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A single bio-energetics growth and reproduction model for the oyster *Crassostrea gigas* in six Atlantic ecosystems

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Abstract:

Many studies based on bioenergetics growth models have investigated the effects of environmental factors on oyster (*Crassostrea gigas*) growth and physiology. However, most of these models are site-specific and cannot be applied to other culture sites without the re-estimation of parameters or re-formulation of some processes. We aimed to develop a generic growth model suitable for application in contrasting environments, with a constant set of parameters. We tested the oyster-DEB model (Bourlès *et al.* 2009) for the stimulation of *C. gigas* growth in different cohorts (spats and adults) at major shellfish culture sites in France, in several years: Arcachon (1993–1994); Marennes-Oléron (2007); Quiberon (1999, 2000, 2001); Rade de Brest (2008); Baie du Mont-Saint-Michel (2003); Baie-des-Veys (2002). These different ecosystems offer a wide range of values for the two forcing variables of the model: water temperature (range: 6-24 °C) and phytoplankton concentration (annual average: 110–700 x 10^3 cell.l^{-1}). The validation data (dry flesh mass of *C. gigas*) were obtained from various growth surveys carried out by IFREMER. The oyster-DEB model simulated the oyster growth dynamics of both spat and adult stages of *C. gigas* accurately over time at the various culture sites. The model captures: *i*) the active spring growth; *ii*) the timing and amplitude of spawning events; and *iii*) the lean periods (*i.e.* loss of dry flesh mass) in autumn and winter. The half-saturation coefficient X_k is the only model parameter that varied between sites and years. This environment-specific coefficient reflects variability in the food of the oysters: quantitative and qualitative effects of the inorganic material and of the phytoplankton species on the feeding response of *C. gigas*. With a single set of parameters (other than for X_k), this is thus the first bio-energetic growth model for *C. gigas* robust enough and of a sufficiently generic nature for the accurate simulation of oyster growth in different Atlantic ecosystems.

Highlights

► A generic growth model of the oyster *Crassostrea gigas* that is suitable for a generic application, *i.e.* with a constant set of parameters, in contrasting Atlantic environments and for different cohorts (spats and adults) was developed. ► The resulting oyster-DEB model simulated the oyster growth dynamics of both spat and adult stages of *C. gigas* accurately over time at the various culture sites. The model captures: *i*) the active spring growth; *ii*) the timing and amplitude of spawning events; and *iii*) the loss of dry flesh mass in autumn and winter. ► The half-saturation coefficient X_k is the only model parameter that varied between sites and years. This environment-specific coefficient reflects variability in the food of the oysters.

Keywords: DEB theory; modelling; bivalves; *Crassostrea gigas*; phytoplankton; temperature effect; coastal environment.

1. Introduction

The Pacific oyster *Crassostera gigas* is a key worldwide species in natural marine ecosystems and marine aquaculture, and is one of the best known non-indigenous animals living on the coasts of north-western Europe (Troost 2010). *C. gigas* was introduced into Europe by and for human activities (shellfish culture) in the early 1970s. It is typically an invasive species: it has managed to establish itself successfully in contrasting environmental conditions, inducing many changes in the ecosystems in which it implants itself due to its considerable filtration capacity and sediment biodeposition and its ability to form extensive reef structures (Troost 2010). In France, it is also a key economic species in the shellfish market, with an annual production of 120,000 t, worth about €270 million per year (Buestel *et al.* 2009). This importance of the Pacific oyster in both natural and production systems has stimulated considerable recent interest in the factors underlying its growth and reproduction performances, particularly in the eco-physiology and bioenergetics of *C. gigas*.

The physiological processes and energetics of marine bivalves in response to environmental fluctuations can be described by energetic budget models, which have been extensively used for shellfish species in aquaculture (*e.g.* Héral, 1993; Dowd, 1997; Bacher *et al*., 1998; Grant *et al*., 2003; Duarte *et al.* 2010). Many of the energetic models for bivalves are net production models (*e.g.* Ross and Nisbet, 1990; Raillard *et al*., 1993; Smaal and Widdows, 1994; Barillé *et al*., 1997; Campbell and Newell, 1998; Scholten and Smaal, 1998; Ren and Ross, 2001) based on the Scope for Growth (SFG) concept (Bayne and Newell, 1983). Dynamic energy budget (DEB) models, by contrast, describe the rates at which organisms assimilate and utilise energy for maintenance, growth and reproduction. The DEB theory is based on physical and chemical assumptions for individual energetics (Kooijman, 2010), whereas SFG models are based on energetics calculated empirically from allometric relationships (Nisbet *et al*., 2000; Van der Meer, 2006). DEB modelling has also been applied to various bivalves (*e.g.* Van Haren and Kooijman, 1993; Ren and Ross, 2005; Cardoso *et al*., 2006; Rosland *et al.* 2009).

The first DEB model for *C. gigas* was developed by Pouvreau *et al*. (2006). It was subsequently improved by Bourlès *et al*. (2009). This model simulates changes in flesh dry mass (growth and reproduction) in adult *C. gigas,* from two environmental parameters: temperature and food concentration. In the initial model, Pouvreau *et al*. (2006) used chlorophyll *a* (chl *a*) concentration as proxy for food availability and for the forcing of the model, but recommended the improvement of this proxy in subsequent studies. In the second version of the model, Bourlès *et al*. (2009) showed that the replacement of chl *a* by phytoplankton concentration refined the description of the food available to the oyster throughout the year. This first individual bio-energetic model for adult *C. gigas* has also been used at various scales, including those of the population (Bacher and Gangnery, 2006) and ecosystem (Grangeré *et al.*, 2009, 2010), and has been adapted for the larval stage of *C. gigas* (Rico Villa *et al*., 2010). This model seems to be the first suitable for use in different environments and at different biological scales without requiring a significant change in structure or parameterisation. Ren and Schiel (2008), in New Zealand, also developed a bioenergetic model for *C. gigas* based on the DEB theory, with parameters very different in some cases from the values of van der Veer *et al*. (2006). Application of the model of Ren and Schiel (2008) to other sites and environmental conditions has, however, yet to be demonstrated. Indeed, this model has been validated solely for a duration of five months in winter, excluding the period of gamete release, and in particular for sets of environmental conditions in which chl *a* concentrations are low (between 0.2 and 3 µg L^{-1}) and temperatures are restricted to the 12 to 16°C range.

In this context, the aim of this study was to assess the robustness and "generic" nature of the oyster DEB model by applying it to the principal oyster-growing regions of the Channel and

Atlantic coasts. We tested the model on a diverse range of oyster-farming sites, with contrasting environmental and production conditions, representative of the diversity of French production. The sites studied were the basins of Arcachon and Marennes-Oléron, the bay of Quiberon, Mont-Saint-Michel Bay, Baie-des-Veys and Brest Harbour. For each of these regions, the data series chosen for each single site comprised measurements over time of the forcing variables (temperature and phytoplankton concentration) and the validation data (dry flesh mass of the oysters).

2. Materials and methods

2.1. Study sites

Six sites along the French Channel and Atlantic coasts (Fig. 1) were selected for study, based on their contrasting environments in terms of both thermal and trophic conditions. Following a south-to-north gradient and, as a function of the years studied, the study sites were: 1) Tès (1993-1994) in the Arcachon Basin (AR; Fig. 1, inset 1); 2) D'Agnas (2007) in the Marennes-Oléron Basin (MO; Fig. 1, inset 2); 3) Men er Roué (1999 to 2001) in Quiberon Bay (QB; Fig. 1, inset 3); 4) Lanvéoc (2008) in Brest Harbour (BR, Fig. 1, inset 4); 5) Saint-Benoît (2003) in Mont-Saint-Michel Bay, for three age classes (1, 2 and 3 years) of *C. gigas* (CA, Fig. 1, inset 5); 6) Grandcamp (March 2002 to September 2003) in Baie-des-Veys (BV, Fig. 1, inset 6).

