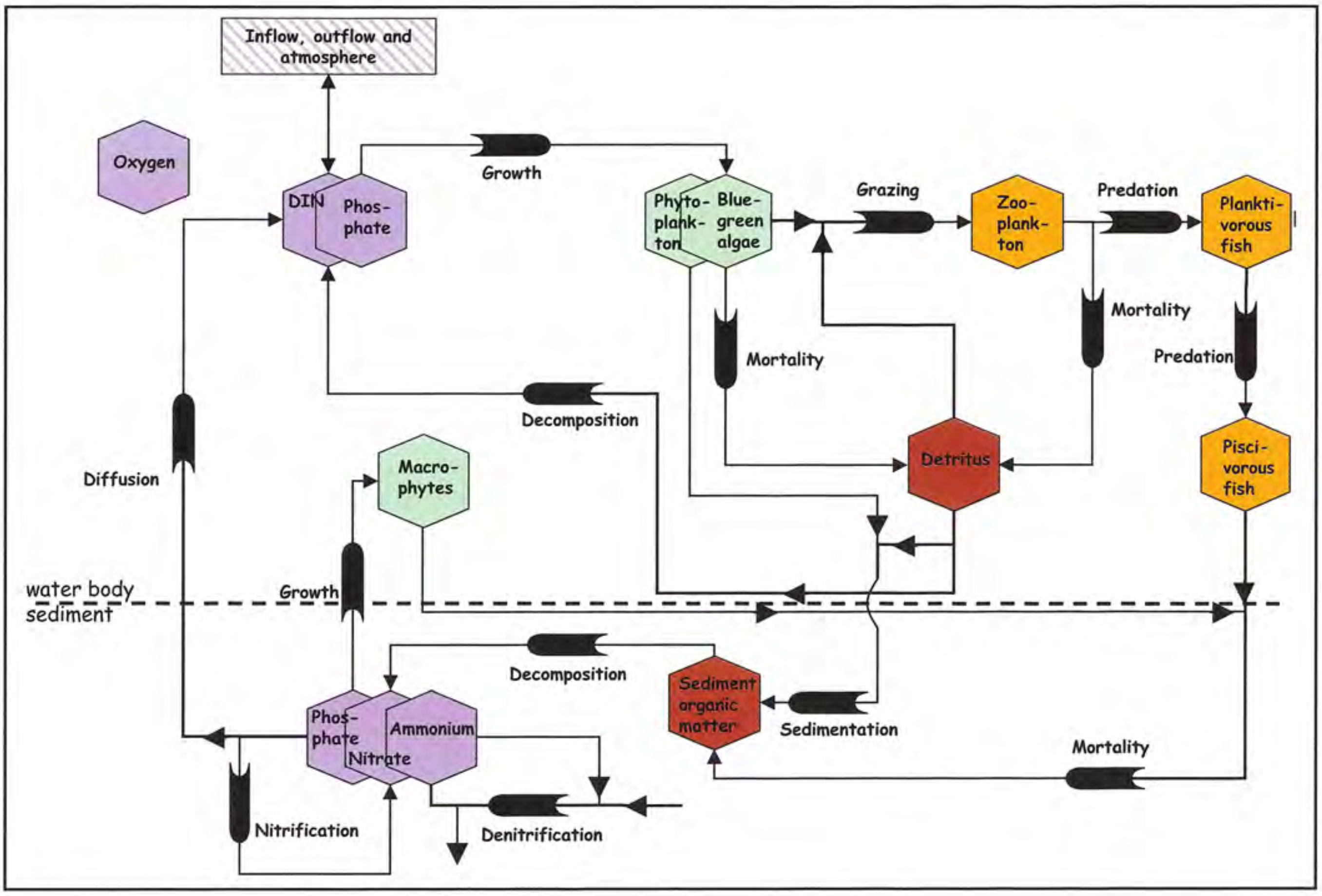
SMHI

No 16, 2002

Reports Hydrology



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a biogeochemical lake model (including literature review of processes)

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Report Summary / Rapportsammanfattning

Issuing Agency/Utgivare Swedish Meteorological and Hydrological Institute SE-601 76 NORRKÖPING Sweden	Report number/Publikation RH No. 16 Report date/Utgivningsdatum September 2002

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Title (and Subtitle)/Titel

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Abstract/Sammandrag

The biogeochemical lake model BIOLA was developed to be used for eutrophication studies in Sweden. Eutrophication is a threat for lakes in populated areas, and this model was developed to be a tool for managing lakes suffering from eutrophication. There are several measures that can be taken to reduce eutrophication. When considering different measures simulations of their effects, with models such as BIOLA, can contribute with information.

The model is a biogeochemical lake module coupled to a one-dimensional hydrodynamic model. The model simulates the continuous change of lake stratification and water quality due to weather, inflow, outflow and biogeochemical processes in the lake and in the sediments. It simulates changes over time in nutrient and biological state at different depths. The most important variables simulated by the model are inorganic nutrients and phytoplankton in the water. Other variables include nutrients and organic matter in the sediments.

The model has shown to be able to simulate changing nutrient and plankton dynamics. The result from three studied lakes are reviewed.

Key words/sök-, nyckelord
biogeochemistry, lake modelling, eutrophication

Supplementary notes/Tillägg	Number of pages/Antal sidor	Language/Språk
	69	English

ISSN and title/ISSN och titel

0283-1104 SMHI Reports Hydrology

Report available from/Rapporten kan köpas från:

SMHI
SE-601 76 NORRKÖPING
Sweden

Contents

1 Introduction

The BIOgeochemical LAke model BIOLA was developed during 2000-2001 at the Swedish Meteorological and Hydrological Institute (SMHI). Eutrophication is a threat for lakes in populated areas, and this model was developed to be a tool for managing lakes suffering from eutrophication. When considering different measures for eutrophication remedy actions simulations of their effects can contribute to the decision. The main objective of developing the model was to simulate the effect on the seasonal dynamics of nutrient and ecological state in the lake caused by changed nutrient supply to the lake. Secondary objectives were to synthesise information about the lake modelled, and to simulate other in-lake measures to reduce eutrophication. The model was developed for eutrophic lakes in Sweden within the Swedish Water Management Research Program (VASTRA), and was financed by the Swedish Foundation for Strategic Environmental Research (MISTRA) and SMHI.

The model is a biogeochemical lake module coupled to a one-dimensional hydrodynamic model (simulated by PROBE, see below). The combined PROBE-BIOLA model simulates the continuous change of lake stratification and water quality due to weather, inflow, outflow and processes in the lake and in the sediments. It simulates changes over time in nutrient and biological state at different depths. Modelled variables include nutrient and algal concentrations in the lake as well as nutrients and organic matter in the sediments. The model has to be tuned for the conditions in the lake to be modelled, but only a few parameters in the model are necessary to calibrate.

2 PROBE and the hydrodynamic model

The biogeochemical module is coupled to a hydrodynamic model, which is set up with the equation solver PROBE (Svensson, 1998b). The model simulates vertically varying variables but the lake is assumed to be horizontally homogeneous. It is divided in N-2 layers numbered (I=) 2 to N-1 from bottom and up (Figure 1). Unbalanced in- and outflows causes the thickness of the uppermost cell and the number of cells to vary with varying water level during a simulation. The vertical co-ordinate, z, is measured from the deepest bottom and *ZDIM* denote the level of the water surface, while z_s is the distance from the water surface (i.e. *ZDIM-z*). The time step may vary, but typically 10 minutes are used.

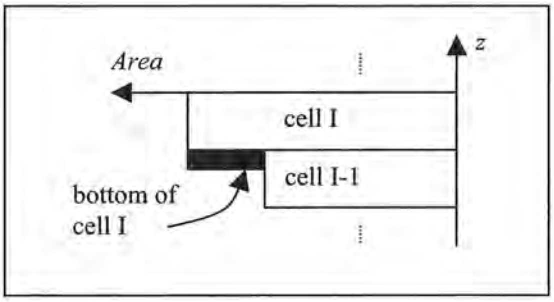

Figure 1. Illustration of cell grid of PROBE and BIOLA.

The hydrodynamic model simulates the mixing and temperature (T) of the lake using meteorological forcing (air temperature, wind, relative humidity and cloud coverage) and inflow/outflow records. Solar radiation is estimated from time of year, latitude and cloud coverage (Omstedt, 1990). The turbulent mixing is included in the mean-flow and heat equations as a vertical exchange coefficient. The turbulent mixing is modelled with a two-equation turbulence model (the k-ε model) which calculates the exchange coefficient (also called turbulent eddy viscosity). It is assumed that all variables are mixed with the same field of turbulence (including those of BIOLA below). Further description of PROBE applications in lakes and seas may be found in Sahlberg (1988), Omstedt (1990), and Sahlberg and Olsson (2000).

3 The biogeochemical model – BIOLA

The biogeochemical module is build to be used with PROBE. The transport equations (1-2) are simulated within PROBE, with biological and chemical processes as sink and source terms.

$$\frac{\partial C}{\partial t}+v\frac{\partial C}{\partial z}=\frac{1}{A}\frac{\partial}{\partial z}\left(A\nu\frac{\partial C}{\partial z}\right)+\Phi+\phi \tag{1}$$

$$\frac{\partial C}{\partial t}=\Phi+\phi \tag{2}$$

Sources and sinks are denoted Φ and ϕ respectively. These are calculated by BIOLA and described in more detail in Section 4. Note that sinks (ϕ) are negative. C denotes concentration, t is time, v is vertical velocity, A is horizontal area (varying with depth), and ν is turbulent eddy viscosity. For sediment variables and macrophytes, which are attached to the bottom, advection and diffusion is zero, and the transport equation is reduced to (2). In addition, fish are assumed to be independent of advective flow.

Nutrient supply through inflow and loss of dissolved and particulate material in the water through outflow are external processes incorporated in the model (1). Besides the sources and sinks in the transport equation, additional sources and sinks form boundary conditions. These include exchange of oxygen through the lake surface and atmospheric deposition of nutrients. The external factors are described in Section 5.

3.1 State variables

The biogeochemical model encompasses the elements carbon (C), nitrogen (N), phosphorus (P) and oxygen (O_2). Totally 14 variables are included in the model (phosphate, dissolved inorganic nitrogen, oxygen, dissolved phosphorus in sediment, dissolved ammonium in sediment, dissolved nitrate in sediment, phytoplankton, blue-green algae, zooplankton, fish (planktivorous and piscivorous), detritus and sediment organic matter; Table 1). The variables can be divided into groups with inorganic, living organic and dead organic variables (Table 1). Inorganic carbon is not modelled, neither is nitrogen and phosphorus bound in

Table 1. State variables included in the model.

Inorganic variables	Symbol	Unit	Living organic variables	Symbol	Unit
Phosphate	PO4	mg P L^{-1}	Phytoplankton	A	mg C L^{-1}
Dissolved inorganic nitrogen	DIN	mg N L^{-1}	Blue-green algae	A_{NFIX}	mg C L^{-1}
			Zooplankton	Z	mg C L^{-1}
Oxygen	O2	mg O_2 L^{-1}	Planktivorous fish	FA	mg C L^{-1}
Dissolved phosphorus in sediment water	BIP	g P m^{-2}	Piscivorous fish	FB	mg C L^{-1}
			Macrophyte	M	mg C L^{-1}
Dissolved ammonium in sediment water	BNH4	g N m^{-2}	Dead organic variables	Symbol	Unit
Dissolved nitrate in sediment water	BNO3	g N m^{-2}	Detritus	D	mg C L^{-1}
			Sediment organic matter	B	g C m^{-2}

organic matter. The latter are assumed to be a constant fraction of the organic matter (see Section 3.2 below). Two functional groups of phytoplankton is included. The phytoplankton variable simulates all phytoplankton except blue-green algae, which are modelled separately.

The state variables are simulated as concentrations (Table 1). Sediment variables are simulated per unit sediment area, while dissolved and particulate variables in the water are calculated by volume. For sediment variables the value for cell I denote the sediment at the bottom of that cell (Figure 1). For the other variables the value for cell I denotes the concentration in cell I. The macrophyte variable is an exception. Since macrophytes are not free-living, their concentration for cell I denotes the concentration in the whole water column above the bottom of cell I (Figure 2). The macrophytes are thus assumed uniformly distributed in the water column. This leads to a horizontal variation in macrophyte concentration.

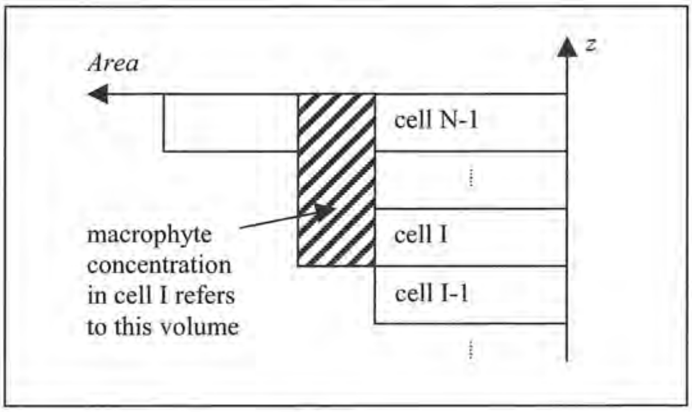

Figure 2. Illustration of macrophyte cell.

All state variables are given a minimum value beyond which it is not reduced more. The sinks of a variable are set to zero when the minimum value is reached. The variables are not allowed to become zero, because the ability to recolonise and grow back then is lost. Oxygen is an exception. Negative oxygen denote presence of hydrogen sulphide, demanding a corresponding amount of oxygen to be oxidised.

3.2 Modelled processes

The modelled processes give the flows between the state variables (Figure 3). The processes are described in detail in the Section 4 and 5. The process equations have different degree of complexity and different origin. They include both experimentally found and more qualitatively hypothesised relations. Table 2 gives an overview of the internal processes modelled and the variables they influence. Totally 44 parameters are used in the process equations. These are described together with the processes in Section 4. All state variables and parameters are summarised in Appendix I.

The process of photosynthesis produces organic matter and oxygen from inorganic nutrients and carbon dioxide (3).

$$106CO_2 + 16NH_3 + H_3PO_4 + 106H_2O \rightarrow (CH_2O)_{106}(NH_3)_{16}(H_3PO_4) + 106O_2 . \quad (3)$$

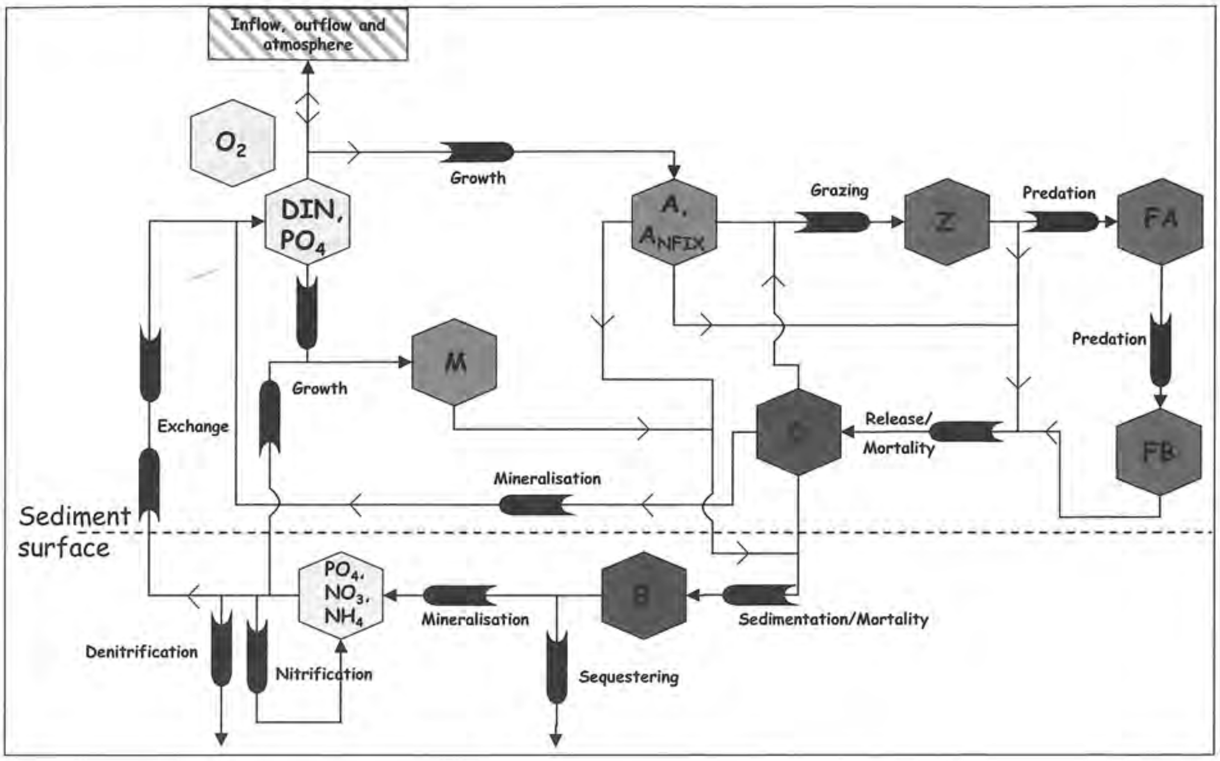

Figure 3. State variables (N,P,C) and processes of the biogeochemical model BIOLA.

Table 2. Modelled internal processes and their influence on the state variables.

