

graphical extent is low). As with the previous steps, duration of any effect of the farm once operations cease is expected to be negligible (low). In total, the **severity** of food limitation caused by the new long-line farm site on other nearby farms is expected to be **low**, and the **probability** that this step in the logic model will occur is **high**. Our knowledge of the processes involved in this type of interaction is good enough that **uncertainty** for this prediction is **low**.

7. New production will affect other areas. When examining potential effects of a long-line farm on larger areas, it is necessary to examine the balance of primary production and the effect of the farm on food concentrations in a larger water body. Primary production varies with meteorological conditions which act on the fresh water and nutrients loadings, light intensity, water temperature and sediment resuspension, and inter-annual variability is probably high. In Marennes-Oléron bay, a comprehensive assessment of primary production showed that primary production is driven by nutrient fluxes, water mixing and light limitation due to turbidity (Struski and Bacher 2006) and its role on carrying capacity has also been assessed (Bacher *et al.* 1998). Although no comparable estimation exists for Aiguillon bay, it is likely that it behaves in the same way because of the similarities between the two ecosystems – for example, macrotidal bays, input from fresh water and nutrients from rivers, sediment resuspension due to currents and waves. Primary production is therefore thought to be a limiting factor for the carrying capacity if mussel production is based solely on primary production at the scale of the bay.

There is also evidence of a relationship between phytoplankton concentration and mussel growth on bouchot in Pertuis Breton (Dardignac-Corbeil 2004) and in Marennes-Oléron Bay (Boromthanasarat *et al.* 1988) and growth of suspended culture mussels has been assessed in Pertuis Breton (Barillé 1996). The effect of phytoplankton and turbidity on mussel growth has been assessed by Garen *et al.* (2004) who compared growth in suspended culture and bouchot and showed that mussels on long-lines exhibited the highest growth rate, probably due to differences in immersion time.

Phytoplankton availability is therefore probably the primary limiting factor for growth, but horizontal dispersion probably acts to dilute the available supply of food. The hydrodynamical model implemented in Pertuis Breton and the Marennes-Oléron Bay showed that, in Pertuis Breton, tidal currents frequently exceed 50 cm s^{-1} . Compared to other ecosystems where mussel culture takes place, this intense water movement favours the supply of food particles to individual bivalves. However, the residence time of water within the bay has not been accurately estimated and is probably much higher than in

Marennes-Oléron Bay, where limitation of carrying capacity has been demonstrated. Increased flushing rates would tend to dilute the concentration of phytoplankton in the water body.

Modelling of food depletion in the long-line area has shown that the actual current velocity and mussel density would not result in significant food depletion, even if the long line area was extended. At the local scale of long-lines or bouchots, primary production is negligible compared to the supply of food through advection of phytoplankton and detritus by currents. Simulations of particle movements and fluxes of bivalve food demonstrated that the actual mussel density and lease size had a minor effect on flows of particulate organic matter and phytoplankton, and that water exchange was high enough to support the additional mussel production proposed.

Interactions between cultivated areas generally occurs when the combination of water residence time, shellfish standing stock and primary production limits food availability (Smaal *et al.* 1998; Guyonnet *et al.* 2005; Bacher *et al.* 1998). In Pertuis Breton, long-lines and bouchots are operated in different areas, separated by a few kilometres, which minimises the potential for interactions.

The likely degree of change (severity) is **low** and limited to the area of the lease site and immediately downstream of it. If the production were removed any effect on the system is not likely to persist even for a short period of time. The **severity** is therefore **Low**. **Probability** that this prediction is correct is high and the **Uncertainty** associated with this prediction is **Moderate** because of a lack of accurate information on some physical parameters such as flushing time. Even so, the variation in environmental forces that are evident in the existing conditions are expected to be representative of the range of environmental variation.

