previous sections, as they relate to the relative role of wild species in drawing down POM and to the consequent valuation of the regulatory ecosystem service provided for nutrient removal. As noted by Ferreira and Bricker (2016), there is some inconsistency in the current approach to valuation of nitrogen (and phosphorus) removal, which at present considers only the harvested component, based, e.g., on nitrogen content in tissue and shellfish landings (e.g., Oyster BMP Expert Panel 2016 recommendations for harvested tissue only, removal in shell and by denitrification are still under consideration by the Panel).

Based on this premise, it is not possible to make a case for regulatory ecosystem services with respect to nutrient removal when dealing with natural populations, including natural or restored reefs of the same species that are cultivated because the organisms remain in the water (although the nutrients are not dissolved in the water column but sequestered, at least temporarily, in animal tissues).

Ferreira and Bricker (2018) present a complementary approach for valuation, which focuses on a key primary symptom of eutrophication (chlorophyll), rather than the causative factors (nutrient loading). This is consistent with regulation in both the United States and Europe, where water quality thresholds are based on what the EU WFD terms biological quality elements, including phytoplankton (see, e.g., Bricker et al. 2003—United States; Ferreira et al. 2011—EU).

The assessment of the role of different filter-feeders in chlorophyll drawdown at an ecosystem scale is a methodological challenge because it can only be executed by means of system-scale models such as the ones applied herein. Nevertheless, because for an analysis of habitat-scale interactions between cultivated and wild species, such models are also a requirement and it was possible to examine scenarios for both LIS and BEL that consider four different situations: (1) the standard model with both cultivated and wild components, (2) a model with no filter-feeders present, and (3) the two complementary situations, i.e., with and without aquaculture or natural populations.

Results for LIS and BEL are presented in Tables 11 and 12. In each case, the chlorophyll P_{90} was used as a typical maximum for the primary symptom (Bricker et al. 2003). Daily model outputs were used for analysis, and the P_{90} per box was determined, and also the overall P_{90} considering raw data for all the boxes shown.

Although results for LIS reflect limited bioextraction, because of the relatively low stocking densities of both oysters and

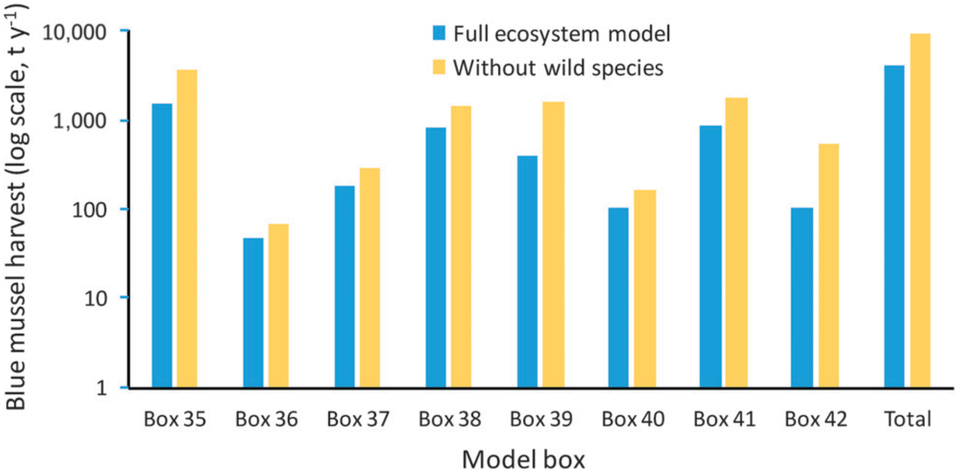

Figure 7. Blue mussel harvest in BEL for Model Year 9, with and without wild species active. Note *Y* axis in log scale, box locations are shown in Figure 4.

TABLE 10.

Blue mussel harvest in BEL for Model Year 9 with and without wild species.

