PRIMARY RESEARCH PAPER

Possible effects of global climate change on the ecosystem of Lake Tanganyika

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Abstract Any change in the air temperature, wind speed, precipitation, and incoming solar radiation induced by increasing greenhouse gasses and climate change will directly influence lakes and other water bodies. The influence can cause changes in the physical (water temperature, stratification, transparency), chemical (nutrient loading, oxygen) and biological (structure and functioning of the ecosystem) components of the Lake. In this work an influence of the likely effects of the climate change on the above three components of Lake Tanganyika are studied by means of a simple ecological model. Simulations for the years 2002–2009 have been performed using the wind and solar radiation data from the National Centres for Environmental Protection (NCEP) reanalysis. Various possible climatic scenarios are studied by changing the surface layer depth, its temperature and the wind stress. Any change in any of the above physical forcing parameters modifies the timing and intensity of the dry season peaks of the biogeochemical parameters. It is seen that the gross production increases as temperature of the surface layer increases and its depth decreases. High temperature and low wind stress, reduces the biomass. The effects of a slight increase in lake water temperature on the Lake Tanganyika ecosystem might be mitigated by increased windiness, if the latter was sufficient to induce greater mixing.

Keywords Lake Tanganyika · Ecological and hydrodynamic model · Climate change · Sensitivity analysis

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Introduction

The East African rift valley lakes are amongst the oldest on Earth. Lake Tanganyika (containing about 17% of the world freshwater) is one of the largest amongst them. It is a long, narrow and deep lake, situated between 3°20′ and 8°45′S and 29°05′ and 31°15′E (Fig. 1). It is meromictic in nature (complete

overturning of water never takes place). Thermal stratification in the Lake is well marked and varies above the permanent anoxic hypolimnion (Beauchamp, 1939; Coulter and Spigel, 1991). The epilimnion undergoes seasonal temperature changes, whereas the hypolimnion is a vast reservoir of nutrients largely isolated from surface influences (Hecky et al., 1991; Edmond et al., 1993). The region around the Lake undergoes two main seasons: a 4–5 months long cool 'dry season', characterised 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, during which the winds are weaker and mainly from northeast (Coulter & Spigel, 1991). The stratification breaks down during the dry season, whereas in the wet season it is similar all along the length of the Lake (Coulter & Spigel, 1991; Naithani et al., 2002; Verburg et al., 2003; Naithani et al., 2003). Primary production in the epilimnion depends primarily upon the supply of nutrients from the hypolimnion by means of entrainment because of upwelling caused by the high persistent winds of the dry season (Coulter, 1991; Naithani et al., 2007a, b). The Lake is important for its numerous endemic species (Coulter, 1991). Because of its old age and meromictic nature, it is considered to have long, continuous, high-resolution record of the past climate in its sediments (Coulter, 1991). The lake provides fresh water and an inexpensive protein diet to the people of the four riparian nations (Coulter, 1991; Ogutu-Ohwayo et al., 1997; Jorgensen et al., 2006). Any change in its production will affect these people.

The overall productivity of a lake is closely linked to the availability of nutrients and light (Wetzel, 1983). Light is in abundance in Lake Tanganyika, because of its proximity to the equator. The high transparency (secchi disk depth of about 12 m on average) and the low average chlorophyll *a* (1 μg/l) in the surface pelagic water indicate that the lake may be considered as oligotrophic, although strong mixing events may lead to algal blooms (Hecky et al., 1991; Plisnier et al., 1999; Jorgensen et al., 2006; Verburg & Hecky, 2009). The supply of nutrients to the surface layer in the Lake strongly depends upon the hydrodynamical processes induced by temperature and wind stress. The wind stress pushes the warm epilimnion surface water away from the southern end of the lake towards the north. This induces upwelling at the south and accumulation of water in the epilimnion in the north (Beauchamp,
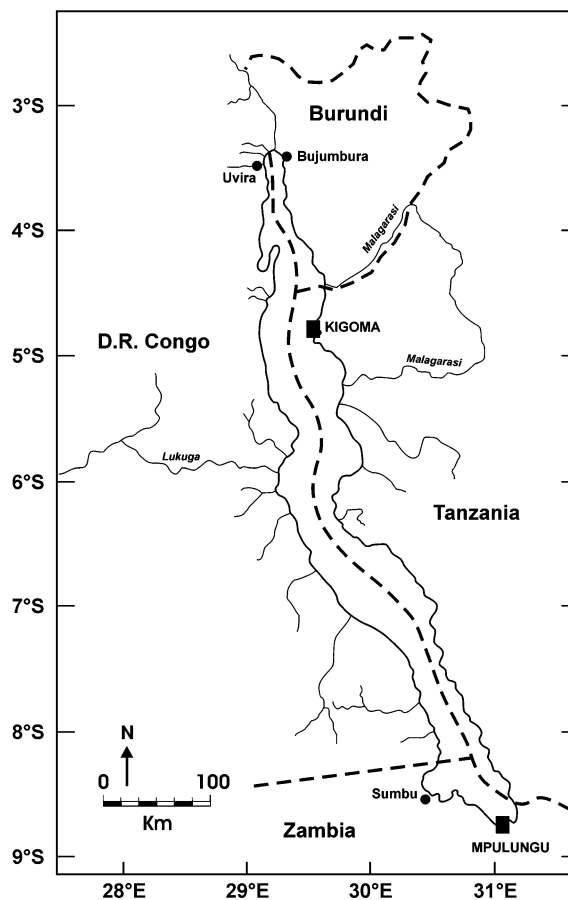
Fig. 1 Geographic map of Lake Tanganyika

