

A simple model of the eco-hydrodynamics of the epilimnion of Lake Tanganyika

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SUMMARY

1. The ecosystem response of Lake Tanganyika was studied using a four-component, nutrient–phytoplankton–zooplankton–detritus, phosphorus-based ecosystem model coupled to a nonlinear, reduced-gravity, circulation model. The ecosystem model, an improved version of the earlier eco-hydrodynamics model developed for Lake Tanganyika, was used to estimate the annual primary production of Lake Tanganyika and its spatial and temporal variability. The simulations were driven with the National Centres for Environmental Protection (NCEP) records for winds and solar radiation forcing.
2. The simulated annual cycles of the four ecosystem variables and the daily net primary production were compared with the observations. The comparison showed that simulations reproduced realistically the general features of the annual cycles of epilimnial phosphate, net primary production and plankton dynamics.
3. The climatic simulations for the years 1970–2006 yielded a daily averaged integrated upper layer net production ranging from 0.11 to 1.78 g C m⁻² day⁻¹ and daily averaged chlorophyll-*a* (chl-*a*) from 0.16 to 4.3 mg m⁻³. Although the nutrient concentrations in the epilimnion during the strong wind years were high, the net production was low, which is partly because of the greater vertical mixing, produced by strong winds, exposing the phytoplankton to low light conditions in deeper waters. The simulated annual net production and chl-*a* agreed quite well with observed production available in the literature.
4. We envisage using this model to predict the future scenarios of primary productivity in the lake.

Keywords: eco-hydrodynamics, ecosystem model, Lake Tanganyika, primary-production, reduced-gravity model

Introduction

Lake Tanganyika is a large Rift Valley lake (on average 670 km long, 50 km wide, 570 m deep) situated in East Africa between 3 and 9°S. It has two main basins in the north and south with maximum

depths of around 1320 and 1470 m, respectively, separated by a sill of 600 m. Thermal stratification in the lake is well marked and varies seasonally above the permanent hypolimnion (Coulter & Spigel, 1991). The water temperature in the lake varies from 24 to 28 °C in the surface layer to around 23.5 °C in the bottom layer. The main seasons around the lake are 4–5 months long (May–September) ‘dry season’, characterized by cooler dry weather and fairly constant southeasterly (trade) winds from around May to September, and a ‘wet season’ for the rest of the year,

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during which the winds are weaker and mainly from northeast (Coulter & Spigel, 1991). Wind speed during the dry season reaches 7–9 m s⁻¹ with gusts of 10–12 m s⁻¹. The wind stress pushes the warmer surface water away from the southern end of the lake towards the northern end and there is a well-known compensating upwelling in the south.

In Lake Tanganyika the growth of phytoplankton is generally nutrient limited, and photosynthesis depends on wind-driven vertical mixing processes that supply nutrients from deep waters to the illuminated mixed layer (Hecky, Spigel & Coulter, 1991). Through increased water density gradients, climate warming has apparently slowed vertical mixing, reducing the exchange rates between shallow and deep water and thus primary production (Verburg, Hecky & Kling, 2003).

Knowledge of the primary productivity of Lake Tanganyika is limited to observations carried out for a few years at few coastal regions, along with some ship-based measurements over the whole length of the lake (Hecky *et al.*, 1981; Hecky & Kling, 1981; Langenberg, 1996; Salonen *et al.*, 1999; Sarvala *et al.*, 1999a; Cocquyt & Vyverman, 2005; Descy *et al.*, 2005). Numerical modelling could improve our understanding of the spatial and temporal distribution of nutrients and primary productivity of the lake and our aim here was to simulate biological and chemical processes in the planktonic system. These are important in estimating the annual primary productivity of the whole lake and the amount of carbon available to higher trophic levels. Such estimates of the annual primary productivity can further be used to study the sensitivity of lake ecosystem to past and future climate variability and change.

The Lake Tanganyika ecosystem has been modelled using a three-component nutrient–phytoplankton–zooplankton model, coupled to a hydrodynamic model (Naithani *et al.*, 2007). The hydrodynamic model is based on nonlinear, reduced-gravity equations with entrainment included. This type of model has been used previously to study productivity–upwelling relationships, climatological upwelling intensity, present and past primary productivity, the palaeocean and organic-rich sediment deposits etc. in the ocean (Luthar, O'Brien & Prell, 1990; Handoh *et al.*, 1999; Handoh & Bigg, 2001). Here, we improved the model by incorporating a detritus pool and by parameterizing ecosystem processes better (Moll,

1998; Dzierzbicka-Glowacka, 2002; Miller, 2005). Theoretically, the ecosystem model could be improved further by resolving the phytoplankton and zooplankton to species, and by including a complete microbial loop. However, all this complexity and the increasing number of components would require many more model parameters to describe the ecosystem. For Lake Tanganyika our knowledge of most of these parameters is poor and specifying appropriate values is therefore difficult. This would also increase the number of observations and measurements needed to calibrate the model properly. For this reason we kept the model as simple as possible. River inputs have not been included in the present ecosystem model, because the pelagic system accounts for most of the production of organic carbon in the lake (Hecky & Fee, 1981). The great volume of Tanganyika, together with its relatively arid climate, limits the direct effect of river inflows on the pelagic system, and the water turnover time based on river inflows is about 1000 years (Hecky, 1978). This reduces the immediate influence of the catchment just as the pelagic ocean is little affected by annual riverine inputs (Coulter & Spigel, 1991).

In this paper, we present simulations of the annual primary productivity of the lake under the prevailing actual circulation and solar radiation, compare with actual observations the regional patterns generated by the model, and model climatic influences on lake ecosystem since 1970.

Methods

The model

Circulation model The circulation model was the modified version of the nonlinear, two-layer, reduced-gravity model developed for Lake Tanganyika and used in earlier studies (Naithani, Deleersnijder & Plisnier, 2002, 2003; Naithani & Deleersnijder, 2004). The present version included entrainment and detrainment terms (Naithani *et al.*, 2007). Model equations are:

$$\frac{\partial \xi}{\partial t} + \frac{\partial(Hu)}{\partial x} + \frac{\partial(Hv)}{\partial y} = w_e \quad (1)$$

$$w_e = \left(\frac{3}{20}\right)^{1/2} \frac{(\tau_x^2 + \tau_y^2)^{1/2}}{(\epsilon g H)^{1/2}} - w_d - \frac{\xi}{r_{tt}} \quad (2)$$

$$\begin{aligned} \frac{\partial(Hu)}{\partial t} = & -\frac{\partial(Huu)}{\partial x} - \frac{\partial(Hvu)}{\partial y} + fHv \\ & -gH\frac{\partial\varepsilon\xi}{\partial x} + \frac{\partial}{\partial x}\left(HA_x\frac{\partial u}{\partial x}\right) \\ & + \frac{\partial}{\partial y}\left(HA_y\frac{\partial u}{\partial y}\right) + \frac{\tau_x}{\rho_0} + w_e^-u \end{aligned} \quad (3)$$