8. Effect on carrying capacity
Mortality of mussels has been monitored at both long-lines and bouchots, and mortality rates have been at acceptable levels. Given no noticeable effect of the new long-line farm on food supply, an increase in mortality is unlikely to occur. The lack of food reduction on the farm site, on nearby farms, or on the carrying capacity of the bay suggests that changes in carrying capacity in the bay due to the new farm will be very small if they occur at all. Furthermore, any effect on the carrying capacity will be quickly reversed should the farm cease to operate. Therefore, the **severity** of effect on carrying capacity will be **low**. The **probability** that this prediction is correct is thought to be **high**. The **uncertainty** associated with this prediction is medium, as some of the physical processes on which it is based (such as flushing times) remain to be fully documented.

Results are summarised in Table 6.2.I. The final rating for the **Probability** is assigned the value of

the element with the **lowest** level of probability. The final rating for the **Severity** (intensity of interaction) is assigned the value of the step with the **lowest** risk rating. The final rating for the **Uncertainty** is assigned the value of the element with the **highest uncertainty** level. The conclusion of the risk evaluation in both local and distant farms is that the risk of change of carrying capacity is considered as low with a medium uncertainty.

6.2.3.5 Risk estimation

In the earlier description of the potential expansion of farming activities, no special technologies were identified as to be used nor were any specific regulatory requirements mentioned that might reduce the effect of the new farm from that which might be anticipated based on the consequence assessment. For that reason, the risk level identified in the consequence assessment is the same as that for the risk evaluation. Should any of the recommended risk management activities be undertaken, that level of risk may be modified.

6.2.4 Risk Management

Option evaluation in risk management addresses what might be done to reduce the probability of a risk being expressed, or to reduce the uncertainty in the prediction of the expression of a risk. The process therefore identifies, for each step in the logic model, what could be done to reduce the probability of it occurring. These actions would directly mitigate possible effects. A further contribution to increasing the effectiveness of the risk analysis would be to reduce the uncertainty associated with predicting that the step will happen. Usually this involves further research or development. Table 6.2.II identifies both mitigation measures and research or development activities that could address the risks arising from the additional filtration pressure of mussels at a proposed new cultivation site.

Gouletquer and Héral (1997) noted that the shellfish industry was facing several internal and external constraints affecting overall economic yield and sustainability. The development of an integrated coastal management plan for the Pertuis Charentais is likely to be a major objective in the near future, not only to take into account the requirements of sustainable aquaculture, but also to include other users in the management of the coastal area. Ervik *et al.* (1997) developed a comprehensive methodology, combining models and data collection, to minimise the effects of aquaculture in Norwegian waters. General principles for the monitoring of aquaculture effects have been stated only recently by Fernandes *et al.* (2001) who emphasised the role of whole-system environmental assessments in developing frameworks for the sustainable use of ecosystems – for example, whether the effects of an activity on the environment is unacceptable with respect to the objectives/needs of producers, regulators and stakeholders and the desire to be able to use maintain the uses of an area indefinitely. They proposed a set of recommendations concerning the implementation of a more focused approach to environmental monitoring to contribute to the management of sustainable aquaculture.

The effort in identifying and mapping sites suitable for aquaculture, and monitoring existing sites, is therefore key to mitigation and optimisation of shellfish aquaculture. Over the last 10 years there has been an increasing development of Geographic Information Systems (GIS) and models (see <http://www.fao.org/fi/gisfish/index.jsp>). GIS-based decision support systems (as advocated by Nath *et al.* 2000) constitute a new generation of management tools. Parker *et al.* (1998) organised physical characteristics, such as bathymetry, bottom type, intertidal location, water currents, temperature, and planktonic concentrations into a GIS to predict and map potential growth rates of juvenile shellfish for seeding sites. Similar tools were implemented by Brown and Hartwick (1988), Arnold *et al.* (2000), Congleton *et al.* (1999, 2003), and Vincenzi *et al.* (2006) for shellfish and Pérez *et al.* (2002, 2003, 2005) for fish aquaculture. Most GIS systems are based on maps of environmental data and sometimes outputs from hydrodynamic models are included (Congleton *et al.* 2003). The coupling of biological models to these physical models will allow information and advice on production to be derived (Bacher *et al.* 2003). This will require additional research effort, and the application of ecophysiological, hydrodynamic and ecological models.