2.2. Forcing and validation variables

The environmental factors governing the growth and reproduction of oysters are the temperature of the seawater and the concentration of phytoplankton (after identification of the microalgal species present). Data for these factors are supplied by the Coastal Environment and Aquacultural Resources Laboratories of IFREMER (http://wwz.ifremer.fr/institut_eng/Marine-science/Monitoring). Temperature is measured continually (high-frequency recording) by multiparameter probes (Hydrolab DS5-X OTT probe, NKE YSI probe). Phytoplankton was identified and counted in 1 L samples of seawater taken from each site at a depth of 1 meter below the surface on a fortnightly or monthly basis depending on the site. The phytoplankton samples were fixed in Lugol's solution by a standardised protocol (Aminot and Kérouel, 2004), in the framework of the IFREMER national REPHY network for phytoplankton monitoring. Some non-edible algae impede the growth of *C. gigas* during massive blooms (Bourlès *et al*., 2009). This was confirmed in our study, for *Leptocylindrus minimus* at Marennes-Oléron in summer 2007 and *Lepidodinium chlorophorum* at Quiberon Bay in September 2001. The model was first tested on total counted phytoplankton species, and the poor match observed between simulated and measured oyster growth for these two specific cases led us to exclude these non-edible species for the forcing of the model. *L. minimus* and *L. chlorophorum* did not bloom massively at any other occasion or any site. Except at MO in summer 2007 and QB in September 2001, the annual mean concentration of these two species was less than 5% of the total number of cells per L.

The mean individual dry flesh mass (*DFM*) of *C. gigas*, which was measured at the six sites, at regular intervals with about 10 samples taken annually, was used to validate the model. This variable was obtained by dissecting 30 oysters, freeze-drying the flesh for 48 to 72 hours (depending on the size), then weighing the dried tissue (to the nearest mg). In total, 11 sets of data relating to changes in the dry flesh mass of *C. gigas* were used as the validation data for the model, for the various years studied at the six sites.

2.3. The oyster-DEB model

The DEB model of oyster growth and reproduction used in this study is that described in detail by Bourlès *et al*. (2009). Note that 1) the DEB theory (Kooijman 2010) is based on biological hypotheses describing the flux of energy within an organism in terms of differential equations and parameters specific to each species, estimated independently of environmental conditions; 2) one feature unique to DEB models is the use of a single set of processes and parameters for *C. gigas*, over a large range of forcing variables; 3) the parameter X_K, a component of the law governing ingestion, is the only freely calibrated parameter of the oyster-DEB model required to obtain the best possible fit between simulated and observed growth data for oysters. The oyster-DEB model was implemented with STELLA® 8.0 software.

The initial conditions of the state variables of the model (dry mass of the soma or structure V, energy reserves E and the reserves devoted to reproduction E_R, expressed in terms of energy, in J) were adjusted for each set of data tested (Table 1). The structural volume V was calculated according to the oyster length (L), using the shape coefficient δ and the formulae $V = (\delta.L)^3$. The initial value of E and E_R were deduced to obtain the correct initial total dry mass, as well as realistic initial values for the energy density and gonado-somatic index GI defined as the ratio between the gonad mass and the total flesh mass. Reported temperature and food abundance for the days preceding the start of each monitoring campaign were used to evaluate the distribution of the energy in the animals between the structure, the reserves and the reproductive compartment.

For each simulation, the quality of model adjustment was estimated by fitting a linear regression between observed and simulated values, and comparing the resulting slope and intercept of significant regressions to 1 and 0, respectively.

3. Results

3.1. Forcing variables: environmental conditions

The annual temperature profiles obtained at the various sites highlight the north-south temperature gradient applying to the oyster-rearing sites and are characteristic of the temperature regions of the Channel/Atlantic coasts of France (Figs. 2 & 3). The minimum temperatures in winter (about 6-8°C) are largely similar for the six sites along the north-south gradient. A weak east-west gradient was also observed along the Channel coast, with minimal temperatures of 6°C measured at Baie-des-Veys (BV) in the east. By contrast, summer temperatures followed a clear latitudinal gradient, with a maximum value of 24°C recorded for Arcachon (AR) in 1994, and lower values of 20°C recorded in the more northerly ecosystems, *i.e.* Brest Harbour (BR), Mont-Saint-Michel Bay (CA) and Baie-des-Veys (Fig. 3).

Phytoplankton concentrations differed between sites, and between years at a given site (Figs. 2 & 3). The lowest mean annual concentration of phytoplankton was $1.1 \cdot 10^5$ cell L^{-1}, at QB in 1999 and AR in 1993, whereas the highest mean annual concentration of phytoplankton was $5.7 \cdot 10^5$ cell L^{-1} for MO in 2007. The second highest mean annual concentration of phytoplankton was $2.9 \cdot 10^5$ cell L^{-1} for BR in 2008. For the other sites, depending on the year considered, annual mean values were between 1 and $2 \cdot 10^5$ cell L^{-1}. Phytoplankton blooms were observed mostly in spring (March/April) at all the sites studied (except BR), and there were also some blooms in the summer (June to August) and autumn (end of September for QB and BR; start of November for AR). The most extensive blooms were observed at MO, where concentrations reached about $35 \cdot 10^5$ cell L^{-1} in April 2007. At

the other sites, the phytoplankton blooms were less extensive, with concentrations of between 2.7 and 17.4 · 10^5 cell L^{-1} (Figs. 2 & 3).

3.2. Validation data: oyster growth

The dry flesh masses of the oysters (*DFM*) differed markedly between sites and as a function of the period considered, with ranges of 0.50 to 2.32 g at the end of the monitoring period and 0.22 to 3.34 g before spawning (Figs. 4, 5 and 6, symbols). Differences between age classes were also observed for the CA site (Fig. 6). The initial masses were between 0.03 and 0.07 g for the 1-y old oysters, and between 0.26 and 1.11 g for the 2-y and 3-y old oysters. The final masses, measured at the end of the monitoring period, were between 0.46 and 1.16 g for 1-y old oysters, 1.11 and 1.95 g for 2-y old oysters and up to 2.32 g for 3-y old oysters.

At the various sites, two distinct periods in the year were identified in the profile of change in *DFM* of oysters of 2-yr and 3-yr old over time: i) a period of sustained spring growth until spawning in summer and ii) a period of slower growth in the autumn, with no growth or even shrinkage in winter (Figs. 4, 5 and 6). One-year old oysters (QB99, QB01 and CA03/1) exhibited a positive growth over the fall and winter (Figs. 5, 6). Mean daily growth rates for the 11 sets of data were 3.92% in spring (approximately corresponding to the March-June period), *versus* 0.17% in the autumn (end of August to November), corresponding to a spring growth rate about 20 times higher than that in the autumn. In autumn and winter, there was frequently no growth at all (AR94, QB99, BV, CA, for all three age classes) or even a loss of mass (MO07, QB00, BR08), except for QB01, where estimated growth rate was positive (0.82) in the autumn.

In terms of spawning, the mass loss corresponding to gamete release for adult oysters of two and three years of age was larger in situations of strong spring growth (Figs. 4, 5 and 6). Thus, at Arcachon, the mass loss observed during gamete release was 27% and 54% of the mean mass of *C. gigas* before spawning in 1993 and 1994, respectively, for estimated daily growth rates in spring of 1.3% in 1993 and 2.4% in 1994 (Fig. 4). For 1-y oysters, monitoring at the CA and QB sites did not detect laying, although oysters of this age are capable of laying eggs and small losses of mass were observed (Figs. 5 and 6-CA).

