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Modelling of *Gymnodinium mikimotoï* blooms along the French Atlantic coast: geographical and vertical distributions

Modélisation des blooms de Gymnodinium mikimotoï *le long de la façade atlantique française : répartition spatiale*

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Abstract. – In order to study the occurrence of *Gymnodinium mikimotoï* bloom on the French Atlantic coast, a three-dimensional model of primary production was set up. The biological model was coupled to a hydrodynamic model previously developed at Ifremer, by the intermediary of transport, diffusion and heat fluxes. The cycles of three limiting elements for the phytoplankton growth were modelised: nitrogen, phosphorus and silicon. The second phase of the study aimed at reproducing the summer dinoflagellate blooms. In this new approach a model of the species *Gymnodinium mikimotoï* was coupled with the previous biomass model which provides the physical and chemical environments. The study focuses on the results obtained by this specific sub-model. The parametrisation was based on some physiological studies reported from laboratory cultures and on parameters existing in the literature. Consistent with the observations, the model reproduces the sub-surface cell concentrations, in the zone of minimal turbulence. The formulation retained for the temperature effect on the growth rate leads to a strong influence of temperature on the onset of the bloom and the mortality rate controls the vertical distribution. Nevertheless, as formulated here, the model underestimates the cell density.

Key words. – Turbulence, Dinoflagellate, *Gymnodinium mikimotoï*, model, nutrients

Résumé. – Afin d'étudier les processus de formation des blooms estivaux du dinoflagellé *Gymnodinium mikimotoï*, un modèle de la production primaire sur le plateau continental atlantique français a été développé. Un modèle biologique a été couplé au modèle physique tridimensionnel développé à l'Ifremer, par l'intermédiaire du transport, de la diffusion et des flux de chaleur. Le modèle biologique décrit les cycles de l'azote, du phosphore et du silicium au travers du réseau trophique. Un modèle spécifique de l'espèce *Gymnodinium mikimotoï* a ensuite été introduit. La nouveauté dans cette approche consiste à introduire un modèle de dynamique simple, pour une espèce phytoplanctonique particulière, dans un modèle tridimensionnel physico-biologique de biomasse globale. L'étude présentée ici montre les résultats issus de ce sous modèle. La paramétrisation spécifique à cette espèce est fondée sur une étude bibliographique et sur des expériences en laboratoire. Une des originalités de l'étude réside dans la formulation du taux de mortalité en fonction de la turbulence et de la densité cellulaire. La distribution verticale en subsurface des concentrations en *Gymnodinium mikimotoï* est assez bien reproduite et l'étude est prometteuse. Les maximums de densité cellulaire simulés pour *Gymnodinium mikimotoï* se situent en sub-surface, au niveau de la pycnocline, correspondant à la zone de turbulence minimale. La comparaison avec les mesures de terrain montre que le modèle reproduit correctement la distribution spatiale de cette espèce le long des côtes; néanmoins, il sous-estime les niveaux de concentrations maximales observés. Le choix retenu pour représenter le rôle de la température sur le taux de croissance conduit à un effet prépondérant sur le déclenchement du bloom. Le taux de mortalité contrôle par la suite la distribution verticale.

Mots clés. – Turbulence, Dinoflagellés, *Gymnodinium mikimotoï*, modèle, nutriments

1 INTRODUCTION

There is an increasing concern in the scientific literature about the impacts of harmful algal blooms (Bates *et al.*, 1998; Hallegraeff et Fraga, 1998; Lancelot *et al.*, 1998; Maestrini *et al.*, 1998; Smayda, 1998). Toxins produced during such seasonal dinoflagellate blooms can kill fauna and may induce human toxic effects. Dinoflagellate is not the only group of species associated with toxic blooms, since species like *Heterosigma akashiwo* (Raphidophyceae), identified in the English Channel and along Atlantic coast, are ichtyotoxic (Nézan, 1995). About two percents of the world's species of phytoplankton are potentially toxic (Sournia, 1995). A worldwide increase in toxic phytoplankton blooms has been observed during the last decades, but, beyond changes in the environmental conditions, it may also be due to increasing awareness.

In this study we focus on a particular species, *Gymnodinium mikimotoï*, whose toxin affects the marine fauna and which frequently occurs along the French Atlantic coast since 1978 (Erard *et al.*, 1990; Arzul *et al.*, 1994; Fossat *et al.*, 1999; Sola *et al.*, 1999). *Gymnodinium mikimotoï* is the name used in this paper for this species, which has known five names. Since

July 2000, *Karenia mikimotoï* is the new denomination (Daugbjerg *et al.*, 2000) but previously, it was named *Gyrodinium aureolum*.

