Effect of nutrient input frequency on the structure and dynamics of the marine pelagic community: A modeling approach

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ABSTRACT

An analysis of the induced changes in both total productivity and community structure as a consequence of different pulsed nutrient inputs has been made by using two different ecosystem modeling tools. One was a modified version of the N-based model proposed by Fasham et al. (1990) for pelagic ecosystems and the other the plankton functional type model by Vichi et al. (2007). Both models lead to higher total biomass production with a pulsed nutrient input compared to a continuous supply, affecting both phytoplankton and zooplankton. Detailed responses are, however, different among plankton groups depending on the frequency of pulsed nutrient input and the complexity of the model. The differences in biomass production were higher for an oscillation period of 150–170 days following a sinusoidal supply pattern. A tidal mixing-induced nutrient supply was also simulated by using both models and a larger biomass increment was observed compared to that obtained with the sinusoidal pattern. Finally, a theoretical application of this approach to the pelagic ecosystem of the North Western Alboran Sea shows a preferential selection of diatoms and larger zooplankton under discontinuous nutrient inputs.

1. Introduction

Oceanic systems are characterized by a marked heterogeneity both in the spatial and in the temporal dimensions, discontinuity being the rule rather than the exception. Moreover, spatial and temporal dimensions are tightly connected as larger-scale processes (i.e. basin-scale) present longer variation times (yearly to decadal) while faster processes occur at smaller spatial scales (such as mesoscale tidal fronts) (Stommel, 1963; Haury et al., 1978).

The spatial heterogeneity of biogeochemical variables (i.e. patchiness) has been recognized to have an impact on the primary production of pelagic marine ecosystems (Flierl and Davis, 1993; Dadou et al., 1996). For example, the existence of a nonhomogeneous distribution of chlorophyll in natural surface waters leads to a higher production compared with the situation of equally distributed fields, a fact that has been related to changes in
community structure, to defend against grazing, or to the presence of spatially coherent structures (Martin et al., 2002).

Coupled to this spatial heterogeneity there is a temporal one (Stommel, 1963; Haury et al., 1978) which also occurs at very different scales ranging from hourly (tidal fronts, internal waves) to subinertial (meteorological) or seasonal scale or at even longer scales (annual or decadal) where climate drives fluctuations affecting wide regions of the ocean (El Niño, La Niña, etc.) (McGillicuddy et al., 1998; 2003; Sakamoto et al., 2004). This temporal discontinuity is much more subtle than the spatial one, making it more difficult to address effects on the production of marine systems. However, primary and secondary production in natural aquatic systems are usually partially coupled with a delayed response (e.g. Valiela, 1995) as grazers need more time to react to changes in resource availability (i.e. primary producers) than phytoplankton (nutrients). So it could be expected, given a variable nutrient input, that the percentage of primary production consumed by zooplankton would change compared to a fixed nutrient flow due to the different reaction times and relative coupling of production and consumption processes (see Holt (2008) and references therein).

For example, there is evidence that primary production calculated from biogeochemical models tends to be underestimated compared to estimates derived from satellite data, particularly in shelf-break regions, mainly because of the use of time-integrated calculations (Hofmann, pers. comm). Also, some laboratory works have revealed the influence of temporal heterogeneity of nutrient input on primary (Burmaster, 1979; Sommer, 1986; Yamamoto and Tsuchiya, 1995; Guayadol et al., 2009) and secondary (Svensen et al., 2002; Cottingham and Schindler, 2000) producer biomass in mesocosms enclosures. This confirms the importance of assessing the temporal dynamics of nutrient supply to ecosystems.

This issue should be of paramount importance in coastal and estuarine areas as they are subjected to a particularly high variability in physical forcing. In such areas, plankton dynamics have long been recognized to be strongly related with the variability in external energy supply (Margalef, 1978), so a number of research works have been devoted to the study of coupling between physical forcing and biological processes in these extreme marine ecosystems both by field data sampling (e.g. De Carlo et al., 2007) and by using hydrodynamic-biogeochemical coupled models (Pace et al., 1984; Tanaka and Mackenzie, 2005; Plus et al., 2006; Lancelot et al., 2007; Marinov et al., 2008; Duarte et al., 2008).

Another possible effect of discontinuous nutrient input to marine ecosystem is the change in the structure and composition of the plankton community (Holt, 2008). In this sense, Grover (1991) hypothesized that nutrient storage ability in a fluctuating environment could select large-celled species while smaller cells have competitive advantage under nutrient-limiting and stable conditions (Margalef, 1978; Falkowski and Oliver, 2007). These hypotheses are supported by a number of recent modeling works such as the one by Litchman et al. (2009) and Verdy et al. (2009) which show a selection of larger (smaller) cells in discontinuous (uniform) environments. Also Roelke et al. (1999) showed how the
composition of a phytoplankton community in an estuarine area could be partially controlled by the periodicity and amplitude of the allochtonous nutrient inputs by using a simplified biogeochemical model of the phytoplankton community.

However, to the best of our knowledge, up to now there has not been a comparative analysis studying how changes in the nutrient input pattern could impact the dynamics of generic marine ecosystems including both the phytoplankton and the zooplankton levels. That should be relevant not only because overall biomass of the system could change but also because community composition changes could greatly influence the trophic transfer efficiency to higher trophic levels. That could make a strong difference in the fish biomass available for harvesting especially in coastal regions, home to most of the commercial fisheries.

In the present work, we tried to address this issue by exploring the differences in both community production levels and structure induced by changing the nutrient supply patterns from a constant input to variable supply rates using two very different biogeochemical models, a modified version of the N-based model described by Fasham et al., 1990 and a plankton functional type (PFT) model (Vichi et al., 2007).

Finally, we apply these models to a theoretical case simulating the flow of the surface layer of the North-Western (NW) Alboran Sea as the input of nutrients to this basin through the Strait of Gibraltar presents a highly variable dynamics that is mainly related to tidal forcing (Macías et al., 2007a). Differences in biomass levels in this basin when comparing the case of a continuous injection of nutrients versus a more realistic pulsed dynamics were assessed using both models.

2. Methods

a. Description of models

Two very different models were used to perform the different simulations. One is the well-known N-based, seven-compartment model proposed by Fasham et al. (1990) (Fasham90 from now on) which was originally implemented to simulate the temporal dynamics (in a 1D framework) of an open-ocean mid-latitude site, the BATS (BermudA Time Series) station. This model was intentionally created as very simplistic, only introducing some refinements in the description of the microbial loop which was supposed to be relevant in the BATS site.

The other model used is the PFT model proposed by Vichi et al. (2007) (BFM thereafter; http://bfm.cmcc.it), being a generalization of a former PFT model called ERSEM (Baretta et al., 1995) initially developed to simulate the dynamics of the coastal ecosystem of the North Sea including different nutrients and macroelements as well as more functional groups and higher trophic levels.

i. Fasham90 model. This model simulates nitrogen cycling through seven compartments of the pelagic ecosystem (Fig. 1, left plate). This is a quite simple, well-tested and widely
used model aimed to describe temporal evolution of the pelagic system in temperate seasonally mixed waters and has been chosen due to its relative simplicity and its reasonable simulation results.