6.2.5 Scope of the Risk Assessment

This case study examines some of the effects of shellfish aquaculture at a specific site. The conclusions need to be examined by stakeholders and shellfish farmers, fishermen and regulators through a coherent risk communication process. We did not seek to take into account all the possible effects of a new shellfish development, and some uncertainties remain in the assessment. However, the example illustrates how the assessment of potential effects of filtration pressure on shellfish carrying capacity might be undertaken. The output is site-specific but the use of a standardised procedure has several advantages. Any risk assessment must be seen as a continuously evolving process which should take into account new information and changes the input from stakeholders and scientists. These changes can diminish the uncertainty attached to the risk evaluation or refine the definition of the risk. Information developed for one assessment can also often be applied in other contexts and sites and outputs of the risk assessment in one case can bring valuable information to other assessments. Eventually, the methodology leads to a management plan to mitigate any undesirable effects revealed by the risk evaluation, improvements in the good farm management practices and directs data collection and scientific research to critical areas of uncertainty.

Other environmental consequences of shellfish farming can be recognised, and are related to more complex processes which all fall into the broad framework of Ecosystem Carrying Capacity, as defined by Inglis *et al.* (2000). In a recent review, McKindsey *et al.* (2006) emphasised the changes in the flow of nutrients and materials due to shellfish culture. The shellfish filter large amounts of water and remove suspended particulate material. This can be partly excreted in dissolved form or repackaged and released as faeces and pseudo-faeces. These generally differ from other seston particles in aggregate size and shape, organic matter content and cohesive properties. Sedimentation of these

Table 6.2.1 : Risk estimation based on the logical model.

Steps in the logic model	Intensity/ degree	Geographical extent	Permanence or duration	Severity (H,M,L)	Probability (H,M,L)	Uncertainty (H,M, or L)	Stage of assessment
1. Mussel farming will extend	H	M	H	H	H	N	Release
2. Estimation of filtration indicates that shellfish pump an important volume of water	H	M	H	M	M	L	Release
3. Calculation of food depletion indicator shows that food concentration is decreased by shellfish filtration	L	M	M	M	H	L	Exposure
4. Growth is limited by environmental conditions in the new farm	M	M	H	H	H	L	Exposure
5. Food depletion affects individual growth within the farm	M	M	H	H	L	M	Effect
6. Growth is limited by environmental conditions in areas distant from the new farm	M	M	H	H	H	L	Exposure
7. New production will affect other areas	L	L	L	L	L	M	Effect
8. Change of productivity	L	L	L	L	L	M	Effect

Probability = H – High, M – moderate, L – Low, N – Negligible

Severity = H – high, M – Moderate, L – Low, N – Negligible

Uncertainty = H- Highly uncertain, M – Moderately uncertain, L – Low uncertain, N- Negligible.

particles is likely to occur when current velocity is low, and organic matter would be expected to accumulate on the sediment beneath the cultivation unit. In the field, significant increases in organic matter content and nutrient enrichment have been observed around oyster tables (Sornin *et al.* 1990), oyster reefs (Dame and Prins 1998), mussel beds (Prins *et al.* 1998) and clam beds (Bartoli *et al.* 2001). For instance, in Saldanha Bay (South Africa), biodeposition rates in raft culture were reported by Stenton-Dozey *et al.* (1999). Deposition beneath rafts was attributed to high production of about 105 tonnes wet wt biomass raft⁻¹ yr⁻¹, including mussels and associated fouling organisms. The sedimentation rate within the farm was around 300 kg organic carbon m⁻² yr⁻¹ and 45 kg nitrogen m⁻² yr⁻¹. Chamberlain *et al.* (2006) also estimated biodeposition fluxes due to cultivated mussels in a lagoon in the Saint Laurence estuary (Canada). The maximum biodeposit production recorded was 125.6 mg d⁻¹ ind⁻¹. They extrapolated this measurement to estimate the biodeposition rate from a mussel line as 26.4 kg line⁻¹ d⁻¹ (365.8 m length; stocking density 575 mussels m⁻¹). The accumulation of this organic matter on the sediment would increase the oxygen demand of the bottom sediments. In some cases, an effect on the environment has been documented and motivated further studies in order to predict when and where these effects would be likely to occur (Chapelle *et al.* 2000). It has been noted that the effect can be exacerbated by environmental factors such as high temperature and slow current speeds, which also increase oxygen demand and depletion in bottom waters. As a consequence, anoxia in the