Such blooms require the interaction of favourable conditions; many factors like temperature, salinity, light intensity, nutrient availability and tidal and wind stresses, which have an impact on the water column stability, appear to play a role in the *Gymnodinium mikimotoï* bloom (Holligan *et al.*, 1984; Honjo *et al.*, 1991; Nielsen, 1991; Gentien, 1998). Nevertheless, the relative importance of each process is not yet fully known. Gentien (1998) has registered three cases leading to *Gymnodinium mikimotoï* bloom: (1) in semi-confined water bodies, and in the stratified regions of (2) tidal fronts and (3) river plumes. All those previously reported findings emphasise the major role of water column stability. In stratification conditions, high concentrations of this species are usually found in the pycnocline. Concerning nutrient concentrations, their importance in the occurrence of *Gymnodinium mikimotoï* bloom vary according to the authors. Some of them suspect a major role of the nutrient enrichment and associate outbreaks with man-made nutrients flushed down rivers; while others attach to them a lower interest (Le Fèvre *et al.*, 1986; Le Corre *et al.*, 1992). But the majority seems to agree the importance of regeneration for *Gymnodinium mikimotoï* development. Le Corre et L'Helguen (1993) and Yamaguchi (1994) show that *Gymnodinium* bloom in frontal region can be maintained almost exclusively by in situ remineralization of previous blooms.

In order to understand the mechanisms leading to the initiation and distribution of bloom, a simple dynamic model has been developed. The novel approach consists in inserting a specific *Gymnodinium mikimotoï* model in a biomass model, which provides the physical and chemical characteristics of the environment.

The objective of this model is to contribute to answer to the following question: "How do combinations of meteorological, hydrodynamical and human forcings, influence the formation and the distribution of those blooms ?"

The biomass model is a 3D physical model (Lazure et Jegou, 1998) coupled to a biological model. This model reproduces the seasonal variations of phytoplankton biomass and provides the main environmental features in terms of hydrodynamical and chemical conditions.

The biology of *Gymnodinium mikimotoï* is complex and only the most basic processes required to formulate a population model have been retained. We include a theoretical approach of mortality process associated to the turbulence field.

2 METHOD

2.1 The hydrodynamical context

The 3D-hydrodynamical French Atlantic model has been developed at

IFREMER during the last decade (Lazure et Jegou, 1998). The simulation domain extends from the coast to approximately the 200 m isobath in the west and from the English Channel entrance in the North (49 N) to the Gulf of Cap Breton in the South (44' N). The three main rivers are taken into account: the Loire, the Vilaine and the Gironde. The model uses a traditional rectangular Cartesian grid with an homogeneous square mesh size (25 km^2). Ten vertical layers are used with sigma coordinates whose grid step progressively increases with depth. The numerical scheme uses a 3D finite difference scheme. Vertical eddy viscosity and diffusivity are calculated by the resolution of the turbulent kinetic energy equation and the use of an algebraic formula for the mixing length. The temperature and salinity distributions of the French Atlantic shelf are simulated by solving the conservation equation taking into heat fluxes budget and the surface and fresh water inputs.

The biological dynamic is implemented into this three-dimensional frame, where all state variables are transported by advection and diffusion. The physical and biological model are connected through the diffusion coefficient, the transport, the temperature and heat fluxes (through the effects of temperature on the biological processes and on the light availability for the algal growth) (Loyer, 2001).

2.2 The biological context

The biological scheme is a simplified version representation of the pelagic ecosystem (cf. paragraphe 2.3).

The model is conceptualised for a shelf sea including the shallow sea characteristics for the replenishment of the mixed layer with nutrients from the bottom. Three cycles are modelized, the nitrogen, phosphate and silicate cycles. It takes into account three groups of phytoplankton, the diatoms that contribute to the silicon cycle, and two group of non-siliceous phytoplankton represented by dinoflagellates and nanophytoplankton. In the phytoplankton, only the diatoms sink. The integration of a small class of phytoplankton allows not only to illustrate the more oligotrophic system of the oceanic waters, but also a better representation of the ammonium uptake and regeneration after a microphytoplanktonic bloom. Organic matter is regenerated through the zooplankton excretion, and through the remineralization of dead cells and faeces. However, only a small part of these detritus remains suspended in the water column and immediately regenerated, the major part sediments onto the bottom in these shallow waters. The benthic compartment in the model simulates the storage, regeneration and erosion processes. A detritic pool on the bottom has been introduced to store the major fraction of detritus and to allow replenishment

of the water column. Mortality of phytoplankton has two components, grazing by zooplankton (divided into two size-classes) and a natural mortality rate.

