



## Impact of periodic nutrient input rate on trophic chain properties

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### ABSTRACT

Marine ecosystems are characterized by a strong influence of hydrodynamics on biological processes. The associated models involve the coupling of physical to biological models and therefore require a large number of state variables. The consequent high complexity limits our capacity to perform a complete and detailed study and even prevents any complete mathematical study of these models. It is also difficult to disentangle among all the processes involved, which ones actually drive the system at any moment. Hydrodynamics, among other consequences, affect the way under which the nutrients are supplied to marine ecosystems. The variability of nutrient input rate in marine systems generally results from runs-off in coastal systems and from physical processes (wind forcing and hydrodynamics) in open ocean. This paper is devoted to the study of the effects of the nutrient input rate variability on the dynamics and the functioning of trophic chains. In this context, we aim to provide an understandable study, based on simplified system models. We consider a periodic nutrient input rate and analyze how this variability modifies some system properties: its dynamics, its functioning and its structure. The dynamics is obtained by numerical simulations and when possible, enlighten by already published mathematical results. The functioning is measured by the time averaged state variables during the simulation period, and their variability. The structure concerns the number of surviving populations, a proxy of specific biodiversity. We show how these properties can be affected and provide some conditions under which the modifications can occur. We also highlight that, even if the physical process is the main driving force in the global dynamics, the choice of the biological model is important to understand the biological response of the system to physical forcing.

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### 1. Introduction

A recurrent question in marine systems concerns the relative role of physics and biotic interactions on the structure of communities. Of course, hydrodynamics is a forcing factor having a strong influence on the spatial distribution of plankton and nutrients. This influence can even have very subtle effects, see d'Ovidio et al. (2010) for instance. However, recent studies have demonstrated that biotic interactions also play a crucial role in the formation of spatial patterns, e.g. Hilker et al. (2006), Malchow et al. (2005) or Malchow et al. (2008) and references therein. What is indeed determinant in the coupling between physical and biological processes is the spatio-temporal scale, and when scales match, both types of processes interact and contribute to the formation of patterns. For instance, it is well known that hydrodynamic structures such as turbulent eddies drive the spatial distribution of phytoplankton species at various scales (Seuront et al., 1999). Physical processes can also have direct and

indirect consequences on the higher trophic levels (Seuront and Lagadeuc, 2001).

Because of the different scales involved, the response of individuals to environmental constraints has to be taken into account. This has led to the use of individuals-based models in marine ecosystem studies (Travers et al., 2010; Travers and Shin, 2010 for instance). On the one hand, this approach allows to understand both how the individual properties (metabolism, behavior, ...) respond to physical and chemical variability at small scales, and what the effect of this response is at the community and ecosystem scales. On the other hand, this approach leads once again to complex and unwieldy tools. It is thus relevant to ask if it is possible to build models at the population or community level, which take into account individual properties but which do not contain a complete detailed description. This question needs a transition scale approach. Different families of methods have been proposed in the literature in ecology like the moment approach, Chesson et al. (2005), the interacting particle approach, Morale et al. (2005) or aggregation of variables, Iwasa et al. (1987), Iwasa et al. (1989) or Auger et al. (2008). In Morozov et al. (2012), the authors show how these different approaches have been used to get mathematical formulations of a particular process

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(the predation rate) at the community level from local information at the individual level. It is indeed recognized that the choice of the mathematical formulation can play an important role on the dynamical behavior of a mathematical model, Cordoleani et al. (2011), Myerscough et al. (1996), Fussmann and Blasius (2005), Poggiale et al. (2010), and this choice depends of course on the scale that we are interested in, and finally it depends on the question we want to address.

In this article, we focus on phytoplankton–zooplankton–consumer interaction models in varying environment, where the variability takes place at different scales and is assumed to result from various physical processes. We then analyze the effect of this temporal variability on the population dynamics and community properties and discuss the results in the light of the scale of forcing variability. Two types of population models are used: a common Monod–Herbert model which makes a direct link between resource and consumer, and a more mechanistic model based on Dynamics Energy Budget (DEB) theory, Kooijman (2010), which is built on individual properties and is an interesting approach for considering the individual level in ecosystem theory, Sousa et al. (2010). These models are presented in the next section. We also explain how these models will be studied, by means of numerical simulations. A Fourier analysis allows to understand how the periodic input rate interact with the possible internal fluctuations of the food chain. This analysis is done for a large set of possible periods of the input rate. Then we will study the community structure and functioning. Since the systems fluctuate, we consider the mean of the state variables during an appropriate length of time, for a large number of parameter values. We obtain the distributions of the means and compare the constant input rate case to the periodic input rate case for various periods and amplitudes.

## 2. Materials and methods

In this section, we describe two food chain models, involving a prey (phytoplankton), a predator (zooplankton) and a super-predator (zooplankton consumer). The first one is the Monod–Herbert model (MH), it is based on direct links between resource/prey densities and consumer/predator densities. The other one (DEB) is based on the DEB theory, with two state variables for each population, a reserve density and the structural biomass. In the case of a constant input rate, these models have already been studied. The former model has been studied in Boer et al. (1998) for instance, the latter model has been described in Kooi et al. (1997), the authors provide the bifurcation analysis.