sediment might propagate into the water column and lead to anoxia in the water surrounding cultivated shellfish, with strong adverse consequences for the stock. In a very recent work, Bouchet (2007) showed some effect of oyster culture on sediment quality and macrobenthos communities in Marennes-Oléron Bay due to biodeposition, through processes of recycling of organic matter leading to enhancement of microphytobenthos production, subsequent temporary anoxia and consequential modification of macrobenthos abundance and diversity. The ecological quality was estimated using the AMBI tool which confirmed that the status of the site was medium.

There is no generally applicable statement of the likely effects of shellfish aquaculture on the environment and on the ecosystem carrying capacity. This is mostly due to the recycling capacity of marine ecosystem linked with the fact that shellfish cultivation is always a net sink of nutrients, in contrast to fish aquaculture. Besides, many findings associated with very high densities of shellfish in bottom culture, or at sites with low current velocity (< 20 cms⁻¹) would not apply to suspended culture in places like Pertuis Breton where the intense water mixing will disperse biodeposition and decrease the intensity of the aquaculture footprint on the sediment at the farm site. As a consequence, our example of Risk Assessment is limited to simple cases where our assumptions based on the predominance of food transport and limitation of shellfish growth and production by phytoplankton are valid. More sophisticated tools capable to assess the interactions between all or some

Table 6.2.II : List of mitigation and research or development steps that could be done to improve the risk assessment linked to the identification of new sites for shellfish aquaculture.

Steps in the logic model	Probability (H,M,L)	Mitigation (regulate/design/modified practices)	Uncertainty (H,M, or L)	Research/Development
1. Mussel farming will extend	H	<ul style="list-style-type: none"> Map existing cultivated areas and assess standing stock and productivity Move new sites offshore Replace existing sites Define management options and indicators of sustainability 	N	<ul style="list-style-type: none"> Define acceptable practices of management for a sustainable development of aquaculture, including economic analysis and multi-agents agreement Improve integrated management of the coastal area, including freshwater and land use
2. Estimation of filtration indicates that shellfish pump an important volume of water	M	<ul style="list-style-type: none"> Monitor environmental parameters 	L	<ul style="list-style-type: none"> Measure primary production and develop numerical model coupling hydrodynamics, nutrient input, sediment resuspension and primary production
3. Calculation of food depletion indicator shows that food concentration is decreased by shellfish filtration	H	<ul style="list-style-type: none"> Simulate and map current velocity Compute water residence time and depletion due to filtration 	L	<ul style="list-style-type: none"> Map phytoplankton and turbidity with field surveys and/or satellite images Retrieve bathymetry data and boundary conditions to implement a hydrodynamical model Estimate the change of hydrodynamics due to long-lines
4. Growth is limited by environmental conditions in the new farm	H	<ul style="list-style-type: none"> Assess and monitor the mussel scope for growth 	L	<ul style="list-style-type: none"> Develop and test ecophysiological model to predict scope for growth as a function of food availability
5. Food depletion affects individual growth within the farm	L	<ul style="list-style-type: none"> Compute and estimate residence time of particles over the area in order to assess interactions between cultivated areas 	M	<ul style="list-style-type: none"> Retrieve bathymetry data and boundary conditions to implement a hydrodynamical model coupled to simple ecophysiological models
6. Growth is limited by environmental conditions in areas distant from the new farm	H	<ul style="list-style-type: none"> Compute and estimate residence time of particles over the area in order to assess interactions between cultivated areas as a function of the distance between the farms 	L	<ul style="list-style-type: none"> Test and validate hydrodynamical model, residence time calculation and particles trajectories
7. New production will affect other areas	L	<ul style="list-style-type: none"> Compute and estimate residence time of particles over the area in order to assess interactions between cultivated areas 	M	<ul style="list-style-type: none"> Retrieve bathymetry data and boundary conditions to implement a hydrodynamical model coupled to simple ecophysiological and primary production models

of the ecosystem components will have to be applied (Chapelle *et al.* 2000; Pastres *et al.* 2001; Gibbs 2004). The effect of larger scale effects due to other coastal activities and environmental change will also have to be taken into account (Marinov *et al.* 2007) and therefore this risk assessment methodology combined with Integrated Coastal Zone Management, mapping and modelling tools will be a great help for decision makers.