The algal spring bloom, subsequent to the annual peak in nutrient runoff, the nutrient seasonal evolution and the spatial pattern in chlorophyll *a* concentrations are properly simulated by the model (Loyer, 2001). The two first figures show the spatial pattern of nitrate and chlorophyll *a* in surface during the spring of the year 1995. Inorganic nitrogen (fig. 1) shows very high concentrations in winter and spring, attesting the coastal water enrichment by the river. The phytoplankton development initiation results mainly from the establishment of the haline stratification and from the adequation between the shallow mixed surface layer rich in nutrients and the decrease of suspended matter concentrations. The model reproduces also the high primary production levels that follow the high spring discharges of the Loire

Fig. 1. – Simulated distribution of surface nitrogen concentrations on May 1995 (µmol/l of nitrogen).
Fig. 1. – Calcul de la répartition des concentrations en nitrate en surface en mai 1995 (µmol/l d'azote).

and Gironde rivers with the highest values found in front of estuaries (fig. 2).

2.3 *Gymnodinium mikimotoï* model insertion

The model is elaborated within the frame of the 3D-model described above (fig. 3).

The initial cell concentration on the 1st January of the year is 500 cell.l^{-1}, and is uniformly distributed through the water column and the whole area of concern. Numerical simulations take into account the main physiological features of this species. The parametrisation is based on some physiological studies reported from laboratory cultures and on parameters reported in the literature.

The mortality rate used in the model is adapted by Gentien (1998) and comes from the kernel collision model of Jackson (1990). Mortality formulation is a function of cell concentration and turbulence that induces collision between cells. Thus, the mortality rate depends on the shear strain γ estimated from the turbulent kinetic energy dissipation rate ε and from the kinematic viscosity ν (fig. 4).

This shear rate decreases with increasing vertical column stability. The parameter α represents the probabil-

Fig. 2. – Simulated distribution of surface chlorophyll concentrations on May 1995 (µg/l).
Fig. 2. – Répartition des concentrations en chlorophylle en surface en mai 1995 (µg/l).

Fig. 3. – Biological nitrogen cycle scheme of *Gymnodinium* model.
Fig. 3. – Schéma du cycle de l'azote dans le modèle biologique.

ity for two cells to die after a collision. Formulation of this "stickiness" parameter is based on an assumption related to the excretion of polysaccharides by this phytoplankton species (Jenkinson et Arzul, 1999). This process, which depends on temperature, is maximal at 20 °C (α=1) and close to zero at 15 °C (α=0,05). Between these two thresholds, α is supposed to follow a linear function.

Fig. 4. – Main hypotheses for the *Gymnodinium* model.
Fig. 4. – Principales hypothèses pour le modèle de *Gymnodinium*.

The growth rate results from the multiplication of three limitation terms for the nutrients, the temperature and the light: $\mu=f(N)*f(T)*f(L)$.

The formulation chosen to describe nutrient uptake is the Michaëlis-Menten equation parametrised by the half saturation constant with an inhibition effect of ammonium on the nitrate consumption. According to Le Corre and L'Helguen (1993), *Gymnodinium mikimotoï* thrives mainly on ammonium. Since *Gymnodinium mikimotoï* requires very low nutrient concentrations for growth, values of half saturation constants chosen are low, K_{NO3}=5,0 mmolN.m^{-3}, K_{NH4}=0,01 mmol.m^{-3} and K_{PO4}=0,05 mmol.m^{-3}. This characteristic allows *Gymnodinium* to be a better competitor than other phytoplankton groups modelled in environments dominated by regeneration processes.

Temperature dependence of growth rate is commonly fitted to the Arrhenius equation. However, from in situ measurements on the Ushant front and in the Bay of Brest have shown that *Gymnodinium mikimotoï* from close locations exhibited large variations in optimum temperature. Thus, a third order polynomial function is used to represent the effect of temperature on growth. At temperature lesser than 13°C, the growth rate is close to zero (Youenou et Gentien, pers. comm.) and the optimum is found between 15 and 18°C (Videau, 1989). This is consistent with literature which reports a wide range of this optimum temperature, highly depending on the strain origin.

