
Shellsim: A Generic Model of Growth and Environmental Effects Validated Across Contrasting Habitats in Bivalve Shellfish

Author(s): A. J. S. Hawkins , P. L. Pascoe , H. Parry , M. Brinsley , K. D. Black , C. McGonigle , H. Moore , C. R. Newell , N. O'Boyle , T. Ocarroll , B. O'Loan , M. Service , A. C. Smaal , X. L. Zhang and M. Y. Zhu

Source: Journal of Shellfish Research, 32(2):237-253. 2013.

Published By: National Shellfisheries Association

DOI: <http://dx.doi.org/10.2983/035.032.0201>

URL: <http://www.bioone.org/doi/full/10.2983/035.032.0201>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

SHELLSIM: A GENERIC MODEL OF GROWTH AND ENVIRONMENTAL EFFECTS VALIDATED ACROSS CONTRASTING HABITATS IN BIVALVE SHELLFISH

A. J. S. HAWKINS,^{1*} P. L. PASCOE,¹ H. PARRY,¹ M. BRINSLEY,¹ K. D. BLACK,²
C. McGONIGLE,³ H. MOORE,⁴ C. R. NEWELL,⁵ N. O'BOYLE,⁶ T. O'CARROLL,⁷ B. O'LOAN,⁷
M. SERVICE,⁴ A. C. SMAAL,⁸ X. L. ZHANG⁹ AND M. Y. ZHU⁹

¹Plymouth Marine Laboratory, Natural Environment Research Council, Prospect Place, The Hoe, Plymouth PL1 3DH, UK; ²Scottish Marine Institute, Oban, Argyll PA37 1QA, UK; ³Loughs Agency, 22 Victoria Road, Londonderry BT47 2AB, Northern Ireland; ⁴Agri-Food and Biosciences Institute, Newforge Lane, Belfast BT9 5PX, Northern Ireland; ⁵Maine Shellfish Research & Development, 7 Creek Lane, Damariscotta, 04543 ME; ⁶Clew Bay Marine Forum, Knockbreaga, Newport, Co Mayo, Ireland; ⁷Bord Iascaigh Mhara, Crofton Road, Dun Laoghaire, Co. Dublin, Ireland; ⁸Institute for Marine Resources & Ecosystem Studies, PO Box 177, 4400 AB Yerseke, The Netherlands; ⁹First Institute of Oceanography, State Oceanic Administration, 6 Xianxialing Road, 266061 Qingdao, P.R. China

ABSTRACT Previous shellfish models have, in general, been calibrated for 1 location, unable to simulate growth across habitats that contrast in seston abundance and composition, as may vary between turbid, eutrophic and oligotrophic waters. Here, we describe the generic shellfish model ShellSIM, demonstrating how a common parameter set simulates growth effectively on calibration in the mussel *Mytilus edulis* and oyster *Crassostrea gigas* during normal culture across 9 different locations in Europe and China. Options enable the user to assess the relative values of chlorophyll *a* (CHL, measured in micrograms per liter), total particulate organic matter (POM; measured in milligrams per liter), and total particulate organic carbon (POC; measured in milligrams per liter) as codescriptors of the food available at separate locations. Using CHL as the sole proxy for available organics, together with an average carbon-to-CHL ratio of 50, growth in both *M. edulis* and *C. gigas* was predicted accurately at only 5 locations, primarily those with relatively low average food availability. In contrast, more than 74% of the observed variance in growth was predicted across all 9 locations in each species on inclusion of dynamic relations defining ingestion and absorption of both CHL-rich and all remaining organic matter such as may include bacteria, protozoans, colloids, and/or detritus, thereby helping to account for temporal and spatial changes in dietary composition. The energy content of the remaining organic matter (measured in Joules per milligram) ranged seasonally across all sites from about 2–25 J/mg, and could be predicted with growth from the relative abundance of CHL and POM alone, proving a viable alternative to more technically demanding measures of POC. Fractional contributions of the remaining organic matter to the energy absorbed in both species at each location ranged from less than about 0.4 during the spring to more than 0.8 from late autumn, in negative relation with CHL, thus helping to offset tissue wasting during winter months. We acknowledge model uncertainties, emphasizing the need to balance practicality and affordability against required accuracies. Last, we describe how the generic and multi-site capabilities afforded by ShellSIM, together with real-time outputs ready for integrated modeling of how shellfish influence ecosystem properties and processes, are saving time and resources across a variety of applications.

KEY WORDS: *Mytilus edulis*, *Crassostrea gigas*, mussel, oyster, shellfish growth model, seston energy content, detrital matter, bound water

INTRODUCTION

Growth in the worldwide aquaculture of bivalve shellfish has been prolonged and rapid, with increasing pressure to model sustainable development, preserving the equity and resilience of interlinked social-ecological systems (FAO 2010, Cranford et al 2012, FAO 2012, Samuel-Fitwi et al 2012). Toward delivering those tools, dynamic simulation has proved essential, accounting for associated complexity in animal-environment interrelations through differential equations that integrate time-varying rates of feeding and metabolism as component processes in the simulation of growth and environmental effects (e.g., Ross & Nisbet 1990, Brylinski & Sephton 1991, Powell et al 1992, Raillard et al 1993, van Haren & Kooijman 1993, Barillé et al 1997, Campbell & Newell 1998, Grant & Bacher 1998, Scholten & Smaal 1999, Pouvreau et al 2000, Hawkins et al 2002, Solidoro et al 2000, Ren & Ross 2001, Ren & Ross 2005, Hofmann et al 2006, Pouvreau et al 2006, Ren & Schiel 2008, Spillman et al

2008, Bourlès et al 2009, Grangeré et al 2009, Rosland et al 2009, Rico-Villa et al 2010, Barillé et al 2011, Saraiva et al 2012).

Although responses in bivalve shellfish to the main environmental drivers of temperature and salinity are relatively well defined, feeding behavior has proved more challenging (Ward & Shumway 2004, Cranford et al 2011). Both the quantity and composition of available seston may be highly variable in time and in space (e.g., Héral et al 1983, Smaal et al 1986, Fegley et al 1992, Smaal & Haas 1997, Newell et al 1998, Cranford & Hill 1999). Faced with those variations, differential retentions and processing of separate dietary components have been reported repeatedly, and tend to enhance the ingestion and/or absorption of living microalgae (e.g., Shumway et al 1985, Iglesias et al 1992, MacDonald & Ward 1994, Hawkins et al 1996, Arifin & Bendell-Young 1997, Hawkins et al 1998a, Hawkins et al 1998b, Cranford & Hill 1999, Hawkins et al 1999, Brillant & MacDonald 2000, Pouvreau et al 2000, Ren et al 2000, Hawkins et al. 2001, Urrutia et al 2001, Wong & Cheung 2001, Rueda & Smaal 2002, Beninger et al 2008a, Beninger et al 2008b, Pascoe et al 2009, Yahel et al 2009). Recognizing that shellfish also feed on protozoans,

*Corresponding author. E-mail: ajsh@pml.ac.uk

DOI: 10.2983/035.032.0201

colloids, and decomposing plant fragments, shellfish models have, in some instances, accounted for other components of the organic matter within suspended particles (e.g., Raillard et al 1993, Campbell & Newell 1998, Grant & Bacher 1998, Pouvreau et al 2000, Ren & Ross 2001, Pouvreau et al 2006, Bourlès et al 2009), but without functional relations to simulate dynamic adjustments in the relative processing of separate dietary components. Hawkins et al. (2002) defined functional relations to simulate dynamic adjustments in the differential processing of particulate organics that are rich in chlorophyll *a* versus remaining “detrital” organics when modeling growth in the Chinese scallop, *Chlamys farreri*. Without such relations, as in stochastic simulations using von Bertalanffy’s growth model to account for seasonal effects of water temperature alone (e.g., Melià & Gatto 2005, Griebeler & Seitz 2007), there can be no insight into dynamic consequences of the natural fluctuations in seston availability, whether for growth or for resulting biogeochemical fluxes that affect ecosystem properties and processes (Newell 2004, Coen et al 2011, Ferreira et al 2011). Just as important, the lack of relations defining differential processing of separate dietary components has compromised the ability of previous models calibrated for given species at 1 location to simulate growth at other locations, let alone across contrasting habitats such as turbid, eutrophic, and oligotrophic waters. Furthermore, evolutionary adaptation to specific ecological niches is evidenced from the different comparative ingestion and/or digestion of separate particle types (e.g., Møhlenberg & Riisgård 1978, Shumway et al 1985, Shumway et al 1991, Ward & MacDonald 1996, Bougrier et al 1997, Hawkins et al 1998b, Beninger et al 1999, Hawkins et al unpubl. data). Therefore, a mechanistic basis for such differences also needs to be formulated before the effective parameterization of any generic model structure for different shellfish species. These requirements were confirmed by the findings of Troost et al. (2010) who, when free-fitting the relative contribution of detritus over and above chlorophyll organics to growth observed in cockles and mussels throughout the Oosterschelde in Netherlands, observed that the importance of detritus was both site and species specific.

Hawkins et al. (unpubl. data) define dynamic adjustments between the relative ingestion and absorption of chlorophyll-rich versus remaining organic matter across wide ranges of seston availability and composition in 8 shellfish species. Here, we describe how inclusion of those responses, together with choice of simple environmental measures that account for associated variation in dietary energy contents, are key elements of the generic shellfish model ShellSIM (<http://www.shellsim.com>) (Hawkins et al 2012a), and enhance the ability to simulate growth effectively across contrasting environments using single-parameter sets in 2 of the most widely cultured of shellfish species—the blue mussel *Mytilus edulis* and the Pacific oyster *Crassostrea gigas*.

METHODS

Environmental Measures

Measures of surface seawater temperature (TEMP; measured in degrees Celsius), salinity (SAL; measured in practical salinity units), dissolved oxygen (DO; measured as percent saturation), aerial exposure (fraction of days exposed to air), and seston availability determined as total particulate mass (TPM; measured in milligrams per liter), particulate inorganic mass (PIM; measured in milligrams per liter), particulate

organic mass (POM; measured in milligrams per liter), and chlorophyll *a* (CHL; measured in micrograms per liter) were undertaken at approximately 2 to 4-wk intervals coincident with measures of shellfish growth during normal culture of *Mytilus edulis* Linnaeus and *Crassostrea gigas* Thunberg at 9 locations summarized in Table 1. At 6 of those locations, not including Dungarvan Bay, Killary Harbour, and Sango Bay, seston availability was also measured as particulate organic carbon (POC; measured in micrograms per liter).

Samples for measures of seston availability were collected by filtering seawater samples through 47-mm GF/C filters that had been previously combusted at 450°C for 3 h and weighed, defining TPM as the weight difference after drying the filter and sample at 60°C for 24 h, PIM as the weight difference after combusting at 450°C for 3 h, and POM as TPM – 1.05 × PIM, assuming 5% of PIM is lost as structural water from clay minerals on incineration, which is a conservative correction based on illite (Caillère & Hénin 1963). In this way, we have corrected for losses that might otherwise be attributed to POM (e.g., Mook & Hoskin 1982, Dankers & Laane 1983, Barillé-Boyer et al 2003), which proved necessary when computing dietary energy contents (see Predicting the Energy Content of Detrital Organics).

To measure POC, additional samples were collected by filtering seawater samples through 47-mm GF/C filters that had been previously combusted at 450°C for 3 h, holding the filtered material in HCl vapor for 15 sec to destroy inorganic carbonates, which would have been lost and might otherwise have been attributed to POM on combustion (Hiroya & Szyperski 1975). Each filter was then placed in a separate acid-washed Petri slide and oven dried at less than 40°C before determining the carbon contents of replicated subsamples using a Carlo Erba elemental analyzer with acetanilide at 925°C as a standard.

Chlorophyll *a* was measured in samples that had been collected on 25-mm GF/C filters using standard procedures for acetone extraction and fluorometric analysis (Holm-Hansen et al 1965).

ShellSIM Structure

STELLA research software (version 9.0.3; isee systems, Lebanon, NH), a graphical modeling package, was used to simulate shellfish growth using the Euler algorithm with a time step of 1 day. Variables and interrelations are defined in Table 2, with associated explanation in the subsections that follow. This is the same approach that has been further developed to predict population dynamics and environmental effects, now validated in 13 commonly cultured shellfish species, and is available from Plymouth Marine Laboratory as a dynamic link library compiled for the Microsoft.NET Framework (<http://www.shellsim.com>).

Assessing the Relative Significance of Different Dietary Components

ShellSIM includes options to simulate the differential availabilities, energy contents, and processing of CHL-rich organic matter that is known to be filtered and ingested preferentially (SELORG, milligrams), relative to all remaining organic matter (REMORG, milligrams), according to the approach and observations of Hawkins et al. (unpubl. data).

When wishing to assess the potential for successful prediction of growth on the basis of CHL alone, or when no data are available for POM and no POC, then all suspended organic

TABLE 1.

Sampling summary: locations and dates for measures of environmental drivers and coincident growth in *Mytilus edulis* and *Crassostrea gigas*.