1939; Coulter and Spigel, 1991; Plisnier et al., 1999; Plisnier & Coenen, 2001; Naithani et al., 2002). A counter-current flows south near the thermocline. The annual southern upwelling brings relatively colder nutrient rich deeper water to the biotic and euphotic zone causing higher rates of primary productivity in the Lake (Hecky & Fee, 1981; Hecky & Kling, 1981; Coulter and Spigel, 1991; Hecky et al., 1991; Langenberg, 1996; Plisnier et al., 1999; Plisnier & Coenen, 2001; Langenberg et al., 2003; Naithani et al., 2007a, b). Wind, temperature, incident solar radiation, and water transparency set the critical mixing depth for growth as a function of euphotic zone depth in relation to the depth of the surface mixed layer (Hecky & Kling, 1987; Naithani et al., 2007a, b). Changing climatic scenarios is considered to be affecting the production of the lakes around the world (Edmond et al., 1993; Fee et al., 1996; De Stasio et al., 1996; Mortsch & Quinn, 1996; Schindler et al., 1996; Magnuson et al., 1997;

Livingstone, 2003; O'Reilly et al., 2003; Verburg et al., 2003; Schep et al., 2007; Stenuite et al., 2007; Smol & Douglas, 2007; Izmest'eva & Silow, 2008; Moore et al., 2009; Verburg & Hecky, 2009; Adrian et al., 2009; Tierney et al., 2010). Climate change will presumably affect the ecosystem in the lakes by means of changing temperatures and winds (Schindler et al., 1990; Hondzo and Stefan, 1991, 1993; Stefan et al., 1993; De Stasio et al., 1996; Fee et al., 1996; King et al., 1997; King et al., 1999; Verburg et al., 2003; Verburg & Hecky 2009; Adrian et al., 2009). These are ecologically important as they determine the depth of the surface mixed layer, the photosynthetically available radiation for primary production and the nutrient recycling in the surface layer (Fee, 1979; Fee et al., 1992). Increased temperatures in Lake Tanganyika and Lake Malawi (another deep rift lake in East Africa) have been reported (Verburg et al., 2003; Vollmer et al., 2005; Verburg & Hecky, 2009).

It should be noted that in recent decades the human population and settlements around the lake have expanded resulting in a local overexploitation of its resources, including the possible local depletion of fish stocks (Reynolds & Molsa, 2000; Sarvala et al., 2006; Jorgensen et al., 2006). This might also add to the fact that few fisheries statistics exist for Lake Tanganyika. According to Caljon (1992); Cohen et al. (1993); Ogutu-Ohwayo et al. (1997); Alin et al. (1999); Jorgensen et al. (2006), and Kamenya et al. (2008) extant biodiversity in Lake Tanganyika and other African Great Lakes is threatened by a variety of human activities. They emphasize that the most damaging threat to the Lake's biodiversity appears to be an increased rate of sediment influx, especially from the heavily impacted smaller watersheds of northern Lake Tanganyika, where large-scale defor-estation and farming practices have caused a dramatic increase in soil erosion rates. This could affect the littoral–sublittoral communities. Increasing intensity of rainfall probably also plays a role. However, there is not enough data to precise that. The health of Lake Tanganyika, which is a major source of livelihood and protein to the human community, also depends on the health of its catchment forests, rivers and streams. Studies concerning the influence of climate change on an ecosystem, therefore, should also consider anthropogenic effects. The four riparian countries are joining efforts to address those issues (UNDP/GEF, 2008).

This article presents a numerical study of the response of Lake Tanganyika ecosystem to possible changes in climatic conditions. We have developed various climatic scenarios with varying reference depth of the surface layer, its temperature and wind stress, in order to assess the sensitivity of Lake Tanganyika's biological, chem-ical and physical properties to climate change.

Materials and methods

For this study, a four-component ecosystem model (Nutrient–Phytoplankton–Zooplankton–Detritus, NPZD), coupled to a non-linear reduced-gravity circulation model has been used. The hydrody-namic/circulation model considers the Lake to consist of two homogeneous layers of different density, representing the warm epilimnion (surface mixed layer) and cold dense hypolimnion (lower layer) separated by a thermocline (Naithani et al., 2002, 2003). The lower layer is considered to be much deeper than the surface active/mixed layer. The model is forced with the wind and solar radiation data from the NCEP reanalysis. Earlier studies using this model have shown that in the motion of water there are internal seiches with oscillations similar to that in the forcing winds, using a series of wind pulses including those representing the actual wind conditions over the lake (Naithani et al., 2002, 2003). The simulated oscillations compare satisfactorily with those derived from observed temperature in the Lake (Naithani et al., 2002, 2003). The coupled ecological-hydrodynamic model simulations show also good correspondence with the measurements from the Lake (Naithani et al., 2007a, b).

The circulation model consists of the non-linear, reduced-gravity equations (Naithani et al., 2007b):

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

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

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

$$\frac{\partial (Hv)}{\partial t} = -\frac{\partial (Huv)}{\partial x} - \frac{\partial (Hvv)}{\partial y} - fHu - gH\frac{\partial \varepsilon \xi}{\partial y}$$
$$+ \frac{\partial}{\partial x}\left(HA_x\frac{\partial v}{\partial x}\right) + \frac{\partial}{\partial y}\left(HA_y\frac{\partial v}{\partial y}\right) + \frac{\tau_y}{\rho_0} + w_{\mathrm{e}}^- v$$

$$(4)$$

where x and y are horizontal axes, u and v are the depth-integrated velocity components in the surface layer in the x and y directions, t is the time, x is the downward displacement of the thermocline, $H = h + \xi$ is the thickness of the epilimnion (the surface, well-mixed layer), h is the reference depth of the surface layer (m) and w_{e} is the entrainment velocity (m s^{-1}). The first term on the right hand side of Eq. 2 is inspired by Price (1979), τ_x and τ_y are horizontal components of specific wind stress in the x and y direction (m^2 s^{-2}), $\varepsilon = (\rho_{\mathrm{b}} - \rho_{\mathrm{s}})/\rho_{\mathrm{b}}$ is the relative density difference between the hypolimnion (ρ_{b}) and the epilimnion (ρ_{s}), calculated using the temperature of the surface layer (t_{s}) and bottom layer (t_{b}), 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_{tt}) is needed which slowly nudges the surface layer depth toward its equilibrium position. The relaxation timescale, r_{tt}, 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 surface layer, f is the Coriolis factor (<0 in the southern hemisphere), A_{s} is the horizontal eddy viscosity in the s ($=x$, y) direction, $w_{\mathrm{e}}^- = \frac{w_{\mathrm{e}} - |w_{\mathrm{e}}|}{2}$ is the negative part of the entrainment velocity, i.e., w_{e}^- is equal to w_{e} if $w_{\mathrm{e}} < 0$ and is zero otherwise. Below, we make use of the positive part of the entrainment velocity, which is defined as $w_{\mathrm{e}}^+ = \frac{w_{\mathrm{e}} + |w_{\mathrm{e}}|}{2}$.