### 2.1. Monod–Herbert model (MH)

This MH model involves four state variables, the nutrient concentration  $N(t)$ , the phytoplankton density  $P(t)$ , the zooplankton density  $Z(t)$  and the consumer density  $C(t)$ . The model reads:

$$\frac{dN}{dt} = I(t) - kN - \frac{a_{01}N}{K_{01} + N}P \quad (1a)$$

$$\frac{dP}{dt} = y_{01} \frac{a_{01}N}{K_{01} + N}P - m_1P - \frac{a_{12}P}{K_{12} + P}Z \quad (1b)$$

$$\frac{dZ}{dt} = y_{12} \frac{a_{12}P}{K_{12} + P}Z - m_2Z - \frac{a_{23}Z}{K_{23} + Z}C \quad (1c)$$

$$\frac{dC}{dt} = y_{23} \frac{a_{23}Z}{K_{23} + Z}C - m_3C \quad (1d)$$

where  $I(t)$  is the input rate of nutrient in the system. In a coastal marine ecosystems for instance, this input results from the runoff along the coast or the contribution by rivers. Parameter  $k$  is the nutrient output rate. At each trophic level  $i$ , a consumption function  $G_{ij}(x) = \frac{a_{ij}x}{K_{ij} + x}$  defines the per capita consumption rate of resource  $i$  by a consumer  $j$ , where  $x = S$  for  $i = 0$ ,  $x = P$  for  $i = 1$  and  $x = Z$  for  $i = 2$ .  $y_{ij}$  is the yield coefficient measuring the proportion of resource  $i$  consumed per unit of time and converted in consumer  $j$ .  $m_i$  is the mortality rate of trophic level  $i$ .

### 2.2. DEB model

This model involves seven state variables. Using DEB notations, the state variables are the nutrient concentration  $N(t)$ , the phytoplankton structure  $V_P$ , the phytoplankton reserve density  $e_P$ , the zooplankton structure  $V_Z$ , the zooplankton reserve density  $e_Z$ , the consumer structure  $V_C$  and the consumer reserve density  $e_C$ . The model reads:

$$\frac{dN}{dt} = I(t) - kN - \frac{a_{01}N}{K_{01} + N}V_P \quad (2a)$$

$$\frac{dV_P}{dt} = \frac{v_{01}e_P - \mu_P g_P}{e_P + g_P}V_P - m_1V_P - \frac{a_{12}V_P}{K_{12} + V_P}V_Z \quad (2b)$$

$$\frac{de_P}{dt} = v_{01} \left( \frac{N}{K_{01} + N} - e_P \right) \quad (2c)$$

$$\frac{dV_Z}{dt} = \frac{v_{12}e_Z - \mu_Z g_Z}{e_Z + g_Z}V_Z - m_2V_Z - \frac{a_{23}V_Z}{K_{23} + V_Z}V_C \quad (2d)$$

$$\frac{de_Z}{dt} = v_{12} \left( \frac{V_P}{K_{12} + V_P} - e_Z \right) \quad (2e)$$

$$\frac{dV_C}{dt} = \frac{v_{23}e_C - \mu_C g_C}{e_C + g_C}V_C - m_3V_C \quad (2f)$$

$$\frac{de_C}{dt} = v_{23} \left( \frac{V_Z}{K_{23} + V_Z} - e_C \right) \quad (2g)$$

where  $I(t)$  is the input rate of nutrient in the system and the parameter  $k$  is the nutrient output rate, like in the MH model (1). At each trophic level, there are two state variables, the structural biomass  $V$  and the reserve density  $e$ . The consumption functions are similar as in the MH model. The DEB parameters  $v_{ij}$ ,  $g_x$  and  $\mu_x$  are the energy conductance, the energy investment ratio respectively and the maintenance rate, for each trophic level.  $m_i$  is the death rate of the population at trophic level  $i$ .

### 2.3. Fluctuating input rate $I(t)$ and parameter values

Since we want to understand the effect of nutrient supply fluctuations on the food chain functioning, we compare simulations with varying nutrient supply to simulations with constant nutrient supply, with the same total amount of nutrient provided during the simulation time length. We consider that  $I$  varies periodically with respect to  $t$  and we use  $I(t) = A(1 - \cos(2\pi t/T)) + B$  where  $2A$  is the amplitude of  $I(t)$ ,  $T$  is the period of the fluctuations and  $B$  is the minimal input rate of nutrient. In order to carry out the numerical simulations, we set the parameter values as follows. We first consider the parameter values provided in Boer et al. (1998) for the MH model (1) and in Kooi et al. (1997) for the DEB model (2), they are recalled in Appendix A. We call these sets of parameters the reference parameter sets for each model. We then perturb randomly these reference parameter vectors. The random sampling is made in a subset of the parameter space, in a such

manner that each parameter  $p$  is selected between  $p_r \pm 10\%$ , where  $p_r$  is the reference value obtained from the above mentioned references. The random selection is performed using a Sobol quasirandom sequence algorithm Bratley and Fox (1988). This approach allows to get a best covering of the parameter space region in order to avoid aggregates, which finally permits to make a lower number of simulations.