Process	Sink (ϕ) of	Source (Φ) of
Phytoplankton growth	PO4, DIN	A, O2
Blue-green algae growth including nitrogen fixation	PO4, DIN	A_{NFIX}, O2
Macrophyte growth	BIP, BNH4, PO4, DIN	M, O2
Natural mortality of autotrophs	A_{NFIX}, M	D, B
Zooplankton grazing	A, A_{NFIX}, D	Z, D
Natural mortality of zooplankton	Z	D
Predation on zooplankton	Z	FA
Predation on planktivorous fish	FA	FB
Natural mortality of fish	FB	D
Mineralisation of detritus	D, O2	PO4, DIN
Denitrification	B, BNO3, DIN, D	BNH4, BIP, DIN, PO4
Nitrification	02, BNH4	BNO3
Mineralisation in sediment	B, O2	BNH4, BIP
Permanent sequestering in sediment	B	
Exchange of nutrients between water and sediment	BIP, PO4, BNH4, BNO3, DIN	BIP, PO4, BNH4, BNO3, DIN
Sinking and sedimentation	A, A_{NFIX}, D	A, A_{NFIX}, D, B

The formula of organic matter has a specific relation between different elements. For phytoplankton the relation from (3) is often used (C:N:P=106:16:1), but the stoichiometric ratio may vary between species. In the model the ratio is assumed to be the same in all organic matter (phytoplankton, zooplankton, detritus, fish, sediment) and according to (3) (Table 3). The stoichiometric ratios are used for transformation of organic fluxes to corresponding nutrient fluxes. Other stoichiometric ratios (Table 3) are used to balance the use/produce of different elements during the processes of denitrification and nitrification. Denitrification is a degradation process that uses nitrate to oxidise organic matter (4), while nitrification oxidises ammonium to nitrate with the use of oxygen (5).

$$5CH_2O + 4H^+ + 4NO_3^- \rightarrow 2N_2 + 5CO_2 + 7H_2O\,. \tag{4}$$

$$NH_4^+ + 2O_2 \rightarrow 2H^+ + NO_3^- + H_2O \tag{5}$$

Table 3. Stoichiometric ratios between elements in organic matter and for the denitrification and nitrification processes.

Constant	Ratio	Usage	Parameter values
C_{OC}	O_2/C	in phytoplankton growth/organic matter mineralisation	2.667 mg O_2 (mg C)$^{-1}$
C_{NC}	N/C	in organic matter	0.176 mg N / (mg C)$^{-1}$
C_{PC}	P/C	in organic matter	2.44*10^{-2} mg P / (mg C)$^{-1}$
C_{NP}	N/P	in organic matter	7.2 mg N / (mg P)$^{-1}$
$C_{CNdenit}$	C/N	in denitrification	1.071 mg C (mg N)$^{-1}$
C_{ONnitr}	O_2/N	in nitrification	4.572 mg O_2 (mg N)$^{-1}$

4 Process equations

In this section, equations for the internal sink and source terms of all variables are given and described. In addition parameters are explained and default values given.

4.1 Phytoplankton growth

Phytoplankton growth is modelled proportional to the phytoplankton biomass. The phytoplankton growth rate has a temperature dependent maximum rate, and reduction factors due to light and nutrient availability ((6), Table 4). An Arrhenius function is used for temperature dependence, which gives increasing growth with temperature. This has been shown to be true for a composite phytoplankton community (Chapra, 1997) despite different temperature optimum for different species. A commonly used expression for light limitation with an optimum light intensity is used. The light climate is decreasing exponentially with depth (7), modelled by Steele's equation (Steele, 1962). The light attenuation is described in next section. Nutrient limitation is modelled with a Michaelis-Menten expression with only one limiting nutrient at the time (phosphate or dissolved inorganic nitrogen). Temperature and light on the other hand are regarded as independent functions.

$$\Phi_A = \mu_A * \theta^{T-T_{ref}} * \frac{I(z)}{I_{opt}} * e^{1-\frac{I(z)}{I_{opt}}} * \min\left(\frac{PO4}{k_{PO4}+PO4}, \frac{DIN}{k_{DIN}+DIN}\right) * A \tag{6}$$

$$I(z) = I_0 * e^{-K_d * z} \tag{7}$$

Table 4. Parameters for phytoplankton growth.

Symbol	Parameter	Value	Reference
μ_A	maximum growth rate for phytoplankton at reference temperature	2.0 d^{-1}	Chapra (1997)
θ	general temperature coefficient	1.07	Kirk (1983)
T_{ref}	general reference temperature	20°C	standard value
I_{opt}	optimal light intensity for phytoplankton and blue-green algae	50 W m^{-2}	Chapra (1997); Kirk (1983)
k_{PO4}	half-saturation concentration for phytoplankton and blue-green algae uptake of phosphorus	0.01 mg P L^{-1}	median of several literature values: Riegman *et al.* (2000); Matsuda *et al.* (1999); Tufford and McKellar (1999); Chapra (1997); Scheffer *et al.* (1997); Garnier *et al.* (1995); Seip and Reynolds (1995); Rhee (1978); Lehman *et al.* (1975)
k_{DIN}	half-saturation concentration for phytoplankton and blue-green algae uptake of nitrogen	0.02 mg N L^{-1}	median of several literature values: Matsuda *et al.* (1999); Tufford and McKellar (1999); Chapra (1997); Gu *et al.* (1997); Valiela *et al.* (1997); Garnier *et al.* (1995); Priscu *et al.* (1985); Halterman and Toetz (1984); Axler *et al.* (1982); Rhee (1978); Lehman *et al.* (1975)

The growth process releases oxygen, and consumes phosphate and dissolved inorganic nitrogen, proportionally to the phytoplankton growth ((8-10), Table 3).

$$\Phi_{O2} = C_{OC} * \Phi_A \tag{8}$$

$$\phi_{DIN} = -C_{NC} * \Phi_A \tag{9}$$

$$\phi_{PO4} = -C_{PC} * \Phi_A \tag{10}$$

Phytoplankton respiration is not modelled. In macrophyte dominated lakes, phytoplankton are scarce. This may be partly due to release of growth suppressing chemicals by the macrophytes (Scheffer, 1998). This has not been modelled, since the effect is hard to quantify and probably secondary.

4.2 Light attenuation

Light attenuation ((11), Table 5) depends on the concentration of light absorbing particles, such as algae and detritus. In this model the light attenuation coefficient (K_d) depends linearly on the concentration of macrophytes, phytoplankton, blue-green algae and detritus (12). Thus it incorporates the self-shading effect into algal growth. The attenuation varies between lakes, especially by the background turbidity (e.g. absorption by water, humic substances, inorganic suspended particles). The latter is combined in the rest term (k_w). Therefore light attenuation determined for the lake to be modelled should be used if available.

$$I(z_s) = I_0 * e^{-K_d * z_s} \tag{11}$$

$$K_d = k_w + k_M * M + k_P * (A + A_{NFIX}) + k_D * D \tag{12}$$

Table 5. Parameters for light attenuation.

Symbol	Parameter	Value	Reference
k_w	extinction coefficient of the water	0.04 m^{-1}	Krause-Jensen and Sand-Jensen (1998)
k_M	macrophyte shading coefficient	0.16 $m^2 g^{-1}$	Krause-Jensen and Sand-Jensen (1998)
k_P	shading coefficient for phytoplankton and blue-green algae	0.3 $m^2 g^{-1}$	Krause-Jensen and Sand-Jensen (1998)
k_D	detritus shading coefficient	0.2 $m^2 g^{-1}$	median of several literature values: Scheffer (1998); Savchuk and Wulff (1996); Buiteveld (1995); DiToro (1978)

Macrophytes have a tendency to give clearer water. This is due to limiting the light for phytoplankton growth, as modelled here, but also due to sheltering sediment from wind resuspension and sheltering zooplankton from fish so that they may better control the phytoplankton biomass. The effect of the latter factors has not been included in the model.

4.3 Blue-green algae growth including nitrogen fixation

Modelled blue-green algae, or cyanobacteria, are not nitrogen limited, because they use nitrogen fixation when the Michaelis-Menten expression says phosphate is in excess ((13), Table 6). Nevertheless they grow (14) using DIN (16), if DIN is available. This process has the same formulation as phytoplankton growth, except that blue-green algae have a lower maximum growth rate. This is assumed because of their colony form, which limits their access to nutrients. This extensive form of growth also makes them less edible to zooplankton. Growth based on atmospheric nitrogen has an extra factor (13), which lets the excess of phosphate regulate the growth rate (Savchuk and Wulff, 1996).

$$\Phi_{ANFIX1} = \mu_{ANFIX} * \theta^{T-T_{ref}} * \frac{I(z_s)}{I_{opt}} * e^{1-\frac{I(z_s)}{I_{opt}}} * \frac{PO4}{k_{PO4}+PO4} * \frac{1}{1+\left(\frac{DIN}{PO4*C_{NP}}\right)^4} * A_{NFIX}$$

$$\text{if } \frac{DIN}{k_{DIN}+DIN} < \frac{PO4}{k_{PO4}+PO4} \text{ else } \Phi_{ANFIX1} = 0 \tag{13}$$

$$\Phi_{ANFIX2} = \mu_{ANFIX} * \theta^{T-T_{ref}} * \frac{I(z_s)}{I_{opt}} * e^{1-\frac{I(z_s)}{I_{opt}}} * \frac{PO4}{k_{PO4}+PO4} * A_{NFIX}$$

$$\text{if } \frac{PO4}{k_{PO4}+PO4} \leq \frac{DIN}{k_{DIN}+DIN} \text{ else } \Phi_{ANFIX2} = 0 \tag{14}$$

Blue-green algae take up phosphate (17), in addition to atmospheric or dissolved nitrogen, and produce oxygen (15).

$$\Phi_{O2} = C_{OC} * (\Phi_{ANFIX1} + \Phi_{ANFIX2}) \tag{15}$$

$$\phi_{DIN} = -C_{NC} * \Phi_{ANFIX2} \tag{16}$$

$$\phi_{PO4} = -C_{PC} * (\Phi_{ANFIX1} + \Phi_{ANFIX2}) \tag{17}$$

Table 6. Parameters for blue-green algae growth and nitrogen fixation.

Symbol	Parameter	Value	Reference
μ_{ANFIX}	maximum growth rate for blue-green algae at reference temperature	1.0 d^{-1}	Scheffer *et al.* (1997); Seip and Reynolds (1995)
θ	general temperature coefficient	1.07	Kirk (1983)
T_{ref}	general reference temperature	20°C	standard value
I_{opt}	optimal light intensity for phytoplankton and blue-green algae	50 W m^{-2}	same as for phytoplankton growth
k_{PO4}	half-saturation concentration for phytoplankton and blue-green algae uptake of phosphate	0.01 mg P L^{-1}	same as for phytoplankton growth
k_{DIN}	half-saturation concentration for phytoplankton and blue-green algae uptake of nitrogen	0.02 mg N L^{-1}	same as for phytoplankton growth

There are indications that it is low light that favour blue-green algae in front of phytoplankton and not phosphorus supply or N:P ratio (Scheffer *et al.*, 1997). This has not been considered nor a possible difference in shading by blue-green algae compared to phytoplankton.

4.4 Macrophyte growth

Macrophyte growth depends on temperature, light and nutrient conditions ((18), Table 7). The formulation is similar to other algae growth. Macrophytes may use nutrients from the sediment as well as from the water phase (references in Collins and Wlosinski, 1989). In this model, macrophytes is assumed to take nutrient from the inorganic nutrients in the sediment in the first hand (20-23), but macrophyte growth is not assumed to be limited by the nutrients in the sediment alone (18).

$$\Phi_M = \mu_M * \theta_M^{T-T_{ref}} * \frac{I(z_s)}{I_{Mopt}} * e^{1-\frac{I(z_s)}{I_{Mopt}}} * \min\left(\frac{BIP/d_{sed} + PO4}{k_{MIP} + BIP/d_{sed} + PO4}, \frac{BNH4/d_{sed} + DIN}{k_{MIN} + BNH4/d_{sed} + DIN} \right) * M \tag{18}$$

Table 7. Parameters for macrophyte growth.

Symbol	Parameter	Value	Reference
μ_M	maximum growth rate for macrophytes at reference temperature	0.5 d^{-1}	Fong *et al.* (1993); Krause-Jensen and Sand-Jensen (1998)
θ_M	temperature coefficient for macrophyte	1.04	Santamaría and van Vierssen (1997)
T_{ref}	general reference temperature	20°C	standard value
I_{Mopt}	optimal light intensity for macrophyte	75 W m^{-2}	Kirk (1983)
k_{MIP}	half-saturation concentration for macrophyte uptake of phosphorus	0.005 mg P L^{-1}	model value from Asaeda and van Bon (1997)
k_{MIN}	half-saturation concentration for macrophyte uptake of nitrogen	0.01 mg N L^{-1}	model value from Asaeda and van Bon (1997)
d_{sed}	thickness of active sediment layer	0.1 m	DiGario and Snow (1977)
Δz_{cell}	thickness of lake cell	varying with depth	determined by model setup
$BNH4_{min}$	minimum value of ammonium in the sediment	10^{-10} g N m^{-2}	chosen by author
BIP_{min}	minimum value of phosphate in the sediment	10^{-10} g P m^{-2}	chosen by author

Macrophyte growth produce oxygen (19), which is assumed to be released in cell I, i.e. in the water above the bottom. The nutrient concentration in this cell are used to calculate nutrient limitation. Nutrients from the same cell are used when sediment nutrients are not enough for growth. Notice that the sediment nutrient variables are gram per square meter (g m^{-2}), while the nutrients dissolved in the water are concentrations (mg L^{-1}). Therefore the division by d_{sed} (18) or Δz_{cell} (21,23).

$$\Phi_{O2} = C_{OC} * \Phi_M \tag{19}$$

$$\phi_{BINH4} = -C_{NC} * \Phi_M * z_s \qquad \text{if} \qquad C_{NC} * \Phi_M * z_s < BNH4 - BNH4_{\min} \tag{20}$$

$$\begin{cases} \phi_{BNH4} = -(BNH4 - BNH4_{\min}) \\ \phi_{DIN} = \dfrac{-C_{NC} * \Phi_M * z_s - \phi_{BNH4}}{\Delta z_{cell}} \end{cases} \qquad \text{if} \qquad C_{NC} * \Phi_M * z_s > BNH4 - BNH4_{\min} \tag{21}$$

$$\phi_{BIP} = -C_{PC} * \Phi_M * z_s \qquad \text{if} \qquad C_{PC} * \Phi_M * z_s < BIP - BIP_{\min} \tag{22}$$

$$\begin{cases} \phi_{BIP} = -(BIP - BIP_{\min}) \\ \phi_{PO4} = \dfrac{-C_{PC} * \Phi_M * z_s - \phi_{BIP}}{\Delta z_{cell}} \end{cases} \qquad \text{if} \qquad C_{PC} * \Phi_M * z_s > BIP - BIP_{\min} \tag{23}$$

4.5 Natural mortality of autotrophs

Natural mortality of autotrophs incorporates all mortality except by grazing. Modelled phytoplankton does not suffer from natural mortality, because grazing by zooplankton is assumed to dominate the loss (Scheffer, 1998). Zooplankton does not graze blue-green algae as hard as phytoplankton. Therefore their natural mortality is included in the model, although no default value is given (Table 8). Natural mortality of blue-green algae is modelled as a first-order rate. It only depends on their abundance ((24), Table 8). Dead algae become detritus (25).

$$\phi_{ANFIX} = -m_{ANFIX} * A_{NFIX} \tag{24}$$

$$\Phi_D = -\phi_{ANFIX} \tag{25}$$

Table 8. Parameters for natural mortality of blue-green algae.

Symbol	Parameter	Value	Reference
m_{ANFIX}	mortality rate for blue-green algae	0.0 d^{-1}	no literature value found

For macrophytes, natural mortality ((26), Table 9), is the only sink modelled. Macrophytes may be eaten by fish and birds, although this probably is a small contributor to the food web (Scheffer, 1998). This has not been modelled explicitly, but is included in the natural mortality loss. Macrophytes settle directly on the bottom when they die (27). The mortality is assumed proportional to the biomass (26).

$$\phi_M = -m_M * M \tag{26}$$

$$\Phi_B = -\phi_M * z \tag{27}$$

Table 9. Parameters for macrophyte mortality.

Symbol	Parameter	Value	Reference
m_M	mortality rate for macrophyte	0.05 d^{-1}	model value from Collins and Wlosinski (1989)

4.6 Zooplankton grazing on phytoplankton, blue-green algae and detritus

In the model, zooplankton feed on phytoplankton, blue-green algae and detritus. Since bacteria are not modelled, this food source is not included. The use of different food sources has a stabilizing effect on the zooplankton and phytoplankton populations (Scheffer, 1998).

The modelled grazing depends on the food and amount of grazers present (28-31). The choice between food sources is governed by selectivity coefficients. The selectivity coefficient represent the part of the potential "food" seen as such by the zooplankton. The grazing of autotrophs (28, 29) and detritus (30), result in an increase in zooplankton biomass, but only a part of the consumed food is actually assimilated (Table 10). The efficiency of the assimilation give the growth of the zooplankton (31). The rest of the grazed biomass is released as detritus (32).

$$\phi_A = -k_G * \frac{s_A * A}{k_g + s_A * A + s_{ANFIX} * A_{NFIX} + s_D * D} * Z \tag{28}$$

$$\phi_{ANFIX} = -k_G * \frac{s_{ANFIX} * A_{NFIX}}{k_g + s_A * A + s_{ANFIX} * A_{NFIX} + s_D * D} * Z \tag{29}$$

$$\phi_D = -k_G * \frac{s_D * D}{k_g + s_A * A + s_{ANFIX} * A_{NFIX} + s_D * D} * Z \tag{30}$$

$$\Phi_Z = -e * \left(\phi_A + \phi_{ANFIX} + \phi_D\right) \tag{31}$$

$$\Phi_D = \frac{1-e}{e} \Phi_Z \tag{32}$$

Table 10. Parameters for zooplankton grazing.

Symbol	Parameter	Value	Reference
k_G	grazing rate	0.8 d^{-1}	double the median of several studies with natural food supply, Bosselmann and Riemann (1986)
e	efficiency of zooplankton grazing	0.4	Chapra (1997); Bosselmann and Riemann (1986)
k_g	half-saturation concentration for grazing	0.5 mg C L^{-1}	model value, Chapra (1997); Scavia (1980); Jørgensen (1983)
s_A	selectivity coefficient for grazing on phytoplankton	1.0	Scavia (1980); Knisely and Geller (1986)
s_{ANFIX}	selectivity coefficient for grazing on blue-green algae	0.2	Scavia (1980); Knisely and Geller (1986)
s_D	selectivity coefficient for grazing on detritus	0.4	Scavia (1980)

4.7 Natural mortality of zooplankton

Natural mortality represent different losses of zooplankton including death by diseases and predation by other animals than fish, e.g. larger zooplankton. Predation on zooplankton by fish is treated in the next section. Natural mortality is a first-order process ((33), Table 11). The loss of zooplankton is a source of detritus (34).

$$\phi_Z = -k_{zm} * Z \tag{33}$$

$$\Phi_D = -\phi_Z \tag{34}$$

Table 11. Parameters for zooplankton mortality.

