

Ecosystem simulation modeling of nitrogen dynamics in the restored lake Karla in Greece

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ABSTRACT

Restored lakes are complex dynamic ecosystems. Ecosystem-level modeling of the processes that take place in a lake is a useful tool for understanding lake function and structure and for making predictions. A nitrogen dynamics model for the lake currently undergoing restoration in the area of Karla in Greece is presented. The model includes the area's hydrology and geomorphology and is used to explore the role of different lake structures and functions on nitrogen dynamics in the restored ecosystem, in order to provide a better understanding of the processes involved in nutrient retention by the lake. Seven forms of nitrogen are included in the model: ammonium, nitrite/nitrate, organic, nitrogen stored in algae and macrophytes, and nitrogen stored in active and deep sediments. The processes of ammonification, remineralization, nitrification, denitrification and sedimentation are mathematically modeled using equations from the literature adjusted to the hydrology and special conditions of lake Karla. Results show that most of the incoming nitrogen is sequestered by the lake, while 6.7% of it gets lost in the atmosphere through denitrification. Primary producers play an important role in nitrogen cycling in the lake, while an important part of the nutrient is stored away permanently in deep sediments.

Keywords: Restored lake; Nitrogen; Ecological modeling; Mathematical modeling

1. Introduction

Wetlands are lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface, or the land is covered by shallow water [1]. They store water that can be used for irrigation or for other uses, while they protect from flooding the crops and the inhabited areas downstream. Wetlands are invaluable ecosystems because of the many beneficial properties they have. They regulate the climate of the greater area surrounding them, limiting extreme weather

phenomena. The water, plants and soil in wetlands retain carbon dioxide from the atmosphere, thus helping reduce the greenhouse effect. Wetlands naturally clean the water that flows through them; Mitsch and Gosselink [2] call wetlands the "kidneys" of the earth, as they retain phosphorus, nitrogen and heavy metals from the water as well as pesticides, insecticides and other toxic substances.

Since they can be sinks for almost any chemical, applications of restored wetlands are quite varied, with thousands of applications worldwide treating domestic wastewater, mine drainage, nonpoint source pollution, stormwater runoff, landfill leachate and livestock operations [3]. Wetland and lake restoration require particular

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attention to hydrology, chemical loading, soil physics and chemistry, and area vegetation [4]. Nutrient removal by wetlands is attributed to shallow low-velocity water that allows maximum nutrient absorption and settling, high primary productivity that leads to high nutrient uptake, a combination of aerobic and anaerobic conditions that facilitate chemical transformations, and peat accumulation that permanently buries chemicals. Mathematical modeling in combination with field and experimental data provides a powerful method of evaluating the complex processes operating in such systems, in which the interactions of physical, chemical, microbiological and microbiological processes can be seen [5]. An ecosystem model of the restored Karla lake in Thessaly, Greece was developed, focusing on nitrogen dynamics, thus simulating where and in which form nitrogen is stored in the lake and ultimately predicting overall nitrogen retention by the lake under different hydrologic conditions.

2. Materials and methods

An ecosystem-level model for the fate of nitrogen in a lake was developed and was applied to the conditions relevant to the hydrology and geomorphology of lake Karla. Projections of field data were obtained from the environmental impact assessment (EIA) study for the Karla reservoir [6] and from the Environmental Report prepared by the Greek Ministry of Environment Regional Planning and Public Works [7]. Four submodels were developed, including one for hydrology, primary productivity, sediments and nitrogen using a set of non-linear, ordinary differential equations to describe them. In this paper, emphasis is placed on the presentation of the nitrogen submodel, as the other submodels have been presented elsewhere [8–9]. The model was integrated using the software STELLA™ VIII, a high level visual-oriented programming and simulation language [11]. Fourth-order Runge-Kutta was used as the integration method with a time step of 0.1 week.