Locations	Species	Culture types	Dates	Sites of water sampling and growth validation	Grid references
Belfast Lough, N. Ireland	<i>M. edulis</i>	Bottom	Feb 2005 to Jan 2006	Site BL11*	54°39'57" N, 5°52'21" W
Carlingford Lough, N. Ireland	<i>M. edulis</i>	Bottom	Mar 2005 to Jan 2006	Site CL03*	54°05'16" N, 6°14'18" W
Clew Bay, Ireland	<i>M. edulis</i>	Rope	Feb to Oct 2006	Inislaughil (6 and 18 m depth)	53°51'46" N, 9°37'59" W
	<i>C. gigas</i>	Trestle	Apr to Oct 2006	Inishcarrick*	53°52'43" N, 9°40'17" W
Loch Creran, Scotland	<i>C. gigas</i>	Trestle	Feb to June 2006	Caledonian Oyster Farm	56°30'46" N, 5°23'05" W
Dungarvan Bay, Ireland	<i>C. gigas</i>	Trestle	Jul 2007 to May 2008	North Dungarvan	52°04'30" N, 7°35'05" W
				Mid Dungarvan*	52°03'59" N, 7°35'03" W
				South Dungarvan	52°03'29" N, 7°34'42" W
Lough Foyle, N. Ireland	<i>M. edulis</i>	Bottom	Apr to Jul 2006	Dougold	55°04'64" N, 7°10'67" W
				Steele*	55°07'67" N, 7°10'89" W
Killary Harbour, Ireland	<i>M. edulis</i>	Rope	Aug 2007 to May 2008	Main Channel West (1 and 5 m depth)	53°37'02" N, 9°50'09" W
				Main Channel Mid (1 and 5* m depth)	53°36'18" N, 9°48'16" W
				Main Channel East (1 and 5 m depth)	53°35'60" N, 9°44'57" W
				South Channel West (1 and 5 m depth)	53°36'57" N, 9°50'14" W
				South Channel Mid (1 and 5 m depth)	53°36'10" N, 9°48'18" W
				South Channel East (1 and 5 m depth)	53°35'58" N, 9°44'58" W
Oosterschelde, Netherlands	<i>M. edulis</i>	Bottom	Dec 2005 to Aug 2006	Kijkuit	51°30'18" N, 4°02'59" E
	<i>C. gigas</i>	Bottom	May 2005 to Aug 2006	Zandkreek	51°33'07" N, 3°53'33" E
Sungo Bay, China	<i>C. gigas</i>	Rope	Jan to Aug 2006	East Schelde*	51°30'48" N, 4°08'40" E
				Site 09*	37°03'15" N, 122°33'32" E

* Sites for which representative environmental data are illustrated for each location in Figures 1, 2 and 4.

matter available as food was modeled as SELORG calculated as SELORG

$$\frac{\text{CHL} \times 50}{0.38},$$

with CHL measured in milligrams, where multiplying measured CHL by 50 to give total phytoplankton organic carbon is based on average values measured in nutrient-rich surface waters (Welschmeyer & Lorenzen 1984, Taylor et al 1997) according to Grant & Bacher (1998), and division by 0.38 represents an average conversion to organic matter for natural algal blooms within nearshore waters (Platt & Irwin 1973, Soletchnik et al 1996).

Alternatively, developing the approach taken by Hawkins et al. (2002), when able and wishing to resolve dietary components using additional data for POM and/or POC, ShellSIM simulated additional suspended organic matter surplus to SELORG as REMORG (measured in milligrams) = POM - SELORG, where SELORG (measured in milligrams) was computed as

$$\text{SELORG} = \frac{\text{CHL} \times 12}{0.38},$$

with CHL measured in milligrams, where the C/CHL conversion factor of 12 matched values measured in fast-growing algal monocultures (Taylor et al 1997), and the value was the minimum required to ensure that SELORG did not, on occasion, exceed the

total organic matter indicated from coincident values of POM and/or POC (Hawkins et al unpubl. data).

In contrast to the organic matter within healthy algal monocultures, the energy content of detrital organics may vary greatly, both spatially and seasonally (see Results and Discussion). To help account for this variation and to test further the relative utility of different environmental measures that may be available, ShellSIM contains predictive options as follows:

- Given measures of CHL and POM but no POC, the energy content of REMORG (EREM; measured in Joules per milligram) is calculated as EREM = [(8.25 + (21.24 × (1 - EXP(-2.79 × SELORG)))) + (-0.174 × REMORG)] as presented in Results, Predicting the Energy Content of Detrital Organics.
- Given measures of CHL and POC but no POM, then POM is estimated from POC (POMPOC; measured in milligrams per liter) as POMPOC = [(POC/1,000) × 2.33], and total energy within POM (TOTE; measured in Joules per liter) as TOTE = [47.73 × (POC/1,000)], both according to Platt and Irwin (1973). EREM is then calculated as EREM = [(TOTE - (SELORG × 23.5))/(POMPOC × SELORG)], assuming 23.5 J/mg dry phytoplankton organics (Slobodkin & Richman 1961). This option, in effect, assumes EREM constant at (47.73/2.33) = 20.48 J/mg.
- Given measures of CHL, POM, and POC, the energy content of total particulate organic matter (EPOM; measured in

TABLE 2.

ShellSIM variables and functions used to simulate individual growth in *Mytilus edulis* and *Crassostrea gigas*.

FORCING VARIABLES	
TEMP {°C}	
POM {mg/L}	
POC {µg/L}	
CHL {µg/L}	
FUNCTIONS	
<i>Time</i>	
Day = if year < 1, then int(time) else int(time - 365 * (year - 1))	
Year = (int(time/365) + 1)	
<i>Seston composition</i>	
SELORG = if (CHL > 0 and POC = 0 and POM = 0) then [((CHL ÷ 1,000) × 50) ÷ 0.38] {mg/L} else if (CHL > 0 and POM > 0 and POC = 0) or (CHL > 0 and POM > 0 and POC > 0) then [((CHL ÷ 1,000) × 12) ÷ 0.38] else 0 {mg/L}	
REMORG = POM - SELORG {mg/L}	
EREM = if (CHL > 0 and POM > 0 and POC > 0) then [((POM × ((0.632 + (0.086 × (POC ÷ (POM × 1,000)) × 100)) × 4.187)) - (SELORG × 23.5)) ÷ REMORG] {J/mg} else if (CHL > 0 and POM > 0 and POC = 0) then [(8.25 + (21.24 × (1 - EXP(-2.79 × SELORG)))) + (-0.174 × REMORG)] {J/mg} else if (CHL > 0 and POM = 0 and POC > 0) then 20.48 else 0 {J/mg}	
<i>Temperature effects</i>	
TEF {fraction}	
TEM {fraction}	
TEF <i>M. edulis</i> = [($a - (b \times (\text{TEMP} - c)^2)$) ÷ ($a - (b \times (15 - c)^2)$)]	
TEF <i>C. gigas</i> = [(($a + (b \times \text{TEMP}) + (c \times \text{TEMP}^2)$) ($(a + (b \times \text{TEMP}) + (c \times \text{TEMP}^2))$)]	
TEM = [$\text{EXP}(a \times \text{TEMP})$ ÷ $\text{EXP}(a \times 15)$]	
<i>Ingestion</i>	
NIRSELORG = (if CHL < 0.01 then 0 else [$(b \times \text{SELORG}) \times \text{TEF} \times ((\text{WE} \div \text{WS})^{0.62})$] {mg/h}	
NIRREMORG = [$a \times (1 - \text{EXP}(-b \times \text{REMORG})) \times \text{TEF} \times ((\text{WE} \div \text{WS})^{0.62})$] {mg/h}	
<i>Absorption</i>	
NEA = [(NIRSELORG × 23.5) + (NIRREMORG × 0.15 × EREM)] × 0.82 × 24 {J/day}	
<i>Heat losses</i>	
MHL = [4.005 × TEF × $((\text{WE} \div \text{WS})^{0.72}) \times 24$] {J/day}	
THL = [MHL + (0.23 × NEA)] {J/day}	
<i>Excretory losses</i>	
O:N = [10 + (((200 - 10) ÷ MNEA) × NEA)] {ratio}	
EL = [(((THL ÷ 14.06) ÷ 16) ÷ O:N) × 14 × 1,000] {µg NH ₄ /day}	
<i>Net energy balance</i>	
NEB = [NEA - THL - (EL × 0.02428)] {J/day}	
<i>Reproductive losses</i>	
SPAWN = (if SL >= SLM, TEMP >= TTS and COND >= (0.95 × MTA)) then [DSTW × PSTL × 23.5] else 0 {J}	
STATE VARIABLES AND DERIVATIONS	
<i>Shell</i>	
SG = (if COND >= MTA) then [(1 - MTA) × NEB] else 0 {J/day}	
Shell energy (t) = [Shell energy(t - dt) + (SG) × dt] {J}	
Dry shell weight (t) = [Dry shell weight(t - dt) + (Shell energy ÷ (ECS × 1,000)) × dt] {g}	
<i>Soft tissue</i>	
TG = (if COND < MTA) then NEB else if (COND >= MTA) then [MTA × NEB] else 0 {J/day}	
Soft tissue energy (t) = [Soft tissue energy(t - dt) + (TG - SPAWN) × dt] {J}	
Dry soft tissue weight (t) = [Dry soft tissue weight(t - dt) + (Soft tissue energy ÷ (23.5 × 1,000)) × dt] {g}	
<i>Total fresh weight</i>	
Total wet weight = [(Dry shell weight × (1 + WCS)) + (Dry soft tissue weight × (1 + WCT)) × SCW] {live g}	
<i>Shell length</i>	
SL = [$a \times \text{Dry shell weight}^b$] {cm}	

Unless otherwise stated, the same function was used in both species. Refer to Methods for the explanation of functions and definition of acronyms. Information in braces denotes units.

Joules per milligram POM is calculated as EPOM = [(0.632 + (0.086 × (POC ÷ (POM × 1,000)) × 100)) × 4.187], according to Platt and Irwin (1973), applying a conversion of 4.187 J/cal to compute EREM as EREM = [(POM × EPOM) - (SELORG × 23.5)] ÷ REMORG, again assuming 23.5 J/mg dry phytoplankton organics (Slobodkin & Richman 1961).

Ingestion and Absorption

Differential processing of SELORG and REMORG was simulated using relations fitted to experimental measures described by Hawkins et al. (unpubl. data), standardized between species to a common temperature of 15°C. These relations included linear equations that best describe how net ingestion

of SELORG (NIRSELORG; measured in milligrams per hour per gram) varied with SELORG in both *Mytilus edulis* and *Crassostrea gigas* as follows:

1. NIRSELORG in *M. edulis* = $[-0.16 + (3.57 \times \text{SELORG})]$, where adjusted $r^2 = 0.78$, residual $df = 343$, and $P < 0.0001$.
2. NIRSELORG in *C. gigas* = $[-0.33 + (4.11 \times \text{SELORG})]$, where adjusted $r^2 = 0.43$, residual $df = 321$, and $P < 0.0001$.

Alternatively, exponential equations best describe how net ingestion of REMORG (NIRREMORG; measured in milligrams per hour per gram) varied with REMORG in both *Mytilus edulis* and *Crassostrea gigas* as follows:

1. NIRREMORG in *M. edulis* = $[7.10 \times (1 - \text{EXP}(-0.31 \times \text{REMORG}))]$, where adjusted $r^2 = 0.30$, residual $df = 343$, and $P < 0.0001$.
2. NIRREMORG in *C. gigas* = $[8.21 \times (1 - \text{EXP}(-0.34 \times \text{REMORG}))]$, where adjusted $r^2 = 0.30$, residual $df = 321$, and $P < 0.0001$.

Although shellfish consistently digest and absorb the bulk of ingested chlorophyll-rich organics (Hawkins et al 1986, Navarro et al 2009), only a minor fraction of the remaining nonchlorophyll organics ingested with other suspended particles may be hydrolyzable and thus bioavailable (Dauwe & Middelburg 1998, Dauwe et al 1999a, Dauwe et al 1999b, Dell'Anno et al 2000, Danovaro et al 2001, Pusceddu et al 2003). Analyses of the nutritional value of POM within lagoon systems have indicated that labile "biopolymeric" nonphytoplankton organics measured as protein, carbohydrate, and lipid represented an average of about 50% of total POC, and that an average of only about 30% of that labile organic carbon was hydrolyzable (Pusceddu et al 1996, Pusceddu et al 2003). To account for these observations, which proved necessary to simulate growth adequately at contrasting culture locations, net energy absorption (NEA; measured in Joules per day) was computed as $\text{NEA} = [((\text{NIRSELORG} \times 23.5) + (\text{NIRREMORG} \times 0.15 \times \text{EREM})) \times 0.80 \times 24]$, assuming (1) 23.5 J/mg dry phytoplankton organics according to Slobodkin and Richman (1961), (2) 15% of REMORG was hydrolyzable and thus bioavailable, and (3) both SELORG and the hydrolyzable fraction of REMORG were absorbed with a shared efficiency of 80%, representative of values observed for chlorophyll-rich diets in *Mytilus edulis* and *Crassostrea gigas* (Hawkins et al unpubl. data), and where a constant value was consistent with findings that the volume of matter in the digestive system of bivalve shellfish may be balanced against the production and activity of digestive enzymes to maintain absorption efficiency over ranges of food availability (Bayne et al 1989, Ibarrola et al 1998, Ibarrola et al 2000a, Ibarrola et al 2000b, Ibarrola et al 2000c, Navarro et al 2009).