6.2.6 Literature cited

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Annex. Box model

The box model couples food transport, food consumption by the mussel population and mussel growth at the scale of a cultivated area. The concept is the same as used by Bacher *et al.* (2003), except that food and particulate matter concentrations are assumed to be homogeneous within the cultivated area, which is represented as a single box. The transport equation is a mass balance equation accounting for i) the exchange of water between the box and the external part of the cultivated area (Bacher, 1989; Raillard *et al.* 1994 ; Dowd 1997), ii) sinks of particles due to consumption by filter feeders:

$$\frac{dC}{dt} = \frac{Q}{V} (C_e - C) - \frac{N}{V} \cdot f(C, w) \quad (1)$$

where C refers to either phytoplankton, organic or inorganic particulate matter within the box, C_e is the outside concentration, Q the exchange flow ($m^3 s^{-1}$), $f(C, w)$ the individual food consumption, N the total number of mussels, w the mussel tissue dry weight (DW).

Food consumption was calculated using the ingestion rate of mussels rather than the filtration (see ecophysiological model below) since an important fraction of the filtered particles is assumed to remain in the water column as pseudofeces and would be reused by mussels with the same efficiency.

Equation (1) was coupled to the following mussel growth equation:

$$\frac{dw(x, t)}{dt} = g(C, w, T) \quad (2)$$

where T is the water temperature and $g(C, w, T)$ is the growth rate established from the ecophysiological model of Grant and Bacher (1998). Briefly, the model provides two food sources, phytoplankton and detrital POC, where detrital POC = total POC - chlorophyll carbon. Clearance rate ($l h^{-1}$) of particles is a declining function of TPM. Phytoplankton and POC are both cleared at the same rate, and the proportion of the ingested mass that is rejected as pseudo-faeces is related to turbidity using a step function : no rejection at 0–5 $mg l^{-1}$, 20% rejection at the pseudo-faeces threshold up to 10 $mg l^{-1}$, 40% rejection from 10–40 $mg l^{-1}$, and peak rejection (85% of ingesta) above 40 $mg l^{-1}$. Phytoplankton is selected preferentially to detritus. In terms of ingestion, phytoplankton and POC are maintained as separate quantities, each with a defined absorption efficiency (AE), and absorption rates are summed to calculate total absorption. The phytoplankton AE is assumed to be 80% and AE for detrital POC is set at 40%. In contrast to other models using gut capacity and gut passage time to limit ingestion (Scholten and Smaal 1998), daily ingestion can not be higher than a constant value defined as the maximum daily ingestion. The net energy balance is determined as the difference between the rates of assimilation and respiration, and the balance is allocated between somatic tissue and shell. The model predicts changes in both dry tissue weight and shell weight. The respiration equation was modified from Grant and Bacher (1998) to allow a

better fit with observations. The model was also applied to the 'bouchot' dataset for validation and, as a further check, ecophysiological functions were compared to measured values.

Long lines cover an area of 2.5 km^2 . They are arranged in 20 blocks of 12 long lines each. 85 ropes of 6 m length hang on each long-line and the whole area contains about 240 10^6 mussels. We assumed that mussels were homogeneously spread within the box and that trophic conditions were uniform. Boundary conditions were defined for TPM, POM, and phytoplankton concentrations from the field survey. Temperature time-series were used as a forcing function.

The current velocity field was modeled using a hydrodynamical model developed by Brenon and Le Hir (1999) applied to Marennes-Oléron Bay. This model solves Navier-Stokes equations with a finite difference method using a rectangular grid (Struski 2005) and predicts water height and current velocity. Water height and tidal currents were simulated for one month to cover a full spring-neap tidal cycle. To check the validity of the model, we compared the simulated water height in La Pallice harbour to available observations of water height and we found good agreement. Maximum current velocity was mapped from this single simulation and showed that long lines were located in a region of intensive water exchange, with maximum current velocity over 1 $m.s^{-1}$. Current velocity generally depends on tidal coefficient, and the maximum tidal currents varied between 0.5 and 1 $m.s^{-1}$. In the long line area, the current direction lies along a northwest/southeast axis and intensive exchange of water occurs at Pertuis Breton straight.