2.1. Site description – hydrology

The reservoir is located approximately 20 km north-west of the city of Volos in the prefecture of Magnesia, Thessaly, in central Greece (Fig. 1). The elevation-surface-storage curves for the reservoir were obtained from the technical study of the Karla lake and Associated Works [6]. The site hydrology and the calculation of the reservoir volume have been presented elsewhere [12] and will be covered here briefly. The change in volume of the Karla reservoir as a function of time is calculated by a mass balance equation that includes all inflows and outflows. Water is pumped in from the Pineos River (Q_{river}) and is pumped out to cover irrigation needs (Q_{irrig}) of the area. The maximum water level available for irrigation and maximum flood water level are set in the model, follow-

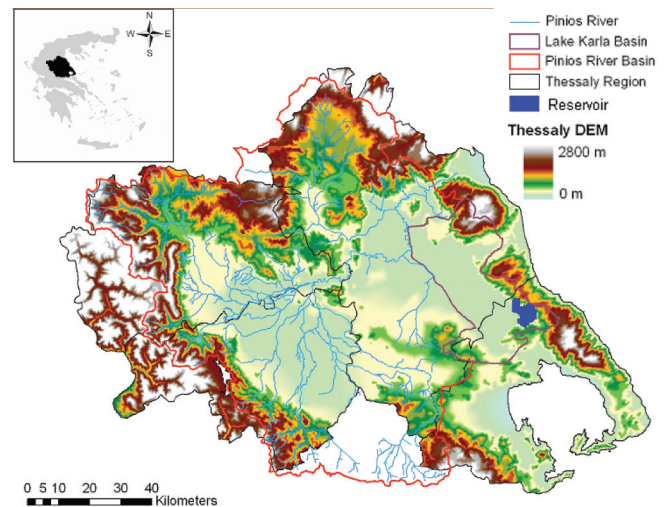


Fig. 1. Map of Thessaly indicating the Penios River and Karla lake basins.

ing the EIA study [6]. Once the maximum flood water level is reached, water is allowed to overflow via a tunnel that discharges water into the adjacent gulf of Pagasitikos (Q_{Pagas}). This way, flooding events are limited. This information is incorporated (with a series of IF-THEN statements) in the development of the hydrologic mass balance for the reservoir. Additional inflows into the reservoir are precipitation (Q_{pptn}), inflow from the watershed due to run-off and floods (Q_{runoff}) and inflow from the surrounding irrigated areas drainage tiles (Q_{drain}). Other outflows include losses to the underlying aquifer (Q_{aquif}), as well as losses due to evapotranspiration (Q_{ET}). To calculate the reservoir surface area (A) corresponding to the volume calculated in the model for each time step, one takes into account reservoir geometry. This is done with the elevation-surface-storage curves; thus, the reservoir volume calculated at each time step is used, and the elevation-surface-storage curves (shown in [8]) allow the calculation of the corresponding surface area. The average water depth in the lake is then found by dividing the calculated storage volume by the corresponding reservoir surface area.

2.2. Nitrogen sub-model

Seven forms of nitrogen were included as seven state variables in the nitrogen sub-model of the lake. The modeling equations were based on models presented in the literature [13–19] with several modifications that reflect the specifics of the Karla lake hydrology and are presented here in detail. All variables used are defined in the list of symbols, with all rates listed in Table 1.

Ammonium nitrogen flows out of the lake through its outflow for irrigation and through its discharge in the Pagasitikos Gulf. Concentrations for all outflows are

Table 1
Different rates used in the model

Rate	Expression	Source
r_{ammon}	$K_{\text{ammon}} \theta^{T-20} [N_{\text{org}}]$	[14]
r_{nitr}	$K_{\text{nitr}} K_{\text{DO}} K_T K_{\text{pH}} [\text{NH}_3]$	[17]
r_{den}	$K_{\text{den}} (1 - K_{\text{DO}}) K_T K_{\text{pH}} [\text{NO}_x]$	[17]
r_{remin}	$K_{\text{remin}} \theta^{T-20} [N_{\text{sed}}]$	[14]
$r_{\text{uptakeNH}_3\text{alg}}$	$\mu_{\text{alg}} \theta^{T-20} \left(\frac{[\text{NH}_3]}{K_{\text{NH}_3} + [\text{NH}_3]} \right) [N_{\text{alg}}]$	[14]
$r_{\text{uptakeNH}_3\text{mac}}$	$\mu_{\text{mac}} \theta^{T-20} \left(\frac{[\text{NH}_3]}{K_{\text{NH}_3} + [\text{NH}_3]} \right) [N_{\text{mac}}]$	[14]
$r_{\text{uptakeNO}_x\text{alg}}$	$\mu_{\text{alg}} \theta^{T-20} \left(\frac{[\text{NO}_x]}{K_{\text{NO}_x} + [\text{NO}_x]} \right) [N_{\text{alg}}]$	[14]
$r_{\text{uptakeNO}_x\text{mac}}$	$\mu_{\text{mac}} \theta^{T-20} \left(\frac{[\text{NO}_x]}{K_{\text{NO}_x} + [\text{NO}_x]} \right) [N_{\text{mac}}]$	[14]
r_{MortAlg}	$K_{\text{MortAlg}} \theta^{T-20} [N_{\text{alg}}]$	[14]
r_{MortMac}	$K_{\text{MortMac}} \theta^{T-20} [N_{\text{mac}}]$	[14]
r_{pcpt}	$K_{\text{pcpt}} [N_{\text{org}}]$	[14]
r_{DS}	$[N_{\text{sed}}] - [N_{\text{sed}}]^0$	[20]