#### 2.4. Numerical studies

Two sets of numerical studies have been performed with both MH and DEB models. The first one deals with a Fourier analysis of model outputs. The spectra are plotted against the periods of the nutrient supply rate. The aim of the second set of studies was to understand if the periodic fluctuations of nutrient input rate modified the trophic chain functioning, and if we could say more on the modifications.

The Fourier analysis was made by varying the nutrient input rate period from 10 to 300 h and for each period, by considering the Fourier spectrum of the state variables during the asymptotic regime. We thus simulate the models during 3000 h and consider only the last 2000 h in order to avoid the initial condition effect and work with stationary time series. This type of analysis has been performed for low and high amplitudes, for both models (MH and DEB).

For the effect of fluctuations on trophic chain functioning, we again considered the asymptotic regime by running the models during 3000 h and analyzing the time series during the last 2000 h. We then calculated the mean of each trophic level biomass, with a without fluctuations of the input rate. In order to get more robust results, we performed this analysis for a large number (1000) of parameter sets, the choice of this number is explained hereafter. We have done this for different nutrient input rate periods and amplitudes, for both models (MH and DEB). The parameter sets are obtained using a Sobol quasirandom sequence in a hypercube around a reference parameter set provided in Boer et al. (1998) for the MH model and in Kooi et al. (1997) for the DEB model, the range for each parameter is more or less 10% around its reference value. 1000 parameter sets is in fact very low since we have 13 parameters for the MH model and 16 parameters for the DEB model. This number has been chosen for the following reasons. First, the Sobol quasirandom sequence allows us to get a well distributed sampling of the parameter domain. Thus we decided to

select an arbitrary number (5000) and to reduce it by a sensible factor to see if the results would be different. The first analysis have been performed with 5000 parameters and the resulting distribution of means obtained for each state variable was very similar with 1000 parameter sets. We thus decided to reduce the time of simulation by finally considering only 1000 parameter sets for each study.

#### 2.5. Some comments on these models

The mathematical formulation of these models in a chemostat would be very similar from a mathematical point of view. Indeed, it would be sufficient to replace  $k$  by the dilution rate  $D$ , the input rate  $I$  by  $DN_{in}$  where  $N_{in}$  would be the nutrient concentration in the chemostat reservoir, and  $m_i$  should be replaced by  $D + m'_i$ . Our Table 1 in Appendix A is based on these relations. It follows that the mathematical analysis provided in the literature on food chains in chemostat, see Boer et al. (1998) and Kooi et al. (1997) for instance, can therefore be easily extended to the MH and DEB models. A bifurcation analysis of a chemostat model in the parameter space  $(N_{in}, D)$  can be somehow interpreted for our models in the parameter space  $(I, k)$ . Experiments with fluctuating concentration  $N_{in}$  in a chemostat would thus provide empirical data related to our theoretical work.

In the case where the input rate  $I$  is a constant, the MH model has been studied in different papers. With  $C(t) \equiv 0$ , we refer for instance to Smith and Waltman (1995) and Li and Kuang (2000). These works provide some results in particular on the role of the parameters  $I$  and  $k$  on the dynamics and on the structure of the community. Among these results, it is shown that a periodic solution can occur. In Boer et al. (1998) (and see references therein), the authors analyze the MH model with a constant value of  $I$  and provide some bifurcation diagrams in the parameter plane  $(I, k)$ . It is shown that complex dynamics can occur (chaotic attractors for instance) and the role played by the parameter  $I$  in the occurrence of complex dynamics is described. It is also shown that for low and for high input rates as well, the consumer goes extinct, it can coexist for intermediate input rates. Moreover, the paper (Smith, 1997) deals with the Droop model for phytoplankton growth in chemostat, which is slightly different from the DEB model but also considers a reserve (or quota) compartment. Results mainly show that, under relevant conditions on  $I$  and on the biological parameter values, the system admits a periodic solution.

**Table 1**

List of the parameters and their units for the MH model and the DEB model. The reference values of these parameters come from Boer et al. (1998) for the MH model and from Kooi et al. (1997) for the DEB model.

MH model			DEB model		
Parameter	Value	Unit	Parameter	Value	Unit
$k$	0.4	$\text{h}^{-1}$	$k$	0.4	$\text{h}^{-1}$
$y_{01}$	0.4	–	$v_{01}$	40	$\text{h}^{-1}$
$y_{12}$	0.6	–	$v_{12}$	0.2	$\text{h}^{-1}$
$y_{23}$	0.6	–	$v_{23}$	0.0756	$\text{h}^{-1}$
$a_{01}$	1.25	$\text{h}^{-1}$	$a_{01}$	1.25	$\text{h}^{-1}$
$a_{12}$	0.33	$\text{h}^{-1}$	$a_{12}$	0.33	$\text{h}^{-1}$
$a_{23}$	0.25	$\text{h}^{-1}$	$a_{23}$	0.25	$\text{h}^{-1}$
$K_{01}$	8	$\text{mg dm}^{-3}$	$\mu_P$	0.025	$\text{h}^{-1}$
$K_{12}$	9	$\text{mg dm}^{-3}$	$\mu_Z$	0.01	$\text{h}^{-1}$
$K_{23}$	10	$\text{mg dm}^{-3}$	$\mu_C$	0.0075	$\text{h}^{-1}$
$m_1$	0.025	$\text{h}^{-1}$	$g_P$	80	–
$m_2$	0.01	$\text{h}^{-1}$	$g_Z$	1	–
$m_3$	0.0075	$\text{h}^{-1}$	$g_C$	0.504	–
			$K_{01}$	8	$\text{mg dm}^{-3}$
			$K_{12}$	9	$\text{mg dm}^{-3}$
			$K_{23}$	10	$\text{mg dm}^{-3}$
			$m_1$	0.5	$\text{h}^{-1}$
			$m_2$	0.2	$\text{h}^{-1}$
			$m_3$	0.15	$\text{h}^{-1}$

