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Modelling the Impact of Microbial Loop on Aquatic Food Webs

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Abstract: In order to control algal blooms, it is necessary to better understand microbial interactions in aquatic ecosystems. Based on the traditional 'Nutrients-Phytoplankton-Zooplankton-Detritus' (NPZD) model, the 'Nutrients-Phytoplankton-Zooplankton-Detritus+Bacteria' (NPZD+B) model has been developed to investigate the impact of the microbial loop on aquatic food webs via nutrient cycling processes. The results of the NPZD+B model showed the positive impact of the microbial loop on phytoplankton growth, and illustrated the importance of 'bottom-up' (resource) control of algal blooms in aquatic ecosystems. The study concludes that the microbial loop is an important model component for simulating water quality dynamics when nutrients are limited in water bodies. The NPZD+B model provides an improved mechanistic understanding of bacteria-phytoplankton interactions in aquatic ecosystems.

Keywords: microbial loop; algal blooms; ecological modelling; aquatic ecosystems.

1. BACKGROUND

Complex microbial interactions in aquatic ecosystems result in diverse planktonic patterns (Li et al., 2012; Li et al., 2013a). The 'microbial loop' concept has been proposed as a key component to describe the complex interactions between microzooplankton and bacteria in aquatic ecosystems, which implies a strong modification of the classical aquatic food web 'nutrients-phytoplankton-zooplankton' paradigm (Azam et al., 1983; Moore et al., 2004).

Conventionally, bacteria mainly remineralize organic matter (Ferrier and Rassoulzadegan 1994, Vadstein 2000). However, bacteria can also compete with phytoplankton for inorganic nutrients (Currie and Kalff 1984, Cotner and Wetzel 1992; Kirchman, 1994). Under nutrient limiting conditions, bacteria compete with phytoplankton for inorganic nutrients, and indirectly limit the primary production of phytoplankton (Joint and Morris, 1982). Microzooplankton graze on bacteria in the microbial loop (Thingstad and Lignell, 1997). Under these conditions, nutrient availability for phytoplankton becomes complicated by nutrient recycling processes (Li et al., 2013b). In particular, when phytoplankton and bacteria compete for the same limiting inorganic nutrients, zooplankton consumption of bacteria results in an increase of phytoplankton biomass (Bratbak and Thingstad, 1985; Brussaard and Riegman, 1998), instead of a decline in phytoplankton biomass (Joint et al., 2002).

In this study, we develop the deterministic 'Nutrients-Phytoplankton-Zooplankton-Detritus+ Bacteria' (NPZD+B) model using fixed literature values for the relevant parameters to investigate the impact of the microbial loop on aquatic food webs, especially phytoplankton growth.

2. METHODS

2.1. Model structures

NPZD: The original ‘Nutrient-Phytoplankton-Zooplankton’ (NPZ) models are universal research tools in oceanography because they incorporate one of the simplest sets of oceanic plankton dynamics (Franks, 2002). Edwards (2001) has added the detritus component into the NPZ models to form the four compartment model ‘Nutrient-Phytoplankton-Zooplankton-Detritus’ (NPZD) model. This model consists of seven processes, especially remineralisation (Figure 1a).

NPZD+B: The ‘Nutrient-Phytoplankton-Zooplankton-Detritus+Bacteria’ (NPZD+B) model incorporated the bacterial compartment into the NPZD model to investigate how the microbial interactions between the heterotrophic bacteria and the microzooplankton grazers influence phytoplankton growth via nutrient recycling processes (Figure 1b). Here we divided zooplankton compartment into two sub-compartments: one was the normal zooplankton group (Z_1), which only grazed on phytoplankton; the other was the microzooplankton group (Z_2), which only grazed on bacteria.