taken equal to the concentration of ammonium nitrogen in the lake, calculated by the model for each time step. Ammonium nitrogen is lost from the lake mass balance through the following processes:

- Nitrification: part of ammonium nitrogen in the lake is converted to nitrites and then nitrates. This is an aerobic process facilitated by the nitrifying bacteria *Nitrosomonas* and depends on temperature, on pH and on dissolved oxygen (DO) concentration in the water (data obtained by the literature and shown in Table 2, with all parameter values shown in Table 3). Correction factors for temperature and pH are included in the model and are less than one when they fall outside the ideal range of, approximately, 27–32°C and 8–9.3, respectively. Fig. 2 presents graphs with those correction factors. A DO correction factor K_{DO} is also included in the model and is calculated using DO concentrations in the lake, as they are reported in the literature (Table 2) and DO saturation levels calculated for temperatures and pressures that are recorded in Karla at the time.

Table 2
Concentrations of inflows used in the model

Quantity	Value	Source
$[\text{NH}_3]_{\text{drain}}$	6.36 g/m ³	[7]
$[\text{NH}_3]_{\text{runoff}}$	2.2 g/m ³	[7]
$[\text{NH}_3]_{\text{Penios}}$	Monthly values for years 1996 to 1998 ranging from 0.01 to 0.69 g/m ³	[15]
$[\text{NO}_x]_{\text{drain}}$	25.29 g/m ³	[7]
$[\text{NO}_x]_{\text{runoff}}$	5.26 g/m ³	[7]
$[\text{NO}_x]_{\text{Penios}}$	Monthly values for years 1996 to 1998 ranging from 0.18 to 15.21 g/m ³	[15]
DO	Monthly values for years 1996 to 1998 ranging from 6.2 to 17.2 g/m ³	[15]
pH	Monthly values for years 1996 to 1998 ranging from 7.72 to 9.04 g/m ³	[15]
N_{algae}	Monthly values for one year ranging from 0.143 to 0.572 g/m ³	[16]
N_{org}	Monthly values for years 1996 to 1998 ranging from 0.7 to 4.02 g/m ³	[15]

- Nitrogen uptake by algae. A form of nitrogen uptake by algae is ammonia; this process uses the values of algae concentration in the lake from the primary productivity sub-model [8].
- Nitrogen uptake by macrophytes. A form of nitrogen uptake by macrophytes is ammonia; this process uses the values of macrophyte concentrations in the lake from the primary productivity sub-model [8].

The mass balance equation used for the calculation of ammonium nitrogen is the following:

$$\begin{aligned}
 V \frac{d[\text{NH}_3]}{dt} = & Q_{\text{drain}} [\text{NH}_3]_{\text{drain}} + Q_{\text{river}} [\text{NH}_3]_{\text{river}} \\
 & + Q_{\text{runoff}} [\text{NH}_3]_{\text{runoff}} + r_{\text{ammon}} V + r_{\text{remin}} V - r_{\text{nitr}} V \\
 & - r_{\text{uptakeNH}_3\text{alg}} V - r_{\text{uptakeNH}_3\text{mac}} V - Q_{\text{irrig}} [\text{NH}_3] \\
 & - Q_{\text{Pagas}} [\text{NH}_3] - Q_{\text{aquif}} [\text{NH}_3]
 \end{aligned} \quad (1)$$