A similar type of analysis is provided for the DEB model in Kooi et al. (1997), still for a constant value of the input rate  $I$  and in the situation where the reserve densities are so fast that quasi-steady state assumption is applied, which is a particular case of the DEB model. It is also shown that for a constant  $I$ , the food chain can exhibit a complex dynamics with chaotic behavior for instance, and that the parameter  $I$  plays a crucial role in the occurrence of this complex dynamics.

In the present paper, we consider variable input rate, focusing on a periodic function of time, and we analyze the effect of this temporal variability on the food chain functioning. For instance, we compare the cases where, during a given period, a given amount of nutrient is first provided at a constant rate and, afterward, at a periodic rate. The role of the period  $T$  and amplitude  $2A$  of the periodic nutrient input rate is studied. Many works have considered periodic forcing in chemostat on predator–prey systems or on competition, with different types of models. We refer to (Zhao, 2003 or Farkas, 1991) for instance. The results focus on the coexistence of several species competing for a few number of limiting nutrient. To our knowledge, there is only very few mathematical results on food chain models like the MH model and even less for models like the DEB one, for time dependent input rate  $I(t)$ .

### 3. Results

#### 3.1. Fourier spectrum analysis

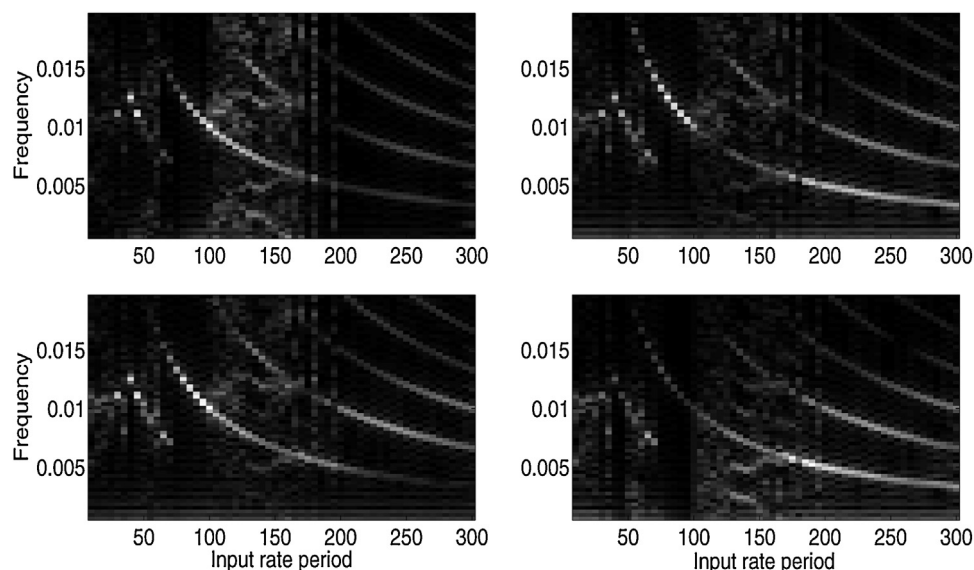
The results obtained for the DEB model are rather similar to the results of the MH model. We thus detail the MH model results and we will discuss the differences between both models afterward. Since the results are very close for the different amplitudes used in the analysis, we first focus on one amplitude in detail and we then briefly describe the slight effect of amplitude. The amplitudes have been chosen according to the following criterion. When the input rate is constant, it is well known that if this rate is low, the system reaches an equilibrium state while if we increase the input rate, the state variables fluctuate. We thus considered two sets of values for the amplitude. It must be noticed that the MH model, with the

reference parameter set and a constant input rate  $I = 10$ , exhibits a periodic behavior with a period around 86 h (frequency around 0.01 Hz, that we will call *internal frequency*).

The main result here is illustrated in Fig. 1. In this figure, we see the spectrum of the asymptotic time series obtained with the MH model. The most important pattern is represented by the hyperbolic white curves which means that the main mode in the Fourier spectrum for each input rate period  $T$  is obtained for the frequency  $1/T$ . This means that the forcing term  $I(t)$  has a strong influence on the dynamics of all the state variables. Furthermore, we can see that for input periods  $T$  between 10 h and around 50 h and between 100 h and 200 h, the spectrum is a bit “noisy”. When  $T < 50$  h, the frequency  $1/T > 0.02$  Hz is too large to appear on the graph and the internal frequency provides the main mode. For  $100 < T < 200$ , the “noise” corresponds to a resonance effect since in this case, the ratio between the internal frequency and the external frequency is close to one. Note that the choice  $A = 5$  and  $B = 5$  corresponding to Fig. 1 leads to an averaged input value of 10, which should have been the same with the choice  $A = 10$  and  $B = 0$ . This averaged level of nutrient input rate is required for getting fluctuations of the populations even for constant input rates. But in the latter case, the input rate fluctuations have larger amplitudes than those obtained with the former case.