The ecosystem model, consisting of dissolved phosphorus (Phos), phytoplankton (Phyto), zooplankton (Zoo) and detritus (Detr) was used (Naithani et al., 2007b). Each component was represented by one state variable only (Fig. 2). 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 was implemented so that the ecosystem variables were transported by advection and diffusion. The model includes primary production (PROD), remineralization within the surface layer, and sedimentation of detritus. Phytoplankton is utilised by copepods (GRAZ), settles slowly (1 m d^{-1}) or dies (MORT$_{\mathrm{a}}$).

Fig. 2 Flow diagram of the ecological parameters considered in the model (Naithani et al., 2007b)
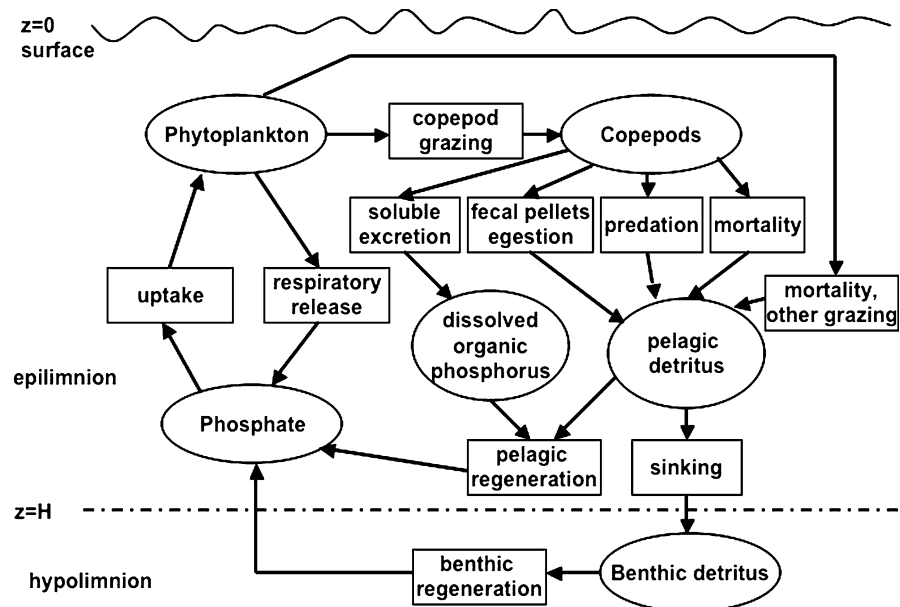
Grazing by copepods is divided into their growth, faecal pellet (FEC) egestion, mortality ($MORT_z$) and excretion (EXC). A small percentage of faeces, dead phytoplankton, and zooplankton are remineralized into phosphate by the microbial food web in the surface layer whereas the rest contributes to the detritus pool. Phytoplankton respiratory release is directly remineralized. The regeneration within the surface layer represents the effect of the microbial food web and also represents the pelagic regeneration. The model is closed by predation from zooplanktivorous fish and sinking of detritus out of the surface layer.

The ecosystem model equations are:

$$\frac{\partial(H\text{Phyto})}{\partial t} = -\frac{\partial(Hu\text{Phyto})}{\partial x}) - \frac{\partial(Hv\text{Phyto})}{\partial y}$$
$$+ \frac{\partial}{\partial x}\left(HK_x\frac{\partial \text{Phyto}}{\partial x}\right) + \frac{\partial}{\partial y}\left(HK_y\frac{\partial \text{Phyto}}{\partial y}\right)$$
$$+ \phi_{he}$$
$$+ H\{\text{PROD} - \text{RESP} - \text{MORT} - \text{GRAZ}\} \quad (6)$$

$$\text{PROD} = r_p \min[2F(I), F(P)]\text{Phyto} \quad (7)$$

$$\text{RESP} = r_a r_p \min[2F(I), F(P)]\text{Phyto} \quad (8)$$

$$\text{MORT}_a = m_a \text{Phyto} \quad (9)$$

$$\text{GRAZ} = r_z \frac{\text{Phyto}}{\text{Phyto} + k_{\text{phyto}}} \text{Zoo} \quad (10)$$

$$F(P) = \frac{\text{Phos}}{\text{Phos} + k_{\text{phos}}} \quad (11)$$

$$F(I) = (1/k_e H)[\arctan(\alpha I_0/2 I_k)$$
$$- \arctan(\alpha I_0 e^{-k_e H/2 \cdot I_k})] \quad (12)$$

$$k_e = 0.066 + 0.07 \frac{\text{Phyto}}{r_c} \quad (13)$$

$$\phi_{he} = w_e^+ \text{Phyto}_h + w_e^- \text{Phyto} \quad (14)$$

$$\frac{\partial(H\text{Zoo})}{\partial t} = -\frac{\partial(Hu\text{Zoo})}{\partial x}) - \frac{\partial(Hv\text{Zoo})}{\partial y}$$
$$+ \frac{\partial}{\partial x}\left(HK_x\frac{\partial \text{Zoo}}{\partial x}\right) + \frac{\partial}{\partial y}\left(HK_y\frac{\partial \text{Zoo}}{\partial y}\right)$$
$$+ \phi_{he} + H\{\text{GRAZ} - \text{EXC}$$
$$- \text{FEC} - \text{MORT}_z - \text{PRED}\} \quad (15)$$

$$\text{EXC} = n_e \text{GRAZ} \quad (16)$$

$$\text{FEC} = n_f \text{GRAZ} \quad (17)$$

$$\text{MORT}_z = m_z \text{GRAZ} \quad (18)$$

$$\text{PRED} = r_f \frac{\text{Zoo}}{\text{Zoo} + k_{\text{zoo}}}\text{Fish} \quad (19)$$