2.2.2. Nitrite/nitrate nitrogen

In the model, no distinction is made between nitrite and nitrate nitrogen; the two quantities are modelled as a single variable (NO_x). NO_x nitrogen flows in the lake through “paths” that are similar to those of ammonium nitrogen, described above. Therefore, there is inflow from Penios River, from the watershed due to floods and area run-off and inflow from the surrounding irrigated areas drainage tiles. As with ammonium nitrogen, the concentrations of these inflows were obtained from the literature and are shown in Table 2. In addition, NO_x nitrogen increases the lake mass balance budget through the processes of nitrification. On the other hand, NO_x nitrogen

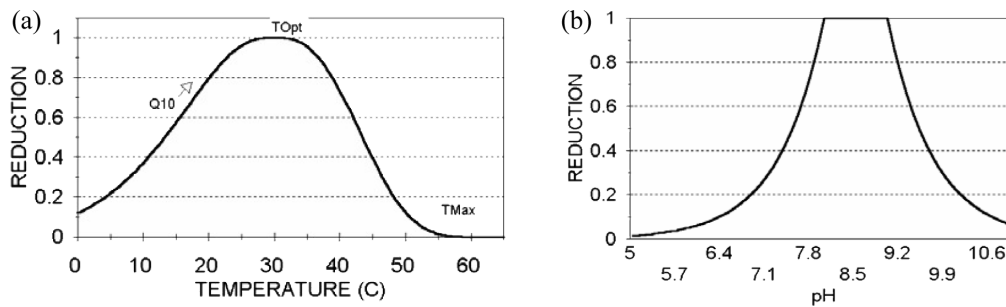


Fig. 2. Correction factors used in the model as a function of (a) temperature, K_T and (b) pH, K_{pH} [17].

decreases the mass balance budget through the process of denitrification, or the anoxic conversion of NO_x 's to nitrogen gas, facilitated by the denitrifying bacteria species *Nitrobacter*, a process that is also temperature-dependent. NO_x nitrogen flows out of the lake through its outflow for irrigation and through its discharge in Pagasitikos Gulf. NO_x nitrogen flows out of the lake through its outflow for irrigation and through its discharge in the Pagasitikos Gulf. NO_x nitrogen is also lost from the lake mass balance through algae and macrophyte uptake.

The mass balance equation used for the calculation of NO_x nitrogen is the following:

$$V \frac{d[\text{NO}_x]}{dt} = Q_{\text{drain}} [\text{NO}_x]_{\text{drain}} + Q_{\text{river}} [\text{NO}_x]_{\text{river}} + Q_{\text{runoff}} [\text{NO}_x]_{\text{runoff}} + r_{\text{nitr}} V - r_{\text{den}} V - r_{\text{uptakeNO}_x, \text{alg}} V - r_{\text{uptakeNO}_x, \text{mac}} V - Q_{\text{irrig}} [\text{NO}_x] - Q_{\text{Pagas}} [\text{NO}_x] - Q_{\text{aquif}} [\text{NO}_x] \quad (2)$$

2.2.3. Nitrogen stored in algae

A separate mass balance is written for the nitrogen stored in algae (N_{alg}). Inflows for this quantity are the uptakes of NH_3 and NO_x by algae, as described above. Additionally, Penios River brings in the lake algae that has nitrogen stored in it, so it is considered an inflow. Outflow of N_{alg} occurs with the outflow of water from the lake either for irrigation, or to Pagasitikos Gulf to prevent flooding. As algae die, the nitrogen stored in them is converted to organic nitrogen (N_{org}).

The mass balance equation used for the calculation of N_{alg} is the following:

$$V \frac{d[\text{N}_{\text{alg}}]}{dt} = Q_{\text{river}} [\text{N}_{\text{alg}}]_{\text{river}} + r_{\text{uptakeNH}_3, \text{alg}} V + r_{\text{uptakeNO}_x, \text{alg}} V - r_{\text{MortAlg}} V - Q_{\text{irrig}} [\text{N}_{\text{alg}}] - Q_{\text{Pagas}} [\text{N}_{\text{alg}}] - Q_{\text{aquif}} [\text{N}_{\text{org}}] \quad (3)$$

2.2.4. Nitrogen stored in macrophytes

A separate mass balance is written for the nitrogen stored in macrophytes (N_{mac}). Inflows for this quantity are the uptakes of NH_3 and NO_x by macrophytes, as described