We have used a modified version of the model described in Fasham et al. (1990) in different aspects. For example, the effect of dilution provoked by the relative change of the mixed layer depth has been removed from the model as this does not apply to our simulation set up. Also, growing and mortality (or breakdown) terms of state variables are density dependent, as later works (e.g. Fasham et al., 1993 and Fasham, 1995) have shown that including this dependency improves the model results in simulating annual cycles in different sites of the world’s ocean. The complete list of model parameters and equations is provided in Appendix A.

ii. BFM model. This plankton functional model was proposed by Baretta et al. (1995) and modified by Vichi et al. (2007). It is a much more complex model with six trophic levels and sixteen functional groups (Fig. 1, right plate). In such a model C, N, P and Si are simulated separately thus allowing a detailed study of the plankton community structure and its biomass composition in terms of biogeochemical elements. Model formulae and parameter values are exactly the same as the ones presented by Vichi et al. (2007) so they have not been included in the Appendix.

Although the use of PFT models is still being debated, (see Anderson et al., 2005) we decided to use this second kind of models because they give highly valuable information about the internal structure of the plankton community that cannot be obtained from the more simple models (Raick et al., 2006).
b. Simulations performed with virtual mesocosm systems

A set of standard simulations were performed simulating a virtual ecosystem in a mesocosm of total volume 1000 L and an input and output flux of 1 L/min (total tank renewal in ca. 17 hours). Irradiance was constant at a value of 1000 W/m² (4600 µE m⁻² s⁻¹) throughout the entire mesocosms (i.e., no horizontal or vertical gradient) to avoid light-limitation of primary production, whereas water temperature was set to 20°C, excluding any effect of thermal stress (by extremely low or high temperatures) on plankton physiology.

In order to minimize the effect of the initial conditions on the model’s results, a spin-up run of 1500 days was made under constant conditions to determine the equilibrium (or near equilibrium) value of each model compartment. After that, each simulation was run up to 500 days with the initial 150 days not being considered in the analysis performed to avoid initial conditions’ influence. Both model’s equations were solved using the ode45 function in Matlab® which adjusts the calculation of the time step to ensure that maximum difference between consecutive integrations is of order $10^{-6}$. The output was collected and stored each 14.4 minutes of simulation, thus storing 100 time steps each day of simulation.

In every simulation, nutrient input is considered to be immediately mixed and homogeneously distributed throughout the mesocosm volume neglecting any spatial heterogeneity in the system.

i. Continuous nutrient input. To get a standard solution as a reference, both models were run simulating a continuous supply of inorganic nutrients to the system by using a constant concentration of nitrogen in the incoming waters. Nitrate concentration was set to 7.14 mmol/m³ for both models while for BFM 1 mmol/m³ of phosphate and 5 mmol/m³ of silicate were prescribed.

The selected ratio yields a nitrogen-limited system in the BFM simulations (N:P<16) enhancing the controlling role of nitrogen to facilitate the comparison with the N-based Fasham90 model. The exceedingly high value of silicate input was chosen to avoid silicate-limiting conditions to diatoms growth which could become dominant with silicate values above 2 mmol/m³ (Egge and Aksnes, 1992). Outflow water presents the same characteristics as the mesocosm’s waters with identical concentration of all constituents of the ecosystems, both living and nonliving.

ii. Sinusoidal pattern of nutrient input. A number of simulations were performed with both models simulating a sinusoidal pattern of inorganic nutrient concentration in the incoming water. Eq. 1 shows the variation in nutrient concentration (in mmol/m³) induced in the mesocosm:

$$\left( \frac{dN}{dt} \right)_{\tan \theta} = \frac{Q}{V} N^*(1 + \sin(\omega t));$$  \hspace{1cm} (1)
where

\[ \omega = \frac{2\pi}{T(\text{days})}; \]  

(2)

\( Q \) is water flux (L/s); \( V \) is mesocosm volume (L) and \( N^* \) is a fixed value of nitrate (7.14 mmol/m³), phosphate (1 mmol/m³) and silicate (5 mmol/m³).

The oscillation periods (“\( T \)” in Eq. 2) selected for the different simulations were: 0.3, 0.8, 2.5, 6.2, 12.5; 31, 62, 125, 169, 251 and 502 days aiming to cover a wide range of temporal scales from quick processes (such as wind or tidal mixing), fortnightly variations (tidal-amplitude variation) or annual-scale processes. The integrated amount of nutrients provided to the system was almost identical in all the simulations with a maximum deviation of 0.4% with respect to the continuous input case. As in the continuous simulations outflowing waters present identical concentration of all constituents of the ecosystem as the mesocosm’s water.

iii. Tidal pattern of nutrient input. To simulate the tidal dynamics of nutrient input to the ecosystem a semidiurnal and fortnightly variation pattern was simulated for both models with two daily high nutrient concentration periods in the inflow of 4 time-step duration (i.e. 57.6 minutes) simulated during 14 days and no input during the next 14 days. In all cases, the total amount of nutrient was adjusted to match that of the continuous supply.

c. Simulation for the NW Alboran Sea

The selected site to perform these simulations was the NW region of the Alboran Sea as this basin is a semi-enclosed area with a restricted and characteristic exchange with the open ocean. The only connection of the Alboran Sea with the world’s ocean is the Strait of Gibraltar (SG in Fig. 2) where an inverse-estuarine circulation occurs with a surface inflow of Atlantic waters and an outflow of deep high-density Mediterranean waters (Armi and Farmer, 1985). A particular place for the water circulation in the Strait is the Camarinal Sill (Parrilla, 1990), located in the western sector of its main channel and with only some 300 m in the deepest central channel. The interaction of tidally-forced water movement with this sharp topography causes intense undulatory processes, such as bores (Boyce, 1975; Armi and Farmer, 1985) or internal waves (Bruno et al., 2002; Vázquez et al., 2008) that are capable to induce mixing between the different water masses present over the sill (Bray et al., 1995; Macías et al., 2006). These mixing processes make the concentration of nutrient in the incoming Atlantic waters extremely variable (Macías et al., 2007a) following clear tidal frequency patterns. The Atlantic Jet entering the Alboran Sea usually extends in a SW-NE direction (Perkins et al., 1990; García-Lafuente et al., 1999), typically extending in the surface water layer (down to 50 meters) and with a width of some 35–40 km (Perkins and Saunders, 1984) being usually found in the vicinity of the Spanish shore (Macías et al., 2007b; 2008).

With this physical framework, the NW Alboran Sea region could be idealized as a big
box (88 km × 45 km × 50 meters depth) to which a discontinuous nutrient supply is simulated using realistic estimations of the Atlantic flux (set to 0.8 Sv; 1 Sv = 10^6 m^3/s, Basheck et al., 2001) with a nutrient concentration depending of the tidal conditions and induced interfacial mixing. The 1D model of along-strait circulation and interfacial mixing developed by Macias et al. (2007a) has been used to compute the nitrogen concentration in the incoming water (see Fig. 10 of Macías et al., 2007a).