$$\frac{\partial(H\text{Phos})}{\partial t} =$$
$$-\frac{\partial(Hu\text{Phos})}{\partial x}) - \frac{\partial(Hv\text{Phos})}{\partial y} + \frac{\partial}{\partial x}\left(HK_x\frac{\partial \text{Phos}}{\partial x}\right)$$
$$+ \frac{\partial}{\partial y}\left(HK_y\frac{\partial \text{Phos}}{\partial y}\right) + \phi_{he} + H\left\{\frac{-(\text{PROD} - \text{RESP})}{\text{CP}_a}\right.$$
$$+ \left.\left(\frac{p_a \text{MORT}_a}{\text{CP}_a} + \frac{(p_f \text{FEC} + p_z MORT_z + \text{EXC})}{\text{CP}_z}\right)\right\} \quad (20)$$

$$\frac{\partial(H\text{Detr})}{\partial t} = -\frac{\partial(Hu\text{Detr})}{\partial x}) - \frac{\partial(Hv\text{Detr})}{\partial y}$$
$$+ \frac{\partial}{\partial x}\left(HK_x\frac{\partial \text{Detr}}{\partial x}\right) + \frac{\partial}{\partial y}\left(HK_y\frac{\partial \text{Detr}}{\partial y}\right) + \phi_{he}$$
$$+ H\{(1 - m_p)\text{MORT}_a + (1 - p_f)\text{FEC}$$
$$+ (1 - p_z)\text{MORT}_z - r_d \text{Detr}\} - w_d \text{Detr} \quad (21)$$

The first four terms on the right-hand side of Eqs. 6, 15, 20, 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 due to phytoplankton and a fraction of the dead phytoplankton, which remain suspended in the water column for a long time. Nutrient limitation is calculated using Michaelis–Menten formula with half-saturation constant as k_{phos}. The model parameters are decided based on the existing literature and were set up in the previous works (Naithani et al., 2007, b). The definition of the parameters and their values are given 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

Table 1 Governing parameters, their description, value, and units used in the model (Naithani et al., 2007b)

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_0	Incident light radiation at the air–water interface	Variable	$\mu E\ m^{-2}s^{-1}$
I_k	Light saturation constant	375	$\mu E\ m^{-2}s^{-1}$
k_e	Light extinction coefficient	Variable	m^{-1}
k_{phos}	Half-saturation constant, uptake	5.0	$\mu g\ P\ l^{-1}$
k_{phyto}	Half-saturation constant, grazing	50.0	$\mu g\ C\ l^{-1}$
k_{zoo}	Half-saturation constant, predation	5.0	$\mu g\ C\ l^{-1}$
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	$\mu g\ C\ l^{-1}$
R_a	percentage of respiration	0.15	–
R_c	Carbon/Chl a 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	ms^{-1}
Zoo_{min}	zooplankton threshold for grazing	2.0	$\mu g\ C\ l^{-1}$

biomass, with mortality rate m_a per day. A small percentage of it is remineralized whereas 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. EXC is the soluble organic material and is remineralized immediately in the water column and replenishes the phosphate pool, whereas proportions of FEC (p_f) and copepod mortality (p_z) are remineralized in the surface layer and the rest settles to the detritus pool. The benthic detritus equation (20) consists of the detrital material sinking out of the water column, which is not remineralized immediately in the surface layer by the microbial food web. The benthic remineralization/decomposition is rather slow (0.02 day^{-1}) compared to the detrital sinking rate (12 m day^{-1}). The

parameters for the ecosystem model are similar to those by Naithani et al. (2007b). Entrainment of phosphate from the hypolimnion was extrapolated exponentially from 45 $\mu g\ P\ l^{-1}$ below 60 m depth to 1 $\mu g\ P\ l^{-1}$ near the surface (Coulter & Spigel, 1991; Plisnier et al., 1996; Plisnier & Descy, 2005). This ensured that the water is richer in nutrients if upwelling occurs from deeper depths.

The equilibrium depth of the thermocline is a parameter that can be modified, as can the surface layer temperature. The temperature of the lower layer is not modified. Model control run refers to the parameters used in the earlier work (Naithani et al., 2007b), with the thermocline at 30 m and the temperature of the surface and lower layers as 27 and 24.5°C, respectively, and forced with NCEP reanalysed winds and solar radiation for the years 2002–2009. The climate change impact is studied by changing the thermocline depth, the surface layer temperature and the wind stress.

Results

First, we studied the influence of the forcing parameters on the time evolution of the physical and biological parameters. This will give insight into the seasonal variation of model-simulated parameters, with changing scenarios.

Changes in the surface layer temperature

Figure 3 shows the time series of model predicted surface layer (epilimnion) depth, and the depth-averaged concentration in the surface layer of phosphate, phytoplankton gross production, phytoplankton biomass and zooplankton biomass. Simulations averaged over the whole lake for various epilimnion temperatures are shown. The plots of the control run are shown in solid line in the Figs. 3, 4, and 5. In general, the time series plots show the increase in the surface layer depth during the dry season of May until September, while it remains shallow during the low wind wet season. Phosphate follows the surface layer depth and shows higher concentration during the dry season and low otherwise. Gross primary productivity (GP) and phytoplankton biomass increase at the beginning of the dry season as the nutrient concentration in the surface layer increased due to entrainment because of upwelling caused by high winds and because the surface layer depth was not too deep. However, they both decrease if the wind stress increases or continues to stay at higher values. The increased surface layer depth caused by persistently higher winds forced the algal community to spend more time in deeper water with reduced light, thereby decreasing the productivity. The second and dominant seasonal peak of the phytoplankton is observed at the end of the dry season when the SE wind diminishes and, subsequently, changes direction, and the surface layer still carrying adequate amounts of nutrients relaxes back to shallower depths. This reflects a trade-off between the availability of nutrients and light. As the density difference between the two layers is decreased, by decreasing t_s, the depth of the surface layer increases and so does the phosphate concentration because of the frequent mixing with bottom nutrient rich water. The peak in the primary productivity linked to the dry season is observed ~ 1 month later. This might be because of the right balance between the surface layer depth and nutrients for

production reached later. Phytoplankton and zooplankton biomasses also show similar behaviour. Increasing t_s from 27 to 28°C, the surface layer depth decreases and so does the entrainment of phosphate. The dry season peaks in the ecological parameters are observed at the same time as for the control run. The peak values of the ecological parameters are not systematically high for all the years for lower surface layer temperature. The year-to-year strength of these peaks depends upon the seasonal winds during that year.