Table 3

Parameters used in the model and their values

Parameter	Value	Source
K_T	Variable (Fig. 2a)	[17]
K_{pH}	Variable (Fig. 2b)	[17]
k_{nitr}	0.135 m/d	[17]
k_{den}	0.1 m/d	[17]
K_{ammon}	0.1/d	[14]
K_{remin}	0.003/d	[14]
K_{MortAlg}	0.3/d	[14]
K_{MortMac}	$\begin{cases} 0.05/\text{d}, \text{ for } T \leq 6^\circ\text{C} \\ 0.05/\text{d}, \text{ for } T \geq 35^\circ\text{C} \\ 0.009/\text{d}, \text{ for } 6^\circ\text{C} < T < 35^\circ\text{C} \end{cases}$	[14]
K_{pcpt}	0.035/d	[14]
K_{NH_3}	18 mg/L	[14]
K_{NO_x}	2 mg/L	[14]
μ_{alg}	0.45/d	[14]
μ_{mac}	0.47/d	[14]
θ	1.042	[14]

above. Outflow of N_{alg} occurs with the death of macrophytes, since the nitrogen stored in them is converted to nitrogen stored in active sediments (N_{sed}).

The mass balance equation used for the calculation of N_{mac} is the following:

$$\frac{d[\text{N}_{\text{mac}}]}{dt} = r_{\text{uptakeNH}_3, \text{mac}} + r_{\text{uptakeNO}_x, \text{mac}} - r_{\text{MortMac}} \quad (4)$$

2.2.5. Organic nitrogen

Another form of nitrogen in the lake is organic nitrogen (N_{org}), which flows in with the inflow of Penios River and flows out of it with the hydrologic outflows (Q_{irrig} , Q_{Pagas} and Q_{aquif}). Inflows to this mass balance are also the quantities released by algae during their death, as described above. The process of ammonification appears as an outflow to this mass balance. Finally, organic

nitrogen is also lost from the lake mass balance through its adsorption by active sediments.

The mass balance equation used for the calculation of N_{org} is the following:

$$V \frac{d[N_{org}]}{dt} = Q_{river} [N_{org}]_{river} + r_{MortAlg} V - r_{ammon} V - r_{pcpt} V - Q_{irrig} [N_{org}] - Q_{Pagas} [N_{org}] \quad (5)$$

2.2.6. Nitrogen stored in active sediments

Another form of nitrogen in the lake is nitrogen stored in active sediments (N_{sed}). As described above, adsorption of N_{org} by sediments and the release of nitrogen as a result of macrophyte death are both inflows to this quantity, while remineralization of sediment nitrogen to ammonium nitrogen is an outflow. The final outflow is permanent storage of nitrogen in the deep sediments.

The mass balance equation used for the calculation of N_{sed} is the following:

$$\frac{d[N_{sed}]}{dt} = r_{pcpt} + r_{MortMac} - r_{remin} - r_{DS} \quad (6)$$

2.2.7. Nitrogen stored in deep sediments

The final point of this model, the sink, is represented by deep sediments (N_{DS}), which are capable of permanently storing nitrogen away from the water column. This variable has a single input from N_{sed} and does not affect

the rest of the model; it starts from zero and is expected to grow as the lake ages.

The mass balance equation used for the calculation of N_{DS} is the following:

$$\frac{d[N_{DS}]}{dt} = r_{DS} \quad (7)$$

Initial values for all quantities were taken either from [6] or [7], or were estimated from relevant values reported in the literature [15,17], taking into account the storage volume and surface area of the reported lake and that of Karla, and sizing them accordingly (Table 4).

Table 4
Initial values of state variables

State variable	Value
NH_3	$43 \cdot 10^6$ g
N_{mac}	$4 \cdot 10^8$ g
N_{alg}	$2.5 \cdot 10^6$ g
N_{org}	0
N_{sed}	0
NO_x	0

3. Results and discussion

The purpose of ecosystem modeling includes integration of collected data, quantitative description of major pathways or processes through different storage