Heat Losses

Calorimetric measures have established that heat losses of feeding and growth in excess of maintenance heat losses (MHL; measured in Joules per day) under conditions of 0 net energy balance increase in linear relation with energy absorption (Hawkins et al 1989, Widdows & Hawkins 1989). Total heat losses (THL; measured in Joules per day) were therefore calculated as $\text{THL} = \text{MHL} + (0.23 \times \text{NEA})$, according to Hawkins et al. (2002), where MHL and the fractional energy cost of feeding and digestion are based on measures of 4.005 J/h/g and

0.23 J/h/g dry soft tissue, respectively, as observed in *Mytilus edulis* acclimated at 15°C and 33‰ (Hawkins et al 1989).

Excretory Losses

Excretory losses as ammonium were calculated from atomic ratios of oxygen consumed to nitrogen excreted (O:N ratio), calculated as $[(\text{O}_2) \div 16] \div [(\text{NH}_4\text{-N}) \div 14]$, where O₂ and NH₄-N are measured in milligrams. Past studies have shown minimum O:N ratios of about 10 after food limitation, increasing to a maximum of about 200 at higher rations (e.g., Bayne & Scullard 1977, Widdows 1978, Epp et al 1988). The O:N ratio was therefore estimated assuming that the O:N ratio increased linearly from minimum to maximum as energy acquisition increased from 0 to the estimated maximum rate of net energy absorption (MNEA; measured in Joules per gram dry soft tissue per day) in each shellfish species (cf. Hawkins et al 2002), where $\text{O:N} = [10 + ((200 - 10) \div \text{MNEA}) \times \text{NEA}]$, using values of 1,250 J/g dry soft tissue/d and 1,350 J/g dry soft tissue/d observed by Hawkins et al. (unpubl. data) for MNEA at 15°C and 33‰ in *Mytilus edulis* and *Crassostrea gigas*, respectively. Excretory losses (EL; measured in micrograms NH₄ per day) were then simulated as $\text{EL} = [((\text{THL} \div 14.06) \div 16) \div \text{O:N}] \times 14 \times 1,000 \times 24]$, where 1 mg O₂ = 14.06 J (Gnaiger 1983).

Energy Balance

Net energy balance (NEB; measured in Joules per day) was computed as $\text{NEB} = [\text{NEA} - \text{THL} - (\text{EL} \times 0.02428)]$, where 1 µg NH₄-N = 0.02428 J (Elliot & Davison 1975).

Shell and Tissue Conversions

Average organic carbon contents (measured as a percentage ± 2 SE; $n = 5$) of total shell mass measured in replicated subsamples of *Mytilus edulis* from the Lynher Estuary, Devon, UK, and *Crassostrea gigas* from the Avon River, Devon, UK, using a Carlo Erba elemental analyzer with acetanilide at 925°C as a standard were $2.25 \pm 0.11\%$ and $0.35 \pm 0.04\%$, respectively. A mean conversion factor of 46 kJ/g organic carbon as established for aquatic invertebrates (Salonen et al 1976) was then used to predict total energy contents of shell (ECS; measured as Joules per total dry milligrams) as $[0.0225 \times 46] = 1.035$ J/total dry mg and $[0.0035 \times 46] = 0.161$ J/total dry mg, respectively. For soft body tissues, we assumed 23.5 J/dry mg (Slobodkin & Richman 1961).

By applying these conversions to measures of dry soft tissue and shell weights recorded during field observations of actual growth at each site, strong linear relations were evident between soft tissue energy (TISE; measured in Joules) and total soft tissue plus shell energy (ALLE; measured in Joules), where $\text{TISE} = [b \times \text{ALLE}]$, when values for the slope b represent the mean tissue allocation (MTA; measured as a fraction), for which values (± 2 SE) in *Mytilus edulis* and *Crassostrea gigas* were 0.68 ± 0.05 ($n = 228$, adjusted $r^2 = 0.97$, $P < 0.0001$) and 0.76 ± 0.04 ($n = 254$, adjusted $r^2 = 0.95$, $P < 0.0001$), respectively.

If the ratio between TISE and ALLE exceeded or equaled MTA, then energy allocation to total soft tissues (TG; measured in Joules per day) was predicted as $\text{TG} = [\text{MTA} \times \text{NEB}]$, and energy allocation to shell (SG; measured in Joules per day) as $\text{SG} = [(1 - \text{MTA}) \times \text{NEB}]$. Otherwise, all available energy was directed to soft tissue growth, helping to maintain TISE following periodic losses of soft tissue through spawning or wasting,

consistent with observations that shell growth is not coupled with tissue growth (e.g., Hilbish 1986).

Energy was converted to dry weight equivalents using the energy contents for dry tissue and shell justified earlier. Conversion from dry to wet equivalents was computed using average (± 2 SE) water contents of shell (WCS; measured as a fraction) and soft tissue (WCT; measured as a fraction) measured in *Mytilus edulis* (0.048 ± 0.007 and 0.804 ± 0.009 , respectively; $n = 76$) and *Crassostrea gigas* (0.189 ± 0.005 and 0.914 ± 0.002 , respectively; $n = 54$) from all sites. Further conversion to total fresh or live weight (TFW; g) accounted for water retained within the shell cavity by applying average (± 2 SE) shell cavity water corrections (SCW; measured as a fraction) to the sum of wet tissue and shell weights as also measured in *M. edulis* (1.485 ± 0.066 ; $n = 76$) and *C. gigas* (1.115 ± 0.009 ; $n = 54$) from all sites.

Conversion to shell length (SL; measured in centimeters) was effected using power relations that best described how SL varied with dry shell weight (DSW; measured in grams) across sites as $SL = [a \times DSW^b]$, where, in *M. edulis*, $a = 2.654$, $b = 0.335$, adjusted $r^2 = 0.99$, residual $df = 74$, and $P < 0.0001$; and, in *C. gigas*, $a = 2.767$, $b = 0.327$, adjusted $r^2 = 0.98$, residual $df = 53$, and $P < 0.0001$.

Reproductive Losses

Spawning was simulated according to the following parameters in each shellfish species: (1) shell length upon maturation (SLM; measured in centimeters); (2) threshold of seawater temperature above which spawning occurs (TTS; measured in degrees Celsius); (3) condition (COND; measured as a fraction) computed as $COND = [\text{soft tissue energy}/(\text{soft tissue energy} + \text{shell_energy})]$; (4) proportion of dry soft tissue lost on each spawning event (PSTL; measured as a fraction), derived by plotting dry tissue loss on spawning versus dry tissue before spawning, assuming that this relation is independent of size in mature individuals as established by Bayne et al. (1983); and (5) maximal number of spawning events per annum (NSE; measured in units).

Using these parameters, energy lost from soft tissues upon spawning (SPAWN; measured in Joules per spawning per animal) was computed according to dry soft tissue weight (DSTW; measured in grams) in *Mytilus edulis* and *Crassostrea gigas* as $SPAWN = [\text{DSTW} \times \text{PSTL} \times 23.5]$ when $SL \geq SLM$ (2 and 5, respectively), $TEMP \geq TTS$ (13 and 19, respectively), and $COND \geq (0.95 \times MTA)$, assuming 23.5 J/mg dry soft body tissue (Slobodkin & Richman 1961), and where values for PSTL were observed experimentally (0.18 and 0.44, respectively), while limiting NSE to 2 (Bayne et al 1983, Hawkins et al 1985, Ren et al 2003, Royer et al 2008).

Effects of Seawater Temperature

Correction factors were applied to simulate effects of seasonal changes in seawater temperature on ingestion rates and MHLs (Table 2). The following relations best describe how clearance rates (CR; measured in liters per hour per gram) under standardized conditions of food availability have been observed to vary with TEMP:

$$\text{CR in } Mytilus edulis = [4.825 - (0.013 \times (\text{TEMP} - 18.954)^2)] \quad (\text{Bougrier et al 1995})$$

$$\text{CR in } Crassostrea gigas = [0.320 + (0.323 \times \text{TEMP}) + (-0.011 \times \text{TEMP}^2)] \quad (\text{fitted to data of Widdows (1978)})$$

Using these curves, factors describing effects on feeding (TEF; measured as a fraction) were computed as $TEF = [(\text{CR predicted at TEMP}) \div (\text{CR predicted at } 15^\circ\text{C})]$ for application to NIRSELORG and NIRREMORG.

Correction factors describing temperature effects on MHLs (TEM; measured as a fraction) were derived assuming that TEM increased continually in logarithmic relation with seawater temperature according to Q_{10} values of 2.10 and 1.96 established in *Mytilus edulis* (Bayne & Newell 1983) and *Crassostrea gigas* (Bougrier et al 1995), respectively. On this basis, TEM was computed as $\text{TEM in } M. edulis = \text{EXP}(0.074 \times \text{TEMP}) \div \text{EXP}(0.074 \times 15)$; and $\text{TEM in } C. gigas = \text{EXP}(0.067 \times \text{TEMP}) \div \text{EXP}(0.067 \times 15)$, assuming energy costs of maintenance recorded in *M. edulis* at 15°C (see Heat Losses) (Hawkins et al 1989).

Effects of Salinity, Dissolved Oxygen, and Aerial Exposure

Lowest values of SAL (25‰) and DO (51%) recorded at all sites were above thresholds below which effects of more than 5% have been recorded on feeding and metabolism in *Mytilus edulis* (24‰ and 25‰, respectively) (Bayne 1975, Almada-Villela 1984) and *Crassostrea gigas* (20‰ and 46‰, respectively) (Brown & Hartwick 1988, Moullac et al 2007). Similarly, *C. gigas* grown on trellises in Dungarvan Bay were exposed to air for an average daily maximum of 0.18 (fraction), which is within the range less than 0.2 that oysters are known to effect full growth compensation (Gillmor 1982). Therefore, it is not necessary to present recorded values for SAL or DO in this article, nor to simulate associated effects.

Effects of Shellfish Size

Relations describing feeding and metabolism were all standardized for an equivalent individual shellfish of 1 g dry soft tissue weight, where the standardized rate SR = $[(\text{SW}/\text{WE})^b \times \text{UR}]$, where SW is the standard weight (1 g), WE is the dry soft tissue weight (measured in grams) of experimental animal, UR is the uncorrected rate, and b is the associated weight exponent. The same exponents were applied in *Mytilus edulis* and *Crassostrea gigas*, but differed according to whether correcting for feeding ($b = 0.62$) or metabolism ($b = 0.72$), as representative values observed both in these and other species of suspension-feeding shellfish (Bayne & Newell 1983, Bougrier et al 1995).

Model Sensitivity and Validation

To compare effects of each model parameter on model output, a single parameter was adjusted either $\pm 10\%$ per model run, requiring 2 runs per parameter, and the average percentage change in live weight resulting from that increase and decrease was used to quantify model sensitivity to that parameter. All analyses were undertaken using steady-state conditions for TEMP (15°C), SAL (33‰), DO (100%), aerial exposure (0.0 fraction), CHL (2 µg/L), and POM (3 mg/L), initializing for *Mytilus edulis* or *Crassostrea gigas* of 2.5 cm SL and running for 100 d.

To help validate ShellSIM outputs, field observations of actual shellfish growth were made under normal culture conditions at the same locations and concurrent with environmental measures described previously (Table 1). On occasion, if project time spans did not allow rearing through the full period of normal culture, both seed and half-grown size classes were deployed.

Each measure of size included average SL (measured in millimeters), total live weight (measured in grams), and dry soft tissue weight (measured in milligrams) for a minimum of 30 individuals at about monthly intervals, taking care to ensure from a single cohort, sieving out fresh settlement as necessary. Simulations of growth were validated by comparing with observed growth as described by Portilla & Tett (2007), classifying performance according to goodness of fit following linear regression on the basis of (1) the proportion of variance explained by each regression and (2) whether slopes and intercepts differ from 1 and 0, respectively; on which basis models can be judged as excellent, good, fair, or poor (Oreskes et al 1994).

RESULTS

Seasonal Changes in Environmental Characteristics

Seasonal changes in TEMP, POM, CHL, and POC are illustrated when measured for each study location in Figure 1. It may be seen that TEMP and CHL varied by an order of magnitude both over time and between sites. Associated changes in the relative availability and energy content of REMORG (measured in milligrams per liter) are illustrated in Figure 2. Remaining organic matter comprised more than 85% of POM at all sites where assessed, but with highly variable energy contents (EREM) that ranged from about 2–25 J/mg, averaging (± 2 SE) 8.1 ± 2.7 J/mg. Associated contributions to the total energy contents of seston (measured as a fraction) never dropped below 0.82, with a maximum of about 0.98 during winter (Fig. 2).