Symbol	Parameter	Value	Reference
k_{zm}	mortality rate for zooplankton	0.005 d^{-1}	Gries and Guede (1999)

4.8 Predation on zooplankton

Planktivorous fish eats zooplankton. The predation depends on prey concentration ((35), Table 12), but the predation pressure increase more than linearly with prey. This is a result of fish switching to zooplankton food when abundant. The predation leads to growth of planktivorous fish (36).

$$\phi_Z = -k_{pA} * \theta^{T-T_{ref}} * \frac{Z^2}{k_Z^2 + Z^2} * FA \tag{35}$$

$$\Phi_{FA} = -\phi_Z \tag{36}$$

Table 12. Parameters for predation on zooplankton.

Symbol	Parameter	Value	Reference
k_{pA}	maximum predation rate on zooplankton at reference temperature	0.1 d^{-1}	median of several values used in models: Persson and Barkman (1997); Janse and Aldenberg (1990)
θ	general temperature coefficient	1.07	model value from Janse and Aldenberg (1990)
T_{ref}	general reference temperature	20°C	model value from Janse and Aldenberg (1990)
k_Z	half-saturation concentration for zooplankton	1.5 mg C L^{-1}	model value from Janse and Aldenberg (1990)

The possibility for fish to have other food sources, e.g. benthic invertibrates, is not modelled. The fish use energy for maintenance, but this is not modelled, i.e. all food (zooplankton) is assumed to result in fish growth. In the model the zooplankton will influence the fish dynamics a lot more than in reality, since these processes are missing. The impact of fish on zooplankton could be modelled without explicitly modelling the fish biomass according to Scheffer (1998).

4.9 Predation on planktivorous fish

Piscivorous fish reduces the planktivorous fish biomass ((37), Table 13). This is modelled the same way as fish predation on zooplankton. The predation results in fish growth (38).

$$\phi_{FA} = -k_{pB} * \theta^{T-T_{ref}} * \frac{FA^2}{k_{FA}^2 + FA^2} * FB \tag{37}$$

$$\Phi_{FB} = -\phi_{FA} \tag{38}$$

Table 13. Parameters for predation on fish.

Symbol	Parameter	Value	Reference
k_{pB}	maximum predation rate on planktivorous fish at reference temperature	0.1 d^{-1}	model value from Persson and Barkman (1997)
θ	general temperature coefficient	1.07	model value from Janse and Aldenberg (1990)
T_{ref}	general reference temperature	20°C	model value from Janse and Aldenberg (1990)
k_{FA}	half-saturation concentration for fish	0.2 mg C L^{-1}	model value from Persson and Barkman (1997)

4.10 Natural mortality of fish

Planktivorous fish are eaten by fish, but no other mortality is modelled. Piscivorous fish mortality is assumed to be a first-order process ((39), Table 14). It results in sediment organic matter (40).

$$\phi_{FB} = -k_{mort} * FB \tag{39}$$

$$\Phi_B = -\phi_{FB} * \frac{A_{cell} * \Delta z_{cell}}{A_{bottom}} \tag{40}$$

Table 14. Parameters for fish mortality.

Symbol	Parameter	Value	Reference
k_{mort}	mortality rate for piscivorous fish	0.0008 d^{-1}	model value from Persson and Barkman (1997)
A_{bottom}	bottom area	varying with depth	determined by input data
A_{cell}	area of lake cell	varying with depth	determined by input data
Δz_{cell}	thickness of lake cell	varying with depth	determined at model setup

Fish can also be consumed by birds, or removed through fishing. In addition piscivorous fish may be cannibals. None of these losses are considered in the model.

4.11 Mineralisation of detritus

Detritus is lost through degradation by microbials ((41), Table 15). This process consumes oxygen (44) and mineralises nitrogen and phosphorus bound in the organic matter (42-43). This maintains the stoichiometric ratio of detritus (Table 3). The modelled degradation depends on temperature (41).

$$\phi_D = -k_d * \theta^{T-T_{ref}} * D \tag{41}$$

$$\Phi_{DIN} = -C_{NC} * \phi_D \tag{42}$$

$$\Phi_{PO4} = -C_{PC} * \phi_D \tag{43}$$

$$\phi_{O2} = C_{OC} * \phi_D \tag{44}$$

Table 15. Parameters for mineralisation of detritus.

Symbol	Parameter	Value	Reference
k_d	degradation rate at reference temperature	0.02 d^{-1}	median of several literature values: Tufford and McKellar (1999); Otten *et al.* (1992); Cole and Likens (1979); Mills and Alexander (1974); Jewell and McCarty (1971)
θ	general temperature coefficient	1.07	same as phytoplankton growth
T_{ref}	general reference temperature	20°C	standard value

4.12 Denitrification

Denitrification is an important process because it removes nitrogen from the lake system. It demands anoxic environment. Thus, if the water contains oxygen the process acts in the sediment. Denitrification may occur in the water if oxygen is depleted. During denitrification organic matter is degraded using nitrate (instead of oxygen). The denitrification results in atmospheric nitrogen (N_2) and inorganic carbon, but these have no source terms since these are not modelled. There are two kinds of denitrification in sediment, the coupled nitrification-denitrification by bacteria and the denitrification of nitrate supplied from the lake water. The model does not separate between these.

Two expressions for denitrification are used, one for denitrification in the sediment (45) and one for denitrification in the water (46) (Table 16). The model only simulates total dissolved inorganic nitrogen in the water, although it is nitrate that is involved in denitrification. Therefore the DIN concentration has been used to estimate the nitrate limitation of denitrification in the water. The limitation is given by the common Michaelis-Menten expression. This process formulation (45-46) differ from most others in BIOLA by not being proportional to the variable in question.

$$\phi_{BINO3} = -k_{dena} * \theta^{T-T_{ref}} * \frac{BNO3}{K_m * d_{sed} + BNO3} * h(O2) \tag{45}$$

$$\phi_{NO3} = -k_{den} * \theta^{T-T_{ref}} * \frac{DIN}{K_m + DIN} * (1 - h(O2)) \tag{46}$$

Table 16. Parameters for denitrification.

Symbol	Parameter	Value	Reference
k_{dena}	maximum areal denitrification rate at reference temperature	0.16 g N m^{-2} d^{-1}	median of several reported recalculated values: Svensson (1998a); Jonsson and Jansson (1997); Mengis *et al.* (1997); Molot and Dillon (1993); Rysgaard *et al.* (1993); Dudel and Kohl (1992); Jensen *et al.* (1992); Bédard and Knowles (1991); Downes (1991); DeLaune *et al.* (1990); Andersen (1977a,b)
k_{den}	maximum denitrification rate at reference temperature	0.03 mg N L^{-1} d^{-1}	median of several reported recalculated values: Svensson (1998a); Jonsson and Jansson (1997); Mengis *et al.* (1997); Molot and Dillon (1993); Rysgaard *et al.* (1993); Dudel and Kohl (1992); Jensen *et al.* (1992); Bédard and Knowles (1991); Downes (1991); DeLaune *et al.* (1990); Messer and Brezonik (1983/84); Andersen (1977a,b)
θ	general temperature coefficient	1.07	Lewandoswki (1982), Messer and Brezonik (1983/1984), Whitehead and Toms (1993)
T_{ref}	general reference temperature	20°C	Lewandoswki (1982)
d_{sed}	thickness of active sediment layer	0.1 m	same value as for nitrification etc.
K_m	half saturation concentration for nitrogen used in denitrification	3 mg N L^{-1}	Messer and Brezonik (1983/1984), Andersen (1977)
$h(O2)$	Heaviside's step function	$\begin{cases} 1 & O2 > 0 \\ 0 & O2 \leq 0 \end{cases}$	

The organic matter degraded during denitrification is proportional to the nitrate used up (47,50). The model assumes that the nitrogen and phosphorus bound in the organic matter are mineralised during the degradation process (48-49,51-52). The denitrification therefore releases a small amount of ammonium/dissolved inorganic nitrogen and phosphorus. This will keep the stoichiometric C:N:P ratio of the organic matter constant.

The equations for sediment denitrification:

$$\phi_B = C_{CNdenit} * \phi_{BINO3} \tag{47}$$

$$\Phi_{BIP} = -C_{PC} * \phi_B \tag{48}$$

$$\Phi_{BINH4} = -C_{NC} * \phi_B \tag{49}$$

The equations for water denitrification:

$$\phi_D = C_{CNdenit} * \phi_{NO3} \tag{50}$$

$$\Phi_{PO4} = -C_{PC} * \phi_D \tag{51}$$

$$\Phi_{DIN} = -C_{NC} * \phi_D \tag{52}$$

4.13 Nitrification

Ammonium in the sediment is oxidised to nitrate if oxygen is present ((53-54), Table 17). Temperature is assumed to regulate the rate in the model, since bacteria are responsible for the process. The process depends on supply of both ammonium and oxygen, and may be controlled by the availability of either. Since the process take place in the sediment but oxygen is supplied from the water above, the oxygen used has to be recalculated to concentration value (55).

$$\phi_{BINH4} = -k_{nitr} * \theta_n^{T-T_{nref}} * \min\left(BINH4, \frac{O2}{C_{ONnitr} * d_{sed}} \right) \tag{53}$$

$$\Phi_{BINO3} = -\phi_{BINH4} \tag{54}$$

$$\phi_{O2} = C_{ONnitr} * \phi_{BINH4} * \frac{A_{bottom}}{A_{cell} * \Delta z_{cell}} \tag{55}$$

Table 17. Parameters for nitrification.

Symbol	Parameter	Value	Reference
k_{nitr}	nitrification rate, depends on d_{sed}	0.08 d^{-1}	Rysgaard *et al.* (1994)
θ_n	temperature coefficient for nitrification	1.1	Heathwaite (1993)
T_{nref}	reference temperature for nitrification	21°C	Rysgaard *et al.* (1994)
d_{sed}	thickness of active sediment layer (where most of the ammonium production occur)	0.1 m	DiGario and Snow (1977)
A_{bottom}	bottom area	varying with depth	determined by input data
A_{cell}	area of the lake cell	varying with depth	determined by input data
Δz_{cell}	thickness of lake cell	varying with depth	determined at model setup

4.14 Mineralisation in sediment

The total degradation of organic matter in the sediment is assumed to depend on temperature and the amount of organic matter. The used temperature relation is the same as for denitrification (45). Here is calculated the aerobic mineralisation of sediment organic matter. The process of denitrification also degrades sediment organic matter, therefore denitrification is subtracted from the total sediment mineralisation to get the part using oxygen ((56), Table 18). During mineralisation of sediment organic matter ammonium and phosphate are released and oxygen consumed (57-59).

$$\phi_B = -\max\left(k_{sm} * \theta^{T-T_{ref}} * B + \phi_B(denitrification), 0\right) \tag{56}$$

$$\phi_{O2} = C_{OC} * \phi_B * \frac{A_{bottom}}{A_{cell} * \Delta z_{cell}} \tag{57}$$

$$\Phi_{BNH4} = -C_{NC} * \phi_B \tag{58}$$

$$\Phi_{BIP} = -C_{PC} * \phi_B \tag{59}$$

Table 18. Parameters for mineralisation in sediment.

Symbol	Parameter	Value	Reference
k_{sm}	mineralisation rate in sediment	0.002 d^{-1}	median of literature values: Jonsson and Jansson (1997); Gale *et al.* (1992); Andersen (1977a,b)
θ	general temperature coefficient	1.07	same as mineralisation of detritus
T_{ref}	general reference temperature	20°C	
A_{bottom}	bottom area	varying with depth	determined by input data
A_{cell}	area of lake cell	varying with depth	determined by input data
Δz_{cell}	thickness of lake cell	varying with depth	determined at model setup

4.15 Permanent sequestering in sediment

Sediment organic matter can be permanently buried and no longer interacting with the lake. This process is modelled as a first-order rate ((60), Table 19). Default is no sequestering, but other has used sequestering rates between 0 and 0.25 d^{-1} (Marmefelt *et al.*, 2000).

$$\phi_B = -k_s * B \tag{60}$$

Table 19. Parameters for permanent sequestering of sediment organic matter.

Symbol	Parameter	Value	Reference
k_s	sequestering rate	0.0 d^{-1}	Marmefelt *et al.* (2000)

4.16 Exchange of nutrients between water and sediment

Dissolved nutrients in sediment pore water may diffuse into the lake water and vice versa ((61-65), Table 20). The sources and sinks therefore only symbol the assumed positive direction of nutrient flow, but can be both positive and negative. The exchange is promoted by benthic animals stirring the sediment. The rate also depends on the concentration gradient between the sediments and the water above. Only the latter is considered in the model. The concentration gradient between the sediment and the water is not given by the model. The modelled concentration is the mean nutrient concentration in the active sediment layer/lake cell. Therefore the concentration gradient is estimated by the difference between these mean concentrations divided by an appropriate distance (i.e. between the depth of mean concentration in the water and the depth of mean concentration in the sediment). The distance of the concentration gradient is assumed to be equal to the thickness of the active sediment layer.

$$\phi_{BIP} = -k_{diff} * \frac{\left(\frac{BIP * (1 - h(O2))}{d_{sed}} - PO4 \right)}{d_{sed}} \tag{61}$$

$$\phi_{BNO3} = -k_{diff} * \frac{(BNO3 - DIN * \Delta z_{cell})}{d_{sed}^{\ 2}} \tag{62}$$

$$\phi_{BNH4} = -k_{diff} * \frac{(BNH4 - 0)}{{d_{sed}}^2} \tag{63}$$

$$\Phi_{PO4} = -\frac{\phi_{BIP} * A_{botten}}{A_{cell} * \Delta z_{cell}} \tag{64}$$

$$\Phi_{DIN} = -\frac{(\phi_{BNO3} + \phi_{BNH4}) * A_{botten}}{A_{cell} * \Delta z_{cell}} \tag{65}$$

It is assumed that if the top sediment is aerobic, all sediment phosphate is absorbed to minerals, while in anaerobic sediment all phosphate is in solution (61). The dissolved inorganic nitrogen in the water is assumed to interact with sediment nitrate (62), while sediment ammonium only diffuses out of the sediment assuming no ammonium in the water (63). This is a crude simplification, but the proportion of different nitrogen components in DIN is not modelled. The sediment nutrient flows (62-63) have to be transformed to corresponding water flows (64-65).

Table 20. Parameters for the exchange of nutrients between water and sediment.

Symbol	Parameter	Value	Reference
k_{diff}	diffusion coefficient for sediment	$1*10^{-9}$ m^2 s^{-1}	median of several literature values: Portielje and Lijklema (1999); James *et al.* (1997); van Rees *et al.* (1996); Rysgaard *et al.* (1994); Amano *et al.* (1992); Sweerts *et al.* (1991); Hordijk *et al.* (1987); Jensen and Andersen (1987); Krezoski *et al.* (1984); Håkansson and Jansson (1983); Cappenberg *et al.* (1982); Hesslein (1980); Freedman and Canale (1977); Kamiyama *et al.* (1977); Schindler *et al.* (1977); Kamp-Nielson (1974)
$h(O2)$	Heaviside's step function	$\begin{cases} 1 & O2 > 0 \\ 0 & O2 \le 0 \end{cases}$	
d_{sed}	thickness of active sediment layer	0.1 m	DiGario and Snow (1977)
A_{bottom}	bottom area	varying with depth	determined by input data
A_{cell}	area of lake cell	varying with depth	determined by input data
Δz_{cell}	thickness of lake cell	varying with depth	determined at model setup

Resuspension of organic matter is not included in the model. The depth of the active sediment layer depends on oxygen conditions, and varies in time and between lakes. This has been ignored in the model.

4.17 Sinking and sedimentation of phytoplankton, blue-green algae and detritus

The sinking of algae and other organic matter are controlled by characteristics like size, density and shape. In the model only the difference in characteristics between variables (phytoplankton, blue-green algae and detritus) are considered and not the variation within each group. The sinking and sedimentation is modelled with different settling velocity for phytoplankton, blue-green algae and detritus ((66), Table 21). Blue-green algae have been given zero velocity because they can regulate their buoyancy (Table 21). The net changes of the variables A, A_{NFIX} and D are calculated by the equation (66), and the source to the sediment by equation (67).

$$\Phi_C = \frac{\partial (v_C * C)}{\partial z} \qquad C = A, A_{NFIX}, D \tag{66}$$

$$\Phi_B = v_C * C \tag{67}$$

Table 21. Parameters for sinking and sedimentation.

Symbol	Parameter	Value	Reference
v_P	sinking velocity of phytoplankton	0.8 m d^{-1}	median of literature values: Broström (1998); James and Bierman (1995); Stabel (1987); Burns and Rosa (1980); Lehman *et al.* (1975); Burns and Pashley (1974)
v_{ANFIX}	sinking velocity of blue-green algae	0.0 m d^{-1}	Burns and Rosa (1980)
v_D	sinking velocity of detritus	1.2 m d^{-1}	median of literature values: Broström (1998); Stabel (1987); Burns and Rosa (1980); Burns and Pashley (1974)

5 External sources and sinks

5.1 River supply

Inflow supplies DIN, phosphate and sometimes dissolved or particulate organic matter (added to the detritus pool). Phytoplankton, blue-green algae and zooplankton are diluted by inflow. Nutrients and plankton are assumed to passively follow the outflow water. Sediment variables, macrophytes and fish are assumed to stay put in the lake, and are not influenced by advective flow. Time series of nutrients and organic matter concentration in inflow are necessary driving data for the model.

5.2 Atmospheric deposition of nitrogen and phosphorus

Atmospheric deposition of nutrients is modelled as a constant flux to the lake surface ((68-69), Table 22). Note that F is directed upward.

$$F_{DIN} = -k_{ndep} * C_{dep} \tag{68}$$

$$F_{PO4} = -k_{pdep} * C_{dep} \tag{69}$$

Table 22. Parameters for atmospheric deposition.