Scenario	Box 35	Box 36	Box 37	Box 38	Box 39	Box 40	Box 41	Box 42	Total
Standard model (t y^{-1})	1,640.48	50.86	193.08	874.98	409.12	110.49	910.82	105.89	4,295.72
No wild species (t y^{-1})	3,883.72	72.34	312.22	1,513.81	1,730.52	173.06	1,881.19	573.90	10,140.76
Difference (t y^{-1})	–2,243.24	–21.48	–119.14	–638.83	–1,321.40	–62.57	–970.37	–468.01	–5,845.04
Percentage change	136.74	42.24	61.71	73.01	322.99	56.63	106.54	441.97	136.07

quahogs, shellfish nevertheless contribute 6.1% to overall chlorophyll removal, and whereas in the separate scenarios oysters remove 1.9%, the wild fishery of hard clams removes 4.7%. There are a number of reasons why the P_{90} change because of oyster + clam removal, when aggregated, will not match the standard model outputs, and should exceed them (6.6% when compared with 6.1%)—foremost is the interaction between the two species in the standard model, which leads to lower oyster harvest and, therefore, to less bioextraction.

This and other aspects are clearer for BEL, where the change in chlorophyll P_{90} when shellfish are switched off is notable: an increase from a baseline of 2.5 to 5.7 μg L^{-1} or 55% reduction due to top–down control. If the two components are considered separately, wild species will reduce the P_{90} by 30.8% and mussels by 45.2%. As described previously, for a correct analysis of the role of shellfish, the model must be run with both components active—the discrepancy in total removal (86% when compared with 55.2%) is now far more obvious and due to the enhanced blue mussel production in the absence of other benthic filter-feeders.

Organically extractive aquaculture is not considered, except as a pressure, in both the EU WFD and MSFD. This unfortunate omission (Ferreira & Bricker 2016) jeopardizes one of the most obvious management tools for eutrophication control. Although the authors do not suggest that top–down control should in any way replace bottom-up approaches to nutrient management, not least because of the issue of moral hazard, it seems unwise to discount the role played by cultivated filter-feeders in regulating environmental conditions.

In both LIS and BEL, these models illustrate a common pattern where, to varying degrees, cultivated and wild species contribute toward improved water quality.

CONCLUSIONS

The inclusion of autochthonous benthic filter-feeders in aquaculture carrying capacity models is shown to provide a set of important insights into ecosystem functioning, particularly with respect to the relative production of both cultivated and wild organisms, and their role in top–down control of eutrophication.

Licensing is often more reliant on local-scale impact simulations, and although such models should certainly form part of the manager's toolset, it is key to underscore that sustainable development must be analyzed through an integrated approach, rather than through a piecemeal process—only after the broader elements of system behavior are understood, should local-scale models be used to inform decision-makers. Ecosystem models can additionally be used to explore scenarios, as illustrated in the two case studies, and scenario outputs can then be nested to drive local-scale models, which would be unable *per se* to translate system-scale changes into local impacts.

Ecosystem models are time-consuming and expensive to develop, but they cost a fraction of the other components required for their successful development. Model costs are typically two orders of magnitude below those of fieldwork, not least because of ship time, deployment of ADCPs, and other moorings and sensors, and one order of magnitude below the laboratory work that typically informs conceptualization of key processes and formulation and parameterization of model equations.

Furthermore, management agencies and industry stakeholders alike must be involved both in the initial development cycle and in subsequent maintenance, and invest from the outset in training and operation of models. For shared operation, the usability of ecosystem models must improve, but the trade-off on this investment is substantial, because stakeholders with continued and committed connections to a particular bay, estuary, or regional sea will critically drive improvements to tools of this nature, provided they find them useful, resulting in jointly curated management frameworks that can be used for multiyear periods.

TABLE 11.

Phytoplankton (chlorophyll) drawdown in LIS, considering four alternative scenarios.

Scenario	Box 23	Box 25	Box 27	Box 30	Box 33	Box 41	Total
Standard model (μg chl L^{-1})	13.5	10.4	8.9	8.3	8.4	10.4	11.1
No shellfish (μg chl L^{-1})	14.4	11.4	9.6	8.9	8.7	10.5	11.8
No eastern oysters (μg chl L^{-1})	13.7	10.7	9.0	8.4	8.5	10.5	11.3
No quahogs (μg chl L^{-1})	14.2	11.1	9.5	8.8	8.6	10.5	11.6
Change due to shellfish (%)	–6.6	–8.7	–7.9	–7.3	–2.8	–0.4	–6.1
Change due to eastern oysters (%)	–1.5	–2.7	–1.8	–1.8	–0.9	–0.1	–1.9
Change due to quahogs (%)	–5.3	–6.0	–6.4	–5.9	–2.2	–0.2	–4.7

TABLE 12.