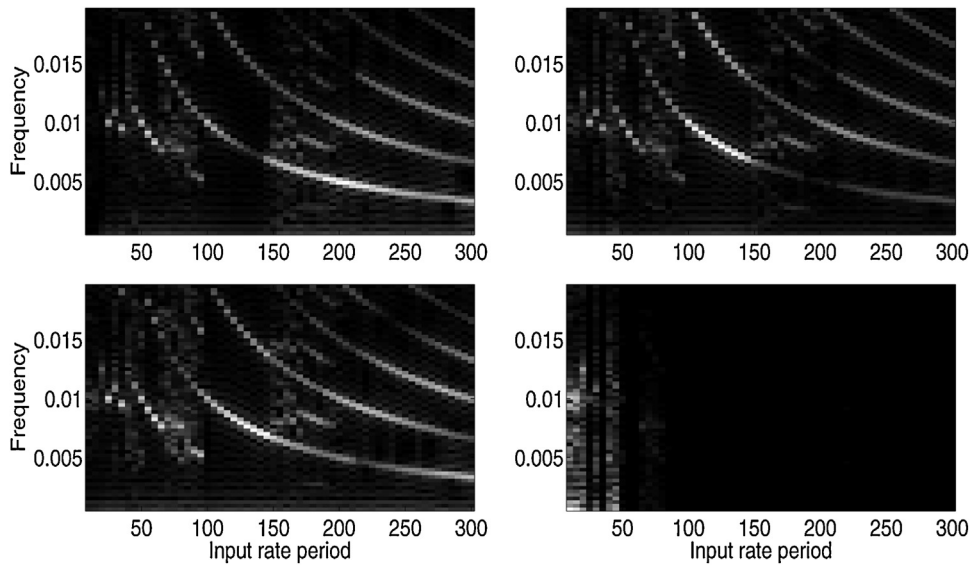
Fig. 2 shows the result for this larger amplitude of nutrient input rates. Similar patterns can be seen. However, for the consumer, the pattern is very different. Indeed, with large input amplitude ( $A = 10$ ), for long periods (around  $T > 80$ ), the consumer is excluded (its biomass tends to zero). This is probably due by too long periods during which the nutrient level was too low to maintain the whole chain. This is supported by the transcritical bifurcation observed in the constant input case for low nutrient input, leading to the extinction of the consumer. The second difference between the spectra built with  $A = 5$ ,  $B = 5$  (Fig. 1) and those with  $A = 10$ ,  $B = 0$ , (Fig. 2) is the level of “noise” on the spectrum, which is lower in the latter case. Indeed, the amplitude of the forcing term is larger, thus the internal fluctuations have less importance.

The last result pointed out in this subsection concerns the comparison with the DEB model outputs. As it can be observed in



**Fig. 1.** The MH model (1), using the reference parameter set (see Appendix A) and  $A = 5$ ,  $B = 5$ , has been simulated during 3000 h. A Fourier analysis has been done on the time series for each state variable, for different input rate period  $T$ , from  $T = 0$  to  $T = 300$ . The height of the spectrum is represented in a gray color. Black corresponds to 0 and the highest values of the spectrum are in white. Each panel corresponds to a different state variable (nutrient = top left, phytoplankton = top right, zooplankton = bottom left and consumer = bottom right).