Symbol	Parameter	Value	Reference
k_{ndep}	yearly deposition of nitrogen	1500 mg N m^{-2} yr^{-1}	Langner *et al.* (1995); Marmefelt *et al.* (2000)
k_{pdep}	yearly deposition of phosphorus	7 mg P m^{-2} yr^{-1}	Areskoug (1993)
C_{dep}	coefficient for change of unit to g m^{-2} s^{-1}	$3.1536*10^{10}$ g mg^{-1} s yr^{-1}	

5.3 Atmospheric exchange of oxygen

Exchange of dissolved oxygen is modelled using saturation deficit ((70), Table 23). The expression is taken from the SCOBI model (Marmefelt *et al.*, 2000).

$$F_{O2} = k_{o12} * \frac{k_{o10} * w + k_{o11}}{\sqrt{k_{o7} - k_{o8} * T_s + k_{o9} * T_s^{\,2}}} * \left((1 + k_{o6}) * O_{sat} - O2\right) \tag{70}$$

w is the wind speed (m s^{-1}), T_s is surface temperature (°C), and the expression within the square root is the Schmidt number (Omstedt, 1991). The saturated oxygen concentration is temperature dependent (71).

$$O_{sat} = e^{k_{o1} + \frac{k_{o2}}{T_s + T_{CK}} + k_{o3} * \ln\left(\frac{T_s + T_{CK}}{k_{o4}}\right) + k_{o5} * (T_s + T_{CK})} \tag{71}$$

Table 23. Parameters for atmospheric exchange of oxygen.

Symbol	Parameter	Value	Reference
k_{o1}	coefficient in oxygen exchange equation	-173.4292	Marmefelt *et al.* (2000)
k_{o2}	coefficient in oxygen exchange equation	24963.39	Marmefelt *et al.* (2000)
k_{o3}	coefficient in oxygen exchange equation	143.3483	Marmefelt *et al.* (2000)
k_{o4}	coefficient in oxygen exchange equation	100	Marmefelt *et al.* (2000)
k_{o5}	coefficient in oxygen exchange equation	-0.218492	Marmefelt *et al.* (2000)
T_{CK}	difference between °C and K	273.15	
k_{o6}	coefficient in oxygen exchange equation	0.025	Marmefelt *et al.* (2000)
k_{o7}	coefficient in oxygen exchange equation	1450	Omstedt (1991)
k_{o8}	coefficient in oxygen exchange equation	71	Omstedt (1991)
k_{o9}	coefficient in oxygen exchange equation	1.1	Omstedt (1991)
k_{o10}	coefficient in oxygen exchange equation	0.17 if $w \leq 3.6$, 2.85 if $3.6 \leq w \leq 13$, and 5.9 if $13 \leq w$	Marmefelt *et al.* (2000)
k_{o11}	coefficient in oxygen exchange equation	0 if $w \leq 3.6$, -9.65 if $3.6 \leq w \leq 13$, and –49.3 if $13 \leq w$	Marmefelt *et al.* (2000)
k_{o12}	coefficient in oxygen exchange equation	5.9	Marmefelt *et al.* (2000)

6 Model application in different lakes

The BIOLA model has been applied to three Swedish lakes; Lake Ringsjön in southern Sweden, Lake Glan in south-eastern Sweden, and Lake Vänern in south-western Sweden. Comparison of results from the applications to the different types of lakes are presented in this section, and especially the parameter values are discussed.

The model versions in the lakes vary, and are described in section 6.1. At set up, initial values of all variables are given, but these are sometimes changed later to get a relatively stable concentration level. Some parameters of the model are then calibrated against measurements. The visual appearance of the time series compared to observations was used for choosing the best parameter values. This was based firstly on the level, and secondly on the seasonal variation of the state variables.

6.1 Descriptions of lakes and model set-ups

Table 24 and 25 summaries the characteristics of the lakes and of the model set-ups. The difference in size of the lakes is striking. Further, Lake Glan and Lake Ringsjön are eutrophic, while Lake Vänern is an oligotrophic brown-water lake. The parameters which were adjusted in the calibrations are given in Table 26.

Table 24. Lake characteristics (data from SMHI (1996) and monitoring programs).

Name	Lake area (km^2)	Mean depth (m)	Mean flow ($m^3 s^{-1}$)	Mean Tot-N (mg L^{-1})	Mean Tot-P (mg L^{-1})	Catchment area (km^2)	Forested area
Lake Glan	75	10	77	1	0.04	13 000	50%
Lake Ringsjön	15	3	4	2	0.08	400	40%
Lake Vänern	5 600	27	550	0.7	0.008	41 000	60%

Table 25. Model set-ups. N is the vertical grid cell number.

Lake	Basin	N	Max depth (m)	Simulation period
Lake Glan	-	30	24	1 October 1987 – 28 September 1998
Lake Ringsjön	Lake Sätoftasjön	20	17.5	1 March 1990 – 31 December 1999
	Lake Östra Ringsjön	20	16.4	
	Lake Västra Ringsjön	14	5.4	
Lake Vänern	northern coast	38	66	1 January 1985 – 31 December 1999
	south-eastern coast	35	55	
	Lake Värmlandsjön	47	108	
	northern Lake Dalbosjön	42	81	
	southern Lake Dalbosjön	29	27	

Table 26. Used parameters for Lake Ringsjön, Lake Glan and Lake Vänern. Only those different from default values are included.

Symbol	Description	Default value	Lake Ringsjön	Lake Glan	Lake Vänern
k_{PO4}	half-saturation concentration for phytoplankton and blue-green algae uptake of phosphorus (mg P L^{-1})	0.01	0.04	0.01	0.001
k_D	detritus shading coefficient (m^2 g^{-1})	0.2	0.2	0.2	0.6
μ_M	maximum growth rate for macrophytes at reference temperature (d^{-1})	0.5	0.5	0.1	-
m_{ANF}	mortality rate for blue-green algae (d^{-1})	0.0	0.002	0.002	0.001
m_M	mortality rate for macrophyte (d^{-1})	0.05	0.05	0.01	-
k_g	half-saturation concentration for grazing (mg C L^{-1})	0.5	1.0	0.5	0.02
s_{ANFIX}	selectivity coefficient for grazing on blue-green algae	0.2	0.2	0.04	0.2
s_D	selectivity coefficient for grazing on detritus	0.4	0.0	0.4	0.0
k_{zm}	mortality rate for zooplankton (d^{-1})	0.005	0.05	0.1	0.04
k_{mort}	mortality rate for piscivorous fish (d^{-1})	0.0008	0.0005	0.0008	-
k_d	degradation rate at reference temperature (d^{-1})	0.02	0.02	0.02	0.0000005
k_{sm}	mineralisation rate in sediment (d^{-1})	0.002	0.02	0.0002	0.000002
k_s	sequestering rate (d^{-1})	0.0	0.0	0.0	0-0.00032
k_{diff}	diffusion coefficient for sediment (m^2 s^{-1})	$1*10^{-9}$	$1*10^{-7}$	$1*10^{-7}$	$9*10^{-12}$-$3*10^{-9}$
v_P	sinking velocity of phytoplankton (m d^{-1})	0.8	0.0005	0.0005	0.06
v_D	sinking velocity of detritus (m d^{-1})	1.2	1.2	1.2	0.006 - 0.01

6.1.1 Model adjustment for Lake Ringsjön

Denitrification was assumed independent of the modelled sediment organic matter (B), i.e. no loss of B during denitrification was modelled. Macrophytes were not included in the model. For Lake Ringsjön, the model was calibrated against observed variables in Lake Västra Ringsjön (Table 26). Observations of nutrient concentration and algal biomass are from regular water investigations in the lake (Bergman, 1997).

6.1.2 Model adjustments for Lake Glan

The oxygen production by macrophyte growth was redirected to the air. A gradual linear transition in phosphate exchange with sediment going from oxic to anoxic conditions was introduced. Observations collected within the catchment's control program, administrated by Motala Ströms Vattenvårdsförbund, were used for calibration. Inflow nitrogen concentrations were taken from a nitrogen model (HBV-N) used in the project 'TRK Belastning till havet' (Transport retention source apportionment – Load to the sea) financed by the Swedish Environmental Protection Agency (NV). Phosphate supply was estimated from observations in the feeder streams (data supplied by Länsstyrelsen Östergötland).

6.1.3 Model adjustments for Lake Vänern

A Langmuir isoterm formulation was used for sorption of phosphate in sediment influencing the phosphate exchange with the water (Ahlkrona, 2002). Resuspension of sediment was included (Ahlkrona, 2002). Fish and macrophytes were not modelled. Lake Vänern has been calibrated for the south-east coast basin, Lake Värmlandssjön and northern Lake Dalbosjön where observations existed. Parameter values were allowed to vary between basins, and different diffusion coefficients for nitrogen and phosphorus were introduced for sediments. Observations of nutrients and TOC were used for inflow concentration (data from Department of Environmental Assessment at the Swedish University of Agricultural Sciences).

6.2 Model results

The simulation of Lake Ringsjön (i.e. Lake Västra Ringsjön) shows a well-mixed lake with a homogeneous temperature most of the time. In Lake Glan and in Lake Vänern (i.e. Lake Värmlandssjön) a thermocline develops during summer. The temperature agrees more or less with observations (e.g. Figure 4) as well as ice thickness, ice formation and ice break up (Figure 5).

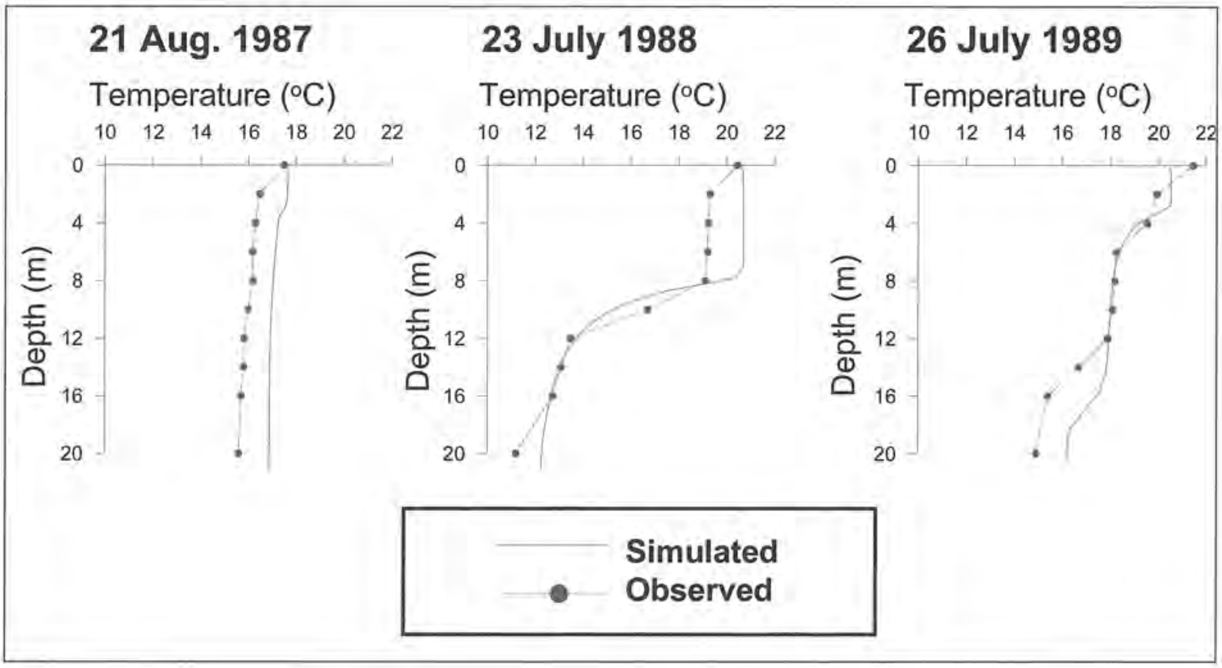

Figure 4. Modelled and observed temperature profiles in Lake Glan.

Dissolved inorganic nitrogen and phosphate are simulated with some discrepancies to observations but both substances show after calibration reasonable concentration levels compared to measurements (mean concentrations in Figure 6). In Lake Ringsjön and Lake Vänern the concentrations are almost homogeneous, while Lake Glan shows some vertical differences.

For mean DIN the seasonal variation is in phase with observations, although the model generally shows not quite enough amplitude in Lake Ringsjön (Figure 6c). In Lake Vänern (Figure 6e) the modelled concentration is almost constant with no seasonal variations. During

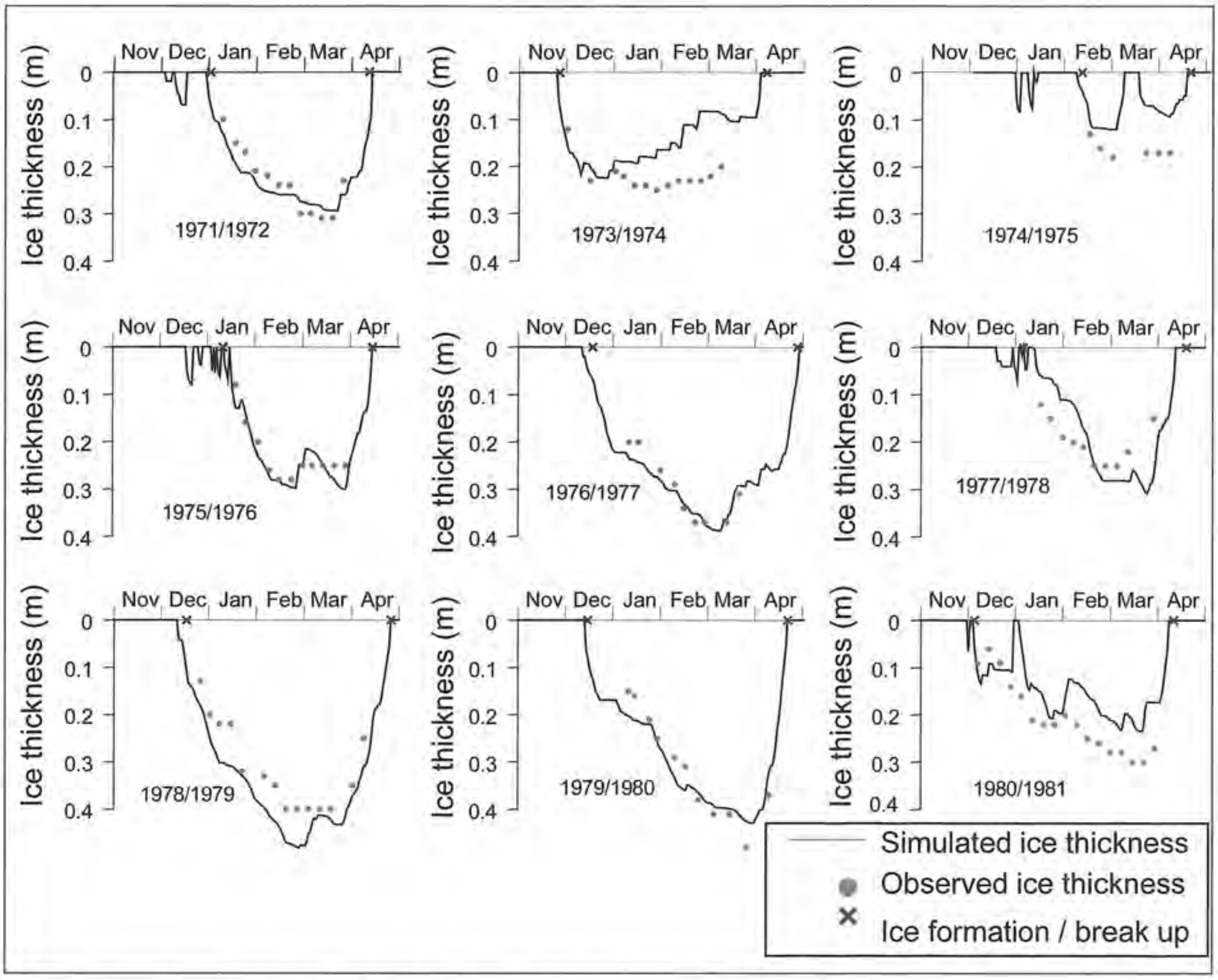

Figure 5. Modelled and observed ice thickness in Lake Glan.

calibration it was found that by increasing the exchange of nitrogen with the sediments, the denitrification rate in Lake Ringsjön increased and the DIN concentrations decreased. Unfortunately the winter concentration decreased too when aiming at decreasing summer concentrations. Thus, the resulting value of the diffusion parameter was a compromise (Table 26). Nevertheless, it was stable enough to be used also in Lake Glan without change. In Lake Vänern on the other hand the exchange of DIN with the sediments had to be reduced unless the DIN concentration should become too low (Table 26). Thus the denitrification in Lake Vänern were relatively minor compared to the other lakes. The parameter values used is outside literature values (Appendix I), but that is not unreasonable since the modelled process represent several exchange mechanisms and not pure diffusion.

For phosphate, on the other hand, the seasonal pattern is not captured correctly in any of the lakes (Figure 6b,d,f), although Lake Vänern seems to lack seasonal variation. The half saturation parameter for algae uptake of nitrogen was the same in all three lake models, but the half saturation parameter for phosphate was calibrated (Table 26). Decreasing the parameter in Lake Vänern made it possible for algae to grow in the low phosphate concentrations present in Lake Vänern, while in Lake Ringsjön it was increased to decrease the algal growth rate and lower the algal concentration.