Changes in the surface layer depth

Next, we studied the possible effects of changing surface layer depth by changing the reference depth of the thermocline (Fig. 4). Increasing the reference thermocline depth naturally increased the depth of the surface layer and entrainment of phosphate from below. However, it decreases the primary productivity as the consequence of light limitation (the ratio of mixing depth/euphotic depth increases). The model shows that the effect of increasing the reference depth of the thermocline has a positive effect on zooplankton biomass. The noticeable effect on the time variation in GP, phytoplankton, and zooplankton is the delay in their dry season peaks. As the reference thermocline goes deeper, their seasonal peak is delayed in time by as far as 1 month. This is probably because of the time the displaced surface layer takes to relax to the optimum depth for phytoplankton growth (explained in the next section along with Fig. 6).

Changes in the wind stress

Figure 5 shows the model simulations for varying wind stress for a reference thermocline depth at 30 m and $t_s = 27$°C. The NCEP wind stress is increased and decreased by the factor given in the legends. Deepening of the surface layer by turbulent entrainment is very well seen. The surface layer depth increases as the wind stress is increased. Phosphate concentration in the surface layer follows the surface layer depth as a probable consequence of turbulence and mixing at depth where concentrations of phosphate are higher. Stronger winds are able to upwell water from deeper layers, where the nutrient concentration is higher than in the shallower waters.
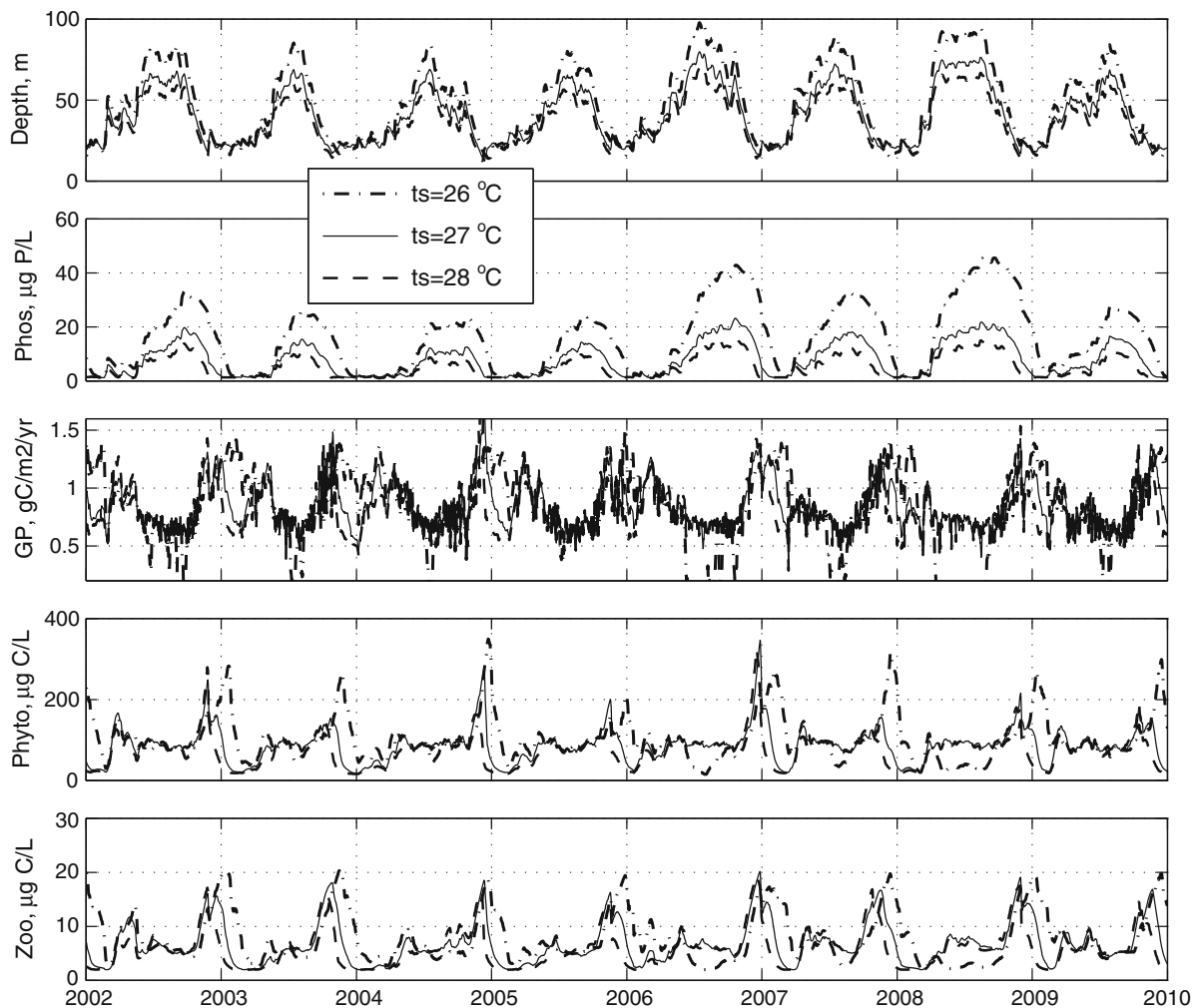
Fig. 3 Time variation of lake averaged parameters for different temperatures of the surface layer for thermocline depth at 30 m over a period of 8 years, from 2002 until 2009

Increasing wind stress delays the seasonal peaks of phytoplankton biomass and zooplankton biomass. For low wind simulations, phosphate becomes limiting for growth.