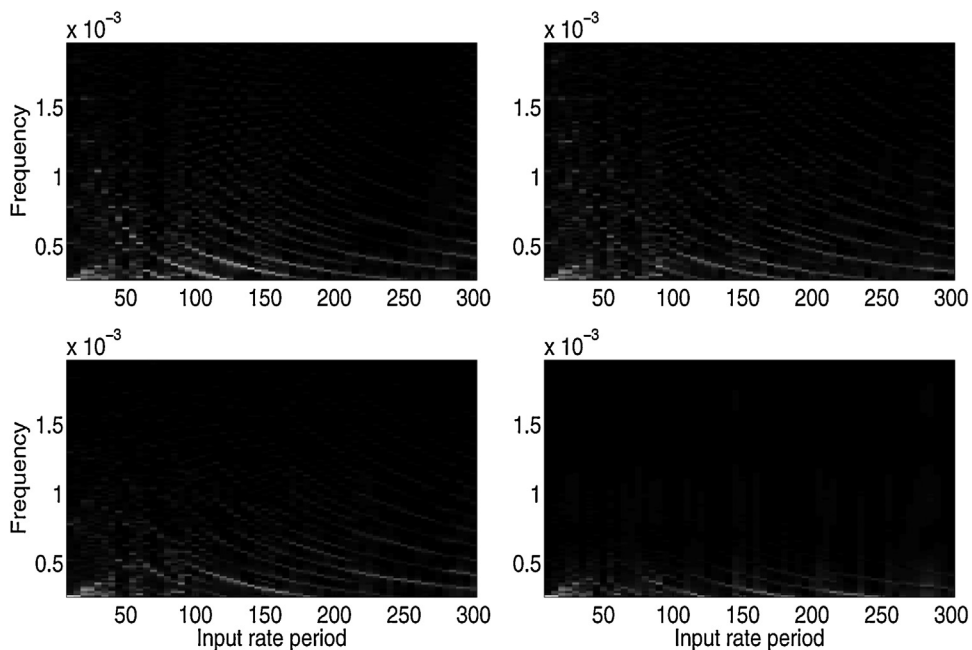


**Fig. 2.** The MH model (1), using the reference parameter set (see Appendix A) and  $A = 10$ , has been simulated during 3000 h. A Fourier analysis has been done on the time series for each state variable, for different input rate period  $T$ , from  $T = 0$  to  $T = 300$ . The height of the spectrum is represented in a gray color. Black corresponds to 0 and the highest values of the spectrum are in white. Each panel corresponds to a different state variable (nutrient = top left, phytoplankton = top right, zooplankton = bottom left and consumer = bottom right).

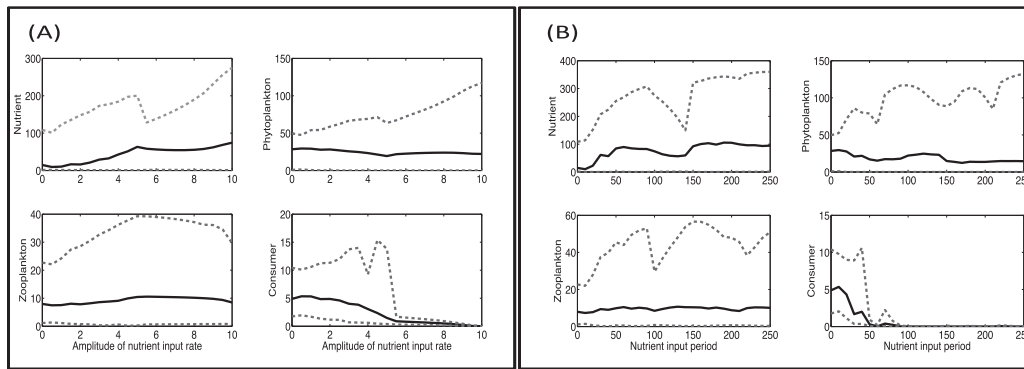
**Fig. 3.** The main pattern is similar for the DEB model but more diffuse. In the DEB model, the relation between the resource concentration in the environment and the biomass state variable of consumer is not direct, since at each level, the resource ingested is first assimilated in a reserve compartment. As we can see in Fig. 3, the main mode in the Fourier spectrum is still obtained for the frequency corresponding to the nutrient input fluctuation. But this mode is not so clear than in the MH model spectra and this can be interpreted by the fact that the response of the different trophic levels to nutrient input variations in the DEB model is less instantaneous than in the MH model.

### 3.2. Response of the population levels to periodic fluctuations

In this subsection, we study how the periodic fluctuations of the nutrient input rate affect the mean (time average) of populations at each trophic level, in the asymptotic regime. We first consider the MH model. In Fig. 4, the mean, maximal and minimal values for each state variable between  $t = 1000$  h and  $t = 3000$  h are represented. On panel (A), they are plotted against the nutrient input rate amplitudes  $A$ , between  $A = 0$  and  $A = 10$  and for  $T = 100$ . We can see that the consumer abundance tends to zero when the amplitude of nutrient input rate is too large. On panel (B), the



**Fig. 3.** The DEB model (2), using the reference parameter set (see Appendix A) and  $A = 5$ ,  $B = 5$ , has been simulated during 3000 h. A Fourier analysis has been done on the time series for each state variable, for different input rate period  $T$ , from  $T = 0$  to  $T = 300$ . The height of the spectrum is represented in a gray color. Black corresponds to 0 and the highest values of the spectrum are in white. Each panel corresponds to a different state variable (nutrient = top left, phytoplankton = top right, zooplankton = bottom left and consumer = bottom right).