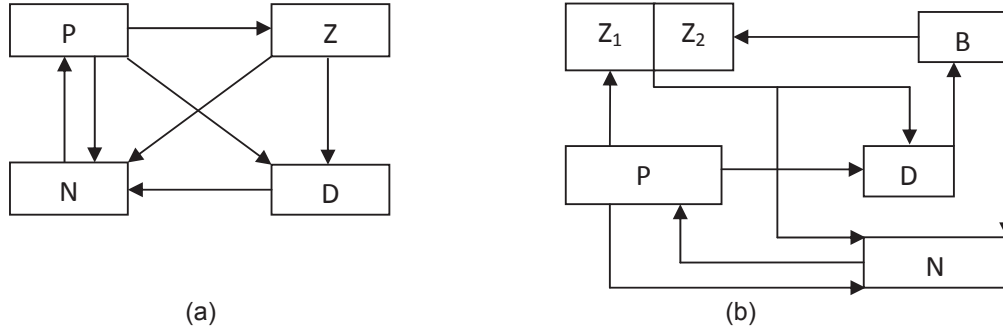


Figure 1. Structure of the NPZD model (a) and the NPZD+B model (b) (Note that P refers to phytoplankton; N refers to nutrients; B refers to the bacterial functional group; D refers to bacteria/fungi-coated detritus; Z_1 refers to normal zooplankton group; Z_2 refers to microzooplankton group).

2.2. Model parameterisation

The compartments and fluxes in the NPZD model and the NPZD+B model were summarised as follows: the nutrient uptake by phytoplankton was based on Michaelis–Menten kinetics, which was limited by light and nutrient availability; all other processes were based on linear first-order kinematics. The equations of these models were compared in Table 1; their modelling parameters were summarised in Table 2.

Nutrient uptake for phytoplankton growth (d_{np})

$$d_{np} = r_{\max} \frac{I_{PAR}}{I_{opt}} \exp\left(1 - \frac{I_{PAR}}{I_{opt}}\right) \frac{N}{\alpha + N} P \text{ with } I_{opt} = \max\left(\frac{1}{4} I_{PAR}, I_{\min}\right) \quad (1)$$

$$\text{Phytoplankton excretion (} d_{pn} \text{)} \quad d_{pn} = r_{pn} P \quad (2)$$

$$\text{Phytoplankton mortality (} d_{pd} \text{)} \quad d_{pd} = m_p P \quad (3)$$

$$\text{Remineralisation of detritus into nutrients (} d_{dn} \text{)} \quad d_{dn} = r_{dn} D \quad (4)$$

$$\text{Zooplankton production (} d_{pz} \text{)} \quad d_{pz} = p_{\max} (1 - \exp(-I_v^2 P^2)) Z \quad (5)$$

$$\text{Zooplankton excretion (} d_{zn} \text{)} \quad d_{zn} = r_{zn} Z \quad (6)$$

$$\text{Zooplankton mortality (} d_{zd} \text{)} \quad d_{zd} = m_z Z \quad (7)$$

$$\text{Bacterial production (} d_{db} \text{)} \quad d_{db} = \mu_B \frac{B}{B + K_B} D \quad (8)$$

Bacterial grazed by microzooplankton (d_{bz})
$$d_{bz} = g_r \frac{B}{K_z + B} B \tag{9}$$

Bacterial excretion (d_{bn})

$$d_{bn} = K_{Be} d_{db} \tag{10}$$

Table 1. The equations for key plankton variables in the NPZD model and the NPZD+B model.

	NPZD	NPZD+B
P	$\frac{dP}{dt} = d_{np} - d_{pn} - d_{pd} - d_{pz}$	$\frac{dP}{dt} = d_{np} - d_{pn} - d_{pd} - d_{pz_1}$
Z	$\frac{dZ}{dt} = d_{pz} - d_{zd} - d_{zn}$	$\frac{dZ_1}{dt} = d_{pz_1} - d_{z_1d} - d_{z_1n}$ $\frac{dZ_2}{dt} = d_{bz_2} - d_{z_2d} - d_{z_2n}$
N	$\frac{dN}{dt} = d_{dn} + d_{zn} - d_{np}$	$\frac{dN}{dt} = d_{bn} + d_{pn} + d_{z_1n} + d_{z_2n} - d_{np}$
D	$\frac{dD}{dt} = d_{pn} + d_{pd} + d_{zd} - d_{dn}$	$\frac{dD}{dt} = d_{pn} + d_{pd} + d_{z_1d} + d_{z_2d} - d_{db}$
B	Null	$\frac{dB}{dt} = d_{db} - d_{bn} - d_{bz_2}$

Table 2. The parameters for the NPZD model and the NPZD+B model.