The response of production rates to light intensity is based upon batch cultures conducted over a range of irradiance (10-100 $\mu mol.m^{-2}.s^{-1}$). The strain used comes from the Bay of Brest. *Gymnodinium mikimotoï* exhibits an adaptation to very low light intensities. The growth rate increases with light intensity up to an optimum estimated at 70 $\mu mol.m^{-2}.s^{-1}$ (Loyer, 2001). This cultures have permitted to evaluate a mean chla/cell ratio of 100000.

$f(N)=\min(f(1),f(2))$ where

$$f(1)=\frac{NO_3}{NO_3+K_{NO_3}+\frac{K_{NO_3}}{K_{NH_4}}\times NH_4}+\frac{NH_4}{NH_4+K_{NH_4}+\frac{K_{NH_4}}{K_{NO_3}}\times NO_3}$$

$$f(2)=\frac{PO_4}{PO_4+K_{PO_4}}$$

$f(T)=\max(f(T);0,05)$ where $f(T)$ is the third order polynomial function described above.

$$f(L)=\frac{L}{L+K_L}$$

with $K_L = 4,8 \mu mol.m^{-2}.s^{-1}$

3 RESULTS

3.1 Horizontal distribution of maxima

At first, we have tested the model response over the year 1995, when a very intense development of *Gymnodinium mikimotoï* occurred from Arcachon to Northern Brittany with a large impact on cultivated mussel (1000 tons killed).

A simulated cell density of *Gymnodinium mikimotoï* is shown in fig. 5. It corresponds to the water column maximum cell concentrations on July 9th 1995. The *Gymnodinium mikimotoï* development is dominant along the south Brittany coast, above the Rochebonne shoal and along the Landes coast (south from Gironde estuary). Simulated blooms in the southern part of the model must be considered with caution, due to the vicinity of the offshore boundary and to lack of particular information about an eventual slope current in this area. The elevated values of cell density observed along these coasts may be explained by a higher availability of ammonium coming from sediment nutrient regeneration. Specific growth rate depends on a combination between low turbulence conditions (at the pycnocline level) and on the nutricline position, so that synchronicity of this two processes enhances the survival rate.

The figure 6 is a national synthetic map on *Gymnodinium mikimotoï* measures made in 1995 by the French REPHY surveillance network; it represents the annual maximum observed on each monitoring sites. The absence of *Gymnodinium* event in the southern part is due to the lack of monitoring point (the only point existing south of the Gironde estuary is located in the Arcachon basin). At the model scale (mesh size of 25 km^2),

Fig. 5. – Simulated spatial distribution of water column maximum cell concentrations (cell.l^{-1}) of *Gymnodinium* on the 12th july 1995.
Fig. 5. – Calcul de la distribution spatiale des maximums des concentrations cellulaires (cell.l^{-1}) dans la colonne d'eau, le 12 juillet 1995.

the bay of Brest and site Poitou-Charente (Pertuis Breton, Pertuis d'Antioche) are not well represented and the model does not reproduce the large concentrations observed. Nevertheless, comparison of coastal field measurements (fig. 6) with model results (fig. 5) shows that spatial distribution of cell concentrations is fairly well represented along the coast; in particular, two patches located in front of the Vilaine and Loire estuaries are identified by the model, but too much offshore. Data obtained by the REPHY do not permit to assess the model accuracy beyond the isobath 50 m, because this database is carried out close to the coast

Fig. 6. – Maximum concentration of *Gymnodinium* for each in situ observation spots during the year 1995. Measures obtained from the French network of phytoplanktonic surveillance (REPHY) ; Belin et Raffin, 1998.
Fig. 6. – Concentrations maximales par site de *Gymnodinium* en 1995. Données observées par le réseau de surveillance du phytoplancton (REPHY) ; Belin et Raffin, 1998.

(in basin, bay, port,...). The lesser concentrations observed in Mediterranean sea could be related to weak inoculation concentrations and by a substitution of other species; the species communities are not the same in Mediterranean sea and along the Atlantic coast.