Simulations were made with the same time-step, irradiance and temperature conditions specified above. The constant environmental conditions were chosen to isolate the effect of the nutrient input discontinuity from other sources of variability (light, temperature . . .). The inclusion of additional variable conditions, although it would have resulted in more realistic simulations, would have made the discussion and interpretation of results much more difficult.

3. Results

The simulation with a continuous supply of inorganic nutrients has been used as the reference run for all the simulations with a discontinuous pattern. Thereby the results have been usually expressed as the difference in biomass of each trophic level/functional group.

Figure 2. South Iberia coast showing the Strait of Gibralta (SG), the Atlantic Jet (AJ, grey arrow) and Western Alboran Gyre (WAG). Black box shows the area considered in the Alboran simulation.
with respect to the standard run calculated according to Eq. 3 (Percentage of Model Bias (PBIAS), Marechal and Holman, 2005).

\[
PBIAS = \frac{\sum_{i=150}^{500} M_i - R_i}{\sum_{i=150}^{500} R_i} \times 100; \quad (3)
\]

\(M_i\) being any model variable at time \(i\) and \(R_i\) the reference variable at time \(i\) (in this particular case the standard run with continuous nutrient input). Statistical significance of calculated PBIAS has been tested applying a T-test for mean comparison (as all biomasses distributions were normally distributed). Associated p-values are presented either in the text or in the corresponding figures.

**a. Sinusoidal input**

The main results obtained when simulating a sinusoidal supply pattern are shown in Figure 3 for both models. There are similar patterns in the results obtained with the two formulations. In both cases, for high frequency oscillations (low periods) the results are quite similar to those obtained with a continuous input, the differences being extremely low (below 1%, Fig. 3) although, due to large sample size, statistically significant (\(p < 0.01\)).

A sustained and significant (p-value < 0.001) increase in biomass values of both phytoplankton and zooplankton is registered using the two models as the oscillation period increases (i.e. lowering the frequency of the pulses) up to a maximum reached around pulses of 150–200 days (Fig. 3), representing two high nutrient concentration periods per year (see Fig. 4). At approximately the same oscillation periods, total inorganic forms of N within the system reach its minimum as can be observed in Figure 3c. With higher periods, the total biomass in the system tends to decrease continuously while total inorganic nitrogen recovers partially (Fig. 3). These general trends were observed for both models and trophic levels showed in Figure 3 except for phytoplankton in the Fasham90 model, which exhibited a continuous biomass increase up to periods of 225 days and a stabilization afterwards (Fig. 3a).

There is also a significant change in the degree of correlation between predator and prey biomass cycles (Fig. 4). As nutrient oscillation period increases, the predator-prey cycles become progressively uncoupled (up to intermediate oscillation periods) as is denoted by the lower values of the linear correlation coefficient between predator-prey biomass (Table 1). Afterwards, a tighter coupling is observed (Fig. 4), as indicated by the higher correlation coefficients in Table 1. Maximum values of biomass also increase with pulsed nutrient to more than 150% for phytoplankton and nearly 50% for zooplankton (Fig. 4) when compared with the continuous supply case.
Figure 3. a) Differences of biomass with the continuous supply simulation as function of the sinusoidal input period. b) The same with the sum of both primary and secondary producers. c) Total free nitrogen in each of the simulations. All differences are significant to 99% confidence except points marked with * (significant to 95%) or with + (not significant).
Figure 4. Examples of temporal evolution of phytoplankton and zooplankton biomass in Fasham90 model as well as nutrient input with a) continuous supply and 31 (b), 169 (c) and 502 (d) days oscillation period. e) Percentage of difference of maximum and minimum values of phyto and zooplankton biomass with respect to the continuous supply (all differences significant to 99%).
The complexity and structure of the BFM allows to analyze separately the effect of the oscillation period of the nutrient concentration in the incoming waters on the different functional groups of both phytoplankton and zooplankton compartments (Fig. 5). When low oscillation periods are simulated, the differences with respect to a continuous supply situation are close to zero for all the phytoplankton functional groups (Fig. 5a). Nevertheless, both diatoms’ and nanoflagellates’ abundances start to increase for oscillation periods above 31 days until periods of 125 days when both groups reach an increase of about 3% (p-value $< 0.001$). From this point onwards, diatom abundance starts to decrease sharply until a negative value of $-11\%$ is reached for the longest periods. Flagellates, on the other hand, keep on increasing their biomass until attaining a maximum value of $5\%$ (p-value $< 0.001$) for periods of 200 days, the shape of the curve being very similar to that resulting for total phytoplankton calculated with the Fasham90 model (Fig. 3a).

The other two functional groups of phytoplankton show a very different pattern. The group called “large phytoplankton” (i.e. large and slow growing species) practically did not react to the nutrient pulses, showing very little (and not significant, $p > 0.05$) differences (Fig. 5a). On the other hand, the picophytoplankton group presents a negative and significant (p-value $< 0.01$) reaction to the pulsed pattern of nutrient input reaching a $-5\%$ decrease of biomass for a 31-day oscillation period and a posterior stabilization around $-1\%$ (p-value $< 0.05$).

A tendency for moderately larger zooplankton biomass is observed for intermediate oscillation periods ($\approx 50–250$ days) except for “carnivorous zooplankton” (Fig. 5b).

<table>
<thead>
<tr>
<th>Oscillation T (days)</th>
<th>Fasham90</th>
<th>BFM</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.3</td>
<td>0.03</td>
<td>0</td>
</tr>
<tr>
<td>0.8</td>
<td>0</td>
<td>-0.01</td>
</tr>
<tr>
<td>2.5</td>
<td>-0.13</td>
<td>0.05</td>
</tr>
<tr>
<td>6.2</td>
<td>-0.35</td>
<td>-0.33</td>
</tr>
<tr>
<td>12.5</td>
<td>-0.57</td>
<td>0.27</td>
</tr>
<tr>
<td>31</td>
<td>-0.70</td>
<td>0.23</td>
</tr>
<tr>
<td>62</td>
<td><strong>-1.16</strong></td>
<td><strong>-2.03</strong></td>
</tr>
<tr>
<td>125</td>
<td><strong>-1.03</strong></td>
<td><strong>-2.08</strong></td>
</tr>
<tr>
<td>169</td>
<td><strong>-3.73</strong></td>
<td><strong>-4.53</strong></td>
</tr>
<tr>
<td>251</td>
<td>5.45</td>
<td>0.84</td>
</tr>
<tr>
<td>502</td>
<td>7.01</td>
<td>7.73</td>
</tr>
<tr>
<td>Tidal mixing</td>
<td><strong>-43.6</strong></td>
<td><strong>-61.7</strong></td>
</tr>
</tbody>
</table>

Positive (negative) values mean a higher (lower) correlation of both variables. Bold values mark the lower correlations.
Figure 5. Biomass difference with respect to the continuous supply in the different functional groups of the BFM model. Sinusoidal input simulations. All differences are significant to 99% confidence except points marked with * (significant to 95%) or with + (not significant).
b. Tidal mixing induced inputs

The percentages of biomass difference in each trophic level and model with respect to the continuous supply simulation are shown in Figure 6. When using the Fasham90 model, only the phytoplankton fraction reacts to the tidal dynamics pattern reaching up to 5% (p-value < 0.001) more biomass than when considering a continuous input of nutrients, while zooplankton does not react.