Description	Symbol	Unit	NPZD	NPZD+B	Literature review
Maximum grazing rate on phytoplankton	p_{max}	d^{-1}	0.2	0.2	1 ^[2] 0.5 ^[3]
Zooplankton excretion rate	r_{zn}	d^{-1}	0.01	0.01	0.01 ^[3]
Zooplankton mortality rate	m_z	d^{-1}	0.02	0.02	0.02-0.07 ^[1] 0.3 ^[2] 0.02 ^[3]
maximum nutrient uptake rate	r_{max}	d^{-1}	1.0	1.0	0.35-3.6 ^[1] 0.5-1.5 ^[2] 0.24-4.56 ^[4]
minimum photosynthetically active radiation (PAR)	I_{min}	W/m ²	25	25	25 ^[3]
phytoplankton mortality rate	m_p	d^{-1}	0.02	0.02	0.02 ^[3]
phytoplankton excretion rate	r_{pn}	d^{-1}	0.01	0.01	0.01 ^[3]

mineralization rate	r_{dn}	d^{-1}	0.007	Null	0.003 ^[3]
half saturation constant	α	$mmol\ N\ m^{-3}$	1.35	1.35	1.35 ^[3]
Ivlev constant	I_v		1.1	1.1	1.1 ^[3]
maximum bacterial DOM uptake rate	μ_B	d^{-1}	Null	0.1	0.05 ^[1] 13.3 ^[2]
DOM excretion	K_{Be}	d^{-1}	Null	0.7	0.7 ^[1]
half saturation constant for bacteria function	K_B	$mmolN\ m^{-3}$	Null	0.97	0.97 ^[1]
grazing rate on bacteria	g_r	d^{-1}	Null	9	0.9 ^[1]
Half saturation constant for grazing	K_z	$mmolN\ m^{-3}$	Null	145.8	145.8 ^[1]

[1] Gal et al. (2009); [2] Van den Meersche et al. (2004); [3]Burchard et al. (2005); [4] Pollinger and Berman (1982); [5] Rhodes and Martin (2010); [6]Heldal and Bratbak (1991); [7]Steward et al. (1996)

2.3. Model setup

A simple 0D model was employed in the Framework for Aquatic Biogeochemical Models (FABM). The seasonality was captured using available field temperature and light data obtained from Lake Kinneret (Israel) from January 1st 1997 to December 31st 1997. All simulations were carried out with a time step of 12 h. The model employs several ODE solvers, and the simplest Euler's method was employed here.

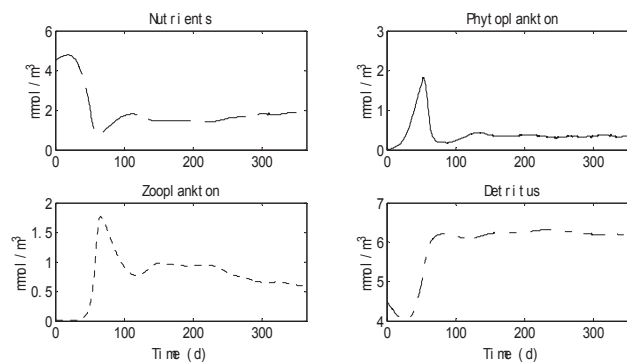
2.4. Analysis approach

The key biological variables (bacteria, phytoplankton, zooplankton) and the nutrient pools (nutrient, detritus) were simulated and analyzed in a phase space. To determine the influence of model structure on key nutrient pathways the nutrient fluxes were averaged over one year.