Changes in the surface layer depth
and its temperature

Figure 6 presents the model simulations for varying thermocline depth and surface layer temperature. Simulations were annually averaged over the whole lake. The 40, 50, and 60 m depth contours are marked. The surface layer depth is greater for lower temperatures than for higher temperatures for the same reference thermocline depth. Similarly, phosphate

concentration increases as the reference thermocline depth increases. Phosphate entrainment increases with deeper surface layer and lower temperature. Lake averaged phytoplankton, on the other hand, is highest with low t_s and shallower thermocline. As the reference thermocline deepens the maximum growth shifts with high t_s. High temperatures and lower thermocline depths are favourable for gross primary production. The Lake averaged light limitation parameter, $F(I)$ also showed similar behaviour to GP, favouring higher temperatures and lower surface layer depths. The zooplankton production, like phytoplankton growth, is favoured at low t_s for a shallower thermocline and high t_s at a deeper thermocline. However, it showed a maximum
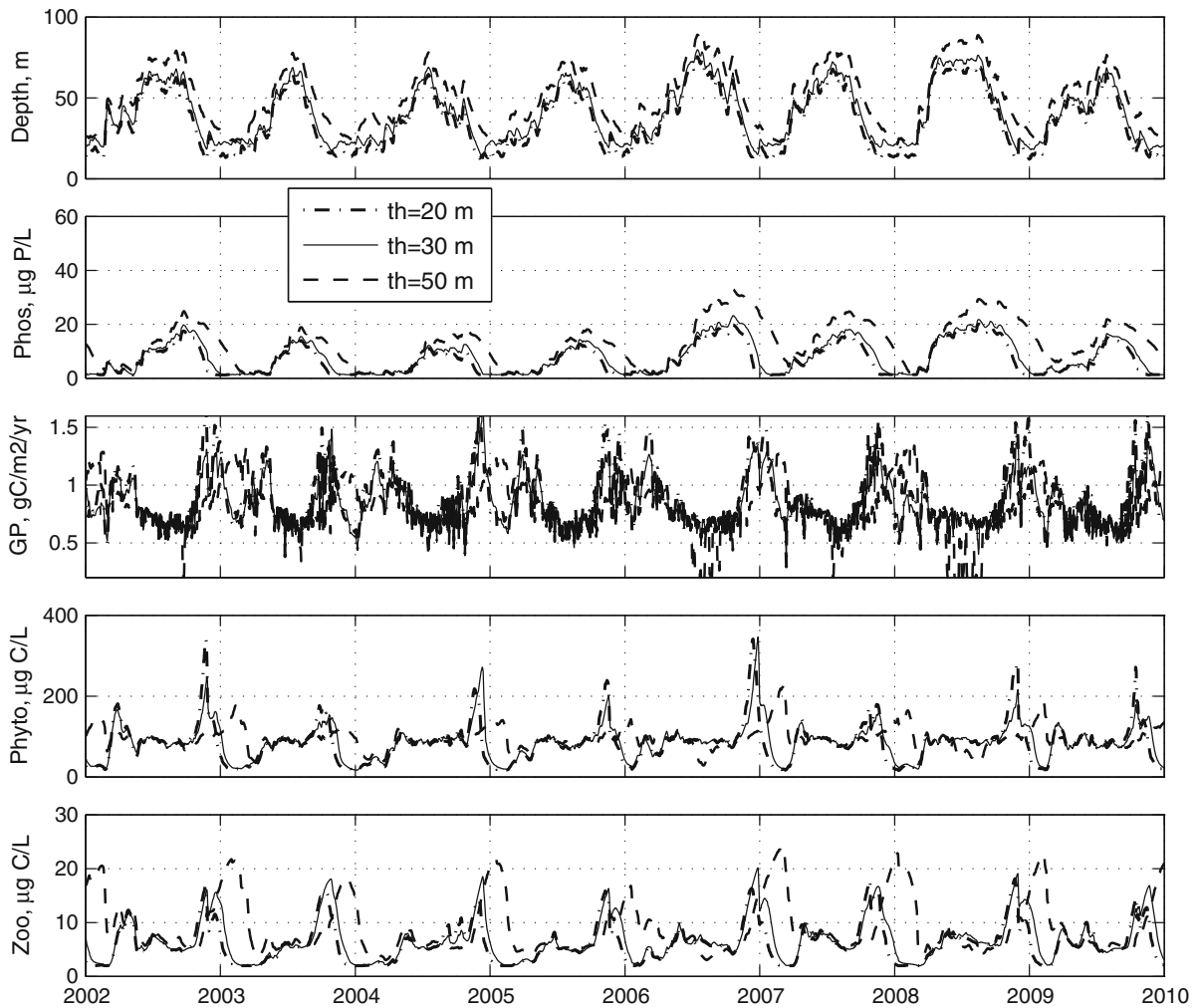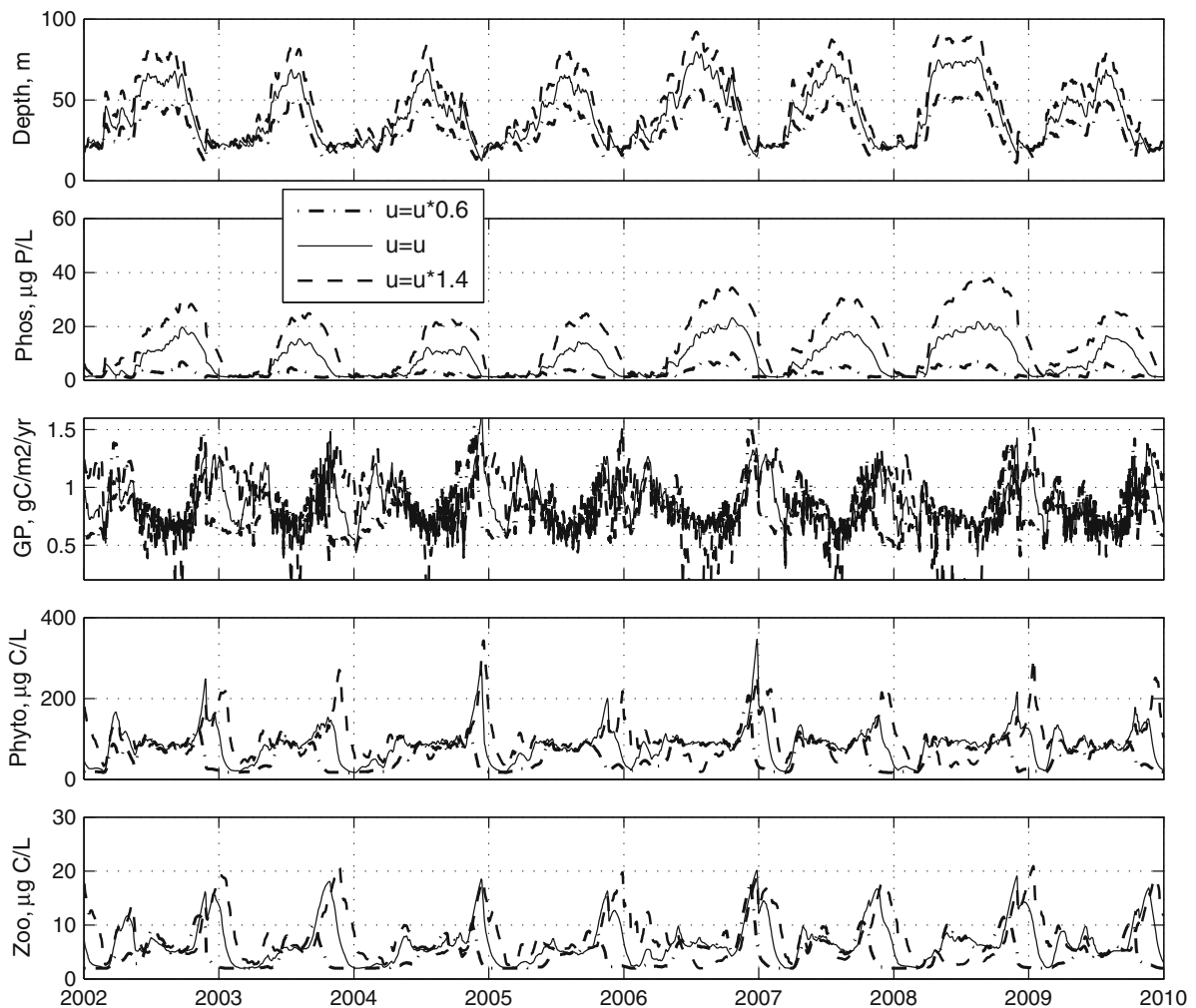
Fig. 4 Time variation of lake averaged parameters for different thermocline depths at a surface layer temperature of 27°C over a period of 8 years, from 2002 until 2009