3.3. Simulated growth of C. gigas

For the 11 sets of data, the simulated values for oyster dry flesh mass (*DFM*) obtained with the model matched the observed values, for both the periods of active growth, mostly in the spring, and periods of mass loss or stalled growth in autumn and winter (Figs. 4, 5 & 6, Table 2). For seven of the 11 sets of data, the values of R^2 for regressions of observed *DFM* against simulated *DFM* exceeded 0.91 (p<0.0001); the slopes were between 0.841 and 1.105 and the intercepts of these regression lines were between -0.155 and 0.198 (Table 4). For the remaining four data sets (AR93, QB99, MO07, CA03/2), R^2 was between 0.8 and 0.9 (p<0.001). For AR93 and QB99, these slightly lower values reflect a slight underestimation of spring growth (Figs. 4 & 5). For MO07, they correspond to an overestimation of growth that was observed from May to mid July 2007 (Fig. 4), and for CA03/2, they reflect an underestimation of the winter growth of 2-y old oysters (Fig. 6).

The amplitude and period of gamete release, as simulated by the model, were consistent with observed values for the seven monitoring campaigns for 2-y and 3-y old oysters (Figs. 4 and 6). Simulations for 1-y old oysters showed either low levels of gamete release (QB99, QB01, Fig. 5), or no gamete release (QB00 and CA03/1, Figs. 5, 6). For QB00, the decrease in *DFM* observed in 1-y old oysters during the summer was correctly simulated by the model,

which predicted a large loss of mass in the summer following a period of sustained growth in the spring (Fig. 5).

The values of the half-saturation coefficient X_K were between 260 and $700 \cdot 10^3$ cell L^{-1} for the 11 data sets used, whereas mean annual phytoplankton concentrations were estimated at 110 to $570 \cdot 10^3$ cell L^{-1} (see section 3.1). Most of the X_K values for the various sites were close to $300 \cdot 10^3$ cell L^{-1}, but two sites had exceptionally high X_K values: greater than $450 \cdot 10^3$ cell L^{-1} at Baie-des-Veys (Fig. 6) and $700 \cdot 10^3$ cell L^{-1} at Marennes-Oléron (Fig. 4). There was a significant linear relationship between X_K and the mean annual concentration of phytoplankton for all 11 data sets (Fig. 7). This relationship can be expressed as follows: $X_K = 1.05 \cdot [\text{phyto}] + 163.48$ ($R^2 = 0.77$; $n = 11$). Thus, the highest estimates of X_K were associated with the highest mean annual phytoplankton concentrations.

4. Discussion

4.1. Generalisation of the oyster-DEB model

The growth dynamics of *C. gigas* were correctly reproduced by the oyster-DEB model *i*) at all sites tested; *ii*) for the three age classes studied and *iii*) throughout the year, both during periods of active growth (essentially in the spring, but sometimes in the summer and autumn) and during periods of mass loss in autumn/winter and more abrupt periods of mass loss in the spring and summer due to spawning (Figs. 4 to 6; Table 2). The oyster-DEB model successfully reproduced the contrasting growth profiles of spring and the autumn-winter period for three age classes of oysters reared simultaneously in the same environment (CA, Mont-Saint-Michel Bay). All the key periods in the growth cycle of farmed *C. gigas*, from the end of the spat stage (*i.e.* one year onwards) were thus faithfully simulated, complementing the validation already reported for larval growth (Rico-Villa *et al*. 2009). This validation thus suggests that the model may be considered generic, not only at the geographic scale (several oyster-rearing sites tested), but also over time (application of the model at the same site over the course of several years) and for oysters of different age classes. This is the first validation of a bioenergetic model for *C. gigas* based on a single set of parameters, in several contrasting environmental conditions, with only one parameter X_K requiring adjustment for each data set. A similar approach is currently being developed for another species of ecological and aquacultural importance, the blue mussel *Mytilus edulis* (Alunno-Bruscia *et al*. in preparation).

The mass losses associated with the release of gametes in the summer were successfully simulated by the model, with a certain consistency, regardless of the age of the oysters (1 to 3 years) and the environmental conditions (Figs. 4, 5 and 6). The simulated dates of gamete release were also close to the actual spawning dates observed *in situ*. No gamete release was observed for 1-y old oysters in Mont-Saint-Michel Bay in 2003. By contrast, gamete release accounted for more than 50% of dry flesh mass loss for the oysters in Brest Harbour in 2008 and in the Arcachon Basin in 1994. Such contrasts are not unusual in *C. gigas* (Berthomé *et al*., 1986). These variations in gamete release highlight differences in the flow of energy and matter between the two principal compartments of the individual, the soma and the reproductive compartment, through the application of the same energy allocation rules to all life stages of the oyster. In younger oysters (smaller in size), a higher proportion of energy is devoted to growth of the soma than to gamete production, whereas the reverse is true for older oysters. These observations are consistent with the hypothesis underlying DEB theory (Kooijman, 2010), according to which the costs of maintaining the soma increase with its size, thereby asymptotically limiting growth in the largest oysters, whereas the investment in reproduction continues to increase proportionally with the size of the soma. One recent study attempted to improve the description of reproductive effort in *C. gigas*

through the use of a DEB model. This study was carried out at three of the six sites studied here (Arcachon, Marennes-Oléron and Brest Harbour) in the years 2008 and 2009; it has led to the proposal of a new set of DEB parameters and a formalism different from that of Bourlès *et al.* (2009), with the addition of a state variable describing gamete production in the spring (Bernard *et al.*, in press -this issue). A comparison between the simulations obtained with the two versions of the model (those of Bourlès *et al*. (2009) and Bernard *et al*. (in press -this issue)) indicated that the model of Bernard *et al.* better described and quantified the reproductive effort.

The demonstration in this work of the generalised application of an oyster-DEB model at different sites nonetheless raises questions about the correctness of the values of parameters estimated in various studies (van der Veer *et al*., 2006; Pouvreau *et al*., 2006; Bourlès *et al*., 2009). Another bio-energetic model based on DEB theory has been developed for *C. gigas* by Ren and Schiel (2008). These authors specified that their model had been applied to and validated in conditions of Pacific oyster rearing specific to New Zealand. The values of the parameters of the Ren and Schiel model (2008) are different from those estimated here: k = 0.65 *vs* 0.45; $[E_G]$ = 2900 *vs* 1900 J·cm^{-3}; $[E_M]$ = 5900 *vs* 2295 J cm^{-3}; $[p_M]$ = 18.5 *vs* 24 J cm^{-3} d^{-1}, for the estimations of Ren and Schiel (2008) and Bourlès *et al*. (2009), respectively. Ren & Schiel (2008) based their parameters estimation on data collected during a short period (6 months from May to October) under a narrow range of temperatures (13-15°C); moreover no spawning for *C. gigas* occurred, which impedes any validation of the k value used by these authors. This may partly explain the differences in the DEB parameters between the two studies. The validations of these two models, which were developed independently for the same species, highlight the need to work towards homogeneity in parameter values, for the construction of a unique, standard growth model based on DEB theory (Kooijman, 2010). The recent work of Bernard *et al.* (in press -this issue) represents an additional step towards the harmonisation of DEB parameters for *C. gigas*.