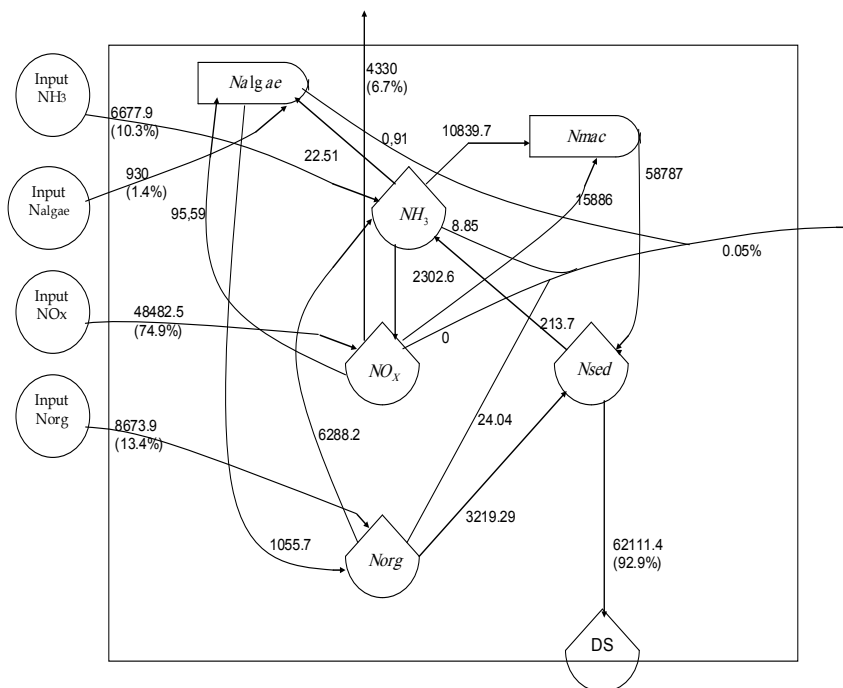


Fig. 3. Flow of nitrogen in the lake (in mg N/m³-y). The numbers in parentheses represent percentage of inflowing nitrogen.

compartments, and presentation of a whole picture at the ecosystem level. One way to achieve this is to draw a system diagram based on modeling results. A conceptual system diagram of the constructed nitrogen model, where the flows of nitrogen are depicted with Odum energy symbols is shown in Fig. 3. With this diagram we can see the flow and fate of the different forms of nitrogen in the lake. The budgets displayed in Fig. 3 are 3-year averages (in mg N/m³-y) and were calculated from simulation results using typical hydrology data based on the EIA study for the Karla lake.

In Fig. 3 6,677 mg NH₃-N/m³-y is shown to flow in the lake from Penios River, drainage and runoff, while the corresponding value for NO_x is 48,482 mg NO_x-N/m³-y. For some flows, these values are also shown as percentages of the total incoming nitrogen. Thus, it is shown that out of the incoming flows, the most important one is that of nitrites/nitrates, since it is approximately 75% of the total incoming nitrogen.

In total, approximately 93% of incoming nitrogen is sequestered by the lake, while 6.7% of it is lost in the atmosphere through the process of denitrification. Flows show that a large percentage of nitrogen is retained by the lake, since it is stored initially in the active sediments and then temporarily in the deep sediments. Therefore, a large portion of incoming nitrogen is converted to N_{sed'} during the death of macrophytes. Part of it of course returns to the water column through the process of ammonification, while an important part is directed towards the deep sediments, where it stays permanently.

Another important flow is that of biological assimilation of nitrogen by macrophytes (70% of incoming nitrogen), which in turn is converted to sediments after their death. If the uptake of nitrogen by macrophytes is compared with that of algae, it is obvious that macrophytes uptake much more nitrogen, which is also expected, due to their much larger biomass.

4. Conclusions

A nitrogen simulation model of the processes expected to take place in the Karla lake, which is undergoing restoration in central Greece was developed. Relevant hydrology, primary producers and seven different types of nitrogen were modeled. Simulations show that the lake retains about 93% of nitrogen that flows in, while over 6% of incoming nitrogen goes to the atmosphere through the process of denitrification. The largest part of nitrogen is stored permanently in the deep sediments, while the water that flows out of the lake is almost free of nitrogen.