Phytoplankton (chlorophyll) drawdown in BEL, considering four alternative scenarios.

Scenario	Box 35	Box 36	Box 37	Box 38	Box 39	Box 40	Box 41	Box 42	Total
Standard model (μg chl L^{-1})	2.9	3.8	1.9	2.5	2.1	2.4	2.3	2.0	2.5
No shellfish (μg chl L^{-1})	6.3	6.5	3.4	5.1	6.3	4.5	5.8	6.7	5.7
No mussels (μg chl L^{-1})	4.0	4.8	2.4	3.6	4.5	3.3	4.1	4.2	3.9
No wild species (μg chl L^{-1})	3.9	4.6	2.5	3.0	2.4	3.0	2.9	2.5	3.1
Change due to shellfish (%)	–54.5	–42.2	–43.7	–50.7	–67.2	–45.9	–59.5	–70.1	–55.2
Change due to mussels (%)	–38.6	–30.4	–26.0	–40.7	–61.8	–34.0	–50.4	–63.5	–45.2
Change due to wild species (%)	–37.0	–26.5	–30.4	–28.2	–28.2	–27.7	–28.6	–37.7	–30.8

ACKNOWLEDGMENTS

The authors gratefully acknowledge funding from the REServ (NOAA/EPA) and TEASMILE (AFBI) projects. The authors would like to thank all project partners for data used for the development of the models in both Long Island Sound, United States, and Belfast Lough, Northern Ireland. In addition, the authors wish to thank to M. Tedesco and C. Vincent for their encouragement through the course of this work. Finally, we are grateful for the review comments received on an earlier draft, which led to a range of improvements to the text.

LITERATURE CITED

Agri-Food Strategy Board (AFSB). 2012. Going for growth—investing in success. A strategic action plan for the Northern Ireland agri-food industry. 85 pp. Available at: http://www.agrifoodstrategyboard.org.uk/uploads/Going%20for%20Growth%20-%20Web%20Version.PDF.

Bricker, S., C. Clement, S. Frew, M. Harmon, M. Harris & D. Pirhalla. 1997. NOAA's estuarine eutrophication survey. Volume 3: North Atlantic Region. Silver Spring, MD: Office of Ocean Resources Conservation Assessment. 46 pp.

Bricker, S. B., J. G. Ferreira & T. Simas. 2003. An integrated methodology for assessment of estuarine trophic status. *Ecol. Modell.* 169:39–60.

Bricker, S. B., J. G. Ferreira, C. B. Zhu, J. M. Rose, E. Galimany, G. H. Wikfors, C. Saurel, R. Landeck Miller, J. Wands, P. Trowbridge, R. E. Grizzle, K. Wellman, R. Rheault, J. Steinberg, A. P. Jacob, E. D. Davenport, S. Ayvazian, M. Chintala & M. A. Tedesco. 2018. The role of shellfish aquaculture in the reduction of eutrophication in an urban estuary. *Environ. Sci. Technol.* 52:173–183.

Byron, C. & B. A. Costa-Pierce. 2013. Carrying capacity tools for use in the implementation of an ecosystems approach to aquaculture. In: Ross, L. G., T. C. Telfer, L. Falconer, D. Soto & J. Aguilar-Manjarrez, editors. Site selection and carrying capacities for inland and coastal aquaculture. FAO/Institute of Aquaculture, University of Stirling, Expert Workshop, December 6–8, 2010. Stirling, the United Kingdom of Great Britain and Northern Ireland. FAO Fisheries and Aquaculture Proceedings No. 21. Rome, Italy: FAO. 46 pp.

Byron, C., J. Link, B. Costa-Pierce & D. Bengtson. 2011a. Modelling ecological carrying capacity of shellfish aquaculture in highly flushed temperate lagoons. *Aquaculture* 314:87–99.