4.2. Phytoplankton concentration as a proxy for food availability in the oyster-DEB model

In a simplified modelling approach, we decided to use phytoplankton concentration as a proxy for food ingestion by oysters. We confirmed the relevance of this proxy for the simulation of *C. gigas* growth at several sites in France. In most bio-energetic models developed to simulate the growth of *C. gigas*, chlorophyll *a* concentration is used as the food proxy (*e.g.* Raillard *et al.,* 1993, Barillé *et al.,* 1997, Ren & Schiel 2008). This was the case, in particular, in the first version of the oyster-DEB model (Pouvreau *et al*. 2006). However, Bourlès *et al*. (2009) showed that phytoplankton concentration was a more pertinent food proxy than chl *a* in the rules governing ingestion in the DEB model, constituting in principle a good trophic indicator capable of reproducing the growth variations observed during the year. Bernard *et al.* (in press -this issue) also showed that phytoplankton concentration was sufficient to simulate the reproductive effort of *C. gigas* at various French sites, with the exception of Bourgneuf Bay, a site for which the available data for phytoplankton did not coincide precisely with the site at which oyster growth was monitored (Barillé *et al.*, in press -this issue). The phytoplankton concentration may not be available systematically in monitoring surveys. It is also more costly or time-consuming compared to chl *a* and is not easily simulated by modelling. Despite these drawbacks, it is still in our view a more reliable and precise food proxy of bivalve diets than the chl *a* concentration which does not allow to distinguish the contribution of the main algae classes or groups. An alternative that could help to reach a compromise between chl *a* and phytoplankton concentrations would be to use new instruments for continuous chlorophyll and photosynthetic activity determination among different algae classes by excitation of pigments with coloured LEDs.

This food proxy can be used to distinguish between the respective contributions of the principal species of microalgae identified as food sources for *C. gigas* and to identify blooms of non-edible algae that are, in principle, not ingested (or assimilated in only very small quantities) by oysters. These blooms may develop to densities exceeding $1 \cdot 10^6$ cell L^{-1}, at times at which the oysters display no significant growth (Bourlès *et al.* 2009). In this study, *L. minimus* reached levels of more than $2 \cdot 10^6$ cell L^{-1} in August 2007 at Marennes-Oléron, but there was no concomitant increase in *DFM*. In this particular case, the DEB model correctly simulated the mass of oyster flesh when the number of *L. minimus* cells was excluded from the forcing of the model. At Quiberon bay, *L. chlorophorum* was the species displaying massive proliferation without the slightest positive effect on oyster growth (Fleury *et al*., 2001); this species was withdrawn for the month of September 2001 from the forcing of the model and the result was a good match between the observed and simulated growth of the oyster. *Tetraselmis sp.* and *Kryptoperidinium foliaceum* were previously subtracted from the concentration of total phytoplankton for forcing of the oyster-DEB model and simulation of the growth of *C. gigas* in an oyster pond (Bourlès *et al*. 2009). This negative effect of some particular algae when at high concentrations may provide an alternative explanation for the intriguing decrease in *Crassostrea virginica* food uptake measured *in situ* (with a pelagic ecosystem tunnel) by Comeau *et al.* (2010) during an autumnal bloom.

The alternative to this empirical approach, based on the subtraction of certain non-edible algae from the food sources of oysters, is to modify specifically the assimilation efficiency (*AE*), fixed globally in the current set of parameters at a constant value of 75%, regardless of the phytoplankton species present and their concentrations (Bourlès *et al*. 2009). This would make it possible to retain non-edible algae among the food potentially ingested by the oyster, but absorbed poorly, if at all (*i.e.* with *AE* values that are either very low or zero). The assimilation efficiency of bivalves may vary according to the species of algae ingested (*e.g.* Ren *et al.*, 2006; for reviews in Bayne & Newell 1983; Gosling 2003), with very low values of *AE* reported in the case of *Tetraselmis suecica* for *Crassostrea virginica* (Romberger & Epifanio 1981) and *C. gigas* (Boglino 2008) in particular, or the value of *AE* may decrease as phytoplankton concentration increases (Kuenster 1988). Moreover, assimilation efficiency may be influenced by water temperature, the organic fraction of the food and non-edible inorganic matter (*e.g.* Hawkins *et al*. 1998; for a review see Gosling 2003) and probably displays seasonal variation due to temporal changes in phytoplankton assemblages. Finally, there is a functional relationship between and interdependency of assimilation efficiency on gut capacity, the residence time of the food in the gut and ingestion rate (Bayne & Newell 1983). This relationship cannot be explicitly formalised in the Holling-type II hyperbolic function describing the energy intake of an organism in DEB theory. It is also not possible to formalise differences in the feeding behaviour of *C. gigas* with respect to different phytoplankton species.

4.3. The environment-specific half-saturation coefficient XK

The half-saturation coefficient X_K for ingestion is the only parameter of this model freely adjusted for each environmental scenario, with values of $260 \cdot 10^3$ cell L^{-1} in Quiberon Bay (1999, Fig. 5) to $700 \cdot 10^3$ cell L^{-1} at Marennes-Oléron (2007, Fig. 7). The higher value reflects poor trophic quality or low appetence of the oysters for the food available. X_K is the only empirical parameter of the oyster-DEB model and it integrates all sources of variation linked to the trophic environment, including the diversity of food sources and seasonal variations in the nutritive quality of food, fluctuations of the selection of particles before ingestion and variability in assimilation efficiency as a function of the food actually ingested. In addition to this integration of environmental variability, X_K also seems to be influenced by the age and/or size of oysters, as shown by the different X_K values obtained for the three age classes of oysters in the same environment (Mont-Saint-Michel Bay, Fig. 6). This may be accounted for by variability in filtration, selection and/or ingestion capacities, due to

differences in the range of prey size as a function of the size of *C. gigas*. Indeed, differences in food source between individuals of the same species but of different age classes have been demonstrated for other bivalves, such as the cockle *Cerastoderma edule* (Sauriau and Kang, 2000).

The adjusted values of the half-saturation coefficient X_K increase linearly with measured phytoplankton concentration (Fig. 7), indicating that the quality of the trophic resource and/or the appetence of the oysters for this resource decrease when phytoplankton concentrations are high (*e.g.* Comeau *et al*., 2010). There are two probable explanations for this significant relationship: *i*) sites with high phytoplankton concentrations (*e.g*. MO07 which is also a very turbid site compared to the other sites; BR08) are generally of lower (or poorer) trophic quality than sites with lower phytoplankton concentrations (*e.g*. AR93 and AR94, QB from 1999 to 2001, CA02), accounting for the lower growth rates of oysters at sites with high phytoplankton abundance compared to sites with low abundance, for the same phytoplankton concentration; *ii*) the physiological flexibility of *C. gigas*, particularly in terms of filtration and food selection organs, gills and labial palps (Barillé *et al*., 2000; Dutertre *et al*., 2007), allows the bivalve to adapt to different particle loads. A high particle load (turbid environment) may lead, in particular, to a decrease in gill area and, thus, to a decrease in the capacity of the animal to filter its food. In the oyster-DEB model, this leads to an increase in X_K, resulting in a positive linear relationship between this factor and the mean annual concentration of phytoplankton.