production for a reference thermocline depth of 50 m and $t_s = 27°C$. It can be seen that the maximum in phytoplankton and zooplankton biomass are mostly concentrated within the surface layer depth of 40 to 60 m.

Changes in the wind stress and the surface layer temperature

Here we will discuss the combined effect of changing wind stress and temperature of the surface layer on the Lake ecosystem (Figs. 7, 8, 9). To do this, we used the NCEP winds for 2002–2009. We increased or decreased them by a certain factor given in the ordinate of these figures. Figures 7, 8, and 9 present

the lake averaged parameters for varying wind stress and t_s, for the reference thermocline at 30, 50, and 70 m, respectively. The surface layer depth and concentration of phosphate increases with high winds and lower temperatures. The phytoplankton growth reaches maximum values at lower wind stress and lower t_s for the reference thermocline at 30 m (Fig. 7). If we increase the wind stress, the phytoplankton growth increases as t_s increases. The growth does not increase monotonically with increasing wind stress or t_s. The maximum growth is seen at 27°C, in spite of increasing stress. A similar trend is seen in zooplankton production. For lower wind stress the gross production is high at lower temperature. Primary production gradually increases with

Fig. 5 Time variation of lake averaged parameters for different wind stress at a thermocline depth of 30 m and surface layer temperature of 27°C over a period of 8 years, from 2002 until 2009

increasing wind stress and higher t_s. The maximum production at highest wind stress is observed at highest t_s. If we move the reference thermocline at 50 m (Fig. 8), the lake averaged phytoplankton show its maximum at high stress and higher t_s. This maximum phytoplankton growth decreases slowly with the combination of lower stress and lower temperatures. Lake averaged zooplankton also show similar behaviour. Taking the reference thermocline further down at 70 m (Fig. 9), shifts the preferred combination of t_s and stress for maximum growth of phytoplankton and zooplankton towards lower stress and higher t_s. In these figures (Figs. 7, 8, 9), once again the maximum in phytoplankton and zooplankton biomass is obtained when the depth of the

surface layer is between 40 and 60 m and the minimum otherwise.