$$\begin{aligned} \frac{\partial(Hv)}{\partial t} = & -\frac{\partial(Huv)}{\partial x} - \frac{\partial(Hvv)}{\partial y} \\ & -fHu - gH\frac{\partial\varepsilon\xi}{\partial y} + \frac{\partial}{\partial x}\left(HA_x\frac{\partial v}{\partial x}\right) \\ & + \frac{\partial}{\partial y}\left(HA_y\frac{\partial v}{\partial y}\right) + \frac{\tau_y}{\rho_0} + w_e^-v \end{aligned} \quad (4)$$

where x and y are horizontal axes, u and v the depth-integrated velocity components in the surface layer in the x and y directions, respectively, t the time, ξ the downward displacement of the thermocline, $H=h+\xi$ the thickness of the epilimnion (the surface, well-mixed layer), h the reference depth of the upper layer (m) and w_e the entrainment velocity (m s^{-1}). The first term on the right-hand side of eqn 2 is inspired by Price (1979), τ_x and τ_y are horizontal components of specific wind stress in the x and y direction ($\text{m}^2 \text{s}^{-2}$), $\varepsilon = (\rho_b - \rho_s)/\rho_b$ is the relative density difference between the hypolimnion (ρ_b) and the epilimnion (ρ_s), respectively, w_d is the detrainment term (m s^{-1}). w_d is defined such that the annual mean of the epilimnion volume remains approximately constant. There are large uncertainties in the parameterization of entrainment and detrainment terms. As a consequence, to avoid occasional spurious values of ξ , a relaxation term (ξ/r_{ts}) is needed which slowly nudges the upper layer depth towards its equilibrium position. The relaxation time scale, r_{ts} is sufficiently long so that the relaxation term is generally smaller than the entrainment and detrainment terms. w_e is positive (negative) in the upwelling (downwelling) regions where water is entrained into (detrained from) the upper layer, f is the Coriolis factor (<0 in the southern hemisphere), A_s is the horizontal eddy viscosity in the $s (=x,y)$ direction, $w_e^- = (w_e - |w_e|)/2$ is the negative part of the entrainment velocity, i.e. w_e^- is equal to w_e if $w_e < 0$ and is zero otherwise. Below, we make use of the positive part of the entrainment velocity, which is defined as $w_e^+ = (w_e + |w_e|)/2$.

The surface layer temperature was predicted using the equation:

$$\begin{aligned} \frac{\partial(H\theta)}{\partial t} + \frac{\partial(Hu\theta)}{\partial x} + \frac{\partial(Hv\theta)}{\partial y} \\ = \frac{\partial}{\partial x}\left(HK_x\frac{\partial\theta}{\partial x}\right) + \frac{\partial}{\partial y}\left(HK_y\frac{\partial\theta}{\partial y}\right) \\ + w_e^+\theta_h + w_e^-\theta + H\frac{(\theta_s - \theta)}{r_{ts}} \end{aligned} \quad (5)$$

where θ is the surface layer temperature, θ_s is the reference temperature of the surface layer, θ_h is the temperature of the hypolimnion water and r_{ts} is the relaxation time scale for surface fluxes.

Equations were discretised on Arakawa's C grid. The model uses the forward-backward time stepping. The lake is represented with a rectangular Cartesian grid with $\Delta x = 6$ km and $\Delta y = 20$ km (Fig. 1). The time step is 30 min. The first year model run was not used for analysis.

Ecosystem model The phytoplankton and zooplankton were represented by one state variable each (Fig. 2).

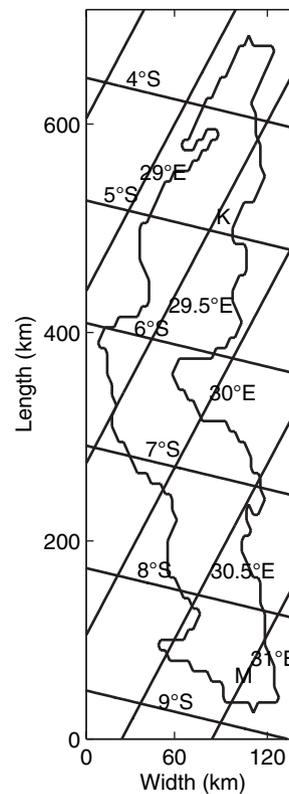


Fig. 1 Map of Lake Tanganyika used in the model with 6 km by 20 km resolution in the x and y direction respectively. M and K indicate the sites used in the study at Mpulungu and Kigoma respectively.

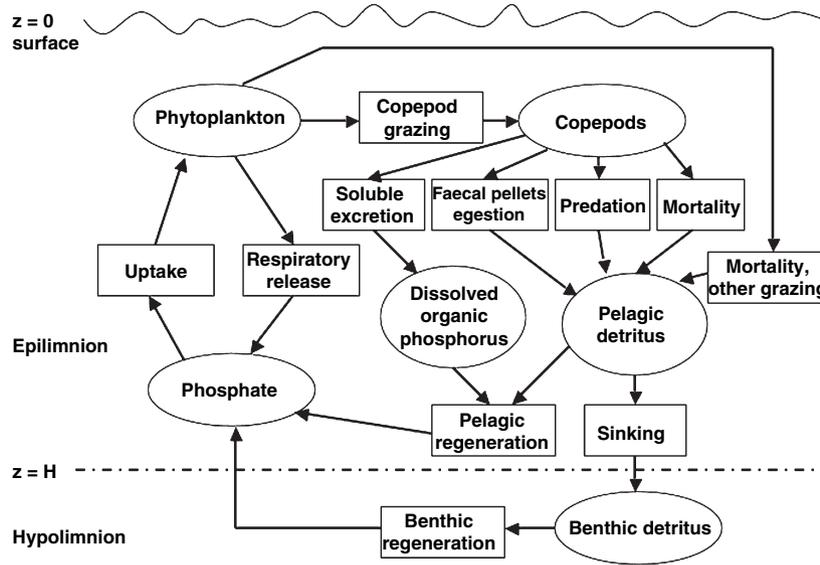


Fig. 2 Flow diagram of the ecological parameters considered in the model.

Phosphorus was the only nutrient simulated in the model to trigger phytoplankton bloom. Järvinen *et al.* (1999) showed that phosphorus and nitrogen were both simultaneously limiting phytoplankton production in Tanganyika, although phosphorus also had a very slight effect alone. The water column dynamics were implemented so that the ecosystem variables were transported by advection and diffusion. The model includes primary production (*PROD*), remineralization within the upper layer, and sedimentation of detritus. Phytoplankton is utilized by copepods (*GRAZ*), settles slowly (1 m day^{-1}) or dies (*MORT_a*). Grazing by copepods was divided into their growth, faecal pellet (*FEC*) egestion, mortality (*MORT_z*) and excretion (*EXC*). A small percentage of faeces, dead phytoplankton and zooplankton are remineralized into phosphate by the microbial food web in the upper layer while the rest contributes to the detritus pool. Phytoplankton respiratory release is directly remineralized. The regeneration within the upper layer represents the effect of the microbial food web and also represents the pelagic regeneration. The model was closed by predation from zooplanktivorous fish and the sinking of detritus out of the surface layer.