A multivariate approach to the feeding response in DEB

Other pathways should be explored to compensate for the empirical estimation of X_K, which varies between sites, making it possible to develop a "multivariate" approach to energy acquisition in *C. gigas* that is not based on a single food proxy and/or a functional response simplified with respect to the alimentary physiology of *C. gigas*. One of these alternative pathways is based on the inclusion of several food sources into the ingestion law, with the aim of better reflecting the contribution of different compartments of the seston as food sources for filter-feeding bivalves, and thus the contribution of these compartments to growth (*e.g.* Cognie *et al*., 2003; Decottignies *et al*., 2007; Marin Leal *et al*., 2008; Lefebvre *et al*., 2009). In environments with high concentrations of inorganic matter, the effect of inedible mineral particles on bivalve filtration may be explicitly integrated into the ingestion law (Kooijman, 2006). Ren (2009) tested this approach with the mussel *Perna canaliculus*. The contribution of suspended organic matter to the food available (expressed in terms of chl *a* concentration) was integrated into a formulation of the functional response *f*, to simulate the growth of cockles (*C. edule*) and mussels (*M. edulis*) in the Oosterschelde (Troost *et al.,* 2010). This contribution was found to be significant in cockles at certain sites. Similarly, the contribution of different genera or families of phytoplankton, the relative contributions of the pelagic phytoplankton and microphytobenthos at certain sites (Marin Leal *et al*., 2008; Lefebvre *et al*., 2009), like that of protists including ciliated and flagellated organisms (Dupuy *et al*., 1999; Trottet *et al*., 2007), could be formalised in terms of *f*. The negative effect of certain algae on the ingestion and growth of filter feeders (*e.g*. Chauvaud *et al*., 2001) and the effect of certain toxic agents (heavy metals, toxic chemicals of natural or anthropogenic origin) or even diseases likely to affect the alimentary physiology of bivalves (Flye-Sainte-Marie *et al.,* 2009) could also be integrated into the structure of the model, through effects on feeding processes or maintenance costs (Casas and Bacher, 2006; Flye-Sainte-Marie *et al.,* 2009).

Another possibility is to model the various processes involved in the feeding of *C. gigas* (filtration, ingestion, assimilation) in the same way as has been done for the mussel *M. edulis* (Saraiva *et al.,* 2011), making use of the concept of "synthesising units" (Kooijman, 1998, 2010). Synthesising units (SU) are generalized enzymes that bind (with a fixed probability) to

substrate molecules (arriving according to a Poisson process), to synthesise products, thereby transforming the arrival fluxes of substrates into a production flux of products (Lika and Papadakis, 2009). If SU are identified with an individual filter feeder, and the product with reserves, the transformation rate is given directly by the functional response *f* (Saraiva *et al.,* 2011). This new modelling approach, involving application of the SU concept, has provided a satisfactory mechanistic description of the feeding processes of *M. edulis* based on published data and has dealt with variability in the amount and quality of food, although uncertainties relating to ingestion in the presence of pseudofaeces production remain. The large set of studies published on the feeding physiology of *C. gigas*, and possible new dedicated experiments, may prove useful for the implementation of a similar approach for Pacific oyster.

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Tables

Table 1. Initial model conditions estimated for each site (AR: Arcachon Basin, MO: Marennes-Oléron, QB: Quiberon Bay, BR: Brest Harbour, CA: Mont-Saint-Michel Bay, BV: Baie-des-Veys, for each year and each age class tested

Site	Year	Age class	Structure V (J)	Reserve E (J)	Reproductive compartment E_R (J)
AR	1993	2 years	4000	800	2100
	1994	2 years	3700	800	2000
MO	2007	3 years	5800	1100	3000
QB	1999	1 year	400	100	200
	2000	1 year	250	50	150
	2001	1 year	250	50	150
BR	2008	2 years	5300	1200	2800
CA	2003	1 year	600	100	300
	2003	2 years	2200	500	1200
	2003	3 years	6800	1400	3600
BV	2002-03	2 years	4000	900	2500

Table 2. Linear regression of observed dry flesh mass against simulated dry flesh mass; regression coefficient R^2, slope, intercept with corresponding p values of testing slopes different from 1 and intercept different from 0. The 11 data sets tested were those for the Arcachon basin in 1993 and 1994 (AR93, AR94), Marennes-Oléron in 2007 (MO07), Quiberon Bay in 1999 (QB99), 2000 (QB00) and 2001 (QB01), Brest Harbour in 2008 (BR08), Mont-Saint-Michel Bay in 2003, for three batches of oysters aged one year (CA03/1), two years (CA03/2) and three years in 2003 (CA03/3) and Baie-des-Veys in 2002-03 (BV02-03).

Regression parameters	**AR93**	**AR94**	**MO07**	**QB99**	**QB00**	**QB01**
R^2	0.805	0.939	0.875	0.850	0.939	0.959
(*p-value*)	*< 0.0001*	*< 0.0001*	*< 0.0001*	*0.0011*	*< 0.0001*	*< 0.0001*
Slope	1.016	0.841	1.033	1.105	1.031	0.933
(*p-value*)	*0.9081*	*0.0256*	*0.0068*	*0.5983*	*0.7348*	*0.3538*
Intercept	-0.076	0.198	0.009	-0.075	-0.015	0.014
(*p-value*)	*0.5899*	*0.0339*	*0.0334*	*0.3340*	*0.7013*	*0.6435*

Regression parameters	**BR08**	**CA03/1**	**CA03/2**	**CA03/3**	**BV02-03**
R^2	0.923	0.951	0.872	0.919	0.928
(*p-value*)	*< 0.0001*	*< 0.0001*	*0.0003*	*< 0.0001*	*< 0.0001*
Slope	1.008	0.955	0.869	1.030	1.072
(*p-value*)	*0.9390*	*0.5991*	*0.1445*	*0.7888*	*0.3805*
Intercept	-0.155	0.113	0.192	-0.093	-0.111
(*p-value*)	*0.5628*	*0.1280*	*0.3035*	*0.7034*	*0.3690*

Figures

Figure 1. Geographic location of the six oyster-rearing zones along the Channel/Atlantic coasts of France at which the oyster-DEB model was tested: the basins of Arcachon (1-AR) and Marennes-Oléron (2-MO), Quiberon Bay (3-QB), Brest Harbour (4-BR), Mont-Saint-Michel Bay (5-CA) and Bei-des-Veys (6-BV). The white stars indicate the oyster-rearing sites and the black stars indicate the location of the hydrological stations. The 20 km scale applies to the maps showing the six oyster-rearing regions in details.