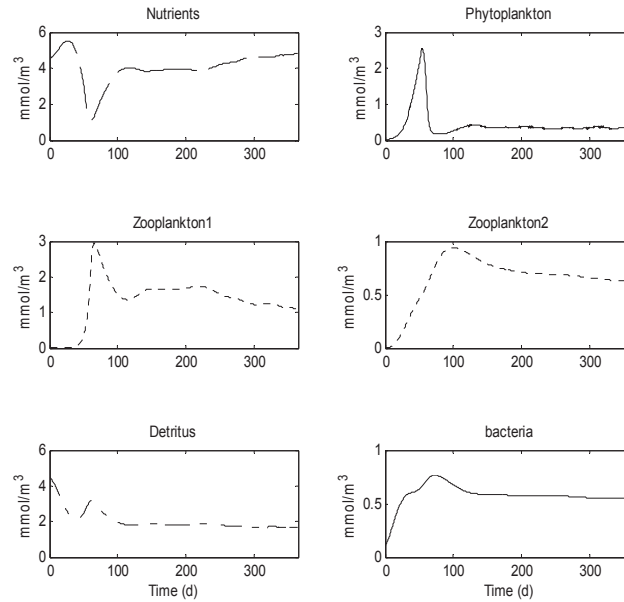
3. RESULTS

3.1. Model simulation

There were some differences in trends and magnitudes of biological variables between the NPZD model and the NPZD+B model (Figure 2). The peak of phytoplankton growth was both captured in the NPZD model and the NPZD+B model. However, the peak of phytoplankton growth in the NPZD+B model was higher than the peak in the NPZD model, which was relevant to the impact of the microbial loop on primary production.



(a)

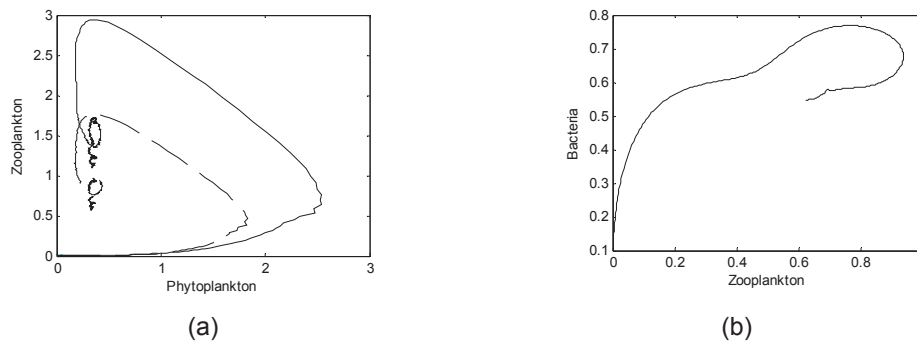


(b)

Figure 2. Simulated results of the NPZD model (a) and the NPZD+B model (b).

3.2. Phase space analysis

The ecosystem relationship in the NPZD model and the NPZD+B model showed the interaction between phytoplankton, zooplankton, and bacteria. The trajectories of phytoplankton vs. zooplankton in the NPZD model and the NPZD+B model moved into a single point in phase space (Figure 3a). When the phytoplankton biomass increased fast, the zooplankton biomass increased slowly. When phytoplankton stopped increasing at around 2 mmol/m³ in the NPZD model and 2.5 mmol/m³ in the NPZD+B model and began to decrease, the zooplankton increased fast. Later when zooplankton reached at the range of 1.5-2 mmol/m³ in the NPZD model or 2.5-3 mmol/m³ in the NPZD+B model, phytoplankton stopped decreasing and zooplankton also correspondingly decreasing very fast. This reflects the predation relationship between phytoplankton and zooplankton in the traditional food web chain. When the microbial loop was included, the phytoplankton vs. zooplankton relationship of NPZD+B was larger than that of NPZD, which illustrates that the microbial loop plays a positive effect on the primary production. The trajectory of zooplankton vs. bacteria in the NPZD+B model was approaching a constant (Figure 3b), which reflects the predation relationship between bacteria and microzooplankton in the microbial loop.



(a)

(b)

Figure 3. Ecosystem relationships between phytoplankton and zooplankton (a); bacteria and zooplankton (b) (dash line refers to the NPZD model; solid line refers to the NPZD+B model).