A four component, phosphorus-based ecosystem model including dissolved phosphorus (*Phos*), phytoplankton (*Phyto*), zooplankton (*Zoo*) and detritus (*Detr*) was used. The ecosystem model equations are:

$$\begin{aligned} \frac{\partial(H\text{Phyto})}{\partial t} = & -\frac{\partial(Hu\text{Phyto})}{\partial x} - \frac{\partial(Hv\text{Phyto})}{\partial y} \\ & + \frac{\partial}{\partial x} \left(HK_x \frac{\partial \text{Phyto}}{\partial x} \right) \\ & + \frac{\partial}{\partial y} \left(HK_y \frac{\partial \text{Phyto}}{\partial y} \right) + \phi_{\text{he}} \\ & + H \left\{ r_p \min[2F(I), F(P)]\text{Phyto} \right. \\ & \quad - r_a r_p \min[2F(I), F(P)]\text{Phyto} \\ & \quad - m_a \text{Phyto} \\ & \quad \left. - r_z \frac{\text{Phyto}}{\text{Phyto} + k_{\text{phyto}}} \text{Zoo} \right\} \end{aligned} \quad (6)$$

$$F(P) = \frac{\text{Phos}}{\text{Phos} + k_{\text{phos}}} \quad (7)$$

$$F(I) = \frac{1}{K_e H} \left[\arctan \left(\frac{\alpha I_0}{2I_k} \right) - \arctan \left(\alpha I_0 e^{-k_e H / 2I_k} \right) \right] \quad (8)$$

$$k_e = 0.066 + 0.07 \frac{\text{Phyto}}{r_c} \quad (9)$$

$$\phi_{\text{he}} = w_e^+ \text{Phyto}_h + w_e^- \text{Phyto} \quad (10)$$

$$\begin{aligned} \frac{\partial(H\text{Zoo})}{\partial t} = & -\frac{\partial(Hu\text{Zoo})}{\partial x} - \frac{\partial(Hv\text{Zoo})}{\partial y} \\ & + \frac{\partial}{\partial x} \left(HK_x \frac{\partial \text{Zoo}}{\partial x} \right) + \frac{\partial}{\partial y} \left(HK_y \frac{\partial \text{Zoo}}{\partial y} \right) \\ & + \phi_{\text{he}} + H \{ \text{GRAZ} - n_e \text{GRAZ} - n_i \text{GRAZ} \\ & \quad - m_z \text{GRAZ} - \text{PRED} \} \end{aligned} \quad (11)$$

$$\text{GRAZ} = r_z \frac{\text{Phyto}}{\text{Phyto} + k_{\text{phyto}}} \text{Zoo} \quad (12)$$

$$\text{PRED} = r_f \frac{\text{Zoo}}{\text{Zoo} + k_{\text{zoo}}} \text{Fish} \quad (13)$$

$$\begin{aligned} \frac{\partial(\text{HPhos})}{\partial t} = & -\frac{\partial(\text{HuPhos})}{\partial x} - \frac{\partial(\text{HvPhos})}{\partial y} \\ & + \frac{\partial}{\partial x} \left(\text{HK}_x \frac{\partial \text{Phos}}{\partial x} \right) + \frac{\partial}{\partial y} \left(\text{HK}_y \frac{\partial \text{Phos}}{\partial y} \right) + \phi_{\text{he}} \\ & + H \left\{ \frac{-(\text{PROD} - \text{RESP})}{\text{CP}_a} + \left(\frac{\text{P}_a \text{MORT}_a}{\text{CP}_a} \right. \right. \\ & \left. \left. + \frac{p_f \text{FEC} + p_z \text{MORT}_z + \text{EXC}}{\text{CP}_z} \right) \right\} \quad (14) \end{aligned}$$

$$\text{PROD} = r_p \min[2F(I), F(P)] \text{Phyto} \quad (15)$$

$$\text{RESP} = r_a r_p \min[2F(I), F(P)] \text{Phyto} \quad (16)$$

$$\text{MORT}_a = m_a \text{Phyto} \quad (17)$$

$$\text{EXC} = n_e \text{GRAZ} \quad (18)$$

$$\text{FEC} = n_f \text{GRAZ} \quad (19)$$

$$\text{MORT}_z = m_z \text{GRAZ} \quad (20)$$

$$\begin{aligned} \frac{\partial(\text{HDetr})}{\partial t} = & -\frac{\partial(\text{HuDetr})}{\partial x} - \frac{\partial(\text{HvDetr})}{\partial y} \\ & + \frac{\partial}{\partial x} \left(\text{HK}_x \frac{\partial \text{Detr}}{\partial x} \right) + \frac{\partial}{\partial y} \left(\text{HK}_y \frac{\partial \text{Detr}}{\partial y} \right) \\ & + \phi_{\text{he}} + H \{ (1 - m_p) \text{MORT}_a \\ & \quad + (1 - p_f) \text{FEC} \\ & \quad + (1 - p_z) \text{MORT}_z \\ & \quad - r_d \text{Detr} \} - w_d \text{Detr} \quad (21) \end{aligned}$$

The first four terms on the right-hand side of eqns 6, 11, 14 and 21 represent the horizontal advection and diffusion of the ecological parameters, u and v are time-dependent horizontal velocities obtained from the circulation model, K_x and K_y are the horizontal diffusion coefficients. The fifth term represents entrainment from hypolimnion. $PROD$ represents the gross primary production limited by light and phosphorus limitations functions $[F(I)$ and $F(P)]$. Underwater light calculation includes self-shading because of phytoplankton and a fraction of the dead phytoplankton which remain suspended in the water column for a long time. Nutrient limitation was calculated using the Michaelis–Menten formula with the half-saturation constant as k_{phos} . The parameters for the ecosystem model are defined in Table 1.