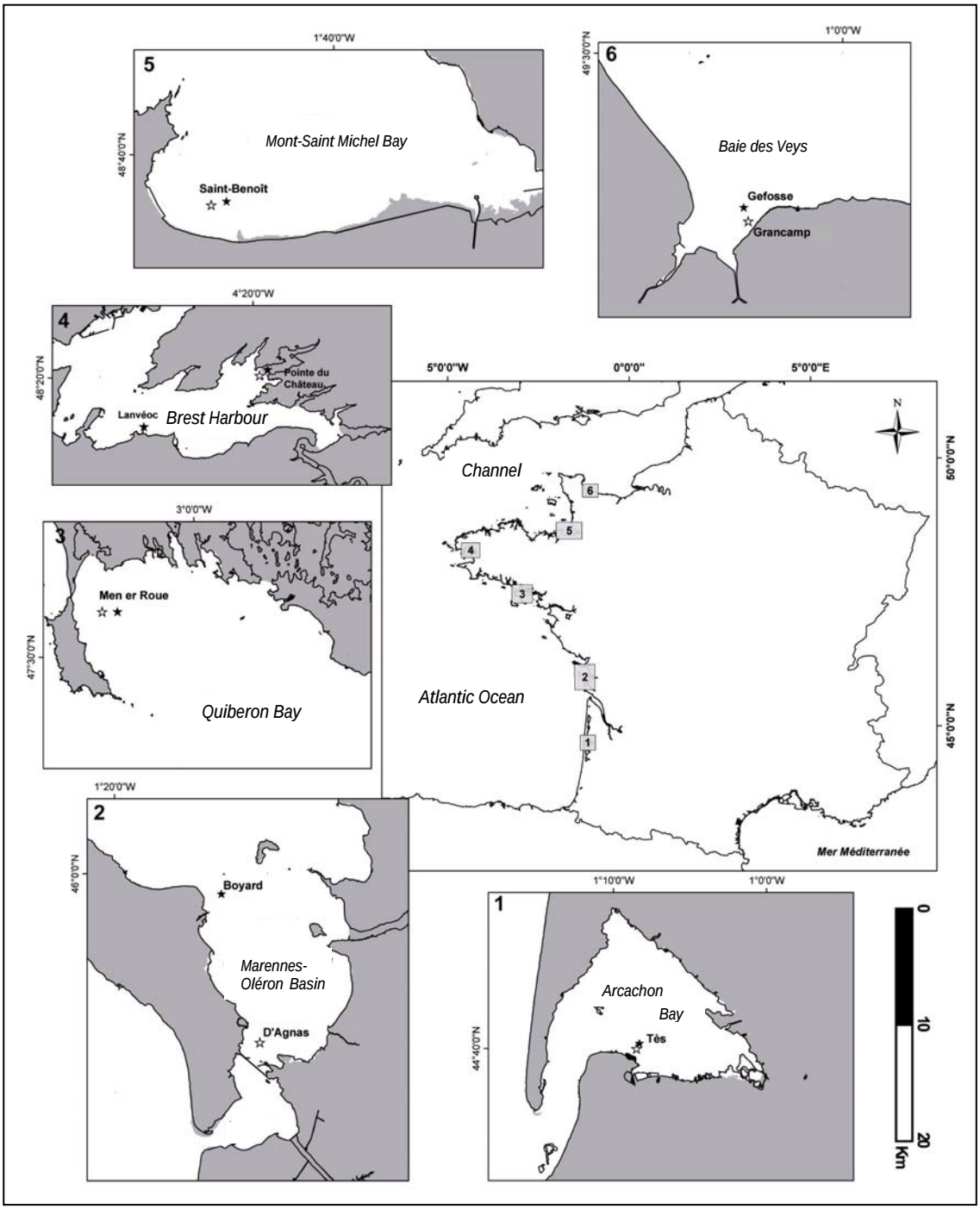

Figure 2. Seawater temperature (°C, grey curve) and phytoplankton concentrations (10^6 cells L^{-1}, black curve), used as forcing variables in the oyster-DEB model in Arcachon Basin (AR) in 1993 and 1994, Marennes-Oléron (MO) in 2007 and Quiberon Bay from 1999 to 2001.

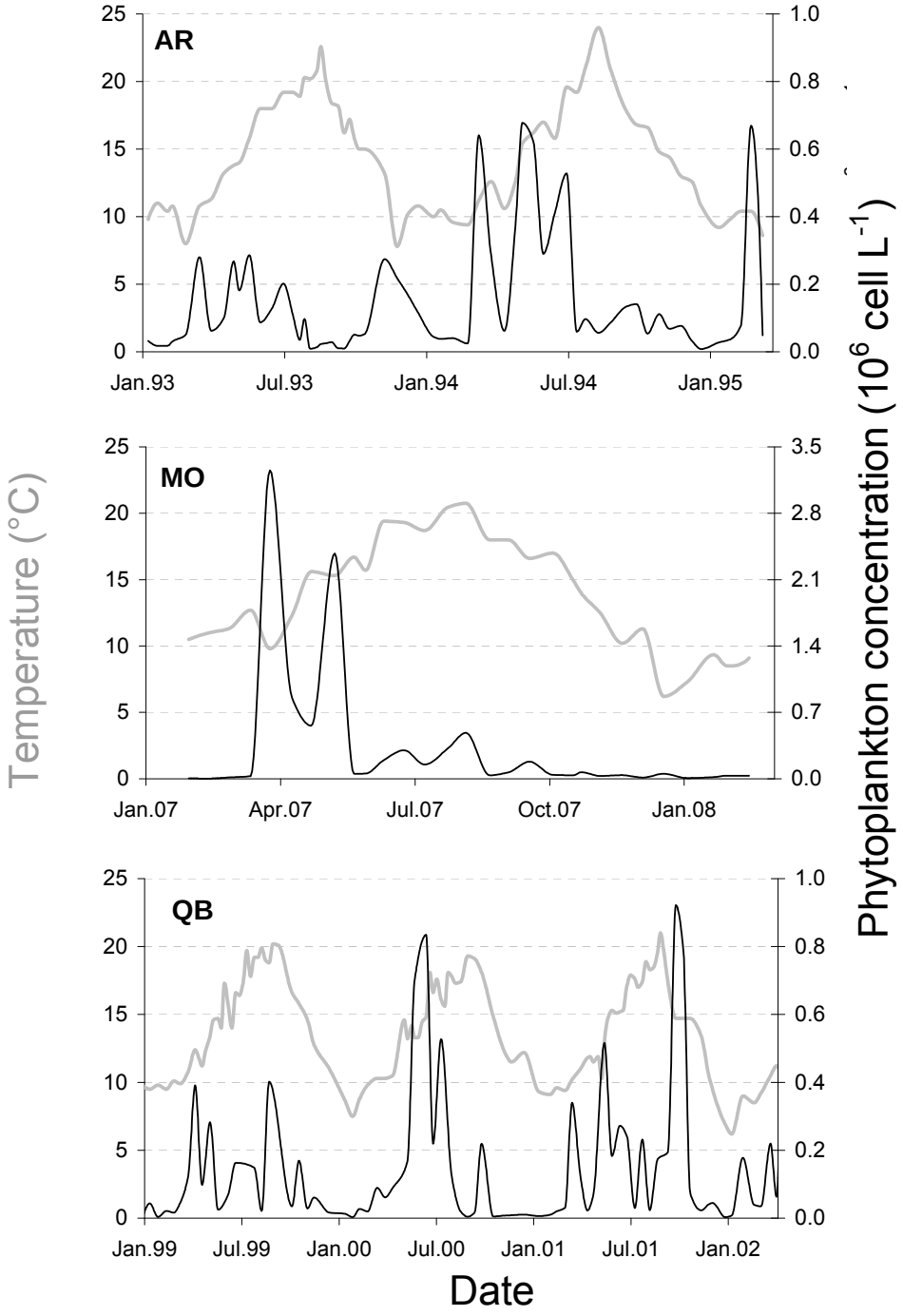

Figure 3. Seawater temperature (°C, grey curve) and phytoplankton concentrations (10^6 cell L^{-1}, black curve), used as forcing variables in the oyster-DEB model in Brest Harbour (BR) in 2008, Mont-Saint-Michel Bay (CA) in 2003) and Baie-des-Veys (BV) in 2002 and 2003.