Predicting the Energy Content of Detrital Organics

The ability to predict variation in EREM without POC data was assessed using EREM, SELORG, and REMORG, each computed from coincident measures of POM, CHL, and POC, as was collected seasonally and during feeding experiments at different study locations (Table 1) (Hawkins et al unpubl. data), when stepwise regression confirmed that EREM was best described by exponential and linear relations with SELORG (measured in milligrams per liter) and REMORG (measured in milligrams per liter) as follows: $EREM = [(8.25(\pm 1.70) + (21.24(\pm 2.66) \times (1 - EXP(-2.79(\pm 0.86) \times SELORG))) + (-0.174(\pm 0.16) \times REMORG)]$, where ± 2 SE are bracketed for each parameter, adjusted $r^2 = 0.52$, residual $df = 284$, and $P < 0.0001$. Maximal values of EREM (21.24 ± 2.66 J/mg) predicted by this equation approximate the energy content of 23.5 J/mg assumed in SELORG (see Ingestion and Absorption). The observation that those maximal values occurred when SELORG was most abundant, declining with increasing REMORG, is consistent with natural cycles during which blooms of primary production ultimately die, with EREM being highest early during the process of decline and decay, and declining thereafter following the transition from SELORG to REMORG. It should be noted that this prediction was dependent on and sensitive to the correction of POM for 5% of PIM lost as structural water on incineration (see Environmental Measures). Without such correction, maximal values simulated for EREM were only 14.1 ± 1.73 J/mg, which would not have afforded a consistent transition and decline from SELORG.

Growth Simulations

Assessing What Measures of Food Availability Are Required to Predict Growth

To assess whether it necessary to account for both chlorophyll-rich and remaining dietary organics when predicting growth in *Mytilus edulis* and/or *Crassostrea gigas* at all sites, measured growth was compared with growth predicted either from (1) CHL alone, multiplying CHL by 50 to give total phytoplankton organic carbon (see Assessing the Relative Significance of Different Dietary Components) or (2) from CHL in combination with POM, multiplying CHL by 12 to give total phytoplankton organic carbon, with associated simulations of SELORG, REMORG, and EREM (see Assessing the Relative Significance of Different Dietary Components and Predicting the Energy Content of Detrital Organics; Fig. 3). When simulated with CHL alone, it is notable that growth was over-predicted for *C. gigas* in Dungarvan Bay and the Oosterschelde, including for *M. edulis* in Belfast Lough, Carlingford Lough, Lough Foyle, and the Oosterschelde (Fig. 3). Nevertheless, selective analyses confirmed that growth was accurately predicted using CHL alone for *M. edulis* in Clew Bay and Killary Harbour ($r^2 = 0.63$), including for *C. gigas* in Clew Bay, Lough Creran and Sungo Bay ($r^2 = 0.82$) (Table 3). Throughout these simulations, average CHL ($\mu\text{g/L} \pm 2\text{SE}$) availabilities in Carlingford Lough (4.9 ± 1.9 , $n = 8$), Lough Foyle (4.8 ± 1.4 , $n = 33$) and the Oosterschelde (2.3 ± 0.6 , $n = 53$) were significantly ($P < 0.05$) higher than in Killary Harbour (1.3 ± 0.3 , $n = 12$) and Lough Creran (0.8 ± 0.4 , $n = 12$), with intermediary values at other locations. Therefore, when using CHL as the sole measure of dietary organics, growth tended to be over-predicted at locations that were on average relatively rich in CHL.

Multiplying CHL by less than 50 to give total phytoplankton organic carbon was not in itself a generic solution to the above discrepancies, for this reduced simulated growth below that observed at locations that were relatively poor in CHL. Instead, when both CHL and POM were used as coincident descriptors of seston availability, multiplying CHL by 12 to give phytoplankton organic carbon, together with associated simulations of SELORG, REMORG, and EREM (see Assessing the Relative Significance of Different Dietary Components and Predicting the Energy Content of Detrital Organics), then predictions of growth were collectively improved throughout all locations in both *Mytilus edulis* ($r^2 = 0.75$) and *Crassostrea gigas* ($r^2 = 0.91$; Fig. 3, Table 3).

Fractional contributions predicted from detrital and bacterial organics (REMORG) to all energy absorbed using both CHL and POM in both *Mytilus edulis* and *Crassostrea gigas* at each location ranged, in general, from less than about 0.4 during spring and summer to more than 0.8 during late autumn and winter (Fig. 4). The similarity of this seasonal cycle between all 9 locations suggests widespread contributions from REMORG in each species, and contributions were most pronounced when CHL was low, helping to offset the tissue wasting that typically occurs at such times (e.g., Hawkins et al 1985, Drudi et al 2007) (Figs. 1 and 4).

Optional Drivers for Simulating the Combined Contributions to Growth of Both Chlorophyll-Rich and Remaining Dietary Organics

To assess the added or separate value of POC relative to POM as codescriptors with CHL of dietary quality when predicting

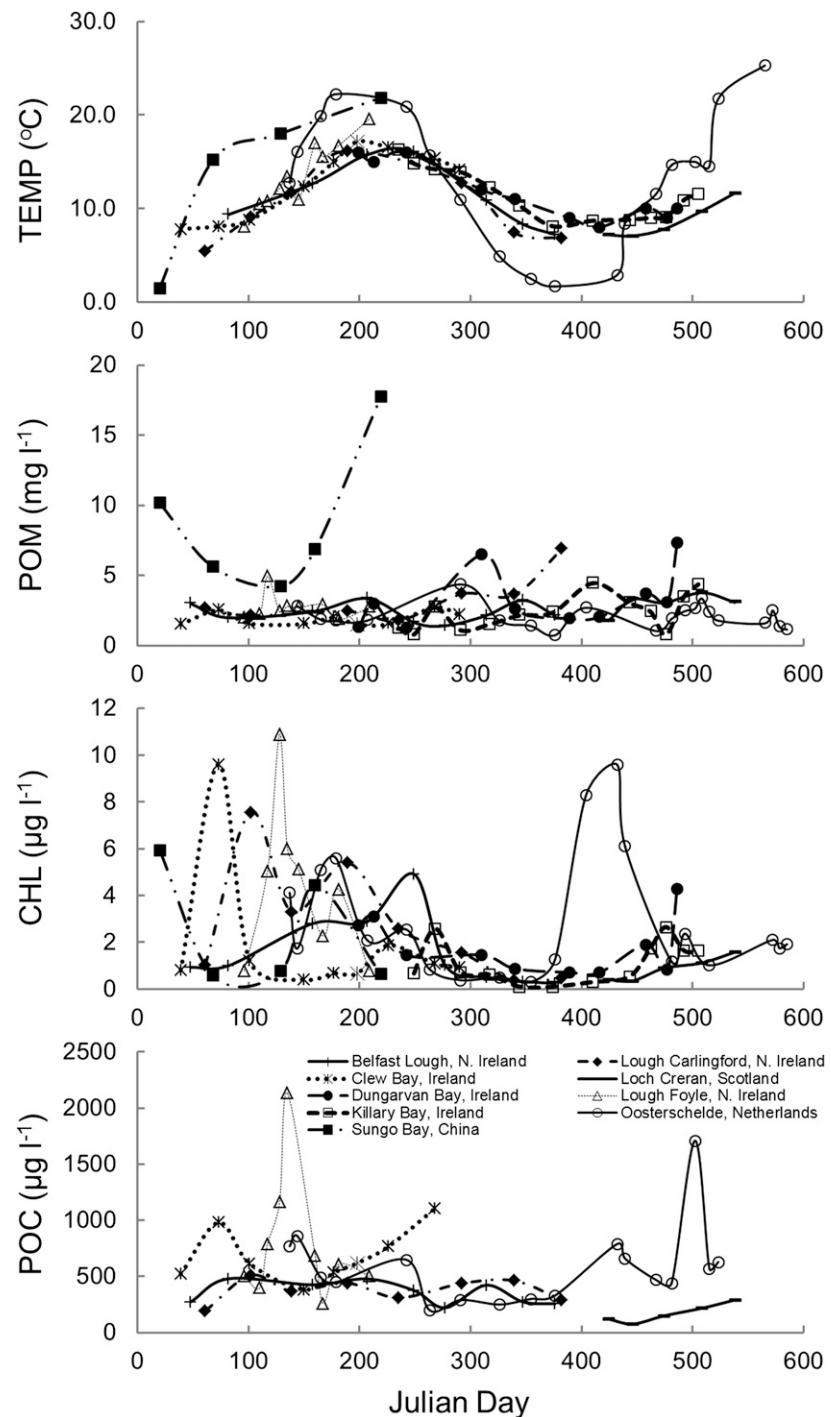


Figure 1. Environmental characteristics. Seasonal changes in temperature (TEMP), particulate organic matter (POM), chlorophyll *a* (CHL), and particulate organic carbon (POC) measured as forcing functions from 9 study locations (Table 1). Values are the average of 3 replicate determinations.

growth in both *Mytilus edulis* and *Crassostrea gigas*, linear regressions were undertaken between measured growth and growth predicted using either (1) CHL and POM, (2) CHL and POC, or (3) CHL, POM, and POC as ShellSIM options accounting for both SELORG and REMORG (see Assessing the Relative Significance of Different Dietary Components; Fig. 5, Table 3). Analyses were restricted to locations where data that had been collected coincidentally for CHL, POM, and POC,

and for *M. edulis* included Belfast Lough, Carlingford Lough, Lough Foyle, and the Oosterschelde, compared with Clew Bay, Lough Creran, and the Oosterschelde for *C. gigas* (Table 1, Fig. 1). Comparison of the resulting multiple correlation coefficients indicates that growth simulations in *C. gigas* using CHL and POC alone ($r^2 = 0.79$), an option assumed constant EREM (see Assessing the Relative Significance of Different Dietary Components), accounted for less of the total variations in

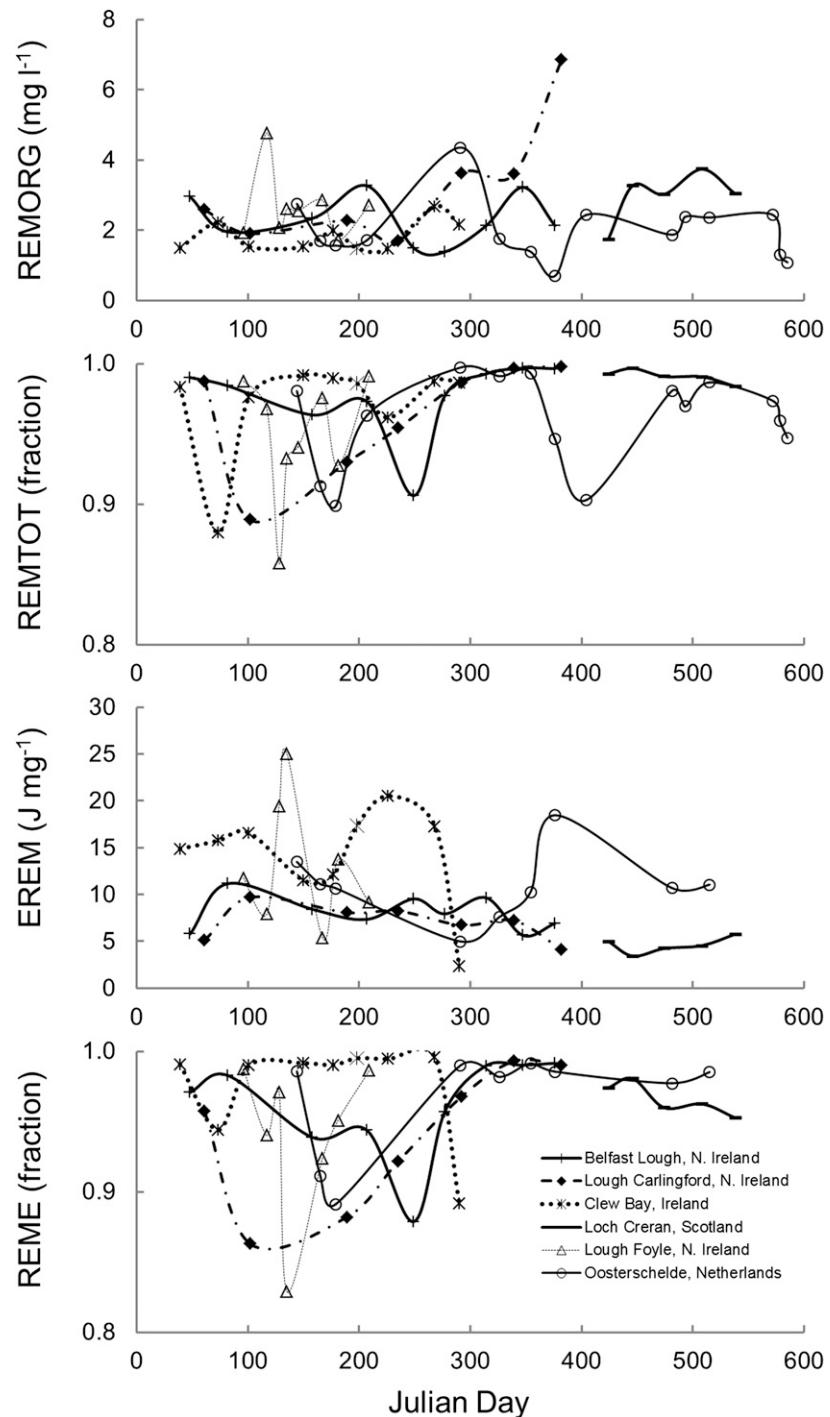


Figure 2. Dietary composition. The abundance of (i) suspended organic matter that was comprised of bacteria, protozoans, colloids and/or detritus (REMORG), (ii) the proportion that remaining organic matter (REMORG) comprised of particulate organic matter (POM) (REMTOT), (iii) the energy content of REMORG (EREM) and (iv) the proportion that energy within REMORG comprised of total seston energy content (REME), each computed as described in the Methods from POM, CHL and POC (Fig. 1) at 6 study locations (Table 1).

measured growth than when estimating variable EREM on the basis either of CHL and POM ($r^2 = 0.93$) or CHL, POM, and POC ($r^2 = 0.86$; see Assessing the Relative Significance of Different Dietary Components and Predicting the Energy Content of Detrital Organics; Fig. 5). Furthermore, growth simulations in both *M. edulis* and *C. gigas* using CHL and POM

($r^2 = 0.85$ and $r^2 = 0.93$, respectively) accounted for more of the observed variations in measured growth than when using either CHL and POC ($r^2 = 0.84$ and $r^2 = 0.79$, respectively) or CHL, POM, and POC ($r^2 = 0.84$ and $r^2 = 0.86$, respectively), indicating that predictions of EREM on the basis of CHL and POM were a viable alternative to measuring POC (Fig. 5).