In the case of the BFM model the phytoplankton again reacts positively reaching almost 2% (p-value < 0.01) more biomass but also zooplankton shows a positive response with an accumulation of nearly 4% (p-value < 0.001) more biomass with respect to the continuous supply simulation.

As with the sinusoidal pattern of supply, a detailed analysis of the effect over each functional group within the BFM model has been made (Fig. 7). In the phytoplankton group, all differences (except for the “large phytoplankton”) are positive and statistically significant with an increase of numerical value with decreasing body size (Fig. 7a). Also, all the groups of zooplankton showed positive differences (Fig. 7b), the most favored being the carnivorous mesozooplankton (+6.2%, p-value < 0.001) and the least, the omnivorous one (+0.4%, p-value > 0.05). The smaller groups (microzooplankton and heterotrophic flagellates) had a mean difference of around 1.2% (with associated p-value < 0.05).
Figure 7. Biomass difference with respect to the continuous supply in the different functional groups of the BFM model. Tidal mixing simulation. All differences are significant to 99% confidence except bars marked with * (significant to 95%) or with + (not significant).
c. Simulation for Alboran Sea

The results obtained simulating the NW Alboran Sea pelagic ecosystem (Fig. 8) are almost identical to those shown for tidal mixing in the previous section (Fig. 6). This is likely as the pattern of nutrient inflow used is quite similar. Nevertheless, in the latter case (Alboran Sea) the computed biomass anomalies are lower (nearly half) than in the former.

As it happened in the tidal mixing inputs simulations, the Fasham90 model only shows a positive reaction to the pulsed supply for phytoplankton (p-value < 0.01) while zooplankton shows a null response. Concerning the BFM model, both phytoplankton and zooplankton show a relative biomass increase reaching nearly +1% and +1.6%, respectively (p-values < 0.01).

However, in spite of this similarity for total biomass and for aggregated trophic levels when a tidal mixing input is simulated, the distribution of this biomass among the functional groups is different (Figs. 7 and 9). In the Alboran Sea case, the relative increase of biomass occurs especially for diatoms (p-value < 0.01) and also, to a lesser degree, for nannoflagellates (p-value < 0.05), while picophytoplankton and large phytoplankton did not show any effect (Fig. 9a).

Regarding zooplankton, contrarily to the previous simulation, carnivorous mesozooplankton (the plankton fraction that has the strongest response in the tidal input simulation,
Figure 9. Biomass difference with respect to the continuous supply in the different functional groups of the BFM model. Alboran Sea application. All differences are significant to 99% confidence except points marked with * (significant to 95%) or with / (not significant).

Figure 9. Biomass difference with respect to the continuous supply in the different functional groups of the BFM model. Alboran Sea application. All differences are significant to 99% confidence except points marked with * (significant to 95%) or with / (not significant).
Fig. 7b) shows a decrease (p-value < 0.01) in biomass compared to that calculated for a continuous input of nutrients, while the other three groups present high positive differences (p-values < 0.01) (Fig. 9b).

4. Discussion

a. Models results

Our simulations have shown that discontinuous patterns of nutrient input seem to have two different, but interconnected, effects on planktonic fractions of marine pelagic ecosystem models. On the one hand clear variations in the abundance of primary and secondary producers have been observed and, on the other, the temporal patterns in which the nutrients are supplied can also induce changes in plankton community composition.

The very similar pattern of biomass anomalies obtained by using both models for the sinusoidal nutrient input (Fig. 3b) could be partially explained by the degree of coupling between phytoplankton and zooplankton biomass cycles. In fact, we can expect a priori that the control of the community structure by a variable nutrient concentration should be mainly related with its effects on the internal structure of the system, including nonlinear feedbacks, different reaction times and other direct and indirect interactions (Holt, 2008).

With a continuous input or with a very short oscillation period (<30 days), the prey-predator cycles are relatively well coupled (Fig. 4a, Table 1) with a nearly constant amplitude and frequency explaining the lack of difference in this range of oscillation (Fig. 3). This situation resembles the usual situation in pelagic low latitude systems where no long-term cycles for nutrient inputs are present but rather a quasi-continuous input is associated with the permanent (but slow) nutrient diapycnal diffusion through the pycnocline or with short scale events such as a storm’s passage (Mann and Lazier, 2006).

The higher biomass accumulation in the system with intermediate (150–180 days) pulse frequencies (Fig. 3) could be explained by the looser coupling of the prey-predator cycles observed in the simulations (Fig. 4c; Table 1) which favor larger amplitude of the cycles with maximum values 150% higher than the standard run and minimum values 95% lower (Fig. 4e). The poorer correlation between predator and prey biomass (Table 1) accounts for a less efficient transference of primary producers’ biomass to the secondary level (i.e there is lower top-down control in the system). This allows the phytoplankton to use the available resources (inorganic nutrients) more efficiently, and so, a higher amount of inorganic material is converted in organic matter increasing the overall biomass of the system. This is confirmed by the significant (p-value < 0.001) lower amount of nitrogen in inorganic form simulated in these conditions (Fig. 3c) which, taking into account that the total amount introduced is equal to the standard run, could only be explained by a higher consumption by primary producers (i.e the system is mainly controlled by bottom-up processes such as nutrient availability).

This maximum in biomass accumulation, thought not very high, is statistically significant (p-value < 0.001) and is reached for both models at oscillation periods of around
150–170 days (Fig. 3b) corresponding to cycles of two high nutrient concentration phases per year. This annual pattern is typical of temperate latitudes where nutrient availability in a shallow mixed layer is higher in the beginning of spring and in the fall (Mann and Lazier, 2006). The fact that both models described originally the behavior of plankton in mid-latitude systems perhaps could hypothetically explain the good response of the virtual communities to this nutrient input pattern (see the original works of Fasham et al. (1990) and Vichi et al. (2007)) as models parameters could already include a tendency to this semiannual periodicity.

Finally, when nutrient pulses are separated by longer time lags, long periods of nutrient-limiting conditions in the system occur (Fig. 4d). The correlation coefficient between phyto and zooplankton biomass increases (Table 1) and, correspondingly, total biomass tends to decrease (Fig. 3b). At the same time, the amount of free inorganic nutrient within the system is significantly higher (p-value < 0.01) (Fig. 3c) in these conditions than when intermediate oscillation periods are simulated, indicating a less intense bottom-up control of the system dynamics by new nutrient availability. In these simulations there were two very clear different periods, one characterized by high nutrient concentration in the system, and the second by extremely low nutrient availability. During the first half of the simulation (high nutrient), the dynamics of the system could be assimilated into the standard run but with higher nutrient availability. However, during the low nutrient period, the community production pattern changes because of nutrient depletion, so the microbial loop and the regeneration of nutrients become more relevant. Actually, the levels of environmental ammonia in the simulations with periods of 250 and 500 days were 20% and 25% higher respectively compared to the continuous supply reference, evidencing the relatively higher relevance of nutrient regeneration in these low-nutrient conditions.