Byron, C., J. Link, B. Costa-Pierce & D. Bengtson. 2011b. Calculating ecological carrying capacity of shellfish aquaculture using mass-balance modelling: Narragansett Bay, Rhode Island. *Ecol. Modell.* 222:1743–1755.

Cochrane, S. K. J., D. W. Connor, P. Nilsson, I. Mitchell, J. Reker, J. Franco, V. Valavanis, S. Moncheva, J. Ekebom, K. Nygaard, R. Serrão Santos, I. Narberhaus, T. Packeiser, W. van de Bund & A. C. Cardoso. 2010. Marine strategy framework directive task group 1 report biological diversity. ICES/JRC. 120 pp.

Connecticut Department of Energy and Environmental Protection (CT DEEP). 2013. 2013 Long Island Sound hypoxia season review. Hartford, CT: Connecticut Department of Energy and Environmental Protection. 31 pp.

Corner, R. A., A. J. Brooker, T. C. Telfer & L. G. Ross. 2006. A fully integrated GIS-based model of particulate waste distribution from marine fish-cage sites. *Aquaculture* 258:299–311.

Cranford, P. J., P. M. Strain, M. Dowd, B. T. Hargrave, J. Grant & M. C. Archambault. 2007. Influence of mussel aquaculture on nitrogen dynamics in a nutrient enriched coastal embayment. *Mar. Ecol. Prog. Ser.* 347:61–78.

Cranford, P. J., J. E. Ward & S. E. Shumway. 2011. Bivalve filter feeding: variability and limits of the aquaculture biofilter. In: Shumway, S. E., editor. Shellfish aquaculture and the environment. Wiley-Blackwell, Oxford, UK. pp. 81–124.

Cromey, C. J., T. D. Nickell & K. D. Black. 2002. DEPOMOD—modelling the deposition and biological effects of waste solids from marine cage farms. *Aquaculture* 214:211–239.

Cubillo, A. M., J. G. Ferreira, S. M. C. Robinson, C. M. Pearce, R. A. Corner & J. Johansen. 2016. Role of deposit feeders in integrated multi-trophic aquaculture—a model analysis. *Aquaculture* 453:54–66.

Denis, L., E. Alliot & D. Grzebyk. 1999. Clearance rate responses of Mediterranean mussels, *Mytilus galloprovincialis*, to variations in flow, water temperature, food quality and quantity. *Aquat. Living Resour.* 12:279–288.

Doering, P. H., C. A. Oviatt & J. R. Kelly. 1986. The effects of the filter-feeding clam *Mercenaria mercenaria* on carbon cycling in experimental marine mesocosms. *J. Mar. Res.* 44:839–861.

Dubois, S., L. Barille & B. Cognie. 2009. Feeding response of the polychaete *Sabellaria alveolata* (Sabellariidae) to changes in seston concentration. *J. Exp. Mar. Biol. Ecol.* 376:94–101.

Ervik, A., A.-L. Agnalt, L. Asplin, J. Aure, T. C. Bekkvik, I. Døskeland, A. A. Hageberg, T. Hansen, Ø. Karlsen, F. Oppedal & Ø. Strand. 2008. AkvaVis—dynamisk GIS-verktøyfor lokalisering av oppdrettsanlegg for nye oppdrettsarter—Miljøkrav for nye oppdrettsarter og laks. Fisken og Havet, nr 10/2008. 90 pp. Havforskningsinstituttet. Fisken og havet 2008-10.

European Commission. 2013. Strategic guidelines for the sustainable development of EU aquaculture—COM/2013/229—Communication to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions (April 29, 2013).

European Commission. 2016. Facts and figures on the common fisheries policy. European Commission, Brussels. 56 pp. Available at: https://

eeas.europa.eu/headquarters/headquarters-homepage/38184/facts-and-figures-common-fisheries-policy_en.

FAO (Food and Agriculture Organization of the United Nations). 2016. The state of world fisheries and aquaculture (SOFIA). Rome, Italy: FAO. 204 pp.