Respiration ($RESP$) was calculated using total respiration (r_p per day) proportional to the

phytoplankton biomass and is regenerated immediately into phosphate. Mortality of phytoplankton ($MORT_a$) is also assumed to be proportional to the phytoplankton biomass, with mortality rate m_a per day. A small percentage of it is remineralized while the rest settles to form the detritus pool. Copepod grazing ($GRAZ$) is proportional to the zooplankton biomass, with maximum grazing rate per day (r_z) multiplied by Michaelis–Menten function of phytoplankton biomass with the half-saturation constant k_{phyto} . Grazing is subject to a threshold Phyto_0 below which grazing ceases. Copepod grazing was divided into four parts, as copepod growth (g_e), excretion (n_e), faecal pellets (n_f) and mortality (m_z), all proportional to grazing. ($g_e + n_e + n_f + m_z = 1$). EXC is the soluble organic material and is remineralized immediately in the water column and replenishes the phosphate pool, while proportions of FEC (p_f) and copepod mortality (p_z) are remineralized in the upper layer and the rest settles to the detritus pool. The remineralized phosphorus contributes to the phosphate pool at the fixed ratio of CP_a and CP_z (Descy & Gosselain, 2004) representing the carbon to phosphorus ratios in algae/phytoplankton and zooplankton respectively.

The benthic detritus eqn 21 consists of the detrital material sedimenting out of the water column, which is not remineralized immediately in the upper layer by the microbial food web. The benthic remineralization is rather slow (0.02 day^{-1}) compared with the detrital sedimentation rate (12 m day^{-1}).

Model forcing

The parameters for the ecosystem model were similar to those by Naithani *et al.* (2007) with a few modifications (Table 1). The CP_a and CP_z ratios used were the mean values found in Lake Tanganyika (Descy & Gosselain, 2004). Some of the other parameters were changed to the values generally accepted in the literature (Moll, 1998; Dzierzbicka-Glowacka, 2002; Miller, 2005), when direct measurements for Lake Tanganyika were not available. Entrainment of phosphate from the hypolimnion was extrapolated exponentially from $45 \mu\text{gP L}^{-1}$ below 60 m depth to $1 \mu\text{gP L}^{-1}$ near the surface (Coulter & Spigel, 1991; Plisnier *et al.*, 1996; Descy & Gosselain, 2004). This ensured that the nutrient concentration is an increasing function of the depth from which these nutrients originate.

Table 1 Governing parameters, their description, value and units used in the model

Symbol	Parameter	Value	Unit
α	Coefficient accounting for the Photosynthetic activity	0.56	–
CP_a	C/P ratio of phytoplankton	58.1	–
CP_z	C/P ratio of zooplankton	77.42	–
I_o	Incident light radiation at the air-water interface	Variable	$\mu\text{E m}^{-2} \text{s}^{-1}$
I_k	Light saturation constant	375	$\mu\text{E m}^{-2} \text{s}^{-1}$
k_e	Light extinction coefficient	Variable	m^{-1}
k_{phos}	Half-saturation constant, uptake	5.0	$\mu\text{g P L}^{-1}$
k_{phyto}	Half-saturation constant, grazing	50.0	$\mu\text{g C L}^{-1}$
k_{zoo}	Half-saturation constant, predation	5.0	$\mu\text{g C L}^{-1}$
m_a	Percentage of phytoplankton mortality	0.15	–
m_z	Percentage of zooplankton mortality	0.1	–
n_e	Percentage of ingestion regenerated as soluble excretion of zooplankton	0.3	–
n_f	Percentage of ingestion egested as faecal pellets	0.3	–
p_a	Percentage of remineralized dead phytoplankton in water column	0.8	–
P_f	Percentage of remineralized faecal pellets in water column	0.4	–
p_z	Percentage of remineralized dead zooplankton in water column	0.8	–
Phyto _{min}	Phytoplankton threshold for grazing	15.0	$\mu\text{g C L}^{-1}$
r_a	Percentage of respiration	0.15	–
r_c	Carbon/chlorophyll- <i>a</i> ratio	100.0	–
r_d	Benthic remineralization rate	0.02	Day^{-1}
r_f	Maximum predation rate	0.2	Day^{-1}
r_p	Maximum uptake/growth rate of phytoplankton	1.4	Day^{-1}
R_z	Copepod grazing rate	0.57	Day^{-1}
w_d	Detritus sinking rate	–12.0	m s^{-1}
Zoo _{min}	Zooplankton threshold for grazing	2.0	$\mu\text{g C L}^{-1}$

In large lakes, greater water column mixing leads to a diminished mean irradiance of the mixed layer, to which phytoplankton entrained in the water are exposed (Tilzer, 1990). Hecky & Fee (1981) observed that the phytoplankton was apparently exposed to lower irradiances in large lakes. According to Tilzer (1990), whenever a large lake is thermally stratified, phytoplankton near the surface adapt to high irradiance whereas the phytoplankton in deep water remains adapted to low light throughout the year. This seems to be the case with the very large and deep Lake Tanganyika and was indeed suggested by the experiments of Sarvala *et al.* (1999a). To account for the adaptation to low light by phytoplankton at greater depths, I_k was extrapolated exponentially from $200 \mu\text{E m}^{-2} \text{s}^{-1}$ below 60 m depth to $375 \mu\text{E m}^{-2} \text{s}^{-1}$ near the surface. This ensured slower and steady adaptation to lower lights by the phytoplankton as the mixing depth increased.

The circulation model was discretized on a 20×6 km grid along the y - and x -directions of the lake respectively. The atmospheric forcing was uniform in space but varied in time. The wind and solar insolation used to initialize the circulation model were

from the National Centres for Environmental Protection (NCEP) reanalyses data. The wind-stress was computed with the y -component of wind, aligned parallel to the length of the lake, i.e. the southeast direction. The initial values of the state-variables were assumed to be zero. The model was run for 1 year before the actual simulation period and therefore, the simulations of the model variables were not sensitive to their initial concentrations/values.

Results

Figure 3 represents the model forcing, model simulations and observations off Kigoma and Mpulungu for the years 2002–06. Winds were high during the dry season (May–September) and low for the rest of the year (Fig. 3a). In 2002 winds were high even during March and April. The depth averaged observed chlorophyll-*a* (chl-*a*) was calculated after interpolating the measurements obtained from 0, 20, 40, 60 and 100 m, respectively, and then averaged over the observed upper layer depth. This makes observations easily comparable with model simulations, which gives the mean over the upper layer. The epilimnion is