However, analyzing phyto- and zooplankton separately, some differences could be observed between the two models. The zooplankton behaves in a similar way when using both formulations and follows the general pattern commented above. Also total phytoplankton in the BFM simulations shows a comparable behavior but, in the Fasham90 simulations, phytoplankton does not decrease for longer periods maintaining a high level of biomass accumulation in the simulations with low frequency of nutrient input (Fig. 3a). This pattern is quite similar to that of the nanoflagellates functional group simulated by BFM that reaches a maximum biomass accumulation at intermediate periods and maintains these levels afterwards (Fig. 5a).

The values for both growth (\( V_p \)) and mortality (\( \mu \)) rates of phytoplankton in Fasham90 and those for the nanoflagellates group in BFM are similar (\( V_p = 2.9 \) d\(^{-1}\) and 2.7 d\(^{-1}\) and \( \mu = 0.045 \) d\(^{-1}\) and 0.05 d\(^{-1}\) respectively) which explains the similarity of the observed results. As the initial intention of the Fasham et al. (1990) work was to propose a model for the oceanic station “S” near Bermuda, it is reasonable that the phytoplankton group included in the model matched the parameters of those species more typical of open ocean systems such as small flagellates (Longhurst, 1998) with high surface/volume (S/V) ratio and fast growing rates (Platt and Denman, 1978). This group seems to react positively to
separate periods of high nutrient concentrations because of its rapid response to favorable conditions (due to the higher S/V ratio) and slower decline due to low mortality rates which allow, in the longer term, to maintain high biomass level even with long periods of nutrient depletion.

In spite of the particular differences observed with each model’s formulation an effect of the discontinuity and frequency of nutrient input is clearly shown by the results of the performed simulations (Fig. 3). The concordance of both models reinforces the conclusions derived from the simulations indicating that number and complexity of PFT included in the model does not decisively influence the results. However, the exact value of the biomass difference should be dependent on the particular configuration of the modeling setup including the water residence time, the induced nutrient concentration and the light and temperature conditions.

On the other hand, while the long term fluctuations (i.e. seasonal, annual) could be reasonably simulated with a sinusoidal function, the short term ones could not be assimilated to this pattern as the more usual forcing below the subinertial range is related to tidal and/or atmospheric forcing (Mann and Lazier, 2006) and in these cases inputs are more concentrated in time taking the shape of isolated pulses (McGillicuddy et al., 1998; Sakamoto et al., 2004). Typical examples of isolated pulses to the photic layer are the mixing processes associated with tidal fronts (McGillicuddy et al., 2003), the pulsed interfacial mixing in the Strait of Gibraltar (Macías et al., 2007a) or the intermittent activation and deactivation cycles of the coastal upwellings associated with wind intensity (e.g. Barton and Hughes, 1982; Macías et al., 2007b). This is the kind of situation to be addressed in the so-called tidal mixing simulations.

The first impression from these tidal input simulations is that biomass increase in the ecosystem is higher than obtained with corresponding periods of the sinusoidal inputs (i.e. with an oscillation period around 30 days), both for the phytoplankton and zooplankton compartments and using both model formulations (Figs. 3 and 6). This is also confirmed by the extremely low cross-correlation coefficient between phytoplankton and zooplankton biomass (Table 1) which reveals a strong uncoupling of production-consumption cycles that could account for a higher biomass accumulation for this tidal pattern of supply. This very same pattern was reported by Holt (2008) using theoretical predator-prey models which predict, for a given amount of resources, that shorter pulses lead to a larger total population response. That author also points to the uncoupling between predator and prey as the main reason of the observed biomass increase with shorter and abrupt resource pulses.

This general pattern seems to indicate that the virtual ecological community represented by both models would be better adapted to this kind of pulsed temporal pattern than to the sinusoidal one. As commented above, this first type of input is more usual at short time-scales in the natural environment and is superposed onto sinusoidal-like seasonal patterns leading to a general tendency favoring biomass accumulation.

Also quite noticeable differences could be observed in the biomass distribution between
the different functional groups using the tidal inputs scheme in BFM (Fig. 7) with respect to the sinusoidal supply (Fig. 5) corroborating the prediction that community structure is controlled (to a certain extent) by resource availability (see Anderson et al., 2008). In this simulation some plankton groups (mainly carnivorous mesozooplankton and picophytoplankton) are extremely favored compared to the sinusoidal input. These differences between both simulations could be partially explained in the light of the food matrix of the BFM model (Table 2) that represents the relative preferences of each predator for each food source and is used in the model to weigh the predation pressure over each functional group (e.g. Vichi et al., 2007a). The observed differences could be explained by chained causes such as (i) tidal mixing favors the biological response of diatoms which increase its biomass due to the skills of this group to grow in such environments due to its nutrient storage capabilities (e.g. Grover, 1991), (ii) this increase drives an increment of omnivorous mesozooplankton as diatoms are the main prey for these organisms (see Table 2) which (iii) induce the increase in carnivorous biomass (which prey mainly on the omnivorous, Table 2), (iv) the more abundant mesozooplankton (both omnivorous and carnivorous) provokes an increase in dissolved ammonia which is used by the picophytoplankton to grow actively, explaining its strong shift from −5% (in the sinusoidal simulations) to +5% (in the tidal mixing ones).

In order to test this hypothesis, an additional simulation was performed with the tidal mixing forcing but removing diatoms from the system. In this case all zooplankton groups as well as picophytoplankton present lower biomass with respect to the continuous supply; this result supports the hypothesis of chained causes presented above.

In the final simulations performed, we tried to apply the scheme of intermittent nutrient pulses to a real case of an environment which could be idealized to a chemostat-culture (though of enormous dimensions) such as the NW region of the Alboran Sea (Fig. 2). Nutrient input to this area comes in a great part from the Strait of Gibraltar and shows a strong tidal dependence (e.g. Macías et al., 2006). We have, thereby, tried to roughly represent the photic layer of the NW Alboran Sea as a big tank with a nutrient input behaving as the one predicted by Macías et al. (2007a). The results for the general trophic
groups (Fig. 8) are quite similar to the one found with the tidal mixing simulations (Fig. 6), though the biomass accumulation achieved in the former is half of the latter. The reason for this weaker effect could be the smaller differences of nutrient input between the neap-spring tidal periods in the Alboran Sea simulation (9–32 mmolN/m$^3$) compared to the tidal mixing simulation (0–180 mmolN/m$^3$). We are well aware that the results of these simulations could not be considered as a realistic representation of the Alboran Sea patterns as the external forcing used is extremely unrealistic (see Materials and Methods section). However this simulation exercise serves just to show the fact that considering a realistic nutrient input dynamics (i.e. realistic tidal pulses) in an oceanographic region could significantly change the resulting production levels as well as the community structure of the pelagic ecosystem, independently of seasonal sources of variability (e.g. changes in light doses or water temperature).

b. Comparison with other data

Though we have not performed new experimental work in order to test the predictions of the used models, there is a number of papers in the literature dealing with both mesocosm experiments, field data and models that report effects of discontinuous nutrient input in marine (and freshwater) environments which can be used to discuss and validate the results presented in this work.

i. Laboratory experiments. It is possible to find a number of research work performed in mesocosm enclosures showing the effect of discontinuous nutrient input on the structure and dynamics of the marine food web and that report patterns similar to those obtained in this paper.