Symbols

[N_{alg}] – Nitrogen concentration in algae, ML⁻³
 [N_{DS}] – Concentration of nitrogen in deep sediments, ML⁻³

[NH₃] – Ammonia concentration, ML⁻³
 [NH₃]_{drain} – Concentration of ammonia in water flowing in from the surrounding irrigated areas drainage tiles, ML⁻³
 [NH₃]_{river} – Concentration of ammonia in water pumped in from Penios River, ML⁻³
 [NH₃]_{runoff} – Concentration of ammonia in runoff flowing in from the watershed, ML⁻³
 [N_{mac}] – Nitrogen concentration in macrophytes, ML⁻³
 [N_{org}] – Concentration of organic nitrogen, ML⁻³
 [N_{org}]_{river} – Concentration of organic nitrogen in water pumped in from Penios River, ML⁻³
 [NO_x] – Nitrates and nitrites concentration, ML⁻³
 [NO_x]_{drain} – Concentration of nitrites/nitrates in water flowing in from the surrounding irrigated areas drainage tiles, ML⁻³
 [NO_x]_{river} – Concentration of nitrites/nitrates in water pumped in from Penios River, ML⁻³
 [NO_x]_{runoff} – Concentration of nitrites/nitrates in runoff flowing in from the watershed, ML⁻³
 [N_{sed}] – Nitrogen concentration in sediments, ML⁻³
 [N_{sed}]₀ – Concentration of nitrogen in sediments at the beginning of each time step, ML⁻³
 A – Reservoir surface area, L²
 DO – Reservoir dissolved oxygen concentration, ML⁻³
 DO_{sat} – Dissolved oxygen saturation level at ambient temperature and pressure, ML⁻³
 K_{ammon} – Maximum rate of ammonification, T⁻¹
 k_{den} – Maximum rate of denitrification, LT⁻¹
 K_{den} – Maximum rate of denitrification-adjusted, (k_{den}A/V), T⁻¹
 K_{DO} – Dissolved oxygen concentration correction factor (DO/DO_{sat})
 K_{MortAlg} – Mortality rate coefficient of algae, T⁻¹
 K_{MortMac} – Mortality rate coefficient of macrophytes, T⁻¹
 K_{NH3} – Half-saturation constant for ammonia, ML⁻³
 k_{nitr} – Maximum rate of nitrification, LT⁻¹
 K_{nitr} – Maximum rate of nitrification-adjusted, (k_{nitr}A/V), T⁻¹
 K_{NOx} – Half-saturation constant for nitrite/nitrate, ML⁻³
 K_{pcpt} – Organic nitrogen precipitation rate coefficient, T⁻¹
 K_{pH} – pH correction
 K_{remin} – Maximum rate of remineralization, T⁻¹
 K_T – Temperature correction
 Q_{drain} – Flowrate of water flowing in from the surrounding irrigated areas drainage tiles, L³T⁻¹
 Q_{irrig} – Flowrate of water pumped out for irrigation, L³T⁻¹
 Q_{Pagas} – Flowrate of water discharged in Pagasitikos Gulf, L³T⁻¹
 Q_{river} – Flowrate of water pumped in from Penios River, L³T⁻¹

Q_{runoff}	– Flowrate of runoff flowing in from the watershed, L^3T^{-1}
r_{ammon}	– Ammonification rate, $ML^{-3}T^{-1}$
r_{den}	– Denitrification rate, $ML^{-3}T^{-1}$
r_{DS}	– Rate of deposition of Nsed to deep sediments, $ML^{-3}T^{-1}$
r_{MortAlg}	– Rate of nitrogen release due to algae mortality, $ML^{-3}T^{-1}$
r_{MortMac}	– Rate of nitrogen release due to macrophyte mortality, $ML^{-3}T^{-1}$
r_{nitr}	– Nitrification rate, $ML^{-3}T^{-1}$
r_{pcpt}	– Rate of organic nitrogen precipitation, $ML^{-3}T^{-1}$
r_{remin}	– Nitrogen remineralization rate, $ML^{-3}T^{-1}$
$r_{\text{uptakeNH}_3\text{alg}}$	– Uptake rate of ammonia by algae, $ML^{-3}T^{-1}$
$r_{\text{uptakeNH}_3\text{mac}}$	– Uptake rate of ammonia by macrophytes, $ML^{-3}T^{-1}$
$r_{\text{uptakeNOxalg}}$	– Uptake rate of nitrites/nitrates by algae, $ML^{-3}T^{-1}$
$r_{\text{uptakeNOxmac}}$	– Uptake rate of nitrites/nitrates by macrophytes, $ML^{-3}T^{-1}$
T	– Water temperature, $^{\circ}C$
V	– Reservoir water volume, L^3
μ_{alg}	– Maximum growth rate of algae, T^{-1}
μ_{mac}	– Maximum growth rate of macrophytes, T^{-1}
θ	– Arrhenius constant

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