Particle trajectories were computed for one tidal cycle at spring tides using the current velocity field from the hydrodynamic model. Particles coming from the inner part of the bay (Aiguillon bay) exit through Pertuis Breton straight in the west or through La Pallice straight in the south. Trajectories also show that the tidal excursion is almost 10 km, which supports the concept of strong water mixing in the inner part of the bay.

Current velocities and water height were used to compute water exchange between the long line area (box) and the outer part of the bay. Average water flow entering and leaving the cultivated area was calculated with the following equation:

$$Q_T = \sum_t \left\{ \sum_{x,y} h(x, y, t) \cdot |U(x, y, t) \cdot N(x, y)| \cdot L \right\} / n$$

Where $U(x, y, t)$ is the current velocity vector at the grid node (x, y) located at the box boundary, $N(x, y)$ is the vector normal to the lease boundary, $h(x, y, t)$ is the water height, L is the mesh size used in the hydrodynamics model (500 m), n is the number of time steps used for the computation. Due to mass conservation, half of total flow enters the cultivated area and the exchange flow was therefore given by:

$$Q = Q_T / 2$$

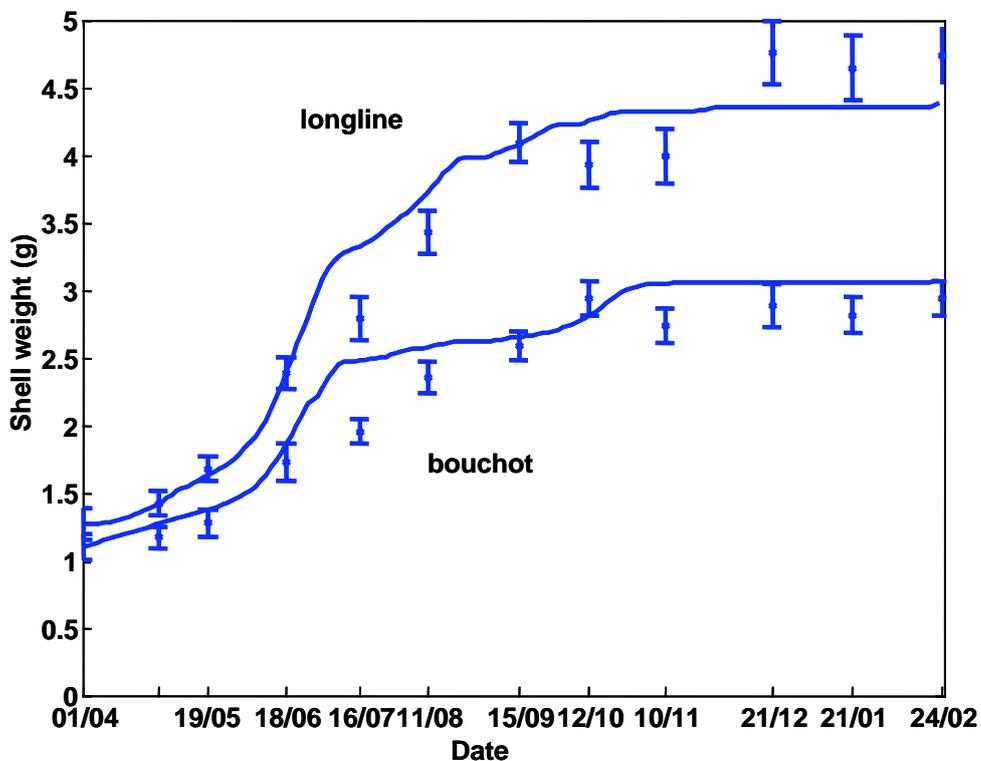
Box volume was equal to :

$$V = \sum_t \left\{ \sum_{x,y} h(x,y,t) \cdot L^2 \right\} / n$$

Where $h(x,y,t)$ is the water height of the grid node (x,y) located inside the box. Exchange flow was equal to $5.2 \cdot 10^3 \text{ m}^3\text{s}^{-1}$ and volume to $2.37 \cdot 10^7 \text{ m}^3$ which yielded a renewal time of 0.05 days.