Svensen et al. (2002) analyzed the results of several mesocosm experiments that included different treatments with variable nutrient inputs. They found that pulsed inputs led to higher chlorophyll levels and to a higher organic matter export (sedimentation), reaching a maximum for a periodicity of the nutrient supply of 10–30 days. With a lower frequency of inputs, the chlorophyll levels fell down again showing a pattern quite similar to that obtained in this paper when using the sinusoidal input pattern (Fig. 3). There are, however, differences in the periods of maximum biomass between the experimental work (10–30 days) and our sinusoidal simulations (150–190 days). These differences could be partially explained by variation in the methodological treatment of nutrient addition between the experimental work and the simulations presented in this work. In the former, no nutrients were added during a number of days, and instantaneous additions were made at specific times. This is clearly different to the settings of sinusoidal simulations presented in this work as in this case, there is a continuous renewal of water from the mesocosm with a slowly changing nutrient concentration in the inflow. However, it is noticeable that, in spite of these methodological differences, the general patterns of biomass levels with respect to nutrient addition frequency are very close in the experiments and in the simulations.
In this same work, Svensen et al. (2002) reported a shift in the phytoplankton community composition was observed with the discontinuous nutrient inputs, with an increase of the relative biomass of flagellates. This observation coincides with predictions of the BFM model, the nanoflagellates being the most favored functional group (Fig. 5a) when simulating a discontinuous nutrient supply.

Also Cottingham and Schindler (2000) analyzed the influence of the zooplankton size structure on the response of phytoplankton to pulsed nutrient inputs and concluded that total biomass of the system (phyto- plus zooplankton) and average individual size of zooplankton increases when nutrients were discontinuously supplied to the system (20–30 days period) agreeing, thereby, with the predictions of the BFM model (Figs. 3 and 5).

**ii. Field data.** Testing the effect of discontinuous nutrient input on real ecosystems is a more difficult task, since they cannot be controlled, as is the case of mesocosm experiments. However, our modeling work can help to explain and understand different patterns found in field data.

One of the more ubiquitous features in the ocean is the presence of deep (or subsurface) chlorophyll maximum (DCM) (Herbland and Voituriez, 1979; Longhurst and Harrison, 1989; Li, 1994). However, the mechanisms that control the origin and position of DCMs are still unclear (see Cullen, 1982; Varela et al., 1992) the competition between light and nutrient availability being the most likely (Klausmeier and Litchman, 2001). Under oligotrophic conditions, the DCM is usually deeper and presents lower chlorophyll concentration than under more productive conditions (Li, 1994). In this poor-nutrients environment small cells usually dominate the DCM assemblage (Bienfang and Szyper, 1981; Ruiz et al., 1996) which has been usually related to better light and nutrient efficiency of such small cells, as photoadaptation can be expected to be relevant (Li and Wood, 1988; Platt et al., 1983). However, another characteristic of these deep environments is that nutrient supply through the nutricline is a slow and continuous process associated with the diffusion mechanisms (Longhurst, 1998). The simulations presented in this work predict a competitive advantage of smaller cells (such as picophytoplankton) with a continuous or a high frequency nutrient supply (Fig. 5a) which could be another mechanism helping to explain the pattern found in these DCMs.

This same effect could help to explain a macroecological pattern of pico- and microplankton distribution found in many different ecosystems such as the North Atlantic Ocean (Li, 2002), the Oregon upwelling system (Sherr et al., 2005) or the southern Iberia coast (Echevarría et al., 2009). All these authors found a negative (positive) relationship between picoplankton (microplankton) biomass and chlorophyll concentration. In all the cases, the higher chlorophyll concentrations correspond to upwelling areas mainly controlled by wind fluctuations that usually show a subinertial (few weeks) scale of variability (Koracin et al., 2004; Pickett and Schwing 2006). In this range of nutrient input oscillation, the BFM model (Fig. 5a) shows a predominance of cells larger than picophytoplankton. In fact, the phytoplankton fractions most affected by the change of period are diatoms and picophyto-
plankton (the smallest one) that show a clear antagonism with a selection for diatoms for shorter periods and the reverse for periods larger than 8 months. Actually this model result shows a shift to a microbial food web for larger periods of nutrient inputs with a decrease especially marked for mesozooplankton and diatoms (Fig. 5). A similar pattern was found by Rodriguez et al. (1998) in the DCM associated with the anticyclonic and cyclonic gyres of the Alboran Sea. They found that the slope of the log-log size spectra was less negative (more abundance of bigger cells) under the cyclonic gyres than under the anticyclonic ones. The former are characterized by higher nutrient supply to the photic layer and by a higher temporal variability in its horizontal and vertical structure (La Violette, 1984; Macías et al., 2007b) while the latter are usually more stable in time and nutrient supply to the upper layer usually occurs mainly by a slow diffusion process across the nutricline. These patterns agree quite well with the predictions of the models as commented in the previous paragraphs.

Also, changes in the lower trophic level composition should have consequences on the higher ones as plankton organisms’ sizes determine the flow of energy and material through the food web (Smetacek, 1999). In this sense, Rykaczewski and Checkley (2008) reported a relationship in the dominance of two species of small pelagic fish (sardine and anchovy) in the California current ecosystem and the predominant upwelling mechanism (coastal-upwelling and wind-curl upwelling). The less-intense but more constant wind-curl upwelling induces smaller phytoplankton cells and zooplankton organisms which are more suitable as food for sardine (which are mainly filter-feeding). On the other hand, the more-intense, located and intermittent coastal upwelling favors larger phyto- and zooplankton which are more adequate for the anchovy bite-feeding strategy. The same general pattern is shown by the BFM model and reflected in Figure 5 for the sinusoidal simulations and in Figure 7 for tidal mixing; intermittent and localized (in time) pulses of nutrients favor the growing of bigger zooplankton organisms.

iii. Modeling works. As previously stated in the introduction, most models in which a variable nutrient input has been considered, have been implemented to represent specific locations subjected to a strong temporal variability such as coastal areas (Pace et al., 1984; Lancelot et al., 2007; Carniel et al., 2007), estuaries (Duarte et al., 2008), bays (Tanaka and Mackenzie, 2005) or lagoons (Plus et al., 2006; Marinov et al., 2008). In none of these works, however, analytical comparisons of the ecosystem state simulating different patterns of external forcing and nutrient supply have been made, as all these models were created to represent the actual behavior of the different ecosystems using the most realistic external conditions available.