3.3. Nutrient fluxes

When bacterial compartment was incorporated into the NPZD models, the microbial loop had a significant influence on mineralization and the zooplankton pool (Figure 4). In the NPZD+B model, the bacterial mineralization increased to 120.1% compared to the other mechanisms, such as zooplankton grazing on bacteria (34.1%) and zooplankton excretion (31.9%) (Figure 4b), which is the primary mechanism of the microbial loop influencing the phytoplankton growth.

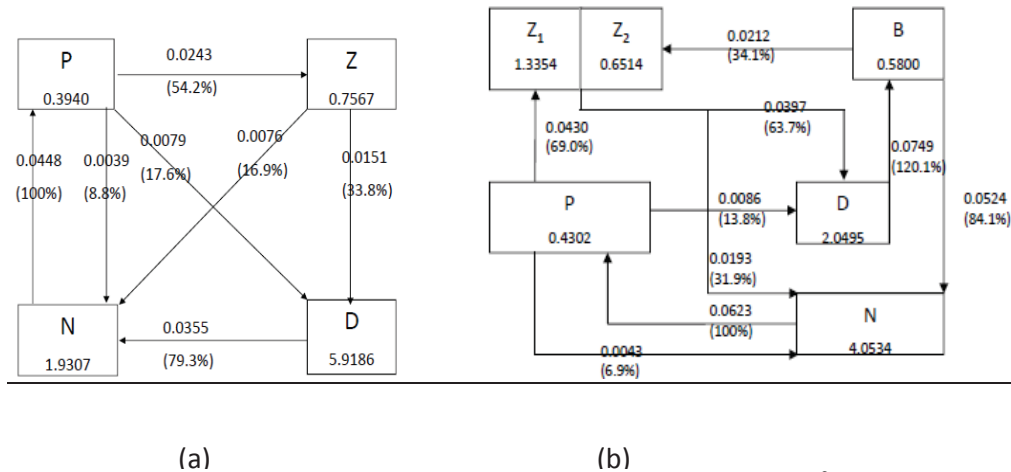


Figure 4. Summary of simulated annual average fluxes and variables (mmol/m^3) for the NPZD model (a) and the NPZD+B model (b).

4. DISCUSSION

The microbial loop has been incorporated into the NPZD model to explore the interactions between different plankton populations (esp., bacteria and phytoplankton). The NPZD+B model for the microbial loop showed the magnitude of the peak of phytoplankton in NPZD+B was larger than the magnitude of the peak of phytoplankton growth in the NPZD model, which indicates that the microbial loop has a positive impact on the primary production of phytoplankton. According to the indirect mutualism theory (Boucher et al., 1982; Stone, 1990), the paradox results from the following conditions: (1) microzooplankton graze on bacteria, which has a negative effect to bacteria; (2) phytoplankton excrete organic matter that may stimulate bacterial growth, which has a positive effect to bacteria; (3) bacteria compete with phytoplankton for inorganic nutrients, which has a negative effect to phytoplankton. Through the (1) and (3) double negative interactions the microbial loop resulted in a net positive impact on phytoplankton primary production. These interactions highlight the importance of the microbial loop on developing algal blooms. When the microbial loop has significant impact on aquatic food webs, such as Lake Kinneret (Hart et al., 2000; Hambright et al., 2007), the ecological models based on the NPZD+B modelling framework can capture the planktonic dynamics successfully (Gal et al., 2009; Makler-Pick et al., 2011; Li et al., 2013a).

The results presented in the paper are highly depending on the choice of parameter values. In the future, the Bayesian approach that combines a description of the state-of-the-art knowledge about parameter values will be applied with measured data to infer the significance of the microbial loop processes in the modeled system. It is also important to consider predation between carnivorous zooplankton, microzooplankton and bacterivorous heterotrophic nanoflagellates. So we can define quantitatively how these microbial interactions influence on phytoplankton growth in aquatic ecosystems, especially the role of the microbial loop on regulating the nutrient fluxes between bacteria, phytoplankton, and zooplankton to shape phytoplankton succession patterns in aquatic ecosystems.

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