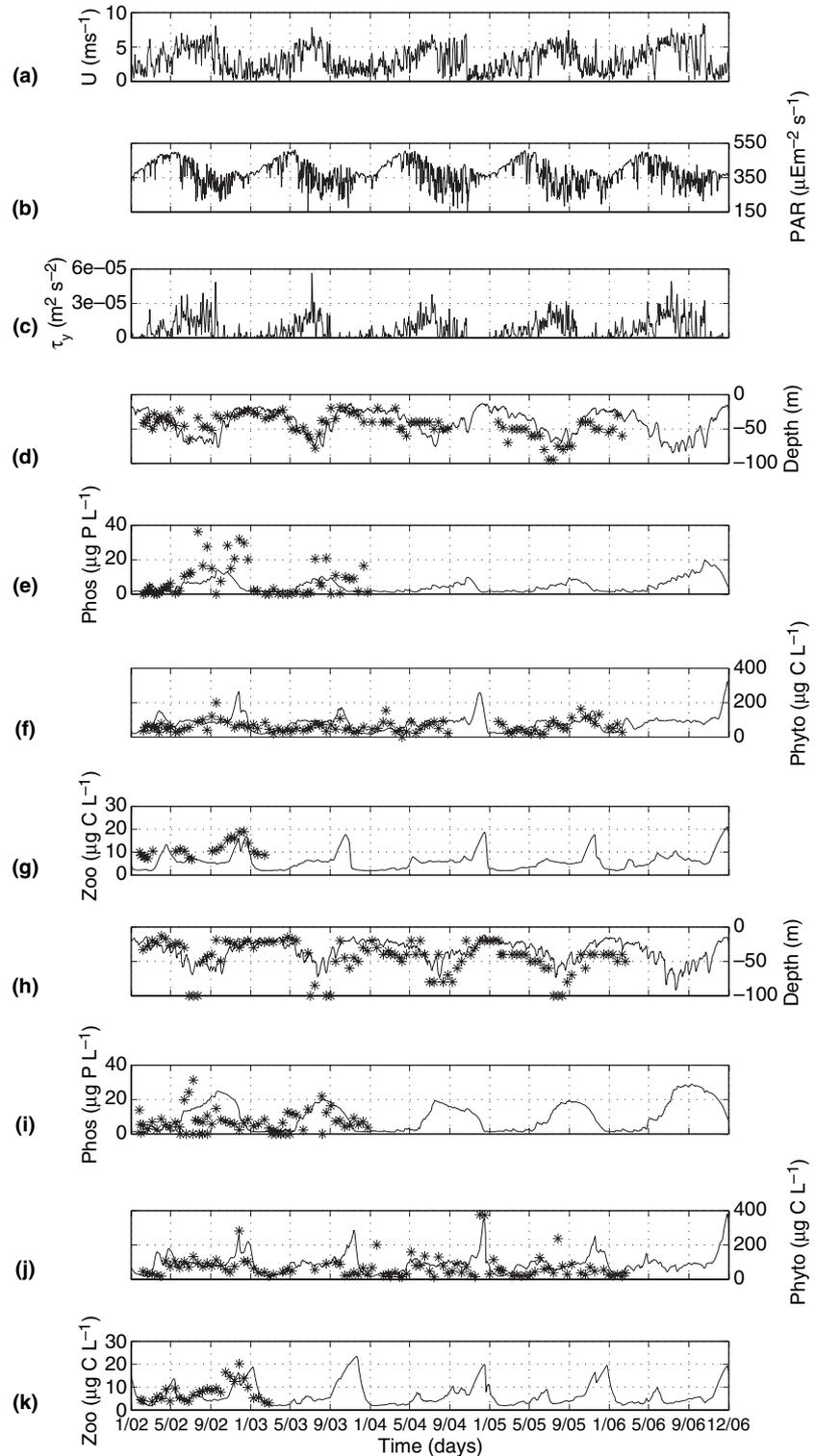


Fig. 3 Time series of daily averaged values of (a) the National Centres for Environmental Protection (NCEP) reanalysed horizontal wind speed, (b) photosynthetic active radiation (PAR), and (c) the *y*-component of wind-stress, model simulated epilimnial depth (d), depth averaged values of phosphate (e), phytoplankton biomass (f) and zooplankton biomass (g) at Kigoma, and model simulated epilimnion depth (h), depth averaged values of phosphate (i), phytoplankton biomass (j) and zooplankton biomass (k) at Mpulungu during the years 2002–06. Observations at Kigoma and Mpulungu are presented by ‘*’.

shallow during low wind wet season and deep during the high wind dry season (Fig. 3d,h). Phosphate follows the mixed layer depth, its concentration being high during deep mixing periods and low otherwise

(Fig. 3e,i). Phytoplankton biomass (Fig. 3f,j) first increased as the nutrient concentration in the upper layer increased because of upwelling caused by high winds. However, the biomass then decreased if the

winds became too high and deep mixing reduced the light in deeper water. Phytoplankton biomass in effect showed a trade-off between the availability of nutrients and light. Sarvala *et al.* (1999b) also reported that, although in principle deep mixing might enhance productivity by increasing nutrient input from the hypolimnion, it also decreased primary production because light becomes limiting for phytoplankton. On average, the plankton biomass in the lake was lower during the dry season and showed peaks from September to November. These peaks correlated with the re-establishment of the upper layer at its equilibrium position, bringing the phytoplankton back to the euphotic zone, after the end of the season with strongest winds in all these years. Zooplankton biomass followed the phytoplankton biomass (Fig. 4).

The observed and predicted depth averaged yearly net primary production ($NP = PROD - RESP$) and mean chl-*a* for the years 2002–06 is given in Table 2. The predicted yearly average values matched well with observations at both stations. The small discrepancies can be attributed to the fact that the observations are taken only twice a month. In the years 2002 and 2006, average daily winds were higher than 5 m s^{-1} for longer than in the other years (Fig. 3a). This resulted in much greater upwelling from deeper

waters and high nutrient entrainment. This was reflected in the slightly higher concentration of chl-*a* in 2002 and 2006 at the two sites than in the other years. The lake-averaged NP was on the average same during these years.

Climatological model run

In order to study the influence of climatic variability on the net productivity of Lake Tanganyika, simulations were carried out for 1970 to 2006 using NCEP data. This period was chosen as it includes the year 1975, when measurements of primary production were carried out rather intensively for the first time (Hecky *et al.*, 1981; Hecky & Fee, 1981; Hecky & Kling, 1981). Climatological model runs are given in Figs 5 & 6. Mean annual wind speed (Fig. 5a) during this period varied between 2 and 4 m s^{-1} , being normally around 3 m s^{-1} except during 1984–92 and 2001–02, when it exceeded 3.5 m s^{-1} . The mean wind speed was lowest in 1974 (2.5 m s^{-1}). The mean annual air temperature (Fig. 5b) increased gradually over the period from 21.5 to $22 \text{ }^\circ\text{C}$. In 1974, low winds were accompanied by low air temperature ($21.3 \text{ }^\circ\text{C}$). Similar air temperatures were observed in 1984 and 1985 but with high winds ($>3.6 \text{ m s}^{-1}$). The highest mean