Nevertheless, in a very recent work, Litchman et al. (2009) developed a phytoplankton competition model for diatoms to test the effect of temporal heterogeneities on the structure of the community. They found that discontinuous nutrient inputs to the system select larger cell sizes compared with an equivalent continuous supply pattern. For these authors this could be the reason for the relatively larger diatom size in marine ecosystems
with respect to freshwater environments as the former are usually more variable in time than the latter. This same effect had also been reported by Verdy et al. (2009) using a generic phytoplankton model, which shows that a constant environment selects for smaller sizes. Again, our own results fit well with these previous works as larger cells (as diatoms) are one of the most favored functional groups both with the sinusoidal pattern (Fig. 5a) and in the Alboran Sea application (Fig 9a).

5. Concluding remarks

In spite of the differences between simulations and/or model formulation described in the previous paragraphs, a clear effect of nutrient supply dynamics on the productivity of marine ecosystem has been established. In the performed simulations, environmental conditions were set as extremely favorable (both light and temperature) and total amount of nutrient supplied to the system was nearly invariable. With these conditions, only the temporal dynamics of nutrient availability in the system is able to create differences of the produced biomass on the order of 5%. So, in order to assess the potential productivity of an ecosystem, not only the total amount of nutrient supplied to the system must be taken into account, but also the frequency and temporal dynamics of such inputs. Our results point to the degree of coupling between the predator-prey biomass cycles as the most probable cause of changes observed in the virtual ecosystem. It has been shown that with two high nutrient periods per year (seasonal scale frequency) the cycles become more uncoupled and so, phytoplankton can transform more quantity of inorganic nutrients into biological material explaining, thereby, the higher overall biomass of the system. As the general rule in natural systems is the discontinuity of nutrient inputs at very different scales, this work has shown theoretically the importance of considering these dynamics for assessing biomass/production levels and/or ecosystem structure in future work.

Also, our results have shown a clear effect not only on biomass yield, but on the community structure as some of the functional groups seem to be more favored than others depending on the nature of pulsed inputs. This has consequences on trophic web dynamics as energy flow would be more or less efficient depending on the biomass distribution between groups (Smetacek, 1999). For example, Pauly and Christensen (1995) proposed that the high fish biomass in upwelling systems is due not only to the high system’s productivity but also because of the temporal discontinuity in nutrient supply, which favours short and redundant food webs. Also, estuarine systems usually have short food web and high energy flows (Baird and Ulanowickz, 1993; Rybarczyk and Elkaim, 2003) which has been related with the variable and pulsed nutrient input to such systems (Lobry et al., 2008). These are but a few examples of the importance of assessing nutrient input dynamics to marine ecosystems.

In conclusion, the use of numerical models as the ones presented here to simulate and study the emergent properties of marine communities, has clearly demonstrated that not only the total amount of nutrient entering the system but the frequency pattern of its input
should be taken into account when analysing the structure of pelagic communities and its connection with hydrodynamic, meteorological and climatological processes.

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APPENDIX

Model parameters and formulations of the modified Fasham model used in the work

a. Model variables and parameters

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Name</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>P</td>
<td>Phytoplankton state variable</td>
<td>State variable</td>
<td></td>
</tr>
<tr>
<td>Z</td>
<td>Zooplankton state variable</td>
<td>State variable</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>Bacteria state variable</td>
<td>State variable</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>Detritus state variable</td>
<td>State variable</td>
<td></td>
</tr>
<tr>
<td>Nn</td>
<td>Nitrte</td>
<td>State variable</td>
<td></td>
</tr>
<tr>
<td>Nr</td>
<td>Ammonia.</td>
<td>State variable</td>
<td></td>
</tr>
<tr>
<td>Nd</td>
<td>DON</td>
<td>State variable</td>
<td></td>
</tr>
<tr>
<td>l</td>
<td>PAR fraction of solar radiation</td>
<td>0.43</td>
<td>Fasham et al., 1990</td>
</tr>
<tr>
<td>a</td>
<td>Air-sea albedo</td>
<td>0.05</td>
<td>Fasham et al., 1993</td>
</tr>
<tr>
<td>oktas</td>
<td>Cloud cover (0–8)</td>
<td>Default: 3</td>
<td>Standard value</td>
</tr>
<tr>
<td>Kw</td>
<td>Attenuation coefficient of water</td>
<td>0.04 m⁻¹</td>
<td>Fasham et al., 1990</td>
</tr>
<tr>
<td>I0</td>
<td>Incident light</td>
<td>1000 (W/m²)</td>
<td>Standard value</td>
</tr>
<tr>
<td>Vp</td>
<td>Phytoplankton maximum growing rate</td>
<td>Temperature dependent</td>
<td>Eppley, 1972</td>
</tr>
<tr>
<td>a</td>
<td>Initial slope of P-I curve</td>
<td>0.05 (Wm⁻²)⁻¹ d⁻¹</td>
<td>Fasham et al., 1993</td>
</tr>
<tr>
<td>k₁</td>
<td>Half saturation constant for nitrate uptake</td>
<td>0.5 mmol m⁻³</td>
<td>Fasham et al., 1990</td>
</tr>
<tr>
<td>k₂</td>
<td>Half saturation constant for ammonium uptake</td>
<td>0.5 mmol m⁻³</td>
<td>Gruber et al., 2006</td>
</tr>
<tr>
<td>mu₁</td>
<td>Maximum phytoplankton mortality rate</td>
<td>0.024 d⁻¹</td>
<td>Gruber et al., 2006</td>
</tr>
<tr>
<td>kₖ</td>
<td>Self-shading coefficient</td>
<td>0.03 (mMol N)⁻¹</td>
<td>Fasham et al., 1990</td>
</tr>
<tr>
<td>γ</td>
<td>Fraction of PP exuded as DON</td>
<td>0.05</td>
<td>Fasham et al., 1990</td>
</tr>
<tr>
<td>psi</td>
<td>Nitrate uptake inhibition (by ammonium)</td>
<td>1.5 (mMol N)⁻¹</td>
<td>Fasham et al., 1990</td>
</tr>
<tr>
<td>g</td>
<td>Maximum zooplankton ingestion rate</td>
<td>0.6 d⁻¹</td>
<td>Fennel et al., 2006</td>
</tr>
<tr>
<td>Symbol</td>
<td>Name</td>
<td>Value</td>
<td>Source</td>
</tr>
<tr>
<td>--------</td>
<td>-------------------------------------------</td>
<td>----------------</td>
<td>-------------------------------</td>
</tr>
<tr>
<td>(\beta)</td>
<td>Zooplankton ingestion efficiency</td>
<td>0.75</td>
<td>Fasham et al., 1990</td>
</tr>
<tr>
<td>(mu_2)</td>
<td>Zooplankton maximum excretion rate</td>
<td>0.1 d(^{-1})</td>
<td>Fasham et al., 1990</td>
</tr>
<tr>
<td>(mu_5)</td>
<td>Zooplankton maximum mortality rate due to consumption</td>
<td>0.05 d(^{-1})</td>
<td>Fasham et al., 1990</td>
</tr>
<tr>
<td>(k_3)</td>
<td>Zooplankton ingestion half saturation constant</td>
<td>3.0 d(^{-1})</td>
<td>Olivieri and Chavez, 2000</td>
</tr>
<tr>
<td>(\delta)</td>
<td>Fraction of zooplankton losses to DON</td>
<td>0.2</td>
<td>Fasham et al., 1993</td>
</tr>
<tr>
<td>(Vb)</td>
<td>Bacterial maximum growth rate</td>
<td>2.0 d(^{-1})</td>
<td>Fasham et al., 1990</td>
</tr>
<tr>
<td>(mu_3)</td>
<td>Bacterial maximum loss rate</td>
<td>0.05 d(^{-1})</td>
<td>Fasham et al., 1990</td>
</tr>
<tr>
<td>(k_4)</td>
<td>Bacterial uptake half saturation constant</td>
<td>0.5 mmol N m(^{-3})</td>
<td>Fasham et al., 1990</td>
</tr>
<tr>
<td>(n_u)</td>
<td>DON:ammonium uptake ratio</td>
<td>0.6</td>
<td>Fasham et al., 1990</td>
</tr>
<tr>
<td>(mu_4)</td>
<td>Detritus maximum breakdown rate</td>
<td>0.05 d(^{-1})</td>
<td>Fasham et al., 1990</td>
</tr>
<tr>
<td>(k_5)</td>
<td>Half saturation constant of phytoplankton mortality</td>
<td>0.2</td>
<td>Popova et al., 1997</td>
</tr>
<tr>
<td>(k_6)</td>
<td>Half saturation constant of zooplankton mortality</td>
<td>0.2</td>
<td>Popova et al., 1997</td>
</tr>
<tr>
<td>(p_1)</td>
<td>Zooplankton preference for phytoplankton</td>
<td>0.5</td>
<td>Fasham et al., 1990</td>
</tr>
<tr>
<td>(p_2)</td>
<td>Zooplankton preference for bacteria</td>
<td>0.25</td>
<td>Fasham et al., 1990</td>
</tr>
<tr>
<td>(p_3)</td>
<td>Zooplankton preference for detritus</td>
<td>0.25</td>
<td>Fasham et al., 1990</td>
</tr>
</tbody>
</table>