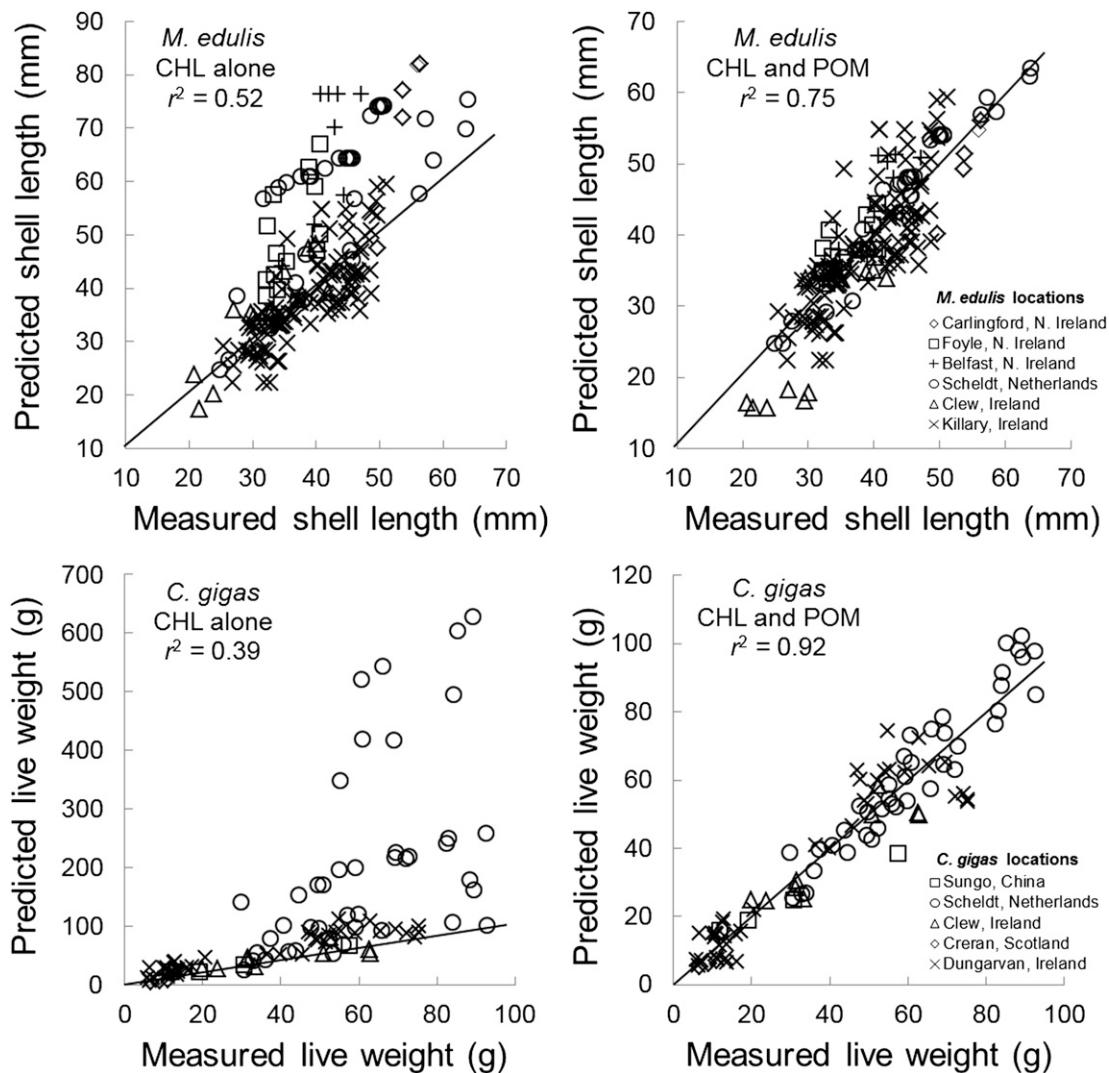


Figure 3. Growth predictions. Relations between measured growth and growth predicted using either chlorophyll (CHL) alone or CHL in combination with particulate organic matter (POM) for *Mytilus edulis* and *Crassostrea gigas* at all study locations. Lines signify perfect equality.

Model Sensitivity and Validation

Average changes in live weight of *Crassostrea gigas* predicted after 100 d under steady-state conditions (see Methods) after adjustments of $\pm 10\%$ in each model parameter were each less than 15%, indicating robust simulation that was not unduly sensitive to any particular element. It is notable that the parameter of greatest influence was the energy content of shell (15%), emphasizing the need for accurate accounting of relative allocation of growth between shell and soft tissue.

Statistics summarized in Table 3 indicate that when observed growth was related to growth simulated using CHL with POM and/or POC, pooling data from all locations as available, the slopes of each fitted linear regressions differed significantly from 0. Furthermore, the only slope that was significantly different from 1 was when using CHL and POC in *Crassostrea gigas*, the difference of which was marginal, and intercepts were, in general, not significantly different from or very close to 0. On this basis, ShellSIM's generic performance when using CHL with POM and/or POC to account for both SELORG and REMORG, applying a single standard set of parameters to predict growth across different

environments, is classified according to Oreskes et al. (1994) as good to excellent in both *Mytilus edulis* and *C. gigas* (Table 3).

DISCUSSION

Numerous previous models of shellfish growth have only proved accurate within the specific environment for which they were calibrated (see Introduction). Here, we have described how the generic shellfish model ShellSIM (<http://www.shellsim.com>) successfully simulates growth across contrasting coastal and estuarine habitats, exemplified using single parameter sets for 2 of the most widely cultured shellfish species: *Mytilus edulis* and *Crassostrea gigas*. Associated measures were undertaken over 3 y at 9 locations, when it was unquestionably significant that complementary projects enabled the consistent application of standardized protocols when measuring seston availability and composition, thus helping ensure the compatibility of data used to drive ShellSIM at different sites. Throughout, our emphasis has been on practicality and affordability, assessing, and comparing the simplest environmental measures to account for associated dietary variation.

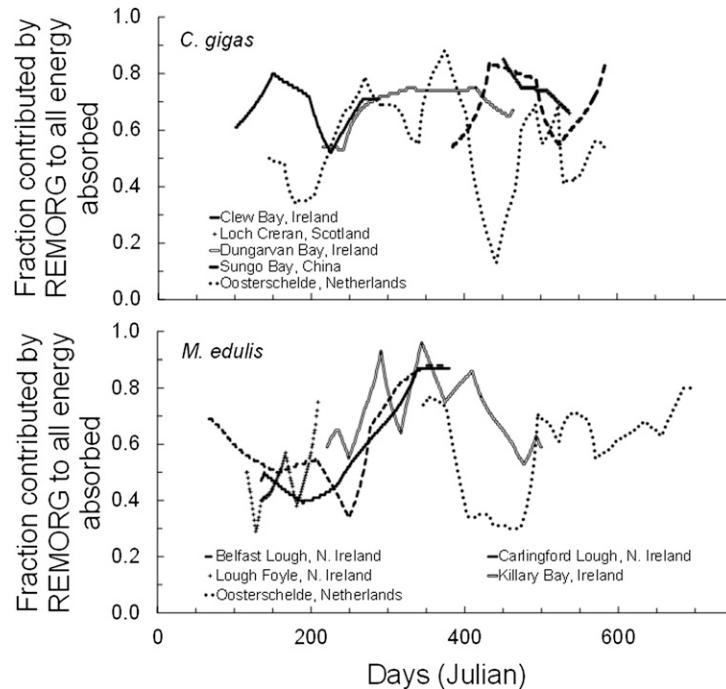


Figure 4. Detrital significance. Fractional contributions from organic matter comprised of bacteria, protozoans, colloids and/or detritus (REMORG) to all energy absorbed in *Mytilus edulis* and *Crassostrea gigas* from 9 study locations (Table 1).

be improved in many ways. For example, there is potential to resolve differences in feeding behavior and/or metabolism that result from genetic variation between stocks of the same species (e.g., Hawkins et al 2000), or to account for adaptations or compensations that may include changes in relative sizes of ctenidium and labial palp (e.g., Essink et al 1989, Barillé et al 2000). Rather than working with generic averages for each species, tailored allometric relations may account for influences of genotype, location, and culture practice on shell shape (e.g., Steffani & Branch 2003, Gardner & Thompson 2009, Cubillo et al 2012). Information on clay composition may help to resolve site-specific differences more completely in the overestimation of POM measured by loss on ignition (Barillé-Boyer et al 2003). Certainly, we need to understand fully the relative bioavailability of ingested organic matter. Future improvements thus include modeling the interactive influences of physical and biological factors on seston abundance, composition, and nutritional value; and drawing on promising observations, which have included (1) a positive relation between concentrations of CHL and biopolymeric organic C, (2) a positive relation between the fractional contribution from microalgae to biopolymeric C and the fraction of that biopolymeric C that is digestible, and (3) inverse relations between the digestible fractions within total associated amounts of biopolymeric matter (Pusceddu et al 2003, Sarà & Pusceddu 2008). Furthermore, although ShellSIM uses chlorophyll *a* as a fixed proxy for the organic matter that may be processed preferentially, resolution of phytoplankton species, CHL class, or size distributions of both CHL and POM available as food (e.g., Spillman et al 2008, Zhang et al 2008, Newell et al 2009) may help account for adaptive adjustments in capture efficiency (Stenton-Dozey & Brown 1992, Barillé et al 1993, Hawkins et al 1999, Beninger et al 2008b, Zhang et al 2010, Ströhmeier et al 2012), with the potential to enhance accuracy over and above standard water filtration methods when measuring what CHL

and POM is truly filtered and ingested (Cranford & Hill 1999). Future models may also benefit from an improved understanding of the relative post-ingestive processing of different particle types, including associated adjustments between the hydrolytic capacity of digestive gland and gut content, which may help to maximize return within a gut passage time (Ibarrola et al. 1998, Ibarrola et al. 2000b, Ibarrola et al. 2000c, Navarro et al 2009). Last, without intending for this list to be exhaustive, there is an established need to account for potential N limitation of growth (cf. Grant & Cranford 1991).

Of course, as our understanding increases, it will be possible to account more fully for the previously mentioned and other uncertainties. But, key to these considerations, will always be the need to balance practicality and affordability against accuracy of growth simulations required within different applications. Meanwhile, applying a single standard set of parameters optimized in each of 14 species to date, ShellSIM has simulated growth to less than a 25% error across wide ranges of environmental and culture practice throughout Europe and Asia (Hawkins et al 2012a). We emphasize that these findings were all observed during normal culture, without accounting for variations in shellfish density or current flow, which, to some extent, is standardized by farmers, would undoubtedly have improved the accuracy of simulated growth. Furthermore, our experimental circumstances were somewhat idealized, not apparently needing to consider the negative effects of harmful algal blooms or pollution. Subject to these and other reservations detailed earlier, associated findings reported in detail here for *Mytilus edulis* and *Crassostrea gigas* are significant for 2 main reasons. First, compared with past models calibrated and optimized per species per site, ShellSIM is a common model structure with a defined list of parameters that simulate effectively on calibration in separate species, the calibrations of which can then be applied across contrasting coastal and estuarine environments, with options that establish