The presence of dinoflagellate in offshore waters has been observed during a cruise conducted in June 1999, on stations 11, 12, 36, 37, 38, 40, 51 (fig. 7) and the taxonomic description has permitted to identify a species belonging to the *Gymnodinium* genus. These stations corresponded to high *Gymnodinium* cell concentrations in the simulation; thus, the model results appear to be in adequation with observations. In these offshore regions, such maxima are found for every year tested by the model.

The simulation indicates that a *Gymnodinium* bloom may take about one month or so to develop from an initial condition of 500 cell.l^{-1} (fig. 8). At the end of summer, the temperature decreases and the water column mixing leads to an increased mortality. The simulation shows that, in addition to low turbulence and nutrient concentrations, the temperature effect on growth also plays a critical role in determining the bloom development.

3.2 Vertical profiles

Figure 9 shows the simulated cell concentrations, ammonium concentrations, density and shear constraint as a function of depth for two stations in front of the Loire and the Vilaine estuaries. We focus on the depth of maximal cell concentration (short line), which we compare to nutrient and density distributions. Maximum cell density is located at the base of the pycnocline at which the lowest turbulent zone can be observed and at the nutricline level.

Thus, the formulation used to simulate the *Gymnodinium* development allows to reproduce the subsurface concentrations without indulging into a formulation of migration processes. The vertical migration of this species may be an important ecological feature if we suppose that the phototropism could be a driving force

Station	Cell concentration in cell.l^{-1} (*Gymnodinium* sp.)
11	1265000
12	467000
36	67000
37	525600
40	40000
51	130000

Fig. 7. – Stations sampled in June 1999 during the cruise Bio-Modycot 99-2.
Fig. 7. – Stations échantillonnées en juin 1999 lors de la campagnes Bio-Modycot 99-2.

Fig. 8. – Simulated temporal evolution of cell concentrations (cell.l^{-1}) over the year 1995 in front of :
a - the Loire estuary (grey round in fig. 9)
b - the Vilaine estuary (white round).

Fig. 8. – Calcul de l'évolution temporelle des concentrations cellulaires (cell.l^{-1}) en 1995 devant :
a - l'estuaire de la Loire (rond gris fig. 9)
b - l'estuaire de la Vilaine (rond blanc).

Fig. 9. – Simulated vertical distributions of :
a - cell concentrations
b - density
c - shear strain
d - ammonium concentrations
in front of the Loire estuary (in grey) and Vilaine estuary (fine line). The horizontal bars correspond to the location of cell concentration maxima.
Fig. 9. – Calcul de la répartition verticale :
a - des concentrations cellulaires
b - de la densité
c - du taux de contrainte de cisaillement
d - des concentrations en ammonium
devant l'estuaire de la Loire (trait épais) et devant l'estuaire de la Vilaine (trait fin). Les barres horizontales localisent le maximum des concentrations cellulaires sur la verticale.

of population movement toward the water masses with the best growth conditions. Nevertheless, here, we hypothesise that other processes can be involved in the observation of subsurface concentrations. And this

model shows that persistence of population in the pycnocline could result from higher survival rates in some low turbulent energy layers.

4 DISCUSSION

The model reproduces the regular onset of growth when temperatures move from a winter low to a summer high. Outbreak occurs after a period of water column stability. Inversely, cell densities diminish during autumn with the temperature and the vertical column stability decreases. The growth rate is enhanced by a good interaction between low turbulence and adequate nutrient availability in front of the Loire and Vilaine estuary. The model can not reproduce the high inshore concentrations. This discrepancy may be due to a too strong mortality induced by an overestimation of the shear constraint. The vertical scheme with ten layers is also one of the model limits. In the same way, the change of sea water properties for layers lower than those described by the model is not taken into account and the validity of the model evaluation of turbulence can be questioned.

The *Gymnodinium mikimotoï* patch south of the Gironde estuary corresponds to local upwelling or to strong mixing induced by the interaction of tidal currents and isles (north of the Gironde estuary) or shoal (Rochebonne) which induce a nutrient release favorable for the *Gymnodinium* growth. Light intensity effect on the growth rate is constant because *Gymnodinium mikimotoï* readily adapts to a large range of light conditions. It allows it to take advantage of the low light intensity of the pycnocline conditions, as well as near the surface in strong light. The mortality rate, which is proportional to the squared cell density, induces severe falls observed on figure 8.