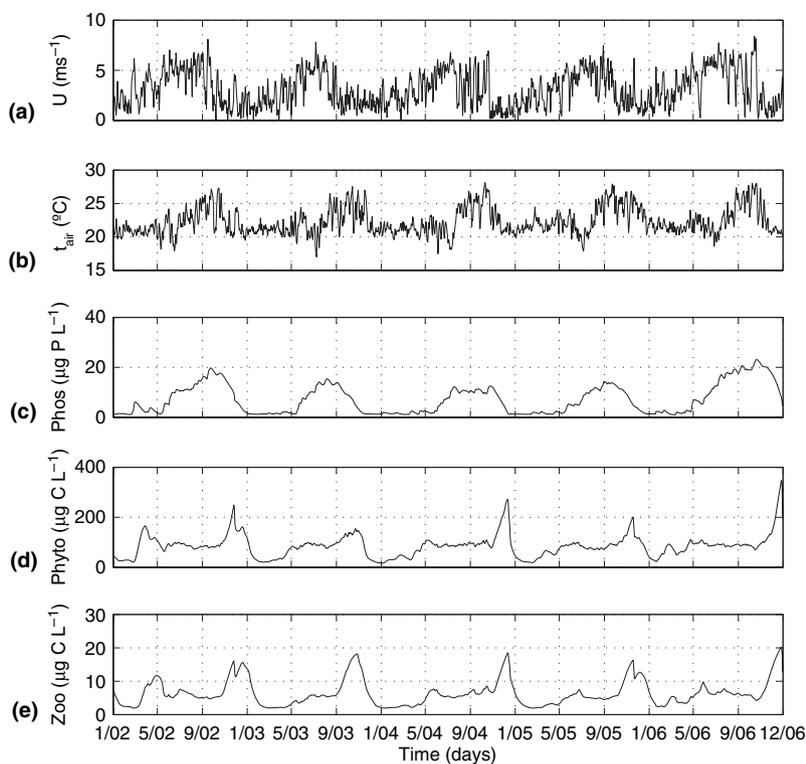


Fig. 4 Time series of daily averaged values of (a) the National Centres for Environmental Protection (NCEP) reanalysed horizontal wind speed, (b) air temperature, (c) depth-averaged values of phosphate, (d) phytoplankton biomass and (e) zooplankton biomass averaged over the whole lake during the years 2002–06.

Table 2 Mean annual NP in the epilimnion and mean chl-*a* from Obs. and model Pre. off Mpulungu, Kigoma and averaged over the whole lake

Year		Mpulungu		Kigoma		Lake average	
		Obs.	Pre.	Obs.	Pre.	Obs.	Pre.
NP							
2002	g C m ⁻² year ⁻¹	–	276.0	–	251.6	–	256.3
	g C m ⁻² day ⁻¹	–	0.75	–	0.69	–	0.70
2003	g C m ⁻² year ⁻¹	–	308.6	–	260.0	–	275.3
	g C m ⁻² day ⁻¹	–	0.84	–	0.71	–	0.75
2004	g C m ⁻² year ⁻¹	–	303.3	–	279.9	–	283.6
	g C m ⁻² day ⁻¹	–	0.83	–	0.76	–	0.77
2005	g C m ⁻² year ⁻¹	–	297.3	–	255.4	–	269.2
	g C m ⁻² day ⁻¹	–	0.81	–	0.70	–	0.74
2006	g C m ⁻² year ⁻¹	–	271.0	–	250.2	–	255.3
	g C m ⁻² day ⁻¹	–	0.74	–	0.69	–	0.70
Chl-<i>a</i>							
2002	mg m ⁻³	0.94 (24)	1.03	0.72 (26)	0.90	–	0.93
2003	mg m ⁻³	0.84 (22)	0.86	0.63 (25)	0.63	–	0.72
2004	mg m ⁻³	0.66 (27)	0.93	0.62 (18)	0.83	–	0.87
2005	mg m ⁻³	0.59 (24)	0.87	0.66 (23)	0.68	–	0.77
2006	mg m ⁻³	0.26 (4)	0.96	0.51 (3)	0.95	–	0.96

NP, net primary production; chl-*a*, chlorophyll-*a*; Obs., observations; Pre., predictions.

The numbers in brackets represents the number of field observations per year used to calculate the yearly average.

annual air temperature (>22.2 °C) was observed in 1987–88, with winds around 3.5 m s⁻¹. This reflects the fact that high winds were not necessarily accompanied by low air temperature. The mean annual photosynthetic active radiation (Fig. 5c) also increased gradually. The increasing trend was most apparent between 1970 and 1981 and from 1998 to 2002 and decreased thereafter, while from 1981 to 1998 it remained more or less constant.

Epilimnial depth (Fig. 5e,j) more or less followed the trend in wind speed, being shallow during calm years and deeper during windy years at both stations. A shallow mixing depth resulted in less nutrients while deep mixing entrained bottom water rich in nutrients (Fig. 5f–k). However, net primary productivity of the lake was higher during shallow mixing periods and low during deep mixing periods, implying less time spent by the phytoplankton in the euphotic layer. Surprisingly, in the year 1974, when the winds were very low resulting in a shallow mixed depth (Fig. 5e–j) and a low concentration of nutrients, the NP was high at both stations (Fig. 5f–k). During this year phytoplankton biomass was high at Mpulungu (Fig. 5m). In 1984–86, when phosphorus concentration in the lake was high and the mixed depth was greater, the phytoplankton biomass was also low, implying that algal cells were spending more time in the light limited

deeper waters. Lower phosphate concentrations during 2000–01 and 2003 were accompanied by lower phytoplankton biomass. The highest phytoplankton biomass at Mpulungu during study was obtained in the years 1991–92, followed by 1987, 1998–99 and 2002. The maximum NP was observed during the years 1974, 1998 and 2003.

The mean lake phosphate concentration (Fig. 6c) followed the wind (Fig. 6a), while the NP (Fig. 6d) showed an inverse relationship with phosphate. The highest mean phytoplankton biomass (Fig. 6e) was obtained in the year 1999. The concentration of nutrients in the upper layer systematically followed wind speed. The lake mean NP was inversely related to wind speed, being high for calm years and *vice versa*. The 1980s and early 1990s were relatively windy and the lake average NP and chl-*a* were correspondingly low. This was also the case for NP at Kigoma and Mpulungu, while at Mpulungu the phytoplankton biomass was rather high in the years 1987 and 1991–92 (Fig. 5m). The mean daily chl-*a* during the whole period of simulation ranged from 0.16 to 4.3 mg m⁻³ in the surface mixed layer, while the net primary production ranged from 0.11 to 1.78 g C m⁻² day⁻¹.