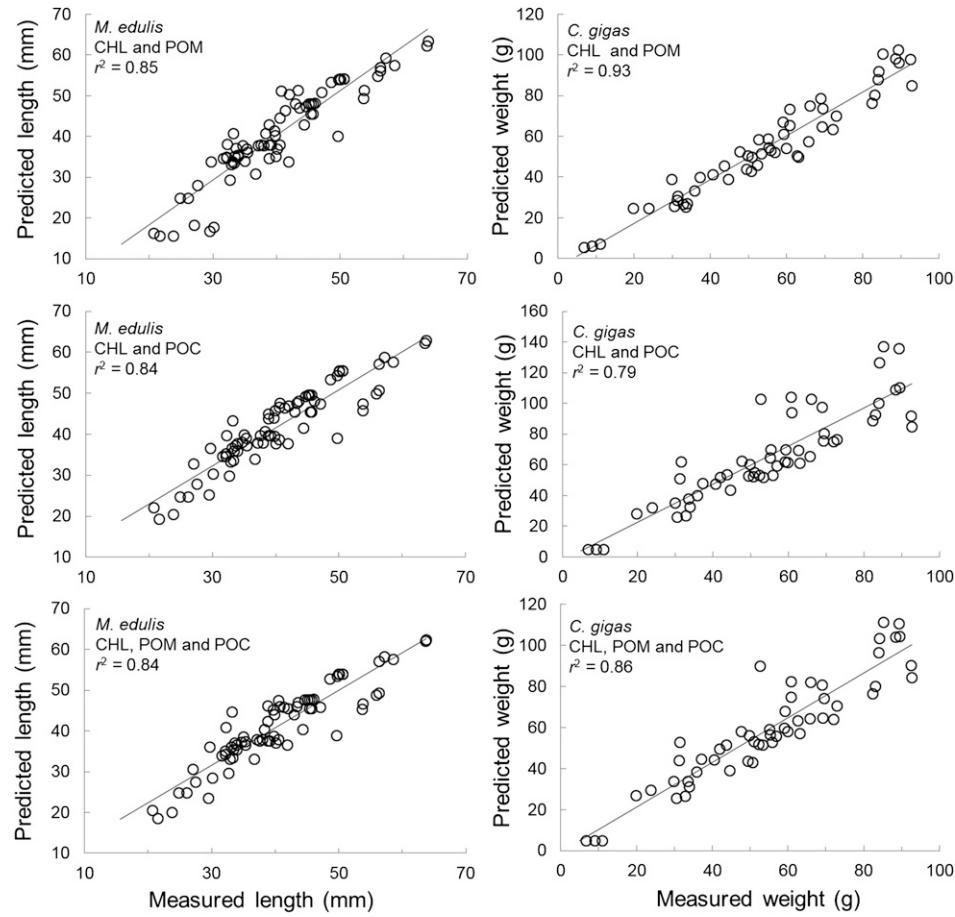


Figure 5. Predictive options. Relations between growth simulated and growth measured in *Mytilus edulis* ($n = 74$) and *Crassostrea gigas* ($n = 52$) over 8–24 mo during normal culture at locations where chlorophyll *a* (CHL), particulate organic matter (POM) and particulate organic carbon (POC) had been collected together, according to predictive options accounting for both CHL-rich organic matter and remaining organic matter using (1) CHL and POM, (2) CHL and POC, or (3) CHL, POM, and POC (refer to Assessing the Relative Significance of Different Dietary Components in the text). Lines were all fitted by linear regression, for which coefficients are summarized in Table 3.

the minimal set of environmental drivers required to simulate effectively at different locations. Second, ShellSIM is comprised solely of experimentally established functional relations, not only between environmental variables and physiology, but also between dependent physiological components of growth. Associated outputs simulate responsive adjustments in clearance rate, oxygen uptake, ammonium loss, fecal loss, and population dynamics, all in real time (<http://www.shellsim.com>), ready for integrated modeling of the feedbacks, both positive and negative, whereby suspension-feeding shellfish influence ecosystem properties and processes (e.g., Newell 2004, Ferreira et al 2011). By accounting for both living and detrital organic matter available as food, ShellSIM is better able to simulate growth, population dynamics, and environmental effects across contrasting locations, with the potential to save significant time and resources, exemplified by a growing track record of applications simulating production capacity and effects in the management of aquaculture at farm scales (Bacher et al 2003, Ferreira et al 2007, Ferreira et al 2009, Newell 2012a, Newell 2012b) (<http://www.marcon.ie/website/html/margisdemo.htm>) and system scales (Duarte et al 2003, Hawkins & Duarte 2003, Ferreira et al 2008, Sequeira et al 2008, Nobre et al 2010, Nunes et al 2011). Currently, ShellSIM is being integrated with other model components within the

geographically transferable GIS-based tool ShellGIS, for which we are tailoring interfaces that enable the user to simulate interactive consequences of culture practice, seeding density, and current speed over time throughout chosen domains (Newell et al 2012a, Newell et al 2012b).

ACKNOWLEDGMENTS

We acknowledge financial support from the EU for contracts 006540 (SSP8) (ECASA), INCO-CT-2004-510706 (SPEAR), and KEYZONES (CRAFT), together with support from DARD-NI for the SMILE project and from Bord Iascaigh Mhara (BIM) for the UISCE project. We are grateful to all the farmers and others who assisted in related data collection and/or experimental work, including Dr. Dai Roberts, Dr. Niall McDonough, Dr. Nuala McQuaid, and Dr. Lynn Browne at Queen's University Marine Laboratory, Portaferry; Judith and Hugo Vajk and their staff, plus Dr Thom Nickell and Christine Campbell at The Caledonian Oyster Co. Ltd., Dunbeg; Emiel Brummelhuis at the Institute for Marine Resources and Ecosystem Studies, Yerseke; and Prof. Li Ruixiang, Wang Xiaona, and Zhang Qinglin at the First Institute of Oceanography, Qingdao. We also thank 2 anonymous referees for helpful corrections and suggestions.

REFERENCES

- Almada-Villela, P. C. 1984. The effects of reduced salinity on the shell growth of small *Mytilus edulis*. *J. Mar. Biol. Assoc. UK* 64:171–182.
- Arifin, Z. & L. I. Bendell-Young. 1997. Feeding response and carbon assimilation by the blue mussel *Mytilus trossulus* exposed to environmentally relevant seston matrices. *Mar. Ecol. Prog. Ser.* 160: 241–253.
- Bacher, C., J. Grant, A. J. S. Hawkins, J. Fang, M. Zhu & M. Besnard. 2003. Modelling the effect of food depletion on scallop growth in Sungo Bay (China). *Aquat. Living Resour.* 16:10–24.
- Barillé, L., J. Haure, B. Cognie & A. Leroy. 2000. Variations in pallial organs and eulatero-frontal cirri in response to high particulate matter concentrations in the oyster *Crassostrea gigas*. *Can. J. Fish. Aquat. Sci.* 57:837–843.
- Barillé, L., M. Héral & A.-L. Barillé-Boyer. 1997. Modélisation de l'éco physiologie de l'huître *Crassostrea gigas* dans un environnement estuarien. *Aquat. Living Resour.* 10:31–48.
- Barillé, L., A. Lerouxel, M. Dutertre, J. Haure, A.-L. Barillé, S. Pouvreau & M. Alunno-Bruscia. 2011. Growth of the Pacific oyster (*Crassostrea gigas*) in a high-turbidity environment: comparison of model simulations based on scope for growth and dynamic energy budgets. *J. Sea Res.* 66:392–402.
- Barillé, L., J. H. M. Prou & S. Bourgrier. 1993. No influence of food quality, but ration-dependent retention efficiencies in the Japanese oyster *Crassostrea gigas*. *J. Exp. Mar. Biol. Ecol.* 171:91–106.
- Barillé-Boyer, A.-L., L. Barillé, H. Massé, D. Razet & M. Héral. 2003. Correction for particulate organic matter as estimated by loss on ignition in estuarine ecosystems. *Estuar. Coast. Shelf Sci.* 58:147–153.
- Bayne, B. L. 1975. Aspects of physiological conditions in *Mytilus edulis* L., with special reference to the effects of oxygen tension and salinity. In: J. S. Gray & M. E. Christiansen, editors. Proceedings of the 9th European Marine Biology Symposium. Chichester: Wiley. pp. 331–349.
- Bayne, B. L., A. J. S. Hawkins, E. Navarro & J. I. P. Iglesias. 1989. The effects of seston concentration on feeding, digestion and growth in the mussel *Mytilus edulis*. *Mar. Ecol. Prog. Ser.* 55:47–54.
- Bayne, B. L. & R. C. Newell. 1983. Physiological energetics of marine molluscs. In: K. M. Wilbur & A. S. Saleuddin, editors. The Mollusca, vol. 4. New York: Academic Press. pp. 407–515.
- Bayne, B. L., P. N. Salkeld & C. M. Worrall. 1983. Reproductive effort and value in different populations of the marine mussel, *Mytilus edulis* L. *Oecologia* 59:18–26.
- Bayne, B. L. & C. Scullard. 1977. Rates of nitrogen excretion by species of *Mytilus* (Bivalvia: Mollusca). *J. Mar. Biol. Assoc. UK* 57:355–369.
- Beninger, P. G., A. Valdizan, B. Cognie, F. Guiheneuf & P. Decottignies. 2008a. Wanted: alive and not dead: functioning diatom status is a quality cue for the suspension-feeder *Crassostrea gigas*. *J. Plankton Res.* 30:689–697.
- Beninger, P. G., A. Valdizan, P. Decottignies & B. Cognie. 2008b. Impact of seston characteristics on qualitative particle selection sites and efficiencies in the pseudolamellibranch bivalve *Crassostrea gigas*. *J. Exp. Mar. Biol. Ecol.* 360:9–14.
- Beninger, P. G., A. Veniot & Y. Poussart. 1999. Principles of pseudofeces rejection on the bivalve mantle: integration in particle processing. *Mar. Ecol. Prog. Ser.* 178:259–269.
- Bougrier, S., P. Geairon, J. M. Deslous-Paoli, C. Bacher & G. Jonquieres. 1995. Allometric relationships and temperature effects on clearance rates and oxygen consumption rates in *Crassostrea gigas* (Thunberg). *Aquaculture* 134:143–154.
- Bougrier, S., A. J. S. Hawkins & M. Héral. 1997. Preingestive selection of different microalgal mixtures in *Crassostrea gigas* and *Mytilus edulis*, analysed by flow cytometry. *Aquaculture* 150:123–134.
- Bouriès, Y., M. Alunno-Bruscia, S. Pouvreau, G. Tollub, D. Leguay, C. Arnaud, P. Gouletquer & S. Kooijman. 2009. Modelling growth and reproduction of the Pacific oyster *Crassostrea gigas*: advances in the oyster-DEB model through application to a coastal pond. *J. Sea Res.* 62:62–71.
- Brillant, M. G. S. & B. A. MacDonald. 2000. Postingestive selection in the sea scallop, *Placopecten magellanicus* (Gmelin): the role of particle size and density. *J. Exp. Mar. Biol. Ecol.* 253:211–227.
- Brown, J. R. & E. B. Hartwick. 1988. Influences of temperature, salinity and available food upon suspended culture of the Pacific oyster, *Crassostrea gigas*: I. Absolute and allometric growth. *Aquaculture* 70:231–251.
- Brylinski, M. & T. W. Sephton. 1991. Development of a computer simulation model of a cultured blue mussel (*Mytilus edulis*) population. *Can. Tech. Rep. Fish. Aquat. Sci.* 1805:1–81.
- Caillère, S. & S. Hénin. 1963. Minéralogie des argiles. Paris: Mason. 150 pp.
- Campbell, D. E. & C. R. Newell. 1998. MUSMOD, a production model for bottom culture of the blue mussel, *Mytilus edulis* L. *J. Exp. Mar. Biol. Ecol.* 219:171–203.
- Coen, L. D., B. R. Dumbauld & M. L. Judge. 2011. Expanding shellfish aquaculture: a review of the ecological services provided by and impacts of native and cultured bivalves in shellfish-dominated ecosystems. In: S. E. Shumway, editor. Shellfish aquaculture and the environment. Chichester: Wiley. pp. 239–318.
- Cranford, P. J. & P. S. Hill. 1999. Seasonal variation in food utilization by the suspension-feeding bivalve molluscs *Mytilus edulis* and *Placopecten magellanicus*. *Mar. Ecol. Prog. Ser.* 190:223–229.
- Cranford, P. J., P. Kamermans, G. Krause, J. Mazurié, B. H. Buck, P. Dolmer, D. Fraser, K. Van Nieuwenhove, F. X. O’Beirn, A. Sanchez-Mata, G. G. Thorarinsdóttir & Ø. Strand. 2012. An ecosystem-based approach and management framework for the integrated evaluation of bivalve aquaculture impacts. *Aquacult. Environ. Interact.* 2:193–213.
- Cranford, P. J., J. Ward & S. E. Shumway. 2011. Bivalve filter-feeding: variability and limits of the aquaculture filter. In: S. E. Shumway, editor. Shellfish aquaculture and the environment. Chichester: Wiley. pp. 81–133.
- Cubillo, A. M., L. G. Peteiro, M. J. Fernandez-Reiriz & U. Labarta. 2012. Density-dependent effects on morphological plasticity of *Mytilus galloprovincialis* in suspended culture. *Aquaculture* 338:246–252.
- Dankers, N. & R. Laane. 1983. A comparison of wet oxidation and loss on ignition of organic material in suspended matter. *Environ. Technol. Lett.* 4:283–290.
- Danovaro, R., A. Dell’Anno & M. Fabiano. 2001. Bioavailability of organic matter in the sediments of the Porcupine Abyssal Plain, northeastern Atlantic. *Mar. Ecol. Prog. Ser.* 220:25–31.
- Dauwe, B. & J. J. Middelburg. 1998. Amino acids and hexosamines as indicators of organic matter degradation state in North Sea sediments. *Limnol. Oceanogr.* 43:782–798.
- Dauwe, B., J. J. Middelburg, P. M. J. Herman & C. H. R. Heip. 1999a. Linking diagenetic alteration of amino acids and bulk organic matter reactivity. *Limnol. Oceanogr.* 44:1809–1814.
- Dauwe, B., J. J. Middelburg, P. Van Rijswijk, J. Sinke, P. M. J. Herman & C. H. R. Heip. 1999b. Enzymatically hydrolyzable amino acids in North Sea sediments and their possible implication for sediment nutritional values. *J. Mar. Res.* 57:109–134.
- Dell’Anno, A., M. Fabiano, M. L. Mei & R. Danovaro. 2000. Enzymatically hydrolysed protein and carbohydrate pools in deep-sea sediments: estimates of the potentially bioavailable fraction and methodological considerations. *Mar. Ecol. Prog. Ser.* 196:15–23.
- Dridi, S., M. Salah Romdhane & M. Elcabsi. 2007. Seasonal variation in weight and biochemical composition of the Pacific oyster, *Crassostrea gigas* in relation to the gametogenic cycle and environmental conditions of the Bizert lagoon, Tunisia. *Aquaculture* 263:238–248.
- Duarte, P., R. Meneses, A. J. S. Hawkins, M. Zhu, J. Fang & J. Grant. 2003. Mathematical modelling to assess the carrying capacity