Numerous factors, light adaptability, no grazing pressure and high sensitivity to low nutrient concentrations, confer a selective advantage to *Gymnodinium mikimotoï*, compared to other simulated groups. For this species, the physical forcing (vertical mixing and temperature distribution) is a primary controller of the planktonic distribution at the spatial and temporal scales. We must be careful to point out that this study is based on data related to a species found in the Bay of Brest. We have reported that species adjust their optimum temperature according to the strain origin. The model, which is a simplified version of the reality, could overestimate the temperature effect on growth. Various workers consider that, qualitatively, it is not the temperatures but their variations which play an important role over the onset of a bloom. Moreover, the model generally underestimates the maximum cell concentrations. This discrepancy may be caused by an underestimation of the growth rate, which does not take into account the probable adaptation of species to the area they live in (coastal or offshore). More, the model does not take into account the two sub-populations of *Gymnodinium*

Fig. 10 – Distribution of chlorophyll *a* concentrations in µg.l^{-1} at station E1 (22 nautical mile south west of Plymouth) for the months March-October. Measurements made during 1975 and 1976 are combined to show temporal and vertical variation for the period March to October, from Holligan and Harbour, 1977.

Fig. 10. – Distribution de la chlorophylle a en µg.l^{-1} à la station E1 en Manche occidentale (22 milles nautiques au large de Plymouth) entre mars et octobre 1975, d'après Holligan and Harbour, 1977.

which may sometimes coexist in culture and in the field forms (Gentien, 1998). This differentiation of sub-populations into two sizes has been observed during the batch cultures performed during this study. The two sub-populations can be distinguished in terms of cell volume and chlorophyll content. If the parameters inducing this differentiation are not yet well defined, this two kinds of cell seem to have different growth rates and different adaptations to the nutrient conditions (Gentien, 1998).

Figure 10 shows the distribution of chlorophyll *a* in the western English

Channel (Holligan and Harbour, 1977); from spring to summer, *Gyrodinium mikimotoï* replaces the diatom population and chlorophyll a becomes concentrated at the subsurface.

The figure 11 shows the simulated cell concentrations as a function of time and depth, in the vicinity of well-known "Ushant front" (see location on fig. 5). The pattern in this figure may be compared with the data of Holligan and Harbour. The maximum cell concentration occurs around end of July and cell densities diminish at the end of August as with the *in situ* data. During the winter period, the cell concentration is fairly weak and uniform from the surface through the bottom. Our model reproduces the gross features of this conceptual model.

5 CONCLUSION

Since this species has been shown to be highly dependent of hydrodynamical conditions and to rely on ammonium concentrations, it has been necessary to include this species model into a standard phytoplankton biomass model, embedded into a 3D hydrodynamical model. Thus, the 3D-pelagic model provides a rather satisfactory estimation of the circulation and turbulence at large scale relatively to the horizontal and vertical dimensions, and an estimation of the main fluxes of matter in the ecosystem.

Numerous factors regulate the magnitude and the seasonal pattern of the blooms. In this model, high temperature, minimum of turbulence and

Fig. 11. – Simulated vertical cell concentrations (cell.l^{-1}) for the period March to December 1995 in the Ushant front system.

Fig. 11. – Calcul de la distribution des concentrations cellulaires (cell.l^{-1}) simulées en *Gymnodinium* dans le système frontal d'Ouessant de mars à décembre 1995.

maximum benthic nutrient regeneration provide the best conditions for the *Gymnodinium mikimotoï* development to occur during summer.

The results suggest that this model is able to reproduce the subsurface cell concentrations of *Gymnodinium mikimotoï.* This distribution is mainly controlled by turbulence and the high capacity of *Gymnodinium mikimotoï* to develop in nutrient regeneration environments. It presents encouraging results. At present, remineralisation rate has been fitted to reproduce at best in situ nutrient concentrations measured in summer. This work will gain a substantial improvement with a better representation of the benthic compartment and with a more refined laboratory study of the coefficient *vs.* temperature.

This model allows to stress the important role of physical processes in determining the vertical cell distribution (higher survival rates in low turbulent energy layers), with a minimum number of parameters (7). Another model on the same species has been developed in Japan (Liu *et al.* 2001) which requires more than 30 parametrizations, including vertical migration whose formulation is not accessible yet to experimentation.

This "species-of-interest" model reproduces the features of the annual cycle as summarized by Holligan and Harbour (1977). It is the first description of a quantitative relation between bloom occurrences of this species and periods of calm weather. This relation between climate and blooms has long been seeked. Due to the highly non linear character of this relationship, modelling was the only tool by which this interaction could be approached.

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