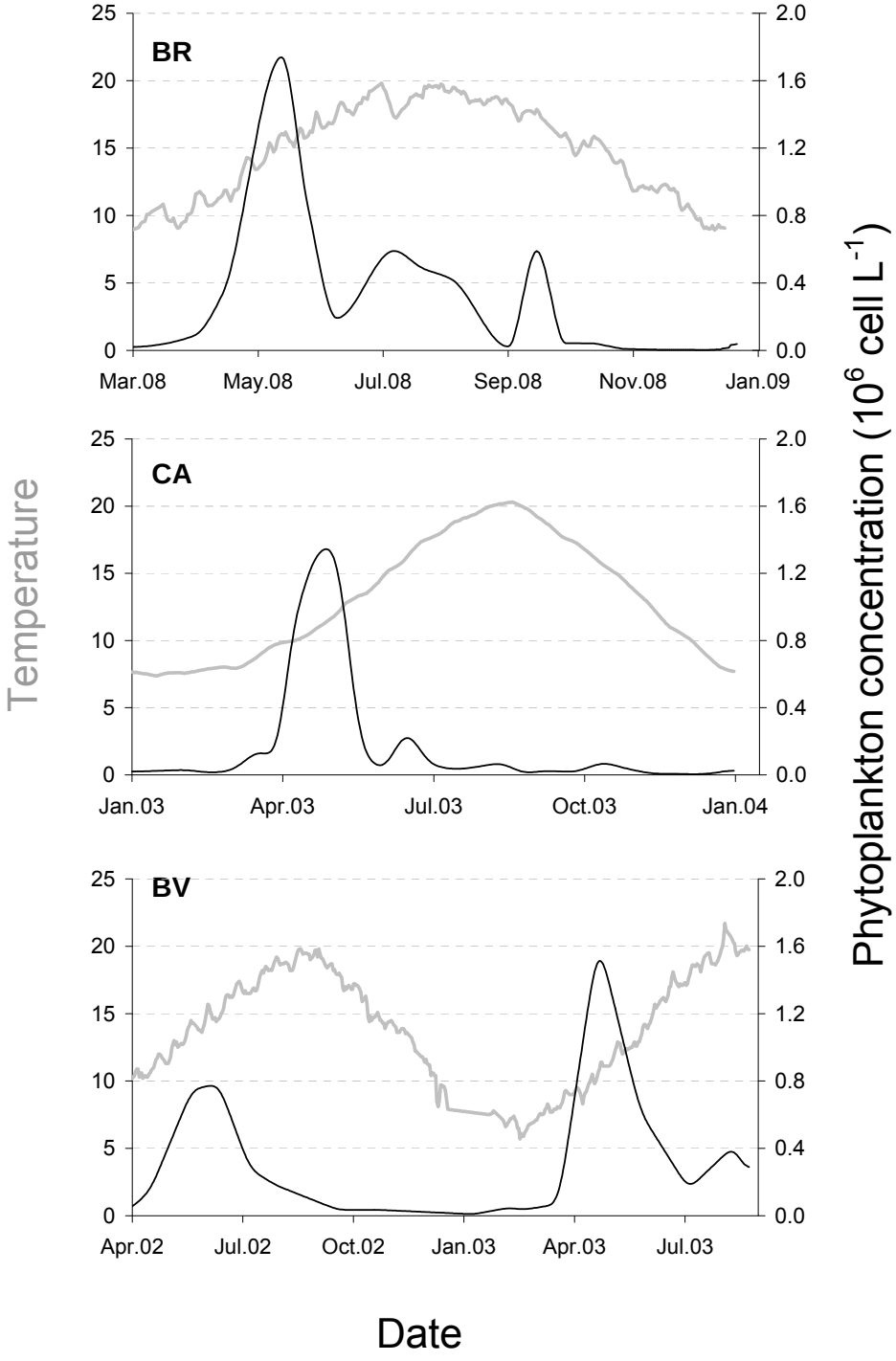

Figure 4. Observed (black symbols: means with 95% confidence intervals (CI)) and simulated (grey curve) dry flesh masses in Arcachon Basin in 199 3 and 1994 and in th e Basin of Marennes-Oléron at the D'Agnas site in 2007. XK is expressed in 103 cell L-1.

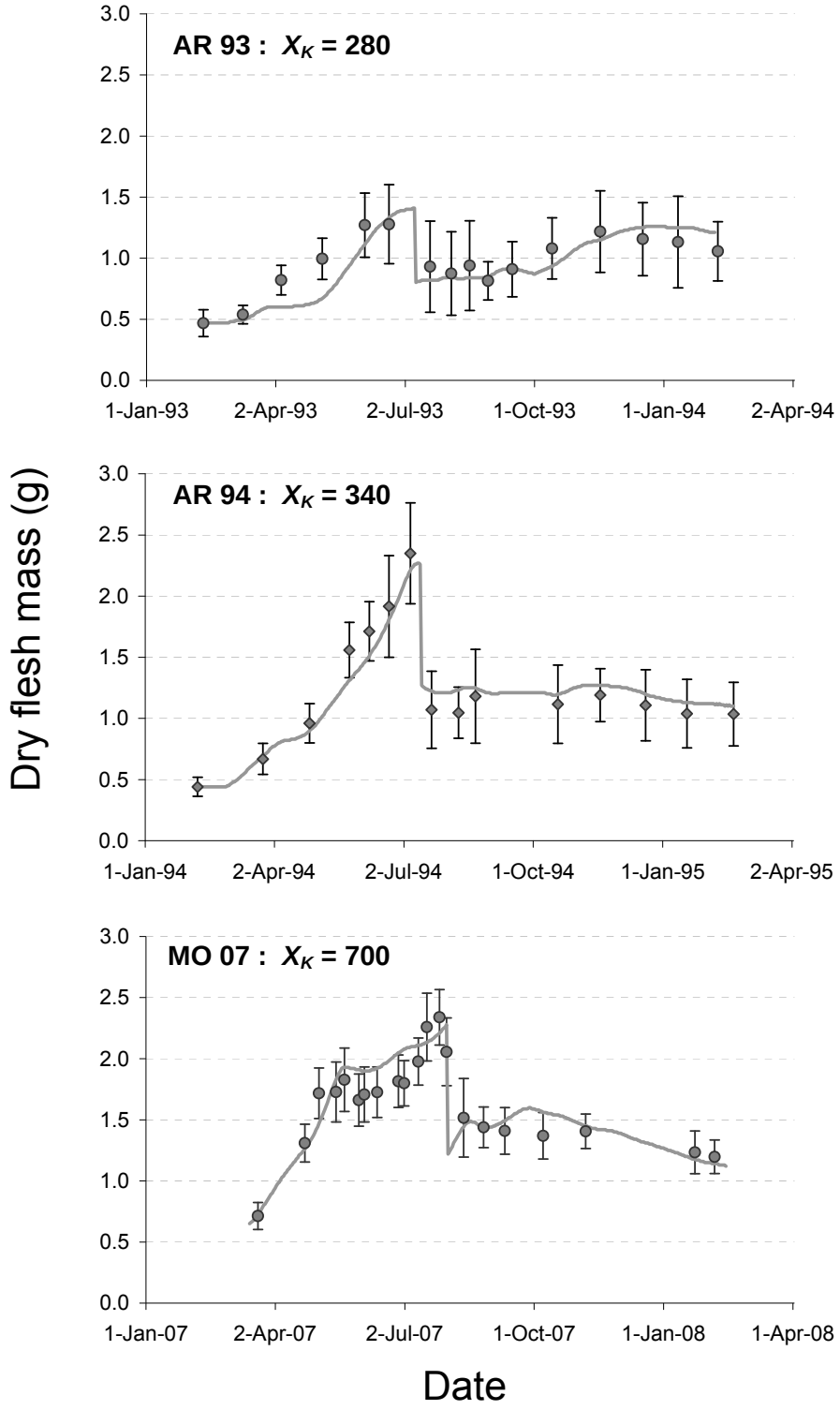

Figure 5. Observed (black symbols: means and 95% CI) and simulated (grey curve) dry flesh masses in Quiberon Bay in 1999, 2000 and 2001. XK is expressed in 103 cell L-1.