- for multi-species culture within coastal waters. *Ecol. Modell.* 168: 109–143.
- Elliot, J. M. & W. Davison. 1975. Energy equivalents of oxygen consumption in animal energetics. *Oecologia* 19:195–201.
- Epp, J., V. M. Bricelj & R. E. Malouf. 1988. Seasonal partitioning and utilisation of energy reserves in two age classes of the bay scallop *Argopecten irradians* (Lamarck). *J. Exp. Mar. Biol. Ecol.* 121:113–136.
- Essink, K., P. Tydeman, F. de Koning & H. L. Kleef. 1989. On the adaptation of the mussel *Mytilus edulis* L. to different environmental suspended matter concentrations. In: R. Z. Klekowski, E. Styczynska-Jurewicz & L. Falkowski, editors. Biochemical and physiological adaptation in marine organisms. 21st European Marine Biology Symposium. Gdansk: Ossolineum. pp. 41–51.
- FAO. 2010. Aquaculture development: 4. Ecosystem approach to aquaculture. FAO technical guidelines for responsible fisheries, no. 5, suppl. 4. Rome: FAO. 53 pp.
- FAO. 2012. The state of world fisheries and aquaculture 2012. Rome: FAO. 209 pp.
- Fegley, S. R., B. A. MacDonald & T. R. Jacobsen. 1992. Short-term variation in the quantity and quality of seston available to benthic suspension feeders. *Estuar. Coast. Shelf Sci.* 34:393–412.
- 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 & S. B. Bricker. 2011. The role of shellfish farms in provision of ecosystem goods and services. In: S. E. Shumway, editor. Shellfish aquaculture and the environment. Chichester: Wiley. pp. 3–26.
- 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. Nickell, R. Pastres, J. Forte, A. Bodoy & S. B. Bricker. 2009. Analyses of coastal and offshore aquaculture: application of the FARM™ model to multiple systems and shellfish species. *Aquaculture* 289:32–41.
- Grant, J. & C. Bacher. 1998. Comparative models of mussel bioenergetics and their validation at field culture sites. *J. Exp. Mar. Biol. Ecol.* 219:21–44.
- Grant, J. & P. J. Cranford. 1991. Carbon and nitrogen scope for growth as a function of diet in the sea scallop *Placopecten magellanicus*. *J. Mar. Biol. Assoc.* 71:437–450.
- Gardner, J. P. A. & R. J. Thompson. 2009. Influence of genotype and geography on shell shape and morphometric trait variation among North Atlantic blue mussel (*Mytilus* spp.) populations. *Biol. J. Linn. Soc. Lond.* 96:875–897.
- Gillmor, R. B. 1982. Assessment of intertidal growth and capacity adaptations in suspension-feeding bivalves. *Mar. Biol.* 68:277–286.
- Gnaiger, E. 1983. Calculation of energetic and biochemical equivalents of respiratory oxygen consumption. In: E. Gnaiger & H. Forstner, editors. Polarographic oxygen sensors: aquatic and physiological applications. Berlin: Springer Verlag. pp. 337–345.
- Grangeré, K., A. Ménesguen, S. Lefebvre, C. Bacher & S. Pouvreau. 2009. Modelling the influence of environmental factors on the physiological status of the Pacific oyster *Crassostrea gigas* in an estuarine embayment: the Baie des Veys (France). *J. Sea Res.* 62:147–158.
- Griebeler E. M. & A. Seitz. 2007. Effects of increasing temperatures on population dynamics of the zebra mussel *Dreissena polymorpha*: implications from an individual-based model. *Oecologia* 151: 530–543.
- Hawkins, A. J. S., B. L. Bayne, R. F. C. Mantoura, C. A. Llewellyn & E. Navarro. 1986. Chlorophyll degradation and absorption throughout the digestive system of the blue mussel *Mytilus edulis* L. *J. Exp. Mar. Biol. Ecol.* 96:213–223.
- Hawkins, A. J. S., B. L. Bayne, S. Bougrier, M. Héral, J. I. P. Iglesias, E. Navarro, R. F. M. Smith & M. B. Urrutia. 1998a. Some general relationships in comparing the feeding physiology of suspension-feeding bivalve molluscs. *J. Exp. Mar. Biol. Ecol.* 219:87–103.
- Hawkins, A. J. S. & P. Duarte. 2003. Modeling ecosystem consequences of species diversity and distribution: a case study addressing multi-species aquaculture in China. In: C. H. R. Heip, H. Hummel, P. H. Van Avesaath & R. M. Warwick, editors. Biodiversity of coastal marine ecosystems: a functional approach to coastal marine biodiversity. Book of abstracts, Renesse, The Netherlands 11–15 May 2002. Yerseke: Netherlands Institute of Ecology-Centre for Estuarine and Marine Ecology. pp. 42–43.
- Hawkins, A. J. S., P. Duarte, J. G. Fang, P. L. Pascoe, J. H. Zhang, X. L. Zhang & M. Zhu. 2002. A functional simulation of responsive filter-feeding and growth in bivalve shellfish, configured and validated for the scallop *Chlamys farreri* during culture in China. *J. Exp. Mar. Biol. Ecol.* 281:13–40.
- Hawkins, A. J. S., J. G. Fang, P. L. Pascoe, J. H. Zhang, X. L. Zhang & M. Y. Zhu. 2001. Modelling short-term responsive adjustments in particle clearance rate among bivalve suspension-feeders: separate unimodal effects of seston volume and composition in the scallop *Chlamys farreri*. *J. Exp. Mar. Biol. Ecol.* 262:61–73.
- Hawkins, A. J. S., M. R. James, R. W. Hickman, S. Hatton & M. Weatherhead. 1999. Modelling of suspension-feeding and growth in the green-lipped mussel *Perna canaliculus* exposed to natural and experimental variations of seston availability in the Marlborough Sounds, New Zealand. *Mar. Ecol. Prog. Ser.* 191:217–232.
- Hawkins, A. J. S., A. Magoulas, M. Héral, S. Bougrier, Y. Naciri-Graven, A. J. Day & G. Kotoulas. 2000. Separate effects of triploidy, parentage and genomic diversity upon feeding behaviour, metabolic efficiency and net energy balance in the Pacific oyster *Crassostrea gigas*. *Genet. Res.* 76:273–284.
- Hawkins, A. J. S., P. Pascoe, H. Parry, K. Black, C. Davis, D. Lan, C. McGonigle, H. Moore, C. Newell, N. O'Boyle, T. O'Carroll, B. O'Loan, R. Pastres, M. Service, A. Smaal, X. Zhang & M. Zhu. 2012a. ShellSIM: a user-friendly software tool predicting growth and environmental interrelations in wide range of bivalve shellfish. In: Book of abstracts, Prague, 1–5 September 2012. Baton Rouge, LA: World Aquaculture Society. p. 464.
- Hawkins, A. J. S., P. N. Salkeld, B. L. Bayne, E. Gnaiger & D. M. Lowe. 1985. Feeding and resource allocation in the mussel *Mytilus edulis*: evidence for time-averaged optimization. *Mar. Ecol. Prog. Ser.* 20: 273–287.
- Hawkins, A. J. S., R. F. M. Smith, B. L. Bayne & M. Héral. 1996. Novel observations underlying fast growth of suspension-feeding shellfish in turbid environments: *Mytilus edulis*. *Mar. Ecol. Prog. Ser.* 131:179–190.
- Hawkins, A. J. S., R. F. M. Smith, S. H. Tan & Z. B. Yasin. 1998b. Suspension-feeding behaviour in tropical bivalve molluscs: *Perna viridis*, *Crassostrea belcheri*, *Crassostrea iradelei*, *Saccostrea cucullata* and *Pinctada margaritifera*. *Mar. Ecol. Prog. Ser.* 166:173–185.
- Hawkins, A. J. S., J. Widdows & B. L. Bayne. 1989. The relevance of whole-body protein metabolism to measured costs of maintenance and growth in *Mytilus edulis*. *Physiol. Zool.* 62:745–763.
- Héral, M., J. M. Deslous-Paoli & J. M. Sornin. 1983. Transferts énergétiques entre l'huître *Crassostrea gigas* et la nourriture potentielle disponible dans un bassin ostréicole: premières approches. *Oceanis* 9:169–194.
- Hilbish, T. J. 1986. Growth trajectories of shell and soft tissue in bivalves: seasonal variation in *Mytilus edulis* L. *J. Exp. Mar. Biol. Ecol.* 96:103–113.
- Hirota, J. & P. Szypner. 1975. Separation of total particulate carbon into inorganic and organic components. *Limnol. Oceanogr.* 28:896–900.
- Hofmann, E. E., J. M. Klinck, J. N. Kraeuter, E. N. Powell, R. E. Grizzle, S. C. Buckner & V. M. Bricelj. 2006. A population dynamics model of the hard clam, *Mercenaria mercenaria*: development of the age- and length-frequency structure of the population. *J. Shellfish Res.* 25:417–444.