Fegley, S. 2001. Demography and dynamics of hard clam populations. In: Kraeuter, J. N. & M. Castagna, editors. Biology of the hard clam. pp. 383–422. Elsevier, Developments in Aquaculture and Fisheries Science – 31.

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

Ferreira, J. G., J. H. Andersen, A. Borja, S. B. Bricker, J. Camp, M. Cardoso da Silva, E. Garcés, A.-S. Heiskanen, C. Humborg, L. Ignatiades, C. Lancelot, A. Menesguen, P. Tett, N. Hoepffner & U. Claussen. 2011. Indicators of human-induced eutrophication to assess the environmental status within the European Marine Strategy Framework Directive. *Estuar. Coast. Shelf Sci.* 93:117–131.

Ferreira, J. G., A. J. S. Hawkins & S. B. Bricker. 2007. Management of productivity, environmental effects and profitability of shellfish aquaculture—the farm aquaculture resource management (FARM) model. *Aquaculture* 264:160–174.

Ferreira, J. G., A. J. S. Hawkins, P. Monteiro, H. Moore, M. Service, P. L. Pascoe, L. Ramos & A. Sequeira. 2008. Integrated assessment of ecosystem-scale carrying capacity in shellfish growing areas. *Aquaculture* 275:138–151.

Ferreira, J. G., A. Sequeira, A. J. S. Hawkins, A. Newton, T. D. Nickell, R. Pastres, J. Forte, A. Bodoy & S. B. Bricker. 2009. Analysis of coastal and offshore aquaculture: application of the FARM model to multiple systems and shellfish species. *Aquaculture* 289:32–41.

Ferreira, J. G., C. Saurel, J. D. Lencart e Silva, J. P. Nunes & F. Vazquez. 2014. Modelling of interactions between inshore and offshore aquaculture. *Aquaculture* 426–427:154–164.

Ferreira, J. G. & S. B. Bricker. 2016. Goods and services of extensive aquaculture: shellfish culture and nutrient trading. *Aquacult. Int.* 24:803–825.

Ferreira, J. G. & S. B. Bricker. 2018. Assessment of nutrient trading services from shellfish farming. In: Smaal, A., J. G. Ferreira, J. Grant, J. K. Petersen & Ø. Strand, editors. Goods and services of marine bivalves.New York, Heidelberg, Dordrecht, London: Springer. In Press.

Filgueira, R. & J. Grant. 2009. A box model for ecosystem-level management of mussel culture carrying capacity in a coastal Bay. *Ecosystems* 12:1222–1233.

Filgueira, R., T. Guyondet, C. Bacher & L. A. Comeau. 2015. Informing marine spatial planning (MSP) with numerical modelling: a case-study on shellfish aquaculture in Malpeque Bay (eastern Canada). *Mar. Pollut. Bull.* 100:200–216.

Filgueira, R., T. Guyondet, L. A. Comeau & J. Grant. 2014. A fully-spatial ecosystem-DEB model of oyster (*Crassostrea virginica*) carrying capacity in the Richibucto Estuary, Eastern Canada. *J. Mar. Syst.* 136:42–54.

Gangnery, A., C. Bacher & D. Buestel. 2004. Application of a population dynamics model to the Mediterranean mussel, *Mytilus galloprovincialis*, reared in Thau lagoon (France). *Aquaculture* 229:289–313.

Henderson, A. R. & I. M. Davies. 2000. Review of aquaculture, its regulation and monitoring in Scotland. *J. Appl. Ichthyology* 16:200–208.

Hibbert, C. J. 1977. Energy relations of the bivalve *Mercenaria mercenaria* on an intertidal mudflat. *Mar. Biol.* 44:77–84.

Karakassis, I., N. Papageorgiou, I. Kalantzi, K. Sevastou & C. Koutsikopoulos. 2013. Adaptation of fish farming production to the environmental characteristics of the receiving marine ecosystems: a proxy to carrying capacity. *Aquaculture* 408–409:184–190.