All the above tests are summarised in Tables 2, 3, 4, 5, and 6. These tables present the percentage change in the average (2002–2009) ecological parameters as compared to the control run simulations with any change in the temperature of the surface layer, reference thermocline depth and wind stress. From these tables, it is clear that an increase in temperature will decrease the phytoplankton and zooplankton biomass (Table 2), whereas increasing the thermocline depth will increase it (Table 3). Decreasing wind stress will also have a negative effect on the growth (Table 4). However, the effects of increasing temperature might be mitigated by
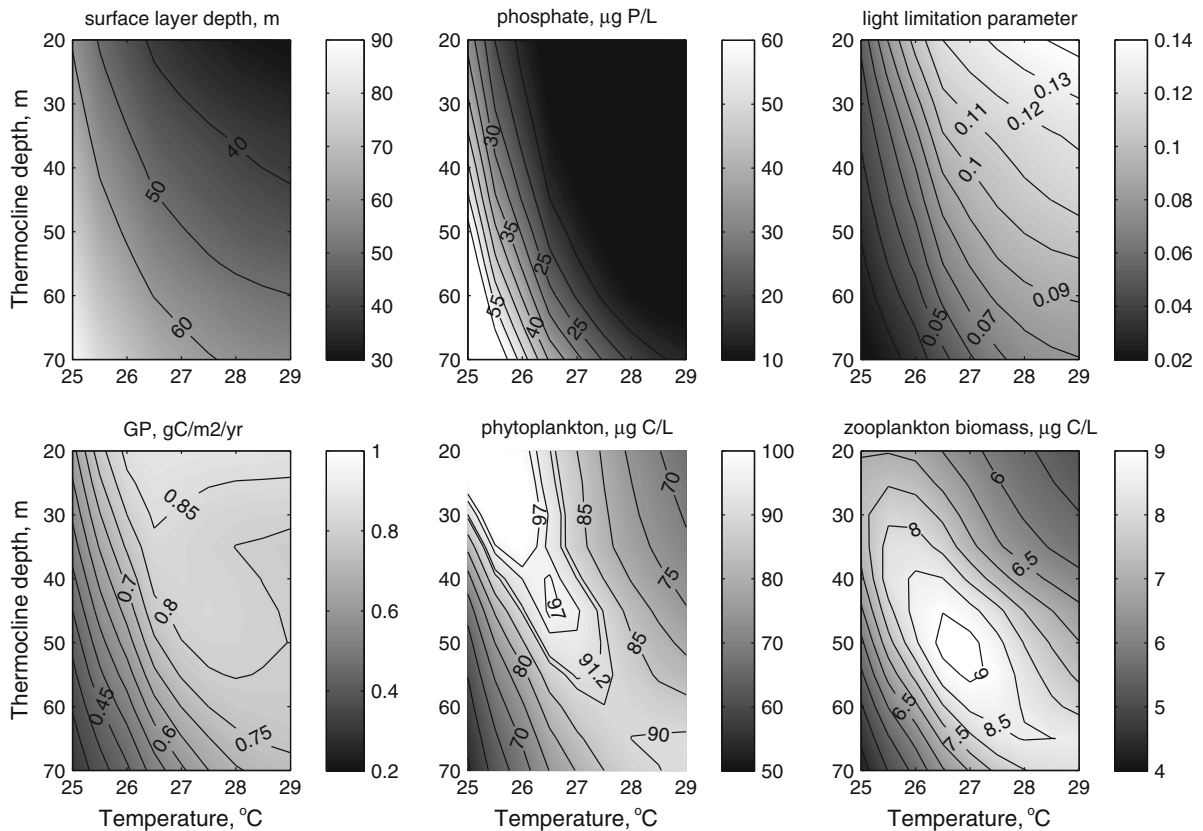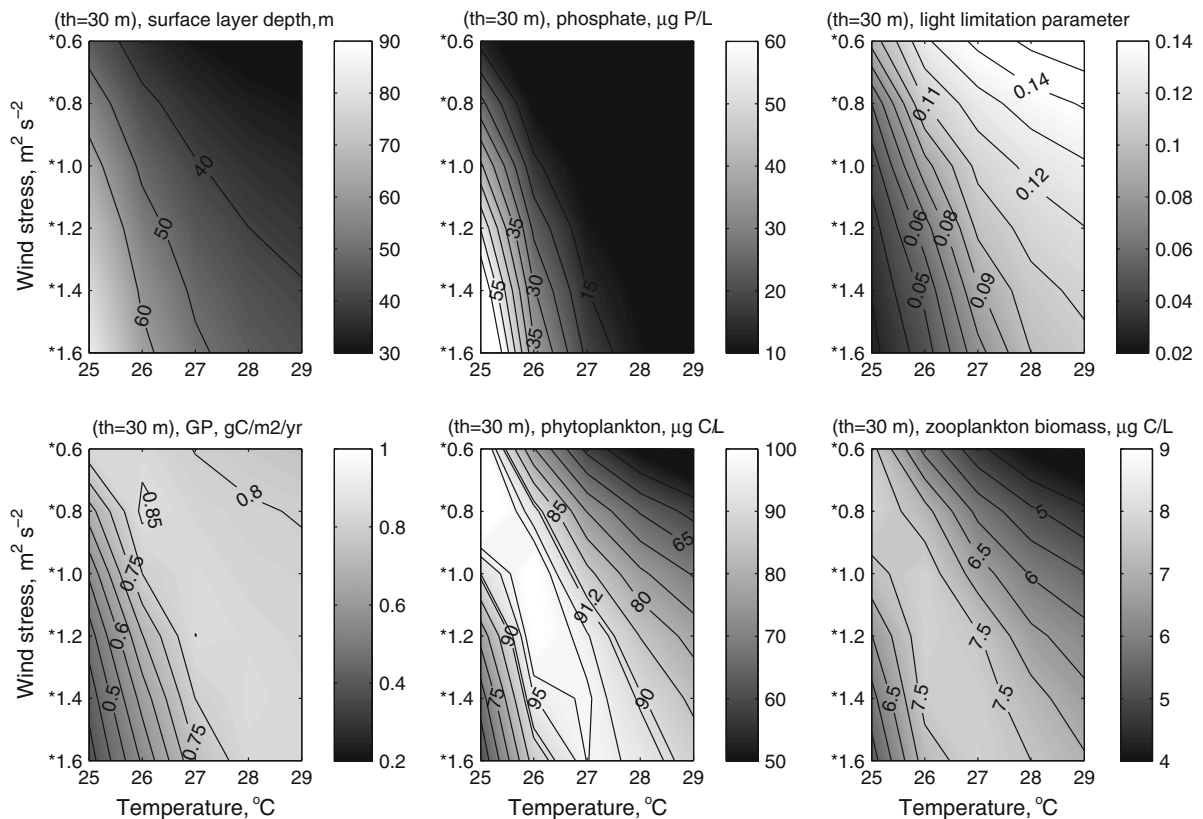
Fig. 6 Lake averaged parameters for various thermocline depths and temperature of the surface layer. In the surface layer depth, the depth contours at 40, 50, and 60 m are marked

increasing winds (Tables 5, 6). This is because high temperatures will result in shallower thermoclines, taking the surface layer away from the nutrient rich deeper water. However, if these high temperatures are accompanied by stronger winds, the resulting wind mixing will bring the nutrients up to the euphotic zone for primary production.

Discussion

This study illustrates how the physical and ecological parameters of Lake Tanganyika might respond to the changes in main climatic parameters. Because of its meromictic