- Holm-Hansen, O., C. J. Lorenzen, R. W. Holmes & J. D. H. Strickland. 1965. Fluorometric determination of chlorophyll. *J. Cons. Int. Explor. Mer.* 30:3–15.
- Ibarrola, I., E. Navarro & J. I. P. Iglesias. 1998. Short-term adaptation of digestive processes in the cockle *Cerastoderma edule* exposed to different food quantity and quality. *J. Comp. Biochem. Physiol. B* 168:32–40.
- Ibarrola, I., M. Etxeberria, J. I. P. Iglesias, M. B. Urrutia & E. Angulo. 2000a. Acute and acclimated digestive responses of the cockle *Cerastoderma edule* (L.) to changes in the food quality and quantity: II. Enzymatic, cellular and tissular responses of the digestive gland. *J. Exp. Mar. Biol. Ecol.* 252:199–219.
- Ibarrola, I., E. Navarro, J. I. P. Iglesias & M. B. Urrutia. 2000b. Temporal changes of feeding and absorption of biochemical components in *Cerastoderma edule* fed algal diet. *J. Mar. Biol. Assoc. UK* 80:119–125.
- Ibarrola, I., E. Navarro & M. B. Urrutia. 2000c. Acute and acclimated digestive responses of the cockle *Cerastoderma edule* (L.) to changes in food quality and quantity: I. Feeding and absorption of biochemical components. *J. Exp. Mar. Biol. Ecol.* 252:199–219.
- Iglesias, J. I. P., E. Navarro, P. Alvarez Jorna & I. Armentia. 1992. Feeding, particle selection and absorption in cockles *Cerastoderma edule* (L.) exposed to variable conditions of food concentration and quality. *J. Exp. Mar. Biol. Ecol.* 162:177–198.
- MacDonald, B. A. & J. E. Ward. 1994. Variation in food quality and particle selectivity in the sea scallop *Placopecten magellanicus* (Mollusca: Bivalvia). *Mar. Ecol. Prog. Ser.* 108:251–264.
- McKee, M. P., J. E. Ward, B. A. MacDonald & B. A. Holohan. 2005. Production of transparent exopolymer particles (TEP) by the Eastern oyster *Crassostrea virginica*. *Mar. Ecol. Prog. Ser.* 288:141–149.
- Melià, P. & M. Gatto. 2005. A stochastic bioeconomic model for the management of clam farming. *Ecol. Modell.* 184:163–174.
- Møhlenberg, F. & H. U. Riisgård. 1978. Efficiency of particle retention in 13 species of suspension-feeding bivalves. *Ophelia* 17:239–246.
- Mook, D. H. & C. M. Hoskin. 1982. Organic determinations by ignition: caution advised. *Est. Coast. Shelf Sci.* 15:697–699.
- Moullac, G. L., I. Quéau, P. L. Souchu, S. X. Pouvreau, J. Moal, J. R. Coz & J. F. Samain. 2007. Metabolic adjustments in the oyster *Crassostrea gigas* according to oxygen level and temperature. *Mar. Biol. Res.* 3:357–366.
- Navarro, E., S. Méndez, I. Ibarrola & M. B. Urrutia. 2009. Comparative utilization of phytoplankton and vascular plant detritus by the cockle *Cerastoderma edule*: digestive responses during diet acclimation. *Aquat. Biol.* 6:247–262.
- Newell, R. I. E. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. *J. Shellfish Res.* 23:51–61.
- Newell, C. R., D. E. Campbell & S. M. Gallagher. 1998. Development of the mussel aquaculture lease site model MUSMOD: a field program to calibrate model formulations. *J. Exp. Mar. Biol. Ecol.* 219:143–170.
- Newell, C. R., C. Davis, A. J. S. Hawkins, J. Richardson, T. Getchis, K. Morris & D. Cheney. 2012a. ShellGIS: a new GIS tool for oyster farm site selection, oyster growth simulation and production carrying capacity. *J. Shellfish Res.* 31:327. (Abstract).
- Newell, C. R., A. J. S. Hawkins, K. Morris, J. Richardson, C. Davis & T. Getchis. 2012b. ShellGIS: a GIS software tool for predicting the growth and environmental impacts of oysters as a function of site selection. In: Book of abstracts, Prague, 1–5 September 2012. Baton Rouge, LA: World Aquaculture Society. p. 462.
- Newell, R. I. E., S. T. Tettelbach, C. J. Gobler & D. G. Kimmel. 2009. Relationships between reproduction in suspension-feeding hard clams *Mercenaria mercenaria* and phytoplankton community structure. *Mar. Ecol. Prog. Ser.* 387:179–196.
- Nobre, A. M., J. G. Ferreira, J. P. Nunes, X. Yan, S. Bricker, R. Corner, S. Groom, H. Gu, A. J. S. Hawkins, R. Hutson, D. Lan, S. Lencart, D. João, P. Pascoe, T. Telfer, X. Zhang & M. Zhu. 2010. Assessment of coastal management options by means of multilayered ecosystem models. *Estuar. Coast. Shelf Sci.* 87:43–62.
- 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.
- Oreskes, N., K. Shrader-Frechette & K. Belitz. 1994. Verification, validation, and confirmation of numerical models in the earth science. *Science* 263:641–646.
- Pascoe, P. L., H. E. Parry & A. J. S. Hawkins. 2009. Observations on the measurement and interpretation of clearance rate variations in suspension-feeding bivalve shellfish. *Aquat. Biol.* 6:181–190.
- Platt, T. & B. Irwin. 1973. Caloric content of phytoplankton. *Limnol. Oceanogr.* 18:306–309.
- Portilla, E. & P. Tett. 2007. Assessing goodness of fit for LESV model (ECASA internal paper). Edinburgh University, Napier. Report, 22 pp. Available at: <http://www.ecasatoolbox.org.uk/the-toolbox/eia-species/models/model-reliability>.
- Pouvreau, S., C. Bacher & M. Héral. 2000. Ecophysiological model of growth and reproduction of the black pearl oyster, *Pinctada margaritifera*: potential applications for pearl farming in French Polynesia. *Aquaculture* 186:117–144.
- Pouvreau, S., Y. Bourles, S. Lefebvre, A. Gangnery & M. Alunno-Bruscia. 2006. Application of a dynamic energy budget model to the Pacific oyster, *Crassostrea gigas*, reared under various environmental conditions. *J. Sea Res.* 56:156–167.
- Powell, E. N., E. E. Hofmann, J. M. Klinck & S. M. Ray. 1992. Modelling oyster populations: I. A commentary on filtration rate: is faster always better? *J. Shellfish Res.* 11:387–398.
- Pusceddu, A., A. Dell’Anno, R. Danovaro, E. Manini, E. Sarà & M. Fabiano. 2003. Enzymatically hydrolyzable protein and carbohydrate sedimentary pools as indicators of the trophic state of detritus sink systems: a case study in a Mediterranean coastal lagoon. *Estuaries* 26:641–650.
- Pusceddu, A., E. Serra, O. Sanna & M. Fabiano. 1996. Seasonal fluctuations in the nutritional value of particulate organic matter in a lagoon. *Chem. Ecol.* 13:21–37.
- Raillard, O., J. M. Deslous-Paoli, M. Héral & D. Razet. 1993. Modélisation du comportement nutritionnel et de la croissance de l’huître japonaise *Crassostrea gigas*. *Oceanol. Acta* 16:73–82.
- Ren, J. S., I. D. Marsden, A. H. Ross & D. R. Schiel. 2003. Seasonal variation in the reproductive activity and biochemical composition of the Pacific oyster (*Crassostrea gigas*) from the Marlborough Sounds, New Zealand. *N. Z. J. Mar. Freshw. Res.* 37:171–182.
- Ren, J. S. & A. H. Ross. 2001. A dynamic energy budget model of the Pacific oyster *Crassostrea gigas*. *Ecol. Modell.* 142:105–120.
- Ren, J. S. & A. H. Ross. 2005. Environmental influence on mussel growth: a dynamic energy budget model and its application to the greenshell mussel *Perna canaliculus*. *Ecol. Modell.* 189:347–362.
- Ren, J. S., A. H. Ross & D. R. Schiel. 2000. Functional descriptions of feeding and energetics of the Pacific oyster *Crassostrea gigas* in New Zealand. *Mar. Ecol. Prog. Ser.* 208:119–130.
- Ren, J. S. & D. R. Schiel. 2008. A dynamic energy budget model: parameterisation and application to the Pacific oyster *Crassostrea gigas* in New Zealand waters. *J. Exp. Mar. Biol. Ecol.* 361:42–48.
- Rico-Villa, B., B. R. Robert & S. Pouvreau. 2010. A dynamic energy budget (DEB) growth model for Pacific oyster larvae, *Crassostrea gigas*. *Aquaculture* 305:84–94.
- Rosland, R., Ø. Strand, M. Alunno-Bruscia, C. Bacher & T. Strohmeier. 2009. Applying dynamic energy budget (DEB) theory to simulate growth and bioenergetics of blue mussels under low seston conditions. *J. Sea Res.* 62:49–61.
- Ross, A. H. & R. M. Nisbet. 1990. Dynamic models of growth and reproduction of the mussel *Mytilus edulis* L. *Funct. Ecol.* 4:777–787.
- Royer, J., C. Seguinéau, K. Park, S. Pouvreau, K. Choi & K. Costil. 2008. Gametogenetic cycle and reproductive effort assessed by two

- methods in 3 age classes of Pacific oysters, *Crassostrea gigas*, reared in Normandy. *Aquaculture* 277:313–320.
- Rueda, J. L. & A. C. Smaal. 2002. Selective ingestion of pelagic versus benthic algae by the cockle *Cerastoderma edule* (Linne, 1758). *J. Shellfish Res.* 21:619–625.
- Salonen, K., J. Sarvala, I. Hakala & M. L. Viljanen. 1976. The relation of energy and organic carbon in aquatic invertebrates. *Limnol. Oceanogr.* 21:724–730.
- Samuel-Fitwi, B., S. Wuertz, J. P. Schroeder & C. Schulz. 2012. Sustainability assessment tools to support aquaculture development. *J. Clean. Prod.* 32:183–192.
- Sarà, G. & A. Pusceddu. 2008. Scope for growth of *Mytilus galloprovincialis* (Lmk., 1819) in oligotrophic coastal waters (southern Tyrrhenian Sea, Italy). *Mar. Biol.* 156:117–126.
- Saraiva, S., J. van der Meer, S. A. L. M. Kooijman, R. Witbaard, C. J. M. Philippart, D. Hippler & R. Parker. 2012. Validation of a dynamic energy budget (DEB) model for the blue mussel *Mytilus edulis*. *Mar. Ecol. Prog. Ser.* 463:141–158.
- Scholten, H. & A. C. Smaal. 1999. The ecophysiological response of mussels (*Mytilus edulis*) in mesocosms to a range of inorganic loads: simulations with the model EMMY. *Aquat. Ecol.* 33:83–100.
- Sequeira, A., J. G. Ferreira, A. J. S. Hawkins, A. Nobre, P. Lourenco, 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.
- Shumway, S. E., T. L. Cucci, M. P. Lesser, N. Bourne & B. Bunting. 1991. Particle selection by three species of scallops. *J. Shellfish Res.* 10:273.
- Shumway, S. E., T. L. Cucci, R. C. Newell & T. M. Yentch. 1985. Particle selection, ingestion and absorption in filter-feeding bivalves. *J. Exp. Mar. Biol. Ecol.* 91:77–92.
- Slobodkin, L. B. & S. Richman. 1961. Calories/gm in species of animals. *Nature* 191:299.
- Smaal, A. C. & H. A. Haas. 1997. Seston dynamics and food availability on mussel and cockle beds. *Estuar. Coast. Shelf Sci.* 45:247–259.
- Smaal, A. C., J. H. G. Verhagen, J. Coosen & H. A. Haas. 1986. Interaction between seston quantity and quality and benthic suspension feeders in the Oosterschelde, The Netherlands. *Ophelia* 26:385–399.
- Soletchnik, P., P. Gouletquer, M. Héral, D. Razet & P. Geairon. 1996. Évaluation du bilan énergétique de l'huître creuse, *Crassostrea gigas*, en baie de Marennes-Oléron (France). *Aquat. Living Resour.* 9:65–73.
- Solidoro, C., R. Pastres, D. Melaku Canu, M. Pellizzato & R. Rossi. 2000. Modelling the growth of *Tapes philippinarum* in North Adriatic lagoons. *Mar. Ecol. Prog. Ser.* 199:137–148.
- Spillman, C. M., D. P. Hamilton, M. R. Hipsey & J. Imberger. 2008. A spatially resolved model of seasonal variations in phytoplankton and clam (*Tapes philippinarum*) biomass in Barbamarco Lagoon, Italy. *Estuar. Coast. Shelf Sci.* 79:187–203.
- Steffani, C. N. & G. M. Branch. 2003. Growth rate, condition and shell shape of *Mytilus galloprovincialis*: responses to wave exposure. *Mar. Ecol. Prog. Ser.* 246:197–209.
- Stenton-Dozey, J. M. E. & A. C. Brown. 1992. Short-term changes in the energy balance of *Venerupis corrugatus* (Bivalvia) in relation to tidal availability of natural suspended particles. *Mar. Ecol. Prog. Ser.* 103:57–64.
- Strøhmeier, T., Ø. Strand, M. Alunno-Bruscia, D. Arne & P. Cranford. 2012. Variability in particle retention efficiency by the mussel *Mytilus edulis*. *J. Exp. Mar. Biol. Ecol.* 412:96–102.
- Taylor, A. H., R. J. Geider & F. J. H. Gilbert. 1997. Seasonal and latitudinal dependencies of phytoplankton carbon-to-chlorophyll *a* ratios: results of a modelling study. *Mar. Ecol. Prog. Ser.* 152: 51–66.
- Troost, T. A., J. Wijsman, S. Saraiva & V. Freitas. 2010. Modelling shellfish growth with dynamic energy budget models: an application for cockles and mussels in the Oosterschelde (southwest Netherlands). *Phil. Trans. R. Soc. B* 365:3567–3577.
- Urrutia, M. B., E. Navarro, I. Ibarrola & J. I. P. Iglesias. 2001. Pre-ingestive selection processes in the cockle *Cerastoderma edule*: mucus production related to rejection of pseudofaeces. *Mar. Ecol. Prog. Ser.* 209:177–187.
- van Haren, R. J. F. & S. A. L. M. Kooijman. 1993. Application of a dynamic energy budget model to *Mytilus edulis* (L.). *Neth. J. Sea Res.* 31:119–133.
- Ward, J. E. & B. A. MacDonald. 1996. Pre-ingestive feeding behaviours of two sub-tropical bivalves (*Pinctada imbricata* and *Arca zebra*): responses to an acute increase in suspended sediment concentration. *Bull. Mar. Sci.* 59:417–432.
- Ward, J. E. & S. E. Shumway. 2004. Separating the grain from the chaff: particle selection in suspension- and deposit-feeding bivalves. *J. Exp. Mar. Biol. Ecol.* 300:83–130.
- Welschmeyer, N. A. & C. J. Lorenzen. 1984. Carbon-14 labeling of phytoplankton carbon and chlorophyll *a* carbon: determination of specific growth rates. *Limnol. Oceanogr.* 29:135–145.
- Widdows, J. 1978. Physiological indices of stress in *Mytilus edulis*. *J. Mar. Biol. Assoc. UK* 58:125–142.
- Widdows, J. & A. J. S. Hawkins. 1989. Partitioning of rate of heat dissipation by *Mytilus edulis* into maintenance, feeding and growth components. *Physiol. Zool.* 62:764–784.
- Wong, W. H. & S. G. Cheung. 2001. Feeding rhythms of the green-lipped mussel, *Perna viridis* (Linnaeus, 1758) (Bivalvia: Mytilidae) during spring and neap tidal cycles. *J. Exp. Mar. Biol. Ecol.* 257: 13–36.
- Yahel, G., D. Marie, P. G. Beninger, S. Eckstein & A. Genin. 2009. *In situ* evidence for pre-capture qualitative selection in the tropical bivalve *Lithophaga simplex*. *Aquat. Biol.* 6:235–246.
- Zhang, J., J. Fang & X. Liang. 2010. Variations in retention efficiency of bivalves to different concentrations and organic content of suspended particles. *Chin. J. Oceanol. Limnol.* 28:10–17.
- Zhang, L. H., X. L. Zhang & M. Y. Zhu. 2008. Preliminary study on selective feeding of the scallop (*Chlamys farreri*) on diatom and dinoflagellate cells. *Adv. Mar. Sci. (China)* 26:372–376.