b) Process equations

Phytoplankton (P):

\[
\frac{dP}{dt} = ((1 - \Omega) \ast J \ast Q \ast P) - G_1 - m_1 - P \ast \left( \frac{\text{flux}}{V} \right); \quad (A.1)
\]

where:

\[
J = \log\left(\frac{\sqrt{J_0^2} + Vp^2 + I_0^2 \ast (Vp \ast a \ast I_0)}{\sqrt{J_0^2} \ast (k_w + (k_c \ast P))} \right)
- \log\left(\frac{\sqrt{J_0^2} \ast e^{-(k_w + k_c \ast P)}}{\sqrt{J_0^2} \ast (k_w + (k_c \ast P))} \ast (Vp \ast a \ast I_0) \right); \quad (A.2)
\]
where:

\[ V_p = 0.6 \times (1.066^T) \]  \quad \text{(A.3)}

with \( T \) in °C.

\[ Q = Q_1 + Q_2; \]  \quad \text{(A.4)}

being:

\[ Q_1 = N_n \frac{e^{-\psi N_r}}{(k_1 + N_n)}; \]  \quad \text{(A.4a)}

\[ Q_2 = \frac{N_r}{(k_2 + N_r)}; \]  \quad \text{(A.4b)}

\[ G_1 = \frac{g \times Z \times p_1 \times p^2}{k_S \times F + F^2}; \]  \quad \text{(A.5)}

being:

\[ F = (p_1 \times P) + (p_2 \times B) + (p_3 \times D); \]  \quad \text{(A.5a)}

\[ F = (p_1 \times P^2) + (p_2 \times B^2) + (p_3 \times B^2); \]  \quad \text{(A.5b)}

\[ m_1 = \mu_1 \times \frac{p^2}{(k_S + P)}; \]  \quad \text{(A.6)}

and flux states for the incoming/outcoming water flux to the simulated box.

Zooplankton (Z):

\[ \frac{dZ}{dt} = (\beta \times (G_1 + G_2 + G_3) - m_2 - m_3) - Z \times \left( \frac{\text{flux}}{V_t} \right); \]  \quad \text{(A.7)}

w:

\[ G_1 = \text{defined above}; \]

\[ G_2 = \frac{g \times Z \times p_2 \times B^2}{k_S \times F + F^2}; \]  \quad \text{(A.8)}

\[ G_3 = \frac{g \times Z \times p_S \times D^2}{k_S \times F + F^2}; \]  \quad \text{(A.9)}

\[ m_2 = \mu_2 \times \frac{Z^2}{(k_6 + Z)}; \]  \quad \text{(A.10)}

\[ m_5 = \mu_5 \times Z^2; \]  \quad \text{(A.11)}
Bacteria (B):

\[
\frac{dB}{dt} = (U_1 + U_2 - G_2 - m_3) - B*\left(\frac{\text{flux}}{V_t}\right); \quad (A.12)
\]

where:

\[
U_1 = B*\frac{Vb*Nd}{k_4 + S + Nd}; \quad (A.13)
\]

\[
U_2 = B*\frac{Vb*S}{k_4 + S + Nd}; \quad (A.14)
\]

being:

\[
S = \min(Nr, nu*Nd); \quad (A.14a)
\]

\[
G_2 = \text{defined above};
\]

\[
m_3 = mu_3*B; \quad (A.15)
\]

Detritus (D):

\[
\frac{dD}{dt} = ((1 - \beta)*(G_1 + G_2) - \beta*G_3 - m_4 + m_1) - D*\left(\frac{\text{flux}}{V_t}\right); \quad (A.16)
\]

where:

\[
m_4 = mu_4*D; \quad (A.17)
\]

and all other parameters have been described elsewhere.

Nitrate (Nn):

\[
\frac{dNn}{dt} = \left(\frac{\text{in Nn*flux}}{V_t}\right) - (J*Q_1*P) - Nn*\left(\frac{\text{flux}}{V_t}\right); \quad (A.18)
\]

where:

\text{in Nn} is the nitrate concentration in the incoming flux.

Ammonium (Nr):

\[
\frac{dNr}{dt} = -(J*Q_2*P) - U_2 + m_3 + (1 - \delta)*m_2 - Nr*\left(\frac{\text{flux}}{V_t}\right); \quad (A.19)
\]

DON (Nd):

\[
\frac{dNd}{dt} = -U_1 + (\gamma*J*Q*P) + m_4 + (\delta*m_2) - Nd*\left(\frac{\text{flux}}{V_t}\right). \quad (A.20)
\]
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