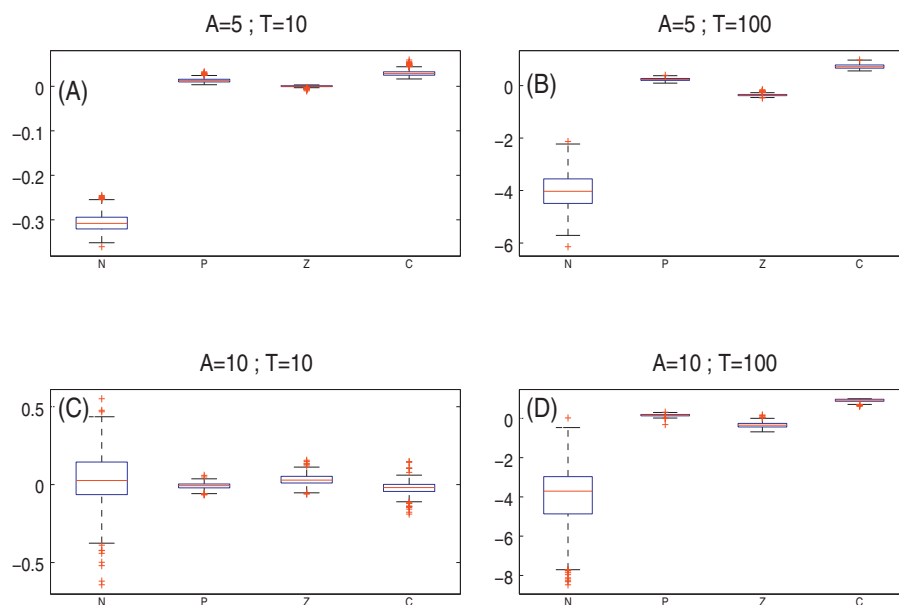


**Fig. 4.** Simulations with the MH model (1) are run, using the reference parameter set (see Appendix A). For each state variable, the mean value (black line), the maximal value (dotted grey lines) and the minimal value (dashed grey lines) are calculated and are plotted against the amplitude  $A$  (panel A) or against the period  $T$  (panel B) of the nutrient input rate. When the amplitude is varying (panel A), the period is fixed to  $T = 100$ . When the period is varying (panel B), the amplitude is fixed to  $A = 10$ .

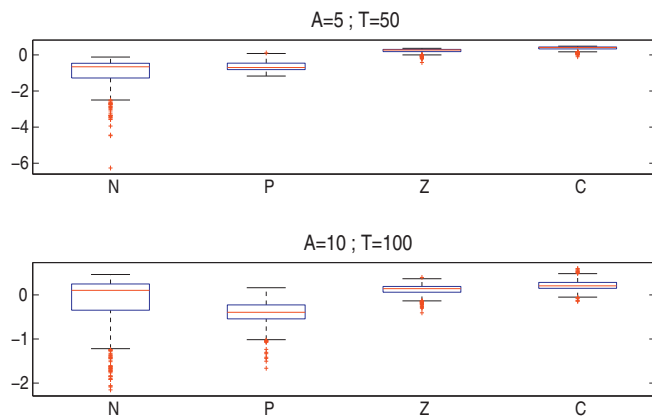
abundance descriptors (mean, maximum, and minimum) are plotted against the period of the nutrient input rate  $T$  between  $T = 0$  and  $T = 250$  h, for  $A = 5$ . This value has been chosen by considering the last graph of panel (A) in Fig. 4 in order to maintain the consumer population, at least for some period values. According to these graphs, we decided to execute simulations with different parameter sets and  $A$  between 0 and 10 and  $T$  between 0 and 100. Fig. 5 illustrates the effect of nutrient input fluctuations. Four graphs are presented, with  $A = 5$  and  $T = 10$  (graph (A)),  $A = 5$  and  $T = 100$  (graph (B)),  $A = 10$  and  $T = 10$  (graph (C)) and  $A = 10$  and  $T = 100$  (graph (D)). In this figure, the distribution of the relative difference of the means, obtained for each random set of parameters, between the constant input rate situation and the periodic one. More precisely, if  $M_1$  denotes the mean value of a state variable with the constant input rate and  $M_2$  denotes the mean value with the periodic input rate, we represented the distribution of:

$$D = \frac{M_1 - M_2}{M_1}$$

When the result is negative, it means that the time average of the state variable is lower in a constant environment than in the fluctuating one, for the same amount of nutrient provided during the whole simulation. We see on graphs (A) and (C), which correspond to a low input rate period  $T = 10$ , that the differences are rather low. In the case (A), we can see that the nutrient is lower in a constant environment than in a fluctuating environment (around 30% lower), but the phytoplankton, the zooplankton and the consumer have close mean values in constant and fluctuating environments. On graphs (B) and (D), we note that the nutrient mean is generally much lower in a constant environment (40% lower in graph (B) and 400% lower in graph (D)). However, the phytoplankton is generally more abundant in a constant environment (25% higher in graph (B) and 20% higher in graph (D)). Finally the consumer biomass is higher in the constant environment (75% higher in graph (B)). However, if we can see in graph (D) that the consumer biomass in a constant environment is around 90% higher than in the fluctuating situation, it is mainly because the abundances are very low (the population is very close to extinction) and thus the decrease induced by fluctuations in this case is not important. Since the differences are much more important for the nutrient level, the box-plot for the other levels



**Fig. 5.** The MH model (1) has been simulated 1000 times with different parameter sets. The parameter sets are chosen according to a Sobol quasirandom sequence. The mean of each state variable is calculated. The figure shows the distribution of the means, for different values of  $T$  and  $A$ . Distributions are presented through box-plot diagrams. The central mark on each box correspond to the median, while the 25th and 75th percentiles correspond to the edges.



**Fig. 6.** The DEB model (2) has been simulated 1000 times with different parameter sets. The parameter sets are chosen according to a Sobol quasirandom sequence. The mean of each state variable is calculated. The figure shows the distribution of the means, for different values of  $T$  and  $A$ . Distributions are presented through box-plot diagrams. The central mark on each box correspond to the median, while the 25th and 75th percentiles correspond to the edges.

seem to be very close to zero (see details in the supplementary material), but the distributions in the case (B) and (D) are significantly different from zero.