Knebel, H. J., R. P. Signell, R. R. Rendigs, L. J. Poppe & J. H. List. 1998. Chapter 1: maps and illustrations showing the acoustic and textural characteristics and the distribution of bottom sedimentary environments, Long Island Sound, Connecticut-New York. In: Poppe, L. J. & C. Polloni, editors. Long Island Sound environmental studies. Woods Hole, MA: U.S. Geological Survey. U.S. Geological Survey Open-File Report 98-502. Available at: https://pubs.usgs.gov/of/1998/of98-502/.

Latimer, J. S., M. A. Tedesco, R. L. Swanson, C. Yarish, P. E. Stacey & C. Garza, editors. 2014. Long Island Sound: prospects for the Urban Sea. New York, Heidelberg, Dordrecht, London: Springer. 558 pp.

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

Long Island Sound Study (LISS). 2017. Stamford, CT: EPA Long Island Sound Office. Available at: www.longislandsoundstudy.net and data at http://lisicos.uconn.edu/.

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

McKinney, R. A., S. M. Glatt & S. R. McWilliams. 2004. Allometric length-weight relationships for benthic prey of aquatic wildlife in coastal marine habitats. *Wildlife Biology* 10:241–249.

Merino, G., M. Barange, J. L. Blanchard, J. Harle, R. Holmes, I. Allen, E. H. Allison, M. C. Badjeck, N. K. Dulvy, J. Holt, S. Jennings, C. Mullon & L. D. Rodwell. 2012. Can marine fisheries and aquaculture meet fish demand from a growing human population in a changing climate? *Glob. Environ. Change* 22:795–806.

National Oceanic and Atmospheric Administration. 2011a. NOAA Aquaculture Policies 2011. Available at: http://www.nmfs.noaa.gov/aquaculture/policy/24_aquaculture_policies.html.

National Oceanic and Atmospheric Administration. 2011b. National shellfish initiative. Available at: http://www.nmfs.noaa.gov/aquaculture/policy/shellfish_initiative_homepage.html.

National Oceanic and Atmospheric Administration. 2016. National ocean policy implementation plan—aquaculture. Available at: http://www.nmfs.noaa.gov/aquaculture/docs/policy/nop_ip_aquaculture.pdf.

National Oceanic and Atmospheric Administration. 2017. Aquaculture in the United States. NOAA Fisheries. Available at: http://www.nmfs.noaa.gov/aquaculture/aquaculture_in_us.html.

Nunes, J. P., J. G. Ferreira, S. B. Bricker, B. O'Loan, T. Dabrowski, B. Dallaghan, A. J. S. Hawkins, B. O'Connor & T. O'Carroll. 2011. Towards an ecosystem approach to aquaculture: assessment of sustainable shellfish cultivation at different scales of space, time and complexity. *Aquaculture* 315:369–383.

Okumuş, I., N. Başcinar & M. Őzkan. 2002. The effect of phytoplankton concentration, size of mussel and water temperature on feed consumption and filtration rate of the Mediterranean mussel (*Mytilus galloprovincialis* Lmk). *Turk. J. Zool.* 26:167–172.

Oyster BMP Expert Panel. 2016. Panel recommendations on the oyster BMP nutrient and suspended sediment reduction effectiveness determination decision framework and nitrogen and phosphorus assimilation in oyster tissue reduction effectiveness for oyster aquaculture practices. Draft report submitted to the Chesapeake Bay Partnership Water Quality Goal Implementation Team, September 22, 2016. Available at: http://www.chesapeakebay.net/calendar/event/24330/. Accessed November 16, 2016.

Radiarta, I. N., S.-I. Saitoh & A. Miyazono. 2008. GIS-based multi-criteria evaluation models for identifying suitable sites for Japanese scallop (*Mizuhopecten yessoensis*) aquaculture in Funka Bay, southwestern Hokkaido, Japan. *Aquaculture* 284:127–135.

Rice, J., C. Arvanitidis, A. Borja, C. Frid & A. Norkko. 2012. Indicators for Sea-floor Integrity under the European Marine Strategy Framework Directive. *Ecological Indicators* 12:174–184.

Rogers, S. I., M. Casini, P. Cur, M. Heat, X. Irigoen, H. Kuos, M. Scheida, H. Sko, K. Stergio, V. Trenkel, J. Wikner & O. Yunev.