The mineralisation of detritus had a high influence on nutrient concentrations in Lake Vänern. The relatively less degradable terrestrial organic matter in this lake is the reason for a low

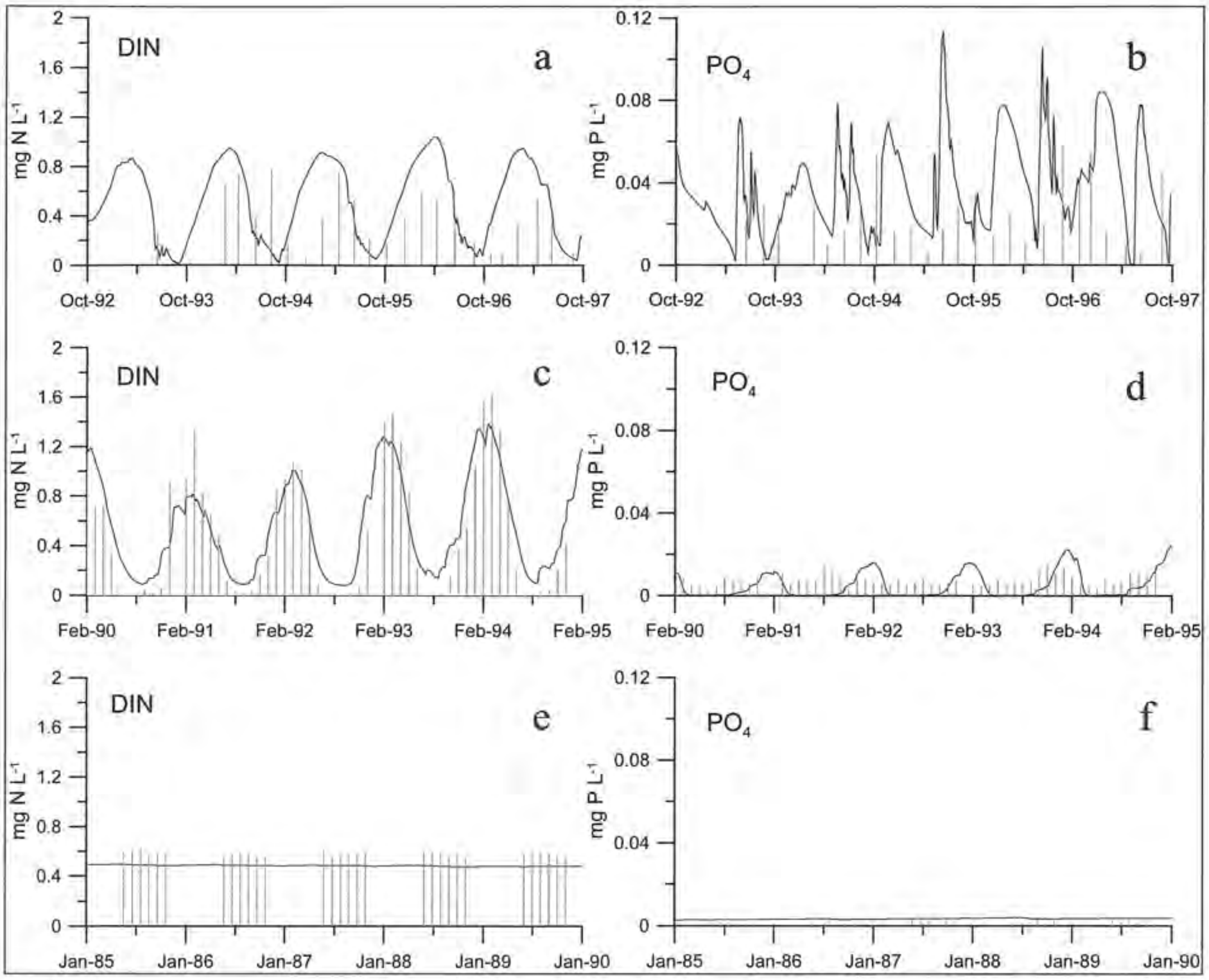

Figure 6. Mean dissolved inorganic nitrogen and phosphate concentration for Lake Glan (a,b), Lake Ringsjön (i.e. Lake Västra Ringsjön) (c,d) and Lake Vänern (i.e. Lake Värmlandssjön) (e,f).

mineralisation rate parameter both in the water and in the sediment (Table 26). The parameter value in Lake Vänern is outside the range found in literature (Appendix I) for degradation of detritus and algal material, but probably not unreasonable for terrestrial organic matter.

The primary producers (i.e. phytoplankton and blue-green algae) directly respond to nutrient concentrations. Both algae show reasonable agreement with observations (Figure 7), but the model does not capture the year to year difference. The timing of algal concentration also needs to be improved (Figure 7a). Natural mortality of blue-green algae is a parameter regulating the relative amount of phytoplankton and blue-green algae (Table 26). The sinking velocity of phytoplankton regulates the concentration of phytoplankton in the water. It varies over a large range in the model. It had to be reduced in especially Lake Glan and Lake Ringsjön unless the phytoplankton would be settling too quickly (Table 26).

Zooplankton is tightly coupled to the phytoplankton and blue-green algae concentrations. Zooplankton mortality influences the algal levels, and could therefore to a small extent be used to regulate their concentration. The parameter was higher in the algal rich Lake Glan (Table 26). In Lake Vänern the low algal concentrations made it necessary to decrease the half saturation parameter for grazing for zooplankton to grow at all (Table 26).

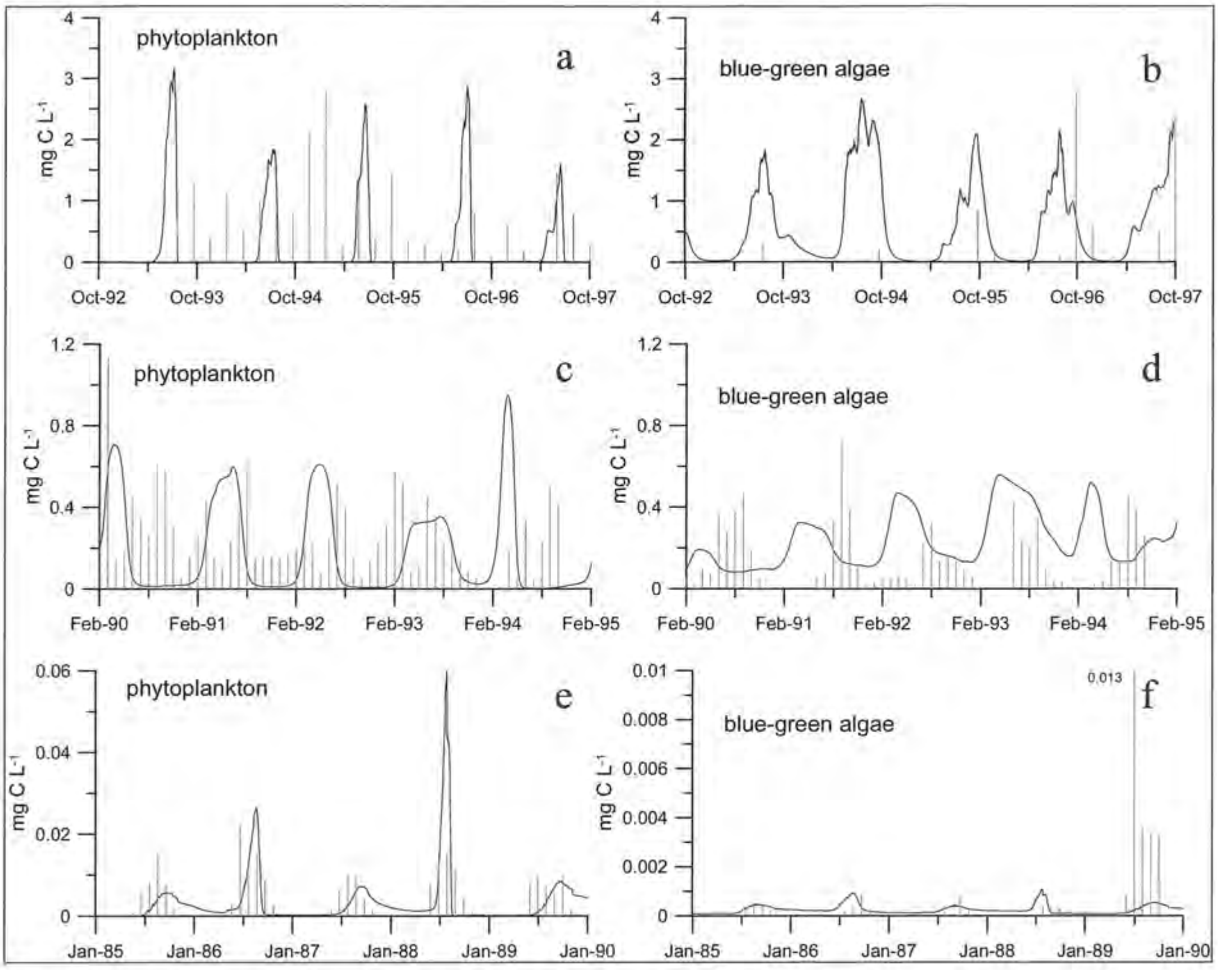

Figure 7. Surface phytoplankton and blue-green algae concentrations for Lake Glan (a,b), Lake Ringsjön (i.e. Lake Västra Ringsjön) (c,d) and Lake Vänern (i.e. Lake Värmlandssjön) (e,f). Note the different scales.

The detritus and sediment parts are unrealistic for Lake Vänern, because of the lake's high input of terrestrial organic matter. The phosphorus in detritus is to high compared to observed total phosphorus (Tot-P) in the lake, because detritus is assumed to have the same P/C ratio as phytoplankton. This phosphorus may not be allowed to reach the water, and is therefore buried in the sediment in the model (i.e. the sequestering rate is not zero, Table 26). Zooplankton in a brown-water lake can have bacteria as an additional food source (Jansson *et al.*, 1999). This could be a reason for their too low concentrations in the model in Lake Vänern. Still, BIOLA can be calibrated to simulate inorganic nutrients and algae reasonably well in this brown-water lake.

An analysis of average flow for specific variables shows that the flows are of different magnitude in the lakes (Table 27 and Table 28). This is natural with the large difference in lake size. More interesting is that the dominating processes vary between the lake models. This is partly due to different model version, but other interesting differences are present as well.

Processes dominating the budgets for dissolved nutrients in the water phase are uptake by phytoplankton and blue-green algae, inflow and outflow, and sometimes exchange with sediments (diffusion). For Lake Vänern the diffusion parameter is lower and the exchange with sediment a less important flow (Table 27). Lake Ringsjön has a large net diffusion of nitrogen into the sediment. This nitrogen is denitrified in the sediment. The extremely large in- and outflows in Lake Värmlandssjön is due to the exchange of water between the two main basins of Lake Vänern. Here water moves to and fro. Notable is also the large influence atmospheric deposition has on the large Lake Vänern.

Table 27. *Average flow of inorganic nutrients in the water (unit kg N/P d^{-1}) based on five years modelling in each lake basin.*

	L. Glan		L. Västra Ringsjön		L. Värmlandssjön	
	DIN	*PO_4*	*DIN*	*PO_4*	*DIN*	*PO_4*
detritus decomposition	320	45	0.5	0.07	20	3
phytoplankton growth	-1100	-150	-9	-1	-430	-60
blue-green algae growth	-1900	-310	-14	-2	-10	-2
denitrification in water	-130	4	0	0	0	0
diffusion from sediment	3100	470	-230	0	-20	-2
inflow	3300	90	480	6	39 000	370
outflow	-3800	-140	-250	-3	-45 000	-310
atmospheric deposition	310	2	60	0.3	2 700	40

Table 28. *Average carbon flow for algae (unit kg C d^{-1}) based on five years modelling in each lake basin.*

	L. Glan		L. Västra Ringsjön		L. Värmlandssjön	
	p.p.	*b.-g. a.*	*p.p.*	*b.-g. a.*	*p.p.*	*b.-g. a.*
growth	6 300	13 000	50	80	2 400	70
grazing	-4 400	-9 100	-50	-30	-2 200	-40
settling	-7	0	-1	0	-200	0
natural mortality	0	-500	0	-30	0	-20
inflow	0	0	53	130	500	20
outflow	-3 200	-2 200	-41	-150	-300	-20

For turn-over processes affecting organic variables (Table 28), a major difference between the lakes is that Lake Västra Ringsjön and Lake Värmlandssjön have inflow of algae and zooplankton from other basins, while Lake Glan don't since it is modelled as a single basin (Table 25). The largest sources are algal growth and in Lake V. Ringsjön inflow. Most of the phytoplankton production is grazed, but less of the blue-green algal production. This since the latter are assumed less edible by the model. Another large loss is outflow. The sinking velocity of blue-green algae is assumed zero by the model (Table 26), thus no settling of these algae occurs (Table 28). On the other hand is natural mortality of phytoplankton not modelled. The phytoplankton sinking velocity in Lake Vänern is larger than in the other lakes making settling a significant sink for phytoplankton there (Table 28).

Acknowledgement

This work was performed within the Swedish Water Management Research Program (VASTRA) which is financed by the Swedish Foundation for Strategic Environmental Research (MISTRA). Additional funding came from Swedish Meteorological and Hydrological Institute (SMHI), and the Swedish Environmental Protection Agency (NV).

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Appendix I Summary of all parameters and state variables in BIOLA

Table AI-1. Parameters in BIOLA with minimum and maximum values found in literature and the BIOLA default value.

Symbol	Parameter	Minimum value	Maximum value	Default value
μ_A	maximum growth rate for phytoplankton at reference temperature (d^{-1})	0.6	10	2.0
θ	general temperature coefficient	1.07	1.17	1.07
T_{ref}	general reference temperature (°C)	-	-	20
I_{opt}	optimal light intensity for phytoplankton and blue-green algae ($W\ m^{-2}$)	25	193	50
k_{PO4}	half-saturation concentration for phytoplankton and blue-green algae uptake of phosphorus ($mg\ P\ L^{-1}$)	0.00003	0.19	0.01
k_{DIN}	half-saturation concentration for phytoplankton and blue-green algae uptake of nitrogen ($mg\ N\ L^{-1}$)	0.005	0.08	0.02
k_w	extinction coefficient of the water (m^{-1})	0	1	0.04
k_M	macrophyte shading coefficient ($m^2\ g^{-1}$)	0.002	0.16	0.16
k_P	shading coefficient for phytoplankton and blue-green algae ($m^2\ g^{-1}$)	0.0004	2.3	0.3
k_D	detritus shading coefficient ($m^2\ g^{-1}$)	0.03	0.4	0.2
μ_{ANFIX}	maximum growth rate for blue-green algae at reference temperature (d^{-1})	0.42	2	1.0
μ_M	maximum growth rate for macrophytes at reference temperature (d^{-1})	0.11	10	0.5
θ_M	temperature coefficient for macrophyte	-	-	1.04
I_{Mopt}	optimal light intensity for macrophyte ($W\ m^{-2}$)	-	-	75
k_{MIP}	half-saturation concentration for macrophyte uptake of phosphorus ($mg\ P\ L^{-1}$)	-	-	0.005
k_{MIN}	half-saturation concentration for macrophyte uptake of nitrogen ($mg\ N\ L^{-1}$)	-	-	0.01
d_{sed}	thickness of active sediment layer (m)	-	-	0.1
m_{ANFIX}	mortality rate for blue-green algae (d^{-1})	-	-	0.0
m_M	mortality rate for macrophyte (d^{-1})	-	-	0.05
k_G	grazing rate (d^{-1})	0.2	2.5	0.8
e	efficiency of zooplankton grazing	-	-	0.4
k_g	half-saturation concentration for grazing ($mg\ C\ L^{-1}$)	-	-	0.5
s_A	selectivity coefficient for grazing on phytoplankton	-	-	1.0
s_{ANFIX}	selectivity coefficient for grazing on blue-green algae	-	-	0.2
s_D	selectivity coefficient for grazing on detritus	-	-	0.4
k_{zm}	mortality rate for zooplankton (d^{-1})	-	-	0.005
k_{pA}	maximum predation rate on zooplankton at reference temperature (d^{-1})	0.05	0.15	0.1
k_Z	half-saturation concentration for zooplankton ($mg\ C\ L^{-1}$)	-	-	1.5

Table AI-1. Continued.

Symbol	Parameter	Minimum value	Maximum value	Default value
k_{pB}	maximum predation rate on planktivorous fish at reference temperature (d^{-1})	0.05	0.13	0.1
k_{FA}	half-saturation concentration for fish (mg C L^{-1})	-	-	0.2
k_{mort}	mortality rate for piscivorous fish (d^{-1})	0.0001	0.015	0.0008
k_d	degradation rate at reference temperature (d^{-1})	0.00005	0.4	0.02
k_{dena}	maximum areal denitrification rate at reference temperature (g N m^{-2} d^{-1})	0.03	1.2	0.16
k_{den}	maximum denitrification rate at reference temperature (mg N L^{-1} d^{-1})	0.01	0.24	0.03
K_m	half saturation concentration for nitrogen used in denitrification (mg N L^{-1})	0.1	84	3
k_{nitr}	nitrification rate, depends on d_{sed} (d^{-1})	-	-	0.08
θ_n	temperature coefficient for nitrification	-	-	1.1
T_{nref}	reference temperature for nitrification (°C)	-	-	21
k_{sm}	mineralisation rate in sediment (d^{-1})	0.00001	0.03	0.002
k_s	sequestering rate (d^{-1})	0	0.25	0.0
k_{diff}	diffusion coefficient for sediment (m^2 s^{-1})	$2.5*10^{-12}$	$2*10^{-8}$	$1*10^{-9}$
v_P	sinking velocity of phytoplankton (m d^{-1})	0.0005	7.5	0.8
v_{ANFIX}	sinking velocity of blue-green algae (m d^{-1})	-	-	0.0
v_D	sinking velocity of detritus (m d^{-1})	0.0005	10	1.2

Table AI-2. Additional parameters in BIOLA with default value.