Simulated and observed mussel growth is shown in the following figure and illustrates the ability of the model to accurately reproduce the growth patterns at two different sites.

Comparison of simulated and observed shell weight of mussels reared on long-lines and bouchot



Equations, parameters and variables used in the ecophysiological model of mussel growth.

Equations	Description
State variables TPM POM CHL DW SW	Total Particulate Matter (mg l ⁻¹) Particulate Organic Matter (mg l ⁻¹) Chlorophyll a mussel Tissue Dry Weight (g) mussel Shell Weight (g)
Forcing functions TEMP	Temperature (°C)
Parameters chl2c=50 pom2c=0.38 CPHY=CHL·chl2c/1000 CDET=POM·pom2c·CPHY	conversion from Chlorophyll a to Carbon (gC gChl ⁻¹) conversion from POM to Carbon (gC gDW ⁻¹) Carbon phytoplankton (mgC l ⁻¹) Carbon detritus (mgC l ⁻¹)
Clearance rate cr1=1.8 cr2=8.6 10 ⁻³ cr3=0.67 if TEMP < 5 frtemp=e ^{((TEMP-5)·0.07)} elseif TEMP >5 & TEMP < 20 frtemp= 1 else frtemp=e ^{((20-TEMP)·0.07)} end CR=CR= (cr1 – cr2·TPM) ·(DW/0.7) ^{cr3} ·24·frtemp	frtemp=temperature effect clearance rate (l d ⁻¹ ind ⁻¹)
Filtration rate FR=CR·TPM if TPM < 5 rej=0 elseif TPM >5 & TPM < 10 rej=0.2 elseif TPM >10 & TPM < 40 rej=0.4 elseif TPM>40 rej=0.7 end	TPM filtration rate (mg d ⁻¹ ind ⁻¹) rej = rejection rate (no unit)
Ingestion rate IR=FR·(1-rej) ir1=600 ir2=0.40 IRmax=ir1·DW ^{ir2} IRTPM=min(IR,Irmax) fq=0.8 IRPHY=IRTPM·CPHYT/TPM/fq IRDET=IRTPM·CDET/TPM	TPM ingestion rate (mg d ⁻¹ ind ⁻¹) TPM maximum ingestion rate (mg d ⁻¹ ind ⁻¹) TPM ingestion rate (mg d ⁻¹ ind ⁻¹) phytoplankton enrichment factor PHYTO ingestion rate (mgC d ⁻¹ ind ⁻¹) DETRITUS ingestion rate (mgC d ⁻¹ ind ⁻¹)
Absorption rate ARPHY=IRPHY·0.8 ARDET=ARDET·0.4 AR=ARPHY+ARDET	PHYTO absorption rate (mgC d ⁻¹ ind ⁻¹) DETRITUS absorption rate (mgC d ⁻¹ ind ⁻¹) total absorption rate
Respiration rate r1= 6.55 r2= 0.454 r3=0.75 RER=(r1+r2·AR)·DW ^{r1}	calibrated calibrated respiration rate (mgC d ⁻¹ gDW ⁻¹)
Carbon budget and growth Budget=AR-RER alloc=0.58 w2c=0.4 s2c=0.08 if Budget>0 dDW=Budget·alloc/w2c/1000 dSW=Budget·(1-alloc)/s2c/1000 else dDW=Budget/w2c/1000 dSW=0 end	Carbon budget (mgC d ⁻¹ gDW ⁻¹) tissue allocation rate - calibrated conversion from DW to Carbon (gC gDW ⁻¹) conversion from SW to Carbon (gC gSW ⁻¹) dDW = dry weight variation (g) dSW = shell weight variation (g)
Integration dt=1 DW=DW+dDW·dt SW=SW+dSW·dt	time step (d) dry weight (g) shell weight (g)