2010. Marine strategy framework directive task group 4 report food webs. ICES/JRC. 63 pp.

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

Ryther, J. H. 1969. Photosynthesis and fish production in the sea. *Science* 166:72–76.

Sequeira, A., J. G. Ferreira, A. J. Hawkins, A. Nobre, P. Lourenço, X. L. Zhang, X. Yan & T. Nickell. 2008. Trade-offs between shellfish aquaculture and benthic biodiversity: a modelling approach for sustainable management. *Aquaculture* 274:313–328.

Silva, C., J. G. Ferreira, S. B. Bricker, T. A. DelValls, M. L. Martín-Díaz & E. Yañez. 2011. Site selection for shellfish aquaculture by means of GIS and farm-scale models, with an emphasis on data-poor environments. *Aquaculture* 318:444–457.

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

Soto, D., J. Aguilar-Manjarrez & N. Hishamunda, editors. 2008. Building an ecosystem approach to aquaculture. FAO/Universitat de les Illes Balears Expert Workshop, May 7–11, 2007, Palma de Mallorca, Spain. FAO Fisheries and Aquaculture Proceedings. No. 14. Rome, Italy: FAO. 221 pp.

Stigebrandt, A., J. Aure, A. Ervik & P. K. Hansen. 2004. Regulating the local environmental impact of intensive marine fish farming. III. A model for estimation of the holding capacity in the MOM system (modelling-ongrowing fish farm-monitoring). *Aquaculture* 234:239–261.

Stokesbury, K. D., E. P. Baker, B. P. Harris & R. B. Rheault. 2011. Environmental impacts related to mechanical harvest of cultured shellfish. In: Shumway, S. E., editor. Shellfish aquaculture and the environment. Oxford, UK: Wiley-Blackwell. pp. 319–338.

Tiller, R., R. Gentry & R. Richards. 2013. Stakeholder driven future scenarios as an element of interdisciplinary management tools; the case of future offshore aquaculture development and the potential effects on fishermen in Santa Barbara, California. *Ocean Coast. Manage.* 73:127–135.

United States House of Representatives 20, 96th Congress. 1980. National Aquaculture Act of 1980. Available at: http://www.nmfs.noaa.gov/aquaculture/docs/aquaculture_docs/nat_aq_act_1980.pdf.

U.S. Department of Commerce. 2011. U.S. Department of Commerce Aquaculture Policy. Available at: http://www.nmfs.noaa.gov/aquaculture/docs/policy/doc_aquaculture_policy_2011.pdf.

Varekamp, J. C., A. E. McElroy, J. R. Mullaney & V. T. Breslin. 2014. Chapter 5: metals, organic compounds, and nutrients in Long Island Sound: sources, magnitudes, trends and impacts. In: Latimer, J. K., M. A. Tedesco, R. L. Swanson, C. Yarish, P. E. Stacey & C. Garza, editors. Long Island Sound: prospects for the urban sea. New York, Heidelberg, Dordrecht, London: Springer. pp. 203–284.

Wilson, J. G. 1990. Gill and palp morphology of *Telinna tenuis* and *T. fibula* in relation to feeding. In: Morton, B., editor. The bivalvia: proceedings of a memorial symposium in honour of Sir Maurice Charles Yonge (1899–1986), Edinburgh, 1986. pp. 141–152. Hong Kong University Press, HKU.

Wolfe, D. A., R. Monahan, P. E. Stacey, D. R. G. Farrow & A. Robertson. 1991. Environmental quality of Long Island Sound: assessment and management issues. *Estuaries* 14:224–236.

World Bank. 2013. Fish to 2030: prospects for fisheries and aquaculture. Agriculture and environmental services discussion paper no. 3. Washington, DC: World Bank Group. Available at: http://documents.worldbank.org/curated/en/458631468152376668/Fish-to-2030-prospects-for-fisheries-and-aquaculture.

Zhang, J., P. K. Hansen, J. Fang, W. Wang & Z. Jiang. 2009. Assessment of the local environmental impact of intensive marine shellfish and seaweed farming—application of the MOM system in the Sungo Bay, China. *Aquaculture* 287:304–310.