Symbol	Parameter	Default value
A_{min}	minimum value of phytoplankton (mg C L^{-1})	10^{-4}
$A_{NFIXmin}$	minimum value of blue-green algae (mg C L^{-1})	10^{-4}
D_{min}	minimum value of detritus (mg C L^{-1})	10^{-10}
Z_{min}	minimum value of zooplankton (mg C L^{-1})	10^{-10}
FA_{min}	minimum value of planktivorous fish (mg C L^{-1})	10^{-10}
FB_{min}	minimum value of piscivorous fish (mg C L^{-1})	10^{-10}
B_{min}	minimum value of organic carbon in the sediment (g C m^{-2})	10^{-10}
BIP_{min}	minimum value of phosphate in the sediment (g P m^{-2})	10^{-10}
$BNH4_{min}$	minimum value of ammonium in the sediment (g N m^{-2})	10^{-10}
$BNO3_{min}$	minimum value of nitrate in the sediment (g N m^{-2})	10^{-11}
$PO4_{min}$	minimum value of phosphate (mg P L^{-1})	10^{-10}
DIN_{min}	minimum value of dissolved inorganic nitrogen (mg N L^{-1})	10^{-10}
$O2_{min}$	minimum value of oxygen (mg O_2 L^{-1})	-4.0
M_{min}	minimum value of macrophyte (g C m^{-2})	10^{-4}
C_{OC}	stoichiometric ratio O_2/C during algae growth/organic matter degradation (mg O_2 (mg C)$^{-1}$)	2.667
C_{NC}	stoichiometric ratio N/C in organic matter (mg N (mg C)$^{-1}$)	0.176
C_{PC}	stoichiometric ratio P/C in organic matter (mg P (mg C)$^{-1}$)	$2.44*10^{-2}$
C_{NP}	stoichiometric ratio N/P in organic matter (mg N (mg P)$^{-1}$)	7.2
$C_{CNdenit}$	stoichiometric ratio C/N during denitrification (mg C (mg N)$^{-1}$)	1.071
C_{ONnitr}	stoichiometric ratio O_2/N during nitrification (mg O_2 (mg N)$^{-1}$)	4.572
k_{ndep}	yearly deposition of nitrogen (mg N m^{-2} yr^{-1})	1500
k_{pdep}	yearly deposition of phosphorus (mg P m^{-2} yr^{-1})	7
C_{dep}	coefficient for change of unit to g m^{-2} s^{-1} (g mg^{-1} s yr^{-1})	$3.1536*10^{10}$
k_{o1}	coefficient in oxygen exchange equation	-173.4292
k_{o2}	coefficient in oxygen exchange equation	24963.39
k_{o3}	coefficient in oxygen exchange equation	143.3483
k_{o4}	coefficient in oxygen exchange equation	100
k_{o5}	coefficient in oxygen exchange equation	-0.218492
T_{CK}	difference between °C and K	273.15
k_{o6}	coefficient in oxygen exchange equation	0.025
k_{o7}	coefficient in oxygen exchange equation	1450
k_{o8}	coefficient in oxygen exchange equation	71
k_{o9}	coefficient in oxygen exchange equation	1.1
k_{o10}	coefficient in oxygen exchange equation	0.17 if $w\leq3.6$, 2.85 if $3.6\leq w\leq13$, and 5.9 if $13\leq w$
k_{o11}	coefficient in oxygen exchange equation	0 if $w\leq3.6$, -9.65 if $3.6\leq w\leq13$, and -49.3 if $13\leq w$
k_{o12}	coefficient in oxygen exchange equation	5.9

Table AI-3. All state variables in BIOLA.

State variables	Symbol
Phosphate	PO4
Dissolved inorganic nitrogen	DIN
Oxygen	O2
Dissolved phosphorus in sediment water	BIP
Dissolved ammonium in sediment water	BNH4
Dissolved nitrate in sediment water	BNO3
Phytoplankton	A
Blue-green algae	A_{NFIX}
Zooplankton	Z
Planktivorous fish	FA
Piscivorous fish	FB
Macrophyte	M
Detritus	D
Sediment organic matter	B

Appendix II Literature review of biogeochemical process formulations in ecological models

Contents

1 Introduction

This is a compilation of biogeochemical lake processes formulated in selected ecological models. The literature review was made to facilitate the development of a biogeochemical lake model (BIOLA) at SMHI.

The most important variables to include in the lake model are nutrients and phytoplankton in the water and phosphorus in the sediment. This was decided in the beginning of the development. Therefore these parts of the models are studied closer than other not so crucial parts. The sediment is important for its possible phosphorus release after reduction of phosphorus in inflow. It was also decided to try and keep BIOLA as simple as possible, and therefore some of the more complex models has been excluded in this review.

Symbols of state variables discussed in this report are gathered in Table AII-1. Some of them are redundant or overlapping as they are used in different models. The variables are modelled in different units in the reviewed models. Phytoplankton, for example, can be modelled as biomass, organic carbon (C), phosphorus (P), nitrogen (N) or chlorophyll a (chl a). The relation between these varies, but constant ratios are sometimes used. Some ratios found are gathered in Table AII-2. If the element ratio in organic matter should vary with time, then phosphorus, nitrogen and carbon must be modelled separately. Some models consider this, but others do not. In addition the ratios may increase in the food chain (Janse and Aldenberg, 1990). This means that predators selectively assimilate the food. This is regulated by excretion.

The sediment is divided in several compartments; e.g. inorganic, organic, interstitial water, passive and active sediment layers. The division is different for different models.

Table AII-1. State variables present in the different models.

Inorganic variables	Symbol	Living organic variables	Symbol	Other variables	Symbol
Phosphate	PO4	Phytoplankton	A	Detritus	D
Nitrate (and nitrite)	NO3	Zooplankton	Z	Particulate organic nitrogen	PON
Ammonium	NH4	Planktivorous fish	FA	Dissolved organic nitrogen	DON
Dissolved inorganic nitrogen	DIN	Predatory fish	FB	Dissolved organic phosphorus	DOP
Oxygen	O2	Macrophytes	M	Particulate organic phosphorus	POP
Temperature	T	Phosphorus in phytoplankton	AP	Sediment phosphorus	BP
Phosphorus in interstitial water in sediment	BI	Nitrogen in phytoplankton	AN	Sediment nitrogen	BN
Nitrate in pore water	BNO			Phosphorus in upper thin sediment layer	BY
Silica	SI				
Light	I				

Table AII-2. Stoichiometric ratios between different elements in organic matter and some other ratios. Reference denotation is found in Table AII-3.

Ratio	Parameter values	References
chl/C	1/100-1/50 g chl/g C	SCOBI
C/chl	50 g C/g chl	JREV
N/chl	7-10 g N/g chl	JREV
N/C	16/(106*12.011) μmole N/μg C	SCOBI
P/chl	2 g P/g chl	WALT
P/chl	0.63-1 g P/g chl	JREV
P/C	1/(106*12.011) μmoll P/μg C	SCOBI
O/C	22.39/12.011 ml O_2/mg C	SCOBI
C/A	0.33-0.6 g C/g dw	JREV
N/A	0.044-0.084 g N/g dw	JREV
P/A	0.011-0.07 g P/g dw	JREV

Bacteria is seldom modelled, I have seen it modelled only once (Jørgensen et al., 1983a). Jørgensen et al. (1983a) attributes this to bacteria having a fairly constant concentration and seldom being measured. Macrophytes are modelled in specific macrophyte models and in PCLAKE (a development of the PCLOOS model). This model is a modelling tool for evaluation of lake restoration scenarios (Janse and van Liere, 1995). The model is very complex, and I have not found any detailed description of it.

The references used in this literature review are grouped into separate models or authors (Table AII-3). The groups have been given names that are used as references for process formulations and parameter values in Section 2.

Table AII-3. Models reviewed.

Name	Type of environment	References
AND	lakes	Andersen (1977)
ASA	eutrophic shallow lakes	Asaeda and Bon (1997)
AST	Lake Ladoga	Astrakhantsev et al. (1996)
COL	reservoirs	Collins and Wlosinski (1989)
JMS	lakes	James (1984)
JORG	lakes (eutrophic)	Jørgensen and de Bernardi (1998); Jørgensen et al. (1986); Jørgensen and Mejer (1977)
JREV	lakes and streams	Jørgensen (1983a); Jørgensen (1983b)
MES	lakes	Messer and Brezonik (1983/1984)
MINL	lakes (eutrophic)	Riley and Stefan (1988)
PCL	hypertrophic shallow lakes	Janse and van Liere (1995); Janse and Aldenberg (1990)
PRS	eutrophic shallow lake	Persson and Barkman (1997)
SCV	Lake Ontario	Scavia (1980)
SCOBI	coastal seas	Anon (2000); Marmefelt et al. (2000); Ahnlund (1999)
SVP	shallow eutrophic lake	Sverdrup et al. (1991)
WALT	stratified lake	Walters (1980)
WHIT	reservoirs and lakes	Whitehead and Toms (1993)

Additional models and process formulations can be found in: Blackburn (1990), Blackburn and Blackburn (1992) (denitrification); Lehman et al. (1975), Patterson et al. (1994), Scheffer et al. (1997), Elliot et al. (2000) (phytoplankton); Hamilton and Schladow (1997), Schladow and Hamilton (1997) (DYREMS Water Quality model); James and Bierman Jr (1995), James et al. (1997), Tufford and McKellar (1999) (variants of WASP Water Quality model); Garnier and Billen (1994), Garnier et al. (2000) (biogeochemical lake model); Park and Uchrin (1997) (SIREM1, Water Quality model including macrophytes); van der Molen et al. (1994), Los and Brinkman (1988) (DBS (DELWAQ-BLOOM-SWITCH) eutrophication model); Håkansson and Carlsson (1995) (LEEDS eutrophication model).

2 Process formulation

The processes are treated below one by one. They are often formulated as a source (Φ_X) or sink (ϕ_X) of the primary variable (index X). This flow has of course a corresponding flow for the receiving variables, but this has not been explicitly written with some exceptions. The different formulations are gathered in tables, sometimes together with parameter values if they were easily found. Note that sinks (ϕ) are negative.

2.1 Phytoplankton growth

Phytoplankton growth is modelled proportional to the phytoplankton biomass (A). Some models divide the phytoplankton into several groups, e.g. green algae (G), blue-green algae (BG), and diatoms (DI). The growth is often modelled as limited by light (μ_{light}), phosphate (μ_{PO4}) or nitrogen (μ_{NO3}, μ_{NH4}). The relative limitation of these is calculated and compared and the most limiting factor decides the primary production through minimisation (1) or through multiplication (2).

$$\Phi_A = \mu_{\max}(T) * \min(\mu_{light}, \mu_{PO4}, \mu_{NO3} + \mu_{NH4}, \mu_{SI}) * A \qquad (1)$$

$$\Phi_A = \mu_{\max}(T) * \mu_{light} * \min(\mu_{PO4}, \mu_{NO3} + \mu_{NH4}) * A \qquad (2)$$

In (1) light is seen as a scarce resource rather than as a rate controlling parameter. Temperature is assumed independent of the other factors. Sometimes (e.g. in SCOBI, cf. Table AII-3) light limitation is also modelled as independent of nutrient limitation (2). The maximum growth rate (given no light or nutrient limitation) is given by μ_{max}. Formulations of the factors are found in Table AII-4, 5 and 6.

Every model, with references in Table AII-3, has its own way of describing the temperature dependence, which it uses for all (or almost all) processes modelled by that model. The SCV model has a complicated expression for temperature dependence, but it has still only three parameters: optimal temperature, maximum lethal temperature and Q_{10} (Table AII-4). The MINL model has different temperature relations for phytoplankton growth and other processes. The relations used by JREV and SCV are more realistic since the rate decreases for both low and high temperatures (Figure AII-1). The first two relations in Table AII-4 seem to be the most common.

Only some models have modelled light (I) limited growth. The formulation of light limitation varies a lot (Table AII-5). Partly the variation depends on the time step and vertical division used by the model. Some have an attenuation coefficient depending on phytoplankton, detritus and/or suspended particles (e.g. SCOBI).

The most common nutrient limitation factors have a Michaelis-Menten formulation (Figure AII-2). This means they depend on a half-saturation concentration parameter. In the SCOBI model the nutrient limitation function also depend on the oxygen level, and for nitrate on the concentration of ammonium (Table AII-6).

Table AII-4. Formulation of maximum phytoplankton growth rate and its dependence on temperature, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
$\mu_{\max}(T)$	$k1 * e^{k2*T-T_0}$	k1=0.59-0.8 d^{-1}, k2=0.0633 $(°C)^{-1}$, T_0=0°C	SCOBI
		k1=0.005 h^{-1}, k2=0.1 $(°C)^{-1}$, T_0=0°C	WALT
	$k1 * a^{T-T_0}$	a=1.07,T_0=293 K	JORG
		T_0=20°C	MINL
		a=1.05 (G)-1.07 (BG), T_0=20°C	PCL
	$k1 * 10^{\frac{T_A}{273+T_0}-\frac{T_A}{273+T}}$	k1=250 (BG)-500 yr^{-1}, T_A=2500-3500 K, T_0=20°C	PRS
	$k1 * e^{-2.3*\left\lvert\frac{T-16.5}{15}\right\rvert}$	k1=2.3-2.53 d^{-1} (calibrated)	JREV
	$k1 * \frac{T}{T_{opt}} * e^{1-\frac{T}{T_{opt}}}$	T_{opt} – optimal temperature	JMS
	$k1 * f(T);$ $f(T) = V^x * e^{x*(1-\upsilon)}$ for $T < T_m$; $V = \frac{T_m - T}{T_m - T_0};$ $x = \left(\frac{w * \left(1 + \left(1 + {}^{40}\!/_{w}\right)^{0.5}\right)}{20}\right)^2;$ $w = \ln(Q_{10}) * (T_m - T_0)$	T_0 – optimal temperature (20-30°C), T_m – maximum lethal temperature (35°C), Q_{10}=1.9 (BG), Q_{10}=2 (all other)	SCV
	$k1$	0.05	JORG
			AST
	$k1 * f(T)$	k1=150 yr^{-1}	SVP

One variant of the MINL model, the PCL, and the JMS models include internal phosphorus and nitrogen concentrations in algae in addition to the P and N of its organic matter. Thus they can simulate the ability of algae to store nutrients for later growth. These are more complex models. Riley and Stefan (1988) states that both Michaelis-Menten and cell quota kinetics (i.e. use of internal nutrients) formulations are useful for lake restoration modelling, and that it is a matter of preference which to choose. In addition, Jørgensen (1983a) states that in lakes the stoichiometric ratios in algae are fairly constant. Since an objective was to keep the model simple, only the Michaelis-Menten type is reviewed here.

The phytoplankton growth is often modelled together with uptake of phosphate and nitrogen, and sometimes also with production of oxygen. These processes are generally calculated as proportional to the phytoplankton growth. The nitrogen can be taken from either ammonium, nitrate or in some cases from the atmosphere (nitrogen fixation). The preference for one or the other is modelled in different ways (see SCOBI, SCV for example).

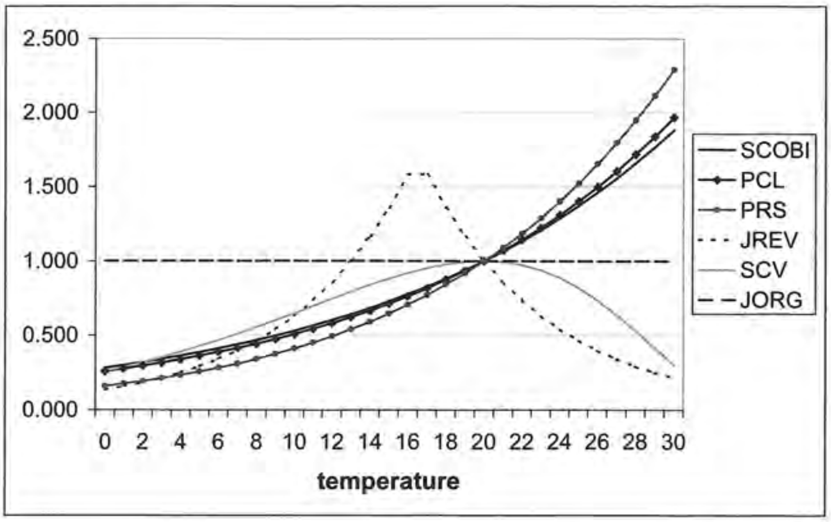

Figure AII-1. The temperature factor for different phytoplankton growth models.

Table AII-5. Formulation of light limitation, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
μ_{light}	1		JORG,AST
	$\frac{I(z)}{I_{opt}} * e^{1-\frac{I(z)}{I_{opt}}}; I(z)=I_0 * e^{-k*z}$	I_{opt}=max(I_0/4, 25 W m^{-2}), k=0.15+0.025A_N, A_N: [μmole N]	SCOBI
		I_{opt}=200 g cal cm^{-2} h^{-1}, k=0.4 m^{-1}	JMS
	$\begin{cases} \frac{I(z)}{I_{opt}} & I(z) \le I_{opt};\ I(z)=I_0 * e^{-k*z} \\ e^{0.1*\left(1-\frac{I(z)}{I_{opt}}\right)} & I(z) > I_{opt} \end{cases}$ $k(z)=k1+\frac{k2}{z} * \int_0^z A(z')dz'$	k1=0.3 m^{-1}, k2=0.04 m^2 (mg chl a)$^{-1}$, A - mg chl a m^{-3}, I_{opt}=115 ly d^{-1}	WALT
	$k1 * \frac{I/k*I_k}{\left(1+\left(I/k*I_k\right)^{k2}\right)^{k3}}$	k=1, k1=1, k2=2, k3=0.5	JREV
		k=2, k1=2, k2=2, k3=1, I_k=0.006 kcal m^{-2} s^{-1} or 150-350 ly d^{-1}	JREV
	$\frac{k * photoperiod}{k2} * \left(e^{-\frac{I_a}{I_s} * e^{-k2*z}} - e^{-\frac{I_a}{I_s} * e^{-k2*z_0}}\right)$	I_a –average yearly solar radiation, k=2.718, k2 =k3*k4*[particle concentration], z_0=0	PRS
		k=2.178/Δz	SCV
	$\frac{1}{1+k * Secchi^{k2}}$	Hill function: k=0.146, n=-2.55, Secchi=3.74-1.74*log(A)	SVP
	$f(I)$		MINL

Table AII-6. Formulation of nutrient limitation, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
μ_{PO4}	$\frac{PO4}{k1+PO4}$	k1=0.1 μg at. L^{-1} (fitted: range 0.1-1.0)	WALT
		k1=0.2 mg P L^{-1}	SVP
		k1=0.004-0.01 mg P L^{-1}	SCV
		k1=0.01-0.02 mg P L^{-1}	JORG
			SVP
		k=0.01 mg L^{-1}	JMS
		k1=0.001-0.15 mg L^{-1}	JREV
	$\frac{PO4}{k1+PO4} * lowox;$ $lowox = \frac{1}{1+\left(\frac{O_{cr}^{2}}{O2}\right)^{oxcr}}$	k1=0.1-1.0 μmole P L^{-1}, O^{2}_{cr}=2, oxcr=6	SCOBI
	$\frac{PO4-k2}{k1+PO4-k2}$		PRS
	$PO4$		AST
μ_{NO3}	1		MINL
	$\frac{NO3}{k1+NO3}$	k1=0.1 mg L-1	JMS
	$\frac{NO3}{k1+NO3} * e^{-k2*NH4} * lowox$	k1=1.0 μmole N L^{-1}, k2=1.5 L μmol^{-1}, lowox – see μ_{PO4}	SCOBI
μ_{NO3} + μ_{NH4}	1		PRS,WALT,JORG,AST,SVP
	$\frac{NH4+NO3}{k+NH4+NO3}$	k=0.000-0.030 mg N L^{-1}	SCV
	$\frac{DIN}{k+DIN}$	k=0.2-0.84 mg L^{-1}	JORG
		k=0.005-0.4 mg L^{-1}	JREV
μ_{NH4}	$\frac{NH4}{k1+NH4} * lowox$	k1=1.0 μmole N L^{-1}, lowox – see μ_{PO4}	SCOBI
μ_{SI}	$\frac{SI}{k+SI}$	k=0.03 mg Si L^{-1} (DI), k=0 (others)	SCV
	1		the other

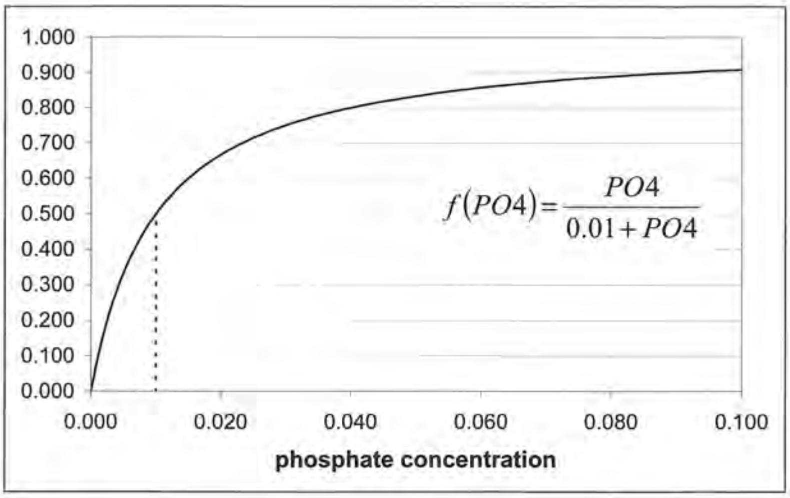

Figure AII-2. Example of a limitation factor for phosphate with half-saturation concentration 0.01.