In order to estimate the bias in the simulated annual production because of NCEP wind forcing, we ran the

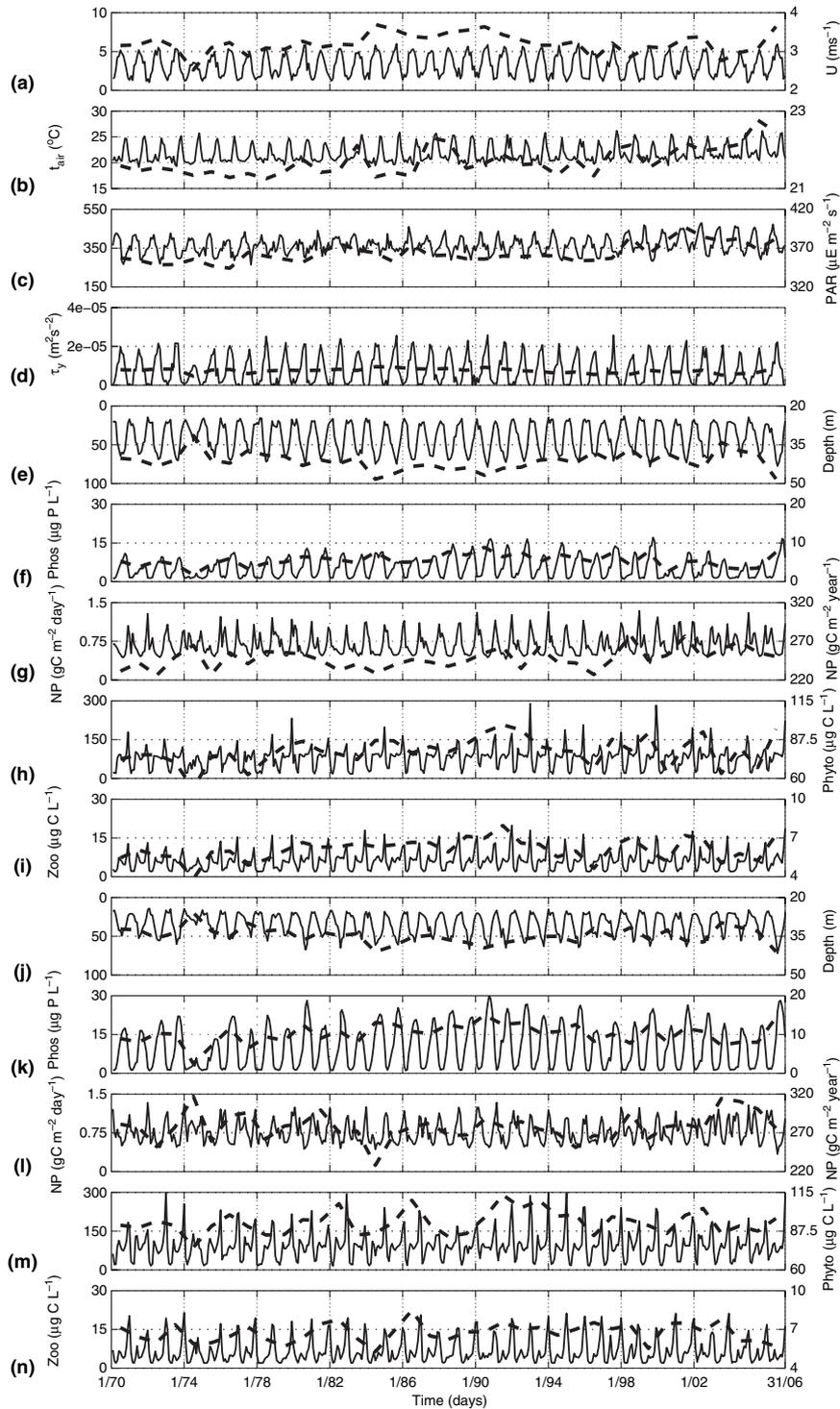


Fig. 5 Time series of daily (solid line) and yearly (dashed line) averaged values of (a) the National Centres for Environmental Protection (NCEP) reanalysed horizontal wind speed, (b) air temperature, (c) photosynthetic active radiation (PAR) and (d) the y -component of wind-stress, (e) model simulated epilimnion depth, (f) depth averaged values of phosphate, (g) net primary productivity (NP), (h) phytoplankton biomass and (i) zooplankton biomass at Kigoma, and (j) model simulated epilimnion depth, (k) depth averaged values of phosphate, (l) net primary productivity (NP), (m) phytoplankton biomass and (n) zooplankton biomass at Mpulungu during the years 1970–2006. The scale for yearly averaged values is shown on the right-hand side of the y -axis.

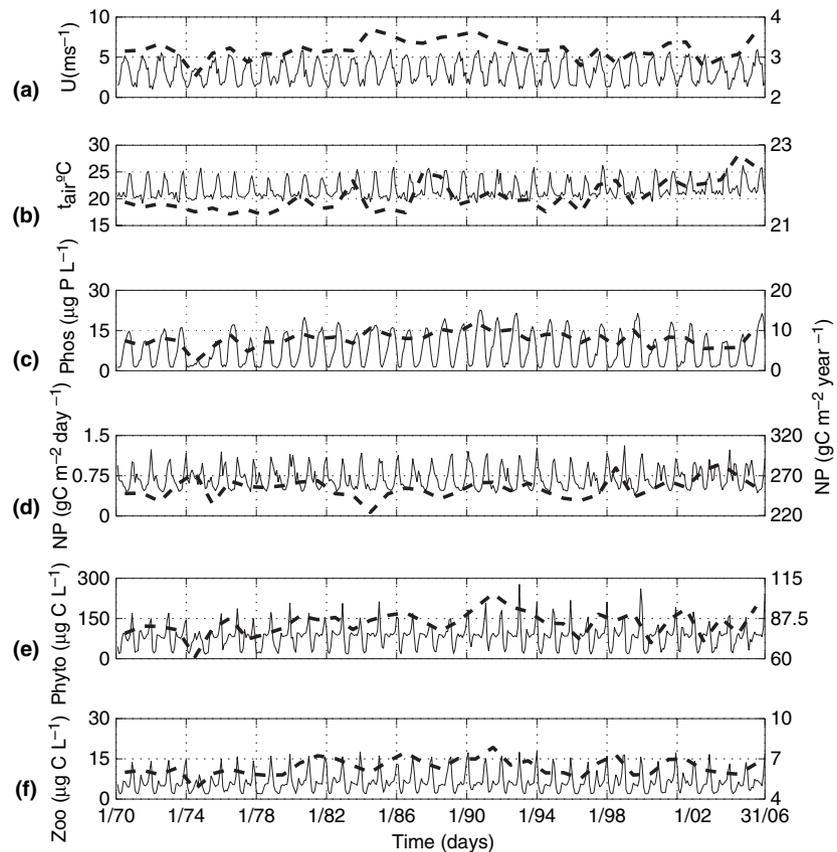


Fig. 6 Time series of daily (solid line) and yearly (dashed line) averaged values of (a) the National Centres for Environmental Protection (NCEP) reanalysed horizontal wind speed, (b) air temperature, (c) model predicted depth-averaged values of phosphate, (d) net primary productivity (NP), (e) phytoplankton biomass and (f) zooplankton biomass averaged over the whole lake during the years 1970–2006. The scale for yearly averaged values is shown on the right-hand side of the y -axis.