We summarize the previous result as follows: the fluctuations have a positive effect on the nutrient level, a negative effect on the phytoplankton level, a positive effect on the zooplankton level and a negative effect on the consumer level. For large amplitudes and low periods, the effects are small and random. We also shown that these results are still true but much diffuse in shorter trophic chain. Even, for a nutrient–phytoplankton system, the effects of fluctuations on the mean of state variables is very low. Indeed, in the nutrient–phytoplankton system, the outputs of the model are strongly correlated to the forcing term and since the constant input rate has the same mean as the fluctuating input rate, it follows that the state variables have very close mean in constant and fluctuating environment. When the length of the food chain increases, the feedback effects of the higher trophic levels enhance the differences between the constant and the fluctuating environment.

With the DEB model, the results are rather different, see Fig. 6. In this figure, two set of simulations are presented, one with  $A = 5$  and  $T = 50$  (low amplitude), the other one with  $A = 10$  and  $T = 100$  (large amplitude). As it can be seen, the distributions of the means are very close to zero, the effect of the fluctuations is much more variable than what we observed in the MH model. We conclude that this more detailed model, containing more state variables, have a much more complex response to the periodic fluctuations of the nutrient input rate. In other words, the choice of the biological part of an ecosystem model remains an important choice, even if we already admit that the physical forcing is the main factor driving the dynamics. For instance, a direct relation between trophic levels lead to robust patterns while indirect relations (use of reserves or quota), which are often more realistic, lead to more complex responses.

#### 4. Discussion and conclusion

In this article, we analyzed the bottom-up effects of fluctuating nutrient uptake on different food chains, starting from the simple nutrient–phytoplankton case to a tri-trophic food chain nutrient–phytoplankton–zooplankton–consumer. For each of the models considered in the paper, we used different parameter sets around a reference parameter set taken from the literature. For this

particular set of parameters, if the mean value of the input rate was taken large enough, oscillations occurred for constant input rate. These intrinsic fluctuations induced by biotic interactions were called internal oscillations. We shown that the nutrient input rate variability has different effects on the system properties. We first shown that the period of input rate provides a clear signature of the Fourier spectrum, regardless the period of the input. However, for low periods, the internal period of the trophic chain drives the main pattern. Furthermore, when the external oscillations (those of the external forcing) had a period of the same order of magnitude as the internal oscillations, a resonance effect was observed on the Fourier analysis. Finally, for long input rate periods, the consumer was excluded. We also shown that the previous results were exhibited by both models (Monod–Herbert and DEB), while the Fourier spectra obtained with the DEB model were more diffuse.

A second set of results shown that the nutrient input rate fluctuations enhances the abundance of nutrient in the environment, meanwhile it decreases the consumer biomass. For the intermediate trophic levels (phytoplankton and zooplankton), the effects depended on the model. With the Monod–Herbert model, the time average phytoplankton biomass is decreased by nutrient rate fluctuations, while the mean zooplankton biomass was increased. We obtained different results with the DEB model. The insertion of reserve compartments lead to more complex responses of the community model to the nutrient input rate fluctuations. The difference of means of the state variables between the constant environment simulations and the periodic input rate case was sometimes positive and sometimes negative, even if the nutrient abundance was essentially enhanced by fluctuations.

To some extent, our results suggest that the nutrient level is mainly driven by the physical forcing, its mean is much sensitive to the fluctuations than the mean of other state variables, for both models. From a modeling point of view, it is enhanced in more complex and detailed systems, as we have seen by comparing the Monod–Herbert model to a DEB one. Furthermore, we observed that the sensitivity of the mean nutrient concentration to the nutrient input rate increases with the length of the food chain. Furthermore, the effect of the nutrient input rate variability on the time average state variables is more robust in systems where the trophic levels are directly linked, like in the Monod–Herbert model, than in models with buffers such as reserves, like in a DEB model.

Consequently, we suggest that when simulating large marine ecosystems with physical models coupled with biological ones, the more complex the biological network is, the more attention must be paid to the effect of the physical forcing on the ecosystem functioning and on the community structure.

Three research directions are envisaged to continue this work. We first aim to provide some mathematical results in order to generalize our results and provide more detailed explanations and the underlying mechanisms of our results. For instance, we started to consider the equilibrium of the food chain models discussed in the present paper, even if an explicit formula for the tri-trophic MH model is already difficult to get (and so complicated that it is not useful). We tried to see if the values of the state variables could be simply related to the input rate  $I$  in the constant input rate case. We expected to see if the Jensen inequality could help to explain our results. The idea is the following. If the equilibrium value of nutrient for instance, is a convex function of  $I$ , we could thus imagine that periodic variations of the nutrient input rate would increase the nutrient. Furthermore, when the system exhibits internal oscillations (case observed if  $I$  is large enough), we can consider that the state variables fluctuate around the values of an unstable equilibrium. But the mean of the state variable is not necessary equal to this equilibrium value, thus any relation

between the equilibrium value and  $I$  would not be useful. Further investigations need to be conducted.

The second research direction concerns the development of mathematical analysis of the MH model. We will focus on bifurcation analysis with the period of nutrient input rate as a bifurcation parameter. From a numerical point of view, more realistic forcing terms (with several periods, intermittent, and so on) should be considered. Finally, it is well known that space occupies a central place in ecology and we will thus work on spatial extensions of the models used in this paper.

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### Appendix A. Parameter values

We recall here the parameter values for models (1) and (2). We arbitrarily took (1) for the initial conditions of all variables.

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