2.2 Nitrogen fixation

Algal growth through nitrogen fixation can occur when there is nitrogen limited conditions in the lake. I have found two SCOBI expressions. The minimum of light and PO4 is determining the limitation in one version (3). The other has multiplicative limitation (4) and also depends on oxygen (Table AII-7). SCV has a simple model, it assumes the half-saturation coefficient for DIN is zero for nitrogen fixation blue-green algae and uses the ordinary growth rate (Table AII-4, Table AII-5, Table AII-6). JREV estimates the nitrogen fixating algae from the concentration inorganic nutrients (Table AII-7).

$$\Phi_A = \eta_{\max} * \eta_{cap} * \min(\mu_{light}, \mu_{PO4}) * A \tag{3}$$

$$\Phi_A = \eta_{\max} * \eta_{cap} * \mu_{light} * \hat{\mu}_{PO4} * lowox * A \tag{4}$$

2.3 Natural mortality of phytoplankton

Mortality of phytoplankton is assumed to result in detritus or directly in inorganic nutrients (MINL). It depends on the concentration of the algae and in some models on temperature ((5), Table AII-8).

$$\phi_A = -f(A,T) * A \tag{5}$$

Table AII-7. Formulation of nitrogen fixation, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
$\eta_{\max}$	$\frac{\eta^{k1}}{k+e^{k2-k3*T}}$	k1=1, k2=28, k3=2 (°C)$^{-1}$, k=1, η=0.5 d^{-1}	SCOBI
	k	0.02 g m^{-3} d^{-1}	JREV
	see phytoplankton growth		SCV
η_{cap}	$\frac{k1}{k2+\left(\frac{NO3+NH4}{PO4*C_{NP}}\right)^{k4}}$	K1=1, k2=1, k4=4, C_{NP} is the phytoplankton N/P ratio	SCOBI
	$\begin{cases}\frac{(5*PO4-DIN)^2}{5*PO4} & 5*\mathrm{PO4}>\mathrm{DIN} \\ 0 & otherwise\end{cases}$	$\frac{A_{NFIX}}{A}=\frac{5*PO4-DIN}{5*PO4}$	JREV
	1		SCV
$\hat{\mu}_{PO4}$	$\frac{PO4}{k1+PO4}$	k1=0.3 µmole P L^{-1}	SCOBI
		k1=0.01 mg P L^{-1}	SCV
	1		JREV
μ_{light}	see phytoplankton growth		SCOBI, SCV
	1		JREV
lowox	see phytoplankton growth		SCOBI
	1		JREV,SCV

Table AII-8. Formulation of natural mortality for phytoplankton, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
$f(A,T)$	k	k=1 d^{-1}, k=0-0.05 d^{-1},	JORG
			AST,SVP
		20-60 yr^{-1}	PRS
		0.05 d^{-1}	SCOBI
	$k*\frac{A}{k2+A}$	k=0.08 d^{-1}, k2=2 µg chl a L^{-1}	SCOBI
	$k*k2^{T-k3}$	k3=20°C	MINL
		k=0.04 d^{-1}, k2=1.05 (G)-1.07(BG), k3=20°C	PCL

2.4 Respiration and excretion of phytoplankton

Not all models include respiration of phytoplankton. Some models model the net growth instead. SCOBI is one of those models. Other models model respiration as proportional to the phytoplankton biomass (6), or independent of phytoplankton (7) (Table AII-9). SCV has a formulation of respiration composed of two terms, one proportional to the growth rate, and one proportional to A (8). The respiration/excretion results in consumption of oxygen, release of phosphate and release of nitrogen. All models do not have release of N and P proportional to the loss of C (cell quota models, e.g. PCL). This allows the P:C ratio in algae to vary with time.

$$\phi_A = -k * \mu_{\max} * A \tag{6}$$

$$\phi_A = -k * \mu_{\max} \qquad \text{(JORG)} \tag{7}$$

$$\phi_A = -k * \mu_{\max} * A - k4 * \Phi_A \qquad \text{(SCV)} \tag{8}$$

Table AII-9. Formulation respiration/excretion of phytoplankton, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
$k * \mu_{\max}$	$\mu_{\max}$ see phytoplankton growth	k=0.02	SCV
		k=0.1	WALT
			JMS,MINL,JORG
	$k * k2^{T-k3}$	k=0.01(BG)-0.03(G) d^{-1}, k2=1.05(G)-1.07(BG), k3=20°C (respiration, excretion below)	PCL
		k2=1.07, k3=293 K	JORG
	$\frac{Q_{\max} + k1}{Q_{\max}} * \frac{A_P/A_C}{k1 + A_P/A_C} * k * k2^{T-k3}$	Q_{max}=0.027 mg P (mg C)$^{-1}$, k1=0.0027 mg P (mg C)$^{-1}$, k, k2, k3 see above, (excretion, include extra factors since cell quota is used)	PCL
	k2*$\mu_{max}/\mu_{max}(T_{ref})$	k2=0.01-0.06 d^{-1}	JREV
$k4$		0.23-0.28	SCV
		0	WALT, MINL, PCL

2.5 Macrophyte growth and mortality

Macrophytes are seldom included in the models reviewed. Specific macrophyte models are rather complicated (ASA). In addition to growth ((9), Table AII-10), respiration ((10), Table AII-11) and mortality ((11), Table AII-12), processes as reuse of dead parts for growth, bird and fish grazing are modelled. Division of the plant in different parts is also found (ASA).

$$\Phi_M = k * f(T) * f(light) * f(\mu_{PO4}, \mu_{NH4}) * f(age) * M \tag{9}$$

Table AII-10. Formulation of macrophyte growth, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
k			ASA
		0.42 d^{-1}	COL
$f(T)$			ASA
		T_{opt}=21°C	COL
$f\begin{pmatrix}\mu_{PO4}\\ \mu_{NH4}\end{pmatrix}$	$\frac{PO4}{k_P+PO4}*\frac{NH4}{k_N+NH4}$	k_P=0.005 mg P L^{-1}, k_N=0.01 mg N L^{-1}	ASA
	$\min\left(\frac{PO4}{k_P+PO4},\frac{NH4}{k_N+NH4}\right)$	k_P=0.005 mg P L^{-1}, k_N=0.01 mg N L^{-1} (calibrated)	COL
$f(light)$	$\frac{PAR}{k_{PAR}+PAR}$	PAR – photosynthetically active radiation	ASA
	$f_2(light)$		COL
$f(age)$	$\frac{age}{k1+age}$	age – age of macrophyte	ASA
	1		COL

Macrophyte respiration has the following general formulation.

$$\phi_M = -k * f(T) * f(light) * M \tag{10}$$

Table AII-11. Formulation of respiration of macrophytes, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
k		1 d^{-1}	ASA
		0.012 d^{-1}	COL
$f(T)$	$-T^2 * k1 + k2$	k1=$6.7*10^{-4}$, k2=0.482	ASA
	1		COL
$f(light)$	1		ASA
	1- $f_2(light)$ (see growth)		COL

Macrophyte mortality has the following general formulation.

$$\phi_M = -f(growth, resp, M_D) * M \tag{11}$$

Table AII-12. Formulation of natural mortality of macrophytes, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
f	$\frac{k}{k+growth-resp+k2*M_D}$	growth and resp according to eq. (9) and (10) above, M_D – dead part of M	ASA
	k	0.05 d^{-1}	COL

2.6 Grazing by zooplankton on plankton and detritus

Zooplankton grazes on phytoplankton (12) and detritus (13), which result in zooplankton growth. In some models, the relative food source eaten is given by selectivity coefficients (Table AII-13 and 14). In all models the grazing is proportional to the zooplankton, Z. It also depend on temperature and the food ((12-13), Table AII-13 and 14).

$$\phi_A = -k * f(T) * g(A,D) * lowox * Z \tag{12}$$

$$\phi_D = -k * f(T) * g(A,D) * lowox * Z \tag{13}$$

Grazing on detritus is similar to the grazing on phytoplankton in the models studied. One of the JORG models and the JREV models graze only on phytoplankton.

Table AII-13. Formulation of grazing on detritus, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
k		1.2-1.8 d^{-1}	SCV
		0.3 d^{-1}	SCOBI
		0, 0.09-0.16 d^{-1}	JORG
$f(T)$	1		SCOBI,JORG
	see phytoplankton growth		SCV
	$k1^{T-k2}$	k1=1.03, k2=293 K	JORG
$g(A,D)$	$\lambda_D * \frac{D^2}{k2*(s_A*A+s_D*D)+s_A*A^2+s_D*D^2}$ $\lambda_D = \frac{s_D*D}{s_A*A+s_D*D}$	k2=100 µg C L^{-1}, s_A=0.5, s_D=0.5, s_A and s_D selectivity coefficients	SCOBI
	$\frac{s_D*D}{k2+s_A*A+s_D*D}$	k2=0.2-0.4 mg C L^{-1}, s_A=0.2-1.0, s_D=0.4	SCV
	$\frac{D}{k3+D}$	k3=0.005 mg P L^{-1}	JORG
lowox	see phytoplankton growth		SCOBI
	1		the other

Table AII-14. Formulation of grazing on phytoplankton, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
k		1.2-1.8 d^{-1}	SCV
		0.3 d^{-1}	SCOBI
		73-256 yr^{-1}=0.2-0.7 d^{-1}	PRS
		0.4-1.1 d^{-1}	JORG
		0.1-2.0 d^{-1}	JREV
		0	WALT
		k=0.1 (BG), k=1 (G), k=0.25 (DI) (selectivity coefficient)	PCL
$f(T)$	1		SCOBI,JORG,JMS
	see phytoplankton growth	T_m=17-40°C, T_0=15-28°, Q_{10}=2-2.4	SCV
	$10^{\frac{T_A}{273+T_0}-\frac{T_A}{273+T}}$	T_A=2500-3500 K, T_0=20°C	PRS
	$k1^{T-k2}$	k1=1.03, k2=293 K	JORG
		k1=1.02-1.14, k2=20°C	JREV
		k1=1.07 (DI), k1=1.08 (G), k1=1.10 (BG), k2=20°C	JREV
	$k1*e^{-2.3*\left\|\frac{T-T_{opt}}{15}\right\|}$	T_{opt}=33°C (BG), T_{opt}=25°C (nanophytoplankton), T_{opt}=20°C (net phytoplankton)	JREV
$g(A,D)$	$A-k2$	k2=0	JMS
		k2=0.5 mg L^{-1}	JREV
	$\lambda_A*\frac{A^2}{k2*(s_A*A+s_D*D)+s_A*A^2+s_D*D^2}$ $\lambda_A=\frac{s_A*A}{s_A*A+s_D*D}$	k2=100 µg C L^{-1}, s_A=0.5, s_D=0.5, s_A and s_D selectivity coefficients	SCOBI
	$\frac{s_A*A}{k2+s_A*A+s_D*D}$	k2=0.2-0.4 mg C L^{-1}, s_A=0.2-1.0, s_D=0.4	SCV
		s_A=1, s_D=0, k2=0.5-4.0 mg L^{-1}	JREV
	$\max\left(0,\frac{k1*A-k2}{k3+k1*A}\right)$	k1=1, k2=0.1 mg P L^{-1}, k3=0.5 mg P L^{-1}, (A is measured in mg P L^{-1})	JORG
		k1=0.01-1 (selectivity for different zooplankton on different algae), k2=0, k3=2-8 mg L^{-1}	PRS
		k1=1, k2=0.5 mg L^{-1}, k3=0.5-4.0 mg L^{-1}	JREV
$k*f(T)$ $*g(A,D)$	$k*\min\left(f(T),f(T)*\frac{k3+k4}{k3+A+D}\right)$; $f(T)=k4*k5^{T-k6}$	k3=0.25 mg C L^{-1}, k4=1.0 mg C L^{-1}, k5=1.05-1.07, k6=20°C	PCL
lowox	see phytoplankton growth		SCOBI
	1		the other

2.7 Faeces from zooplankton or sloppy feeding

In some models zooplankton releases detritus. This may be explained as faeces from zooplankton or sloppy feeding. It is often modelled as a proportion of the grazing ((14), Table AII-15).

$$\phi_Z = a * (\phi_A + \phi_D) \tag{14}$$

Table AII-15. Parameter values of the detritus release rate from zooplankton for different models.

Part	Equation(s)	Parameter values	References
a		0.3	SCOBI
		0.7	PCL
		0.59	JORG

2.8 Excretion from zooplankton, zooplankton respiration

While grazing, zooplankton is sometimes assumed to excrete inorganic nutrients ((15), Table AII-16). Excretion is of minor importance according to Jørgensen (1983a). SCV included a base respiration term (*b*), and the model excretes organic nitrogen instead of inorganic ammonium.

$$\phi_Z = -a * \Phi_Z - b \tag{15}$$

Table AII-16. Formulation of excretion/respiration of zooplankton depending on grazing, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
a		0.3	SCOBI
		0.02-0.16	SCV
b		0	SCOBI
		0.05-0.12 d^{-1}	SCV

Some of the other models model a release of inorganic nutrients, due to zooplankton respiration, that depends directly on Z ((16), Table AII-17).

$$\phi_Z = -a * f(T) * Z \tag{16}$$

Table AII-17. Formulation of excretion/respiration of zooplankton depending on zooplankton, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
a		0.05-0.62 d^{-1}	JORG
		0.1-0.16 d^{-1}	JREV
		0.1 d^{-1}	PCL
$f(T)$	$k2^{T-k3}$	k2=1.03, k3=293 K	JORG
		k2=1.10, k3=20°C	PCL

2.9 Decomposition of detritus

Detritus (organic matter) is decomposed ((17), Table AII-18) during release of ammonium and phosphate and during consumption of oxygen. This is often modelled with constant proportions, but can also vary. Some models have different degradation rate for organic nitrogen and organic phosphorus (Table AII-18). The decomposition often depends on temperature (17) and for SCOBI on light (Table AII-18).

$$\phi_D = -k * f(T,I) * f(D) \tag{17}$$

Most models have a detritus mineralisation that is proportional to the detritus concentration. The only exception I found was AST, which had a constant decomposition.

Table AII-18. Formulation of detritus decomposition, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
k		0.002 d^{-1}	SCOBI
		0.001 $(°C\ d)^{-1}$	SCV
			MINL
		0.04-0.12 d^{-1}, 0.25-0.8 d^{-1}, 0.004 d^{-1}	JORG
		0.02 d^{-1}	PCL
		28 yr^{-1} (orgP)	PRS
		0.001-0.14 d^{-1} (orgN), 0.001-0.4 d^{-1} (orgP)	JREV
$f(T,I)$	1		JORG,AST
	e^{bT}	b=0.15 $(°C)^{-1}$	SCOBI
	$e^{bT} * (k3 + \mu_{max} * \mu_{light})$	μ_{max} and μ_{light} see phytoplankton growth	SCOBI
	a^{T-k2}	a=1.03, k2=293 K	JORG
		a=1.12, k2=20°C	PCL
		a=1.08, k2=20°C	PRS
		k2=20°C	MINL
	T		SCV
$f(D)$	1		AST
	D		the other

2.10 Nitrification

In presence of oxygen, ammonium may transform to nitrate (18). In SCOBI certain levels of oxygen must be present for this to happen, other models only depend on the concentration of ammonium and temperature (Table AII-19).

$$\phi_{NH4} = -k * f(T) * g(O2) * NH4 * h(O2 - k2) \tag{18}$$

Table AII-19. Formulation of nitrification, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
k		0.01 d^{-1} if T<10°C, 0.1 d^{-1} if T>=10°C	SCOBI
		0.005 $(°C\ d)^{-1}$	SCV
		0.03-0.2 d^{-1}	JREV
			MINL
$f(T)$	e^{bT}	b=0.11 $(°C)^{-1}$	SCOBI
	a^{T-k2}	k2=20°C	MINL
	T		SCV
	1		JREV
$g(O2)$	$\frac{O2}{k+O2}$	k=0.01 ml O_2 L^{-1}	SCOBI
	1		SCV,JREV, MINL
h	$h(O2-k2)=\begin{cases}0 & O2<k2\\1 & O2>k2\end{cases}$	k2=0.5 ml L^{-1}	SCOBI
		k2=0	SCV,MINL

2.11 Denitrification in water

Few models model denitrification in the water. During denitrification nitrate are turned into atmospheric nitrogen (N_2). In a variant of the SCOBI model, denitrification only occurs when it is less than the detritus decomposition. The reason is that detritus degrading microbes also are assumed responsible for the denitrification. The SCOBI formulation is pretty complicated ((19), Table AII-20). In Jørgensen (1983a) a simple rate formulation is suggested to work in some cases (JREV in Table AII-20).

$$\phi_{NO3} = -k * \frac{1}{1+\left(\frac{O2}{O_{2d}}\right)^{k1}} * \frac{NO3}{k2+NO3} * NO3 \tag{19}$$

Table AII-20. Parameter values of denitrification in water for different models.