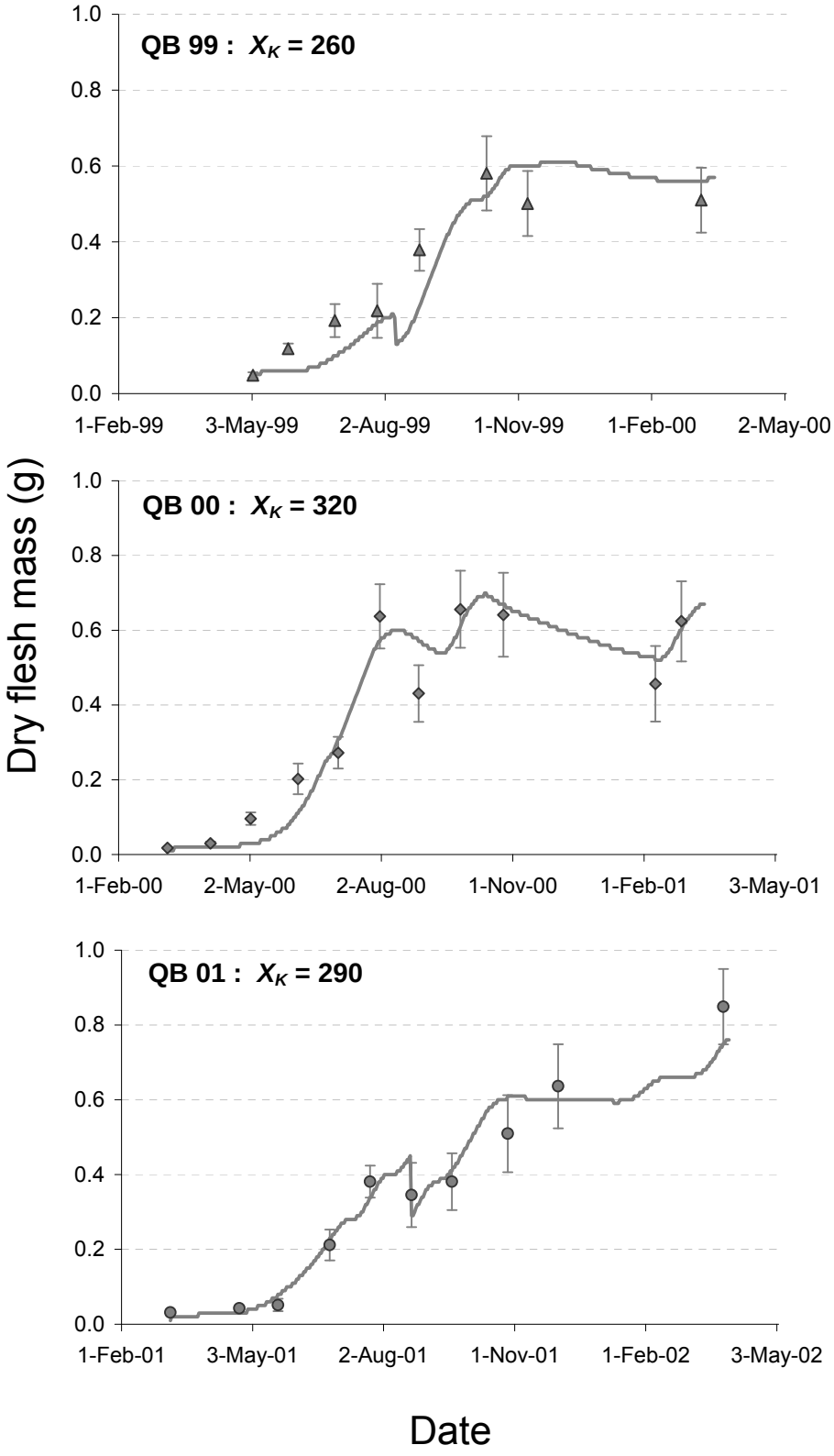

Figure 6. Observed (black symbols: means and 95% CI) and simulated (grey curve) dry flesh masses in Brest Harbour in 2008, Mont-Saint-Michel Bay in 2003 and Baie-des-Veys in 2002-2003. The three simulations at Mont-Saint-Michel Bay (CA) correspond to the three age classes: one year (thin black curve), two years (grey curve) and three years (thick black curve). XK is expressed in 103 cell L-1.

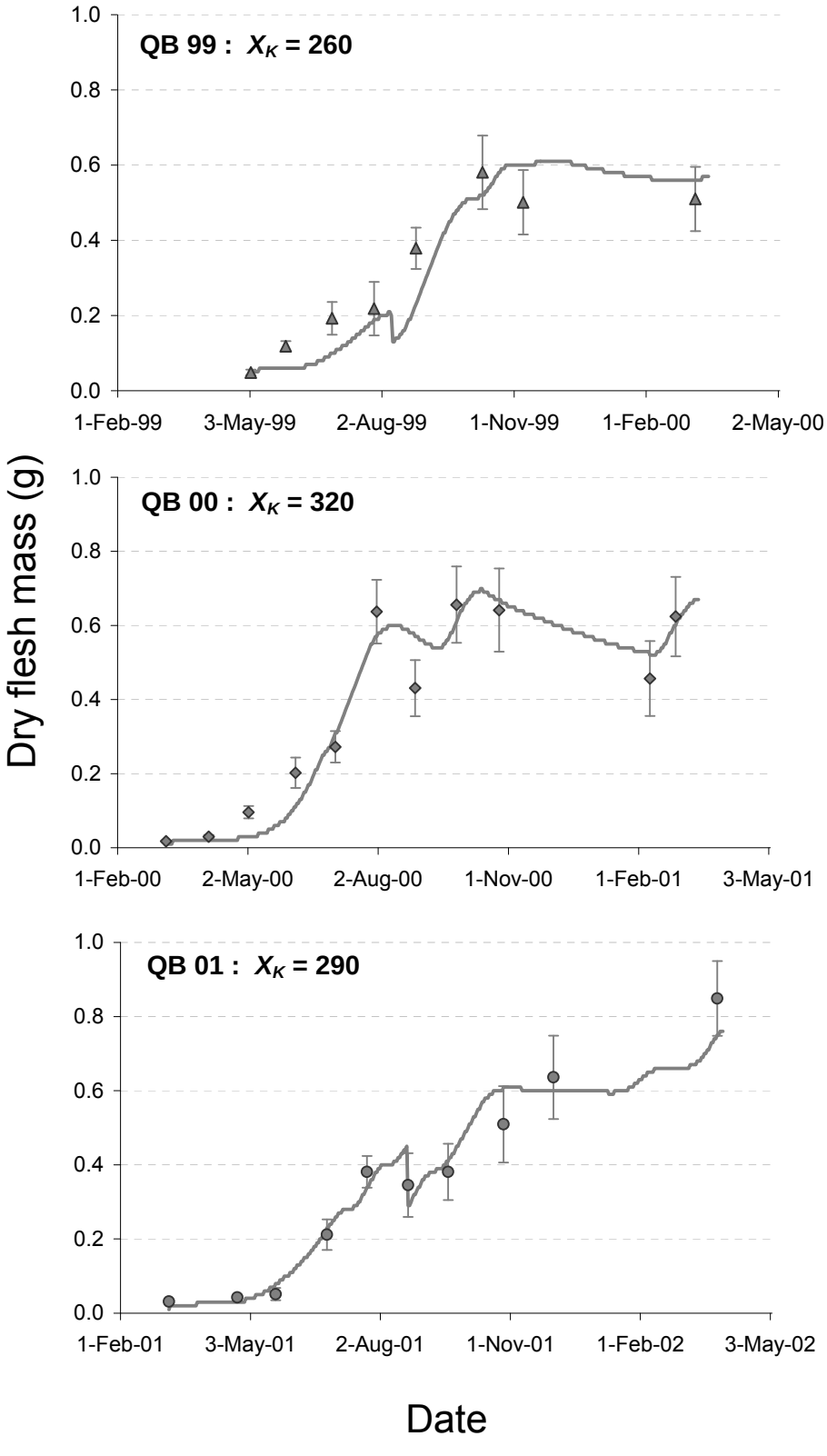

Figure 7. Linear regression (black line: XK =1.05 x [phyt o]+163.48; R^2 = 0.77; n = 11) between mean annual phytoplankton concentr ation and adjusted half -saturation coefficient XK for the 11 simulations in this study (black dots).