Table 3 Percentage difference between model simulations of annual net primary productivity (NP) over the whole lake and at Mpulungu and Kigoma, using observed winds off Mpulungu and National Centres for Environmental Protection (NCEP) wind as forcing factors, respectively, for the period April 1993–March 1994

	Wind scenarios		
	Observed winds	NCEP winds	Per cent difference
NP			
Lake mean	250.4	265.3	5.8
Mpulungu	270.3	274.0	1.3
Kigoma	245.1	261.4	6.6

model using the wind observed at Mpulungu during April 1993 to March 1994 (observations from the FAO/FINNIDA LTR project) and compared them with those obtained with NCEP forcing for the same period (Table 3). The annual simulations with NCEP wind forcing show higher annual production both over the whole lake and at Kigoma by about 6%, while the simulations at Mpulungu were more or less similar. The winds at Mpulungu are representative of those over the southern part of the lake and cannot be

considered to represent fully winds over the northern area of the lake. The northern region occasionally experiences strong northerly winds during the wet season. These brief periods of strong wind are not represented adequately by the winds observed at Mpulungu, and to some extent by NCEP winds. It is evident that with NCEP, wind forcing of the x component of wind stress increases, which accounts for the 6% greater productivity in the northern part of the lake.

Discussion

Observations and measurements on plankton and primary productivity of the lake hitherto have been short term (<1 year) and incomplete in their spatial coverage (Hecky *et al.*, 1991). Hecky & Fee (1981) reported annual net primary production of $290 \text{ g C m}^{-2} \text{ year}^{-1}$ ($0.8 \text{ g C m}^{-2} \text{ day}^{-1}$) for the year 1975. Melack (1980) reported a single pelagic measurement of $0.5 \text{ g C m}^{-2} \text{ day}^{-1}$ in April 1971. Our simulated value of annual net primary productivity for the year 1975 was $235.2 \text{ g C m}^{-2} \text{ year}^{-1}$ ($0.65 \text{ g C m}^{-2} \text{ day}^{-1}$). Note that Hecky & Fee (1981)

measured chlorophyll concentration on two whole lake transects, which traversed Lake Tanganyika from north to south. Each of these transects was completed within 3 weeks in April–May and again in October–November 1975. They chose these two periods to coincide with periods of low algal abundance at the end of the prolonged wet season (October–April) and high algal abundance after dry season mixing (May–September). Moreover, it was assumed that the mean chlorophyll concentrations in April–May and October–November represented, respectively, the 6-month period of low photosynthesis during stratification (January–June), and the period of high photosynthesis during mixing and restratification (June–December) (Hecky *et al.*, 1991). Hecky & Kling (1981) observed the lowest phytoplankton biomass, as low as 60 mg m^{-3} , during the phase of stable stratification and the greatest, as high as 930 mg m^{-3} , at the end of the deep mixing period. Their estimate of chl-*a* in the euphotic layer ranged from 0.1 to 4.5 mg m^{-3} and with an annual mean of 1.2 mg m^{-3} . Our simulations show an annual mean chl-*a* of 0.80 mg m^{-3} averaged in the upper layer. The lower value might be because we took the average over the upper layer while Hecky & Kling (1981) reported the average over the euphotic layer. It should be noted that the model simulations are for the whole year over the whole lake area. The depth profiles of observed chl-*a* show that the maximum chl-*a* is often observed around 20–30 m depth (Salonen *et al.*, 1999; Descy & Gosselain, 2004; Plisnier & Descy, 2005).

Sarvala *et al.* (1999a) reported estimates of primary production of $426\text{--}662 \text{ g C m}^{-2} \text{ year}^{-1}$ for the period July 1993–June 1996. Model prediction of net primary production was $241.08 \text{ g C m}^{-2} \text{ year}^{-1}$. Salonen *et al.* (1999) reported a mean chl-*a* concentration of 1.4 mg m^{-3} in surface water for the whole lake during a cruise in April–May 1995. Their estimate was 1.0 mg m^{-3} for the upper 40 m during this period, 2.2 mg m^{-3} in October–November 1995 and 2.8 mg m^{-3} in November 1996. Langenberg (1996) reported an estimate of $0.6\text{--}1.6 \text{ mg m}^{-3}$ during August–December 1995. Our model predictions for the mean mixed layer over the whole lake during these periods were 0.82 (April–May 1995), 1.49 (October–November 1995), 1.68 (November 1996) and 1.17 mg m^{-3} (August–December 1995). Model predictions are similar to the observations, when it is recalled that the model predictions are

for the whole lake and are an average over the mixed layer.

In conclusion, in the absence of adequate regional, spatial and temporal measurements carried out in Lake Tanganyika, modelling provides a simple alternative for studying lake hydrodynamics and ecosystem functioning. The eco-hydrodynamic-II model, based on a simplified phosphorus cycle and only three prognostic pelagic variables, was able to predict the net primary productivity of the lake. Phosphorus seems to be the most appropriate single nutrient of choice because, in Lake Tanganyika, it appears to be the most limiting. The model simulations successively predicted the present, as well as the past, primary productivity of Lake Tanganyika. The comparison with observations gives confidence in the predicted mean net production of the lake.

The yearly averaged phytoplankton biomass at Kigoma was slightly lower than that at Mpulungu. This agrees with observations and with the observation of Hecky & Kling (1981). They reported that the biomasses were on the average lower at Kigoma with phytoplankton biomass $>100 \text{ mg m}^{-3}$ on only one occasion from mid-March until September.

Long-term climatic simulations were in agreement to Sarvala *et al.* (1999a, 2006), in that at least phytoplankton chlorophyll concentration seems to have remained broadly similar from the 1970s to the present day (excepting some year-to-year fluctuations because of variations in the wind). The case has been most convincingly developed in Sarvala *et al.* (2007). One important finding of the simulations was that light limitation because of deep mixing was more important for phytoplankton production than the enhanced nutrient supply. Negative effects of deep mixing on the phytoplankton biomass were also considered by Sarvala *et al.* (1999b). This means that weakening winds, which in the Tanganyika area have been claimed to be associated with increasing temperatures, might not necessarily lead to lowered productivity.

Our simulations clearly confirmed the findings from previous observations (Langenberg, Sarvala & Roijackers, 2003) that the relationship between mixing depth (changes with warming) and lake productivity is not simple or straightforward. In future we envisage using this model to predict the future scenarios of primary productivity of the lake and to predict fish production. A better understanding of the strength of interaction between the atmospheric forcing and the ecosystem

parameters of the lake is necessary, if we are to predict the potential effects of climate change on production of the lake. Our present circulation model has two weaknesses. First, we have assumed a homogeneous wind field, which is not the case (Bullot, 1977; Savijärvi, 1997; Huttula *et al.*, 1999; Savijärvi & Järvenoja, 2000). Secondly, the vertical structure of the water column stratification in Lake Tanganyika is more complex than implied by the two-layer structure in this model (Craig *et al.*, 1974; Plisnier *et al.*, 1996; Huttula, 1997). In the future it is planned to consider both these points.

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