Part	Equation(s)	Parameter values	References
k		0.5 d^{-1}	SCOBI
		0.002 d^{-1}	JREV
$k1$		6	SCOBI
O_{2d}		0.504	SCOBI
	∞		JREV
k2		1 µmole N L^{-1}	SCOBI
	0		JREV

2.12 Predation on zooplankton/mortality of zooplankton

Natural mortality of zooplankton is modelled in some of the models reviewed. In others the primary death of zooplankton is to be eaten by predators. Predation on zooplankton is sometimes modelled to depend on only the zooplankton like natural mortality ((20), Table AII-21) and not on predators, because these are not modelled.

$$\phi_Z = -k * f(T) * f(Z) * lowox * Z \tag{20}$$

Table AII-21. Formulation of predation/mortality of zooplankton in models not including predators explicitly, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
k		0.1 d^{-1}	SCOBI
		0-0.01 d^{-1}	JORG
		0-0.08 d^{-1}	SCV
			AST,PRS
		0.08-0.15 d^{-1}	PCL
		0.001-0.125 d^{-1}	JREV
$f(Z)$	1		JORG,AST,PCL
	$\frac{Z^n}{k2^n + Z^n}$	n=1, k2=1.0 µg C L^{-1}	SCOBI
		n=2, k2=0.3-0.5 mg P L^{-1}	PRS
		n=2, k2=1.5 mg C L^{-1}	PCL
	$\begin{cases} 1 & Z > Z_{\min} \\ 0 & Z < Z_{\min} \end{cases}$	Z_{min}=0	JORG, JREV
		Z_{min}=0.02 mg C L^{-1}	SCV
$f(T)$	1		AST,SCOBI, PRS, JORG
	$k2^{T-k3}$	k2=1.07-1.10, k3=20°C	PCL
lowox	see phytoplankton growth		SCOBI
	1		the other

JORG has included two types of fish in one of his models. Planktivorous fish (FA) feed on zooplankton (21) with a Michaelis-Menten dependence on the food, but with a minimum concentration, because the fish have to see and find them (Table AII-22). The PCL model only includes one variable of fish (FA), but explicitly models the visibility of the zooplankton to the fish (21).

$$\phi_Z = -k * f(T) * f(Z) * f(vis) * FA \tag{21}$$

Table AII-22. Formulation of predation on zooplankton in models simulating predators explicitly, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
k		0.125 d^{-1}	JORG
		0.15 d^{-1}	PCL
$f(Z)$	$\frac{Z-k1}{k2+Z}$	k1=0.1 mg P L^{-1}, k2=0.3 mg P L^{-1}	JORG
	$\frac{Z^2}{k4^2+Z^2}$	k4=1.5 mg C L^{-1}	PCL
$f(T)$	$k2^{T-k3}$	k2=1.07-1.1, k3=20°C	PCL
	1		JORG
$f(vis)$		*vis* – visibility	PCL
	1		JORG

2.13 Predation on planktivorous fish

In the JORG model with fish, piscivorous fish (FB) feed on planktivorous fish (FA). The predation is modelled to depend on prey by a Michaelis-Menten expression with a threshold concentration for no intake of food at low concentrations ((22), Table AII-23). It also depend on the autotrophs and detritus, because of the increased turbidity they cause (22).

$$\phi_{FA} = -k * \frac{FA - k1}{FA + k2} * \frac{1}{A + D} * FB \tag{22}$$

Table AII-23. Parameter values of predation on fish.

Part	Equation(s)	Parameter values	References
k		0.1 mg P L^{-1} d^{-1}	JORG
k1		0.1 mg P L^{-1}	JORG
k2		0.1 mg P L^{-1}	JORG

2.14 Mortality of predators

The mortality of fish (both types) transforms fish biomass into detritus. JORG modelled it as proportional to the fish biomass ((23-24), Table AII-24), but also have a term which depend on the predation (zooplankton, ϕ_Z, and planktivorous fish, ϕ_{FA}, respectively). This term can be thought of as the faeces of the fish (see next section). The PCL model included respiration, mortality and harvesting terms, where the respiration was a function of temperature.

$$\phi_{FA} = -k * FA \tag{23}$$

$$\phi_{FB} = -k2 * FB \tag{24}$$

Table AII-24. Parameter values of mortality of predators, for different models.

Part	Equation(s)	Parameter values	References
k		0.015 d^{-1}	JORG
	varying over the year	$k<0.003$ d^{-1}	PCL
$k2$		0.01 d^{-1}	JORG

2.15 Excretes and faeces from predators

The JORG model has a similar formulation for faeces from predation on both zooplankton and on fish. PCL has modelled both excretion of inorganic nutrients (25) and organic matter (faeces) (26) from fish (Table AII-25).

$$\Phi_{PO4} = -k * f(T) * FA \tag{25}$$

$$\Phi_D = -a * \phi_{Z/FA} \tag{26}$$

Table AII-25. Formulation of excretion and faeces from predators, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
a		0.35	JORG
		0.4	PCL
			AST
k		0.003 d^{-1}	PCL
$f(T)$	$k2^{T-k3}$	k2=1.07	PCL

2.16 Regeneration in sediment including diffusion

Sediment exchange can be an important process in lakes. The sediment can be a sink of organic matter, and a sink or a source of phosphate. The different models include none, one or several state variables for the sediment, e.g. phosphate in interstitial water, several layers of sediment, active or passive sediments etc. The sediment models are very different and have therefore been treated not grouped after processes but separately. Jørgensen (1983a) says that simple and complex sediment models give completely different responses. The complex ones are needed especially for decreasing P loading scenarios. Schladow and Hamilton (1995) have validated a "simple" model and found that the phosphorus release rate during anoxic conditions was the most sensitive parameter.

The losses of P and N in the sediment of SCOBI depend only on temperature (and the amount of nitrogen and phosphorus in sediment) ((27-28), Table AII-26). One of the processes in JREV is even simpler (Table AII-26).

$$\phi_{BN} = -f(T) * BN \tag{27}$$

$$\phi_{BP} = -f(T) * BP \tag{28}$$

Table AII-26. Formulation of the loss of benthic nutrients, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
$f(T)$	$a * e^{bT}$	a=0.001 d^{-1}, b=0.03 $(°C)^{-1}$	SCOBI
	a	0.95-1.8 d^{-1}	JREV

In SCOBI, part of the nutrient loss in the sediments is released as inorganic nutrients in the water. The amount depends on the oxygen and nitrate condition ((29-31), Table AII-27). The rest of the loss is assumed to be denitrification and sequestering. These nutrients are no longer available to the model.

$$\Phi_{NH4} = -g_1(O2) * \phi_{BN} \tag{29}$$

$$\Phi_{NO3} = -f(NO3) * g_2(O2) * \phi_{BN} \tag{30}$$

$$\Phi_{PO4} = -g(O2) * \phi_{BP} \tag{31}$$

Table AII-27. Formulation of the sources of inorganic nutrients caused by sediment nutrient loss in SCOBI, including parameter values.

Part	Equation(s)	Parameter values	References
$g_1(O2)$	$\begin{cases} 1 & 0 < O2 < k3 \\ 0 & O2 > k3 \end{cases}$	k3=0.5 ml L^{-1}	SCOBI
	complicated expression dividing loss of BN into four sources; denitrification, sequestering, NH4 and NO3	alternative	SCOBI
$f(NO3)$	$1 - \max\left(\frac{NO3}{k + NO3}, k3\right)$	k=1.0 µmole N L^{-1}, k3=0.5, *f* gives the NO3 not denitrified in the sediment	SCOBI
$g_2(O2)$	$-g_1(O2)$		SCOBI
	complicated expression	see $g_1(O2)$	SCOBI
$g(O2)$	$1 - \frac{k1 * O2}{k + O2}$	k=70.2 ml L^{-1}, k1=7.5, *k* gives the PO4 not sequestered in the sediment	SCOBI
	1		SCOBI

JORG has used three different sediment models, but only modelled phosphorus. These have different number of variables: only BP (benthic phosphorus); BP and BI, where BI is phosphorus in interstitial water; BP, BI and BY, where BY is phosphorus in the biologically active thin upper layer in contrast to BP. Only the first two models are described here ((32-33), Table AII-28).

$$\phi_{BP} = -f(T) * BP \tag{32}$$

$$\phi_{BI} = \frac{1}{a_i} * (a_s * \phi_{BP} - Q_d - Q_2) \tag{33}$$

Table AII-28. Formulation of exchange of phosphate with sediment, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
$f(T)$	k	0.002 d^{-1}	JORG
	$k1 * k2^{T-k3}$	k1=0.005 d^{-1}, k2=1.07, k3=20°C	PCL
	1		PRS,SVP
a_i	∞	simplest version	JORG
	$(1-DMU) * \frac{d_s}{d}$	DMU=0.1-0.9 (fraction of dry matter in upper layer), d_s=0.1 m (thickness of upper layer), d=10 m (average depth of water), a_i is the volume ratio: interstitial water/lake volume	JORG
	1		PCL,PRS,SVP
a_s	$DMU * \frac{d_s}{d}$	a_s is the volume ratio: dry sediment/lake volume, see a_i	JORG
	1/por	por=porosity of upper sediment=0.91	PCL
	1		PRS,SVP
Q_d	$a_s * k * BP$	a_s and k see above, flow of P due to diffusion from sediment	JORG
	$\frac{k1 * (BI - PO4) - k2}{k3 * d} * \frac{T}{k4}$	k1=1.2, k2=1.7, k3=1000, k4=280	JORG
	$k1 * \frac{k2}{2} * \frac{(BI - PO4)}{k2}$	k1=0.00004 m^2 d^{-1} – diffusion coefficient, k2=0.02 m – depth of upper sediment layer	PCL
	$\frac{k}{k1} * area * (BI - PO4)$	k – diffusion coefficient, lower for deeper layer, k1 – thickness of diffusionary boundary layer, area – sediment area, BI=k2*BY	PRS
		z=1, BI=0.9 mg P L^{-1}	SVP
Q_2	1		JORG,PRS,SVP
	$k3 * BI$	k3=0.1 d^{-1} – loss constant of interstitial P	PCL

In the two simplest versions of the JORG model the source of phosphate is due to diffusion. The rest of the loss of in BP goes to sequestering and out of the model. In the most complex version (not described here), PO4 is released from the biologically active layer by desorption and biological activity, in addition to diffusion. PCL has a similar model with temperature dependence and diffusion from interstitial water (Table AII-28). PCL models organic C and P in the upper sediment and P in interstitial water.

PRS modelled two layers of sediment. SVP has only one, but both models model the exchange of phosphorus with the sediment as a kind of diffusion. The deeper layer of PRS is similar to the upper, only the upper is included in Table AII-28 .

The JMS model models resuspension, which is not included in this literature review. It also models sediment release of phosphate as a function of sedimentation. The release was zero for anoxic conditions and varying, but below 1, for aerobic conditions.

2.17 Denitrification in sediment

Sediments are the primary location for modelling denitrification in lakes. The process reduces nitrate to atmospheric nitrogen during degradation of organic matter ((34), Table AII-29). SCOBI has indirectly modelled denitrification (see Section 2.16.). The MES model models denitrification with a 50% uncertainty for conditions with sufficient organic carbon supply and aerobic lake sediments. AND has used equations fitted to measurements.

$$\phi_{NO3/BNO} = -k * f(T) * f(NO3, BNO) \tag{34}$$

Table AII-29. Formulation of denitrification in sediments, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
k			WHIT
		$3.5*10^{-4}$ mg N L^{-1} s^{-1}	MES
		12-1429 mg N m^{-2} d^{-1} (anaerob), 161-1429 mg N m^{-2} d^{-1} (aerob)	AND
$f(T)$	$k2^{T-k3}$	k2=1.047, k3=20°C	WHIT
		k2=1.10, k3=35.5°C, 14°C<T<35°C	MES
	1		AND
$f(NO3, BNO)$	$NO3$		WHI
	$\frac{BNO}{k4+BNO}$	k4=3.06 mg N L^{-1}	MES
	$\frac{NO3}{k4+NO3}$	k4=0.1-12 mg N L-1 (anaerob), k4=5-84 mg N L-1 (aerob)	AND

2.18 Sinking and sedimentation of phytoplankton

Some lake models are vertically divided and have a net sink in each layer. Others are vertically integrated and all sinking material settles on a single bottom. The net sinking is modelled as a function of the amount of phytoplankton ((35), Table AII-30).

$$\phi_A = -k * f(A) \tag{35}$$

Table AII-30. Formulation of sinking and sedimentation of phytoplankton, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
k		1	SCOBI
			MINL,WALT,JMS
		0.18 d^{-1}	JORG
		incl. natural mortality	PRS
$f(A)$	$\frac{\partial(k2*A)}{\partial z}$; $k2 = \max(\min(k3*A^2, k4), k5)*k6$; $k6 = \begin{cases} 0 & \frac{\Delta\rho}{\Delta z} > 0.2 \\ 1 - \frac{\frac{\Delta\rho}{\Delta z} - 0.01}{0.2 - 0.01} & 0.01 < \frac{\Delta\rho}{\Delta z} < 0.2 \\ 1 & \frac{\Delta\rho}{\Delta z} < 0.01 \end{cases}$	k2 – sinking velocity, k3=0.2 m s^{-1} (µg chl a $L^{-1})^{-2}$, k4=3.0 m s^{-1}, k5=0.1 m s^{-1}, 0.1 m s^{-1}<k2<3.0 m s^{-1}, ρ - density, z – vertical co-ordinate	SCOBI
	$k2 * \frac{\partial(A)}{\partial z}$; $k2 = \max(\min(k3*A^2, k4), k5)$	k2 – sinking velocity, k3=0.2 m s^{-1} (µ chl a $L^{-1})^{-2}$, k4=3.0 m s^{-1}, k5=0.1 m s^{-1}, z – vertical co-ordinate	SCOBI
	$\frac{1}{area(z)} * \frac{\partial(area(z)*A)}{\partial z}$	area – horizontal lake area, z – vertical co-ordinate	MINL
	$\frac{\partial(A)}{\partial z}$	z – vertical co-ordinate	WALT
	A		JORG,JMS

2.19 Sinking and sedimentation of detritus

The sinking of detritus ((36), Table AII-31) has similar formulation as phytoplankton (35).

$$\phi_D = -k * f(D) \tag{36}$$

Table AII-31. Formulation of sinking and sedimentation of detritus, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
k			MINL,WALT
		0.18 d^{-1}	JORG
	$k = k1 * k6$ $k6 = \begin{cases} 0 & \frac{\Delta\rho}{\Delta z} > 0.2 \\ 1 - \frac{\frac{\Delta\rho}{\Delta z} - 0.01}{0.2 - 0.01} & 0.01 < \frac{\Delta\rho}{\Delta z} < 0.2 \\ 1 & \frac{\Delta\rho}{\Delta z} < 0.01 \end{cases}$	k1=1.5 m s^{-1}, ρ - density, z – vertical co-ordinate	SCOBI
$f(D)$	$\frac{1}{area(z)} * \frac{\partial(area(z) * D)}{\partial z}$	area – horizontal lake area, z – vertical co-ordinate	MINL
	$\frac{\partial(D)}{\partial z}$	z – vertical co-ordinate	WALT, SCOBI
	D		JORG

2.20 Exchange with the atmosphere

Nitrogen is deposited on lakes as nitrate and ammonium. In SCOBI, atmospheric supply of nitrate and ammonium are estimated with data from the MATCH model (Langner et al., 1995). Phosphorus may also be deposited.

Oxygen exchange with the atmosphere is important if oxygen is modelled in the lake. SCOBI and MINL have two similar models (37) depending on oxygen, oxygen saturation, temperature and wind (Table AII-32).

$$\Phi_{O2} = k_0(w,T) * \left(f(T,s) - O2\right) \tag{37}$$

Table AII-32. Formulation of oxygen exchange between the atmosphere and the water, including parameter values, for different models.

Part	Equation(s)	Parameter values	References
$k_0(w,T)$	$k_0 = 5.9 * \frac{a * w + b}{\sqrt{k1 + k2 * T + k3 * T^2}}$; $a = \begin{cases} 0.17 & \mathrm{w} \le 3.6 \\ 2.85 & 3.6 < \mathrm{w} \le 13.0 \\ 5.9 & w > 13.0 \end{cases}$; $b = \begin{cases} 0 & \mathrm{w} \le 3.6 \\ -9.65 & 3.6 < \mathrm{w} \le 13.0 \\ -49.3 & w > 13.0 \end{cases}$	w – wind (m s^{-1}), T – surface temperature (in °C), k1=1450, k2=-71 $(°C)^{-1}$, k3=1.1 $(°C)^{-2}$, a in s m^{-1}	SCOBI
	$k_0 = \frac{a * w^2 + b}{d}$	d – thickness of upper box, a=0.0256 $(\text{miles per hour})^{-2}$, b=0.641	MINL
$f(T,s)$	$f(T,s) = (1+\beta) * O_{sat}$; $O_{sat} = e^{g(T)+h(T)*s}$; $g(T) = k1 + k2/T + k3 * \ln(T/k4) + k5 * T$; $h(T) = k6 + k7 * T + k8 * T^2$	β=0.025, O_{sat} – saturation concentration, s – surface salinity, T – surface temperature (in K), k1=-173.4292, k2=24963.39, k3=143.3483, k4=100, k5=-0.218492, k6=-0.033096, k7=0.00014259, k8=-0.00000017	SCOBI
	$f(T) = O_{sat} = k1 - k2 * T + k3 * T^2 - k4 * T^3$	k1=14.652, k2=0.41022 $(°C)^{-1}$, k3=0.00799 $(°C)^{-2}$, k4=-0.000077774 $(°C)^{-3}$	MINL

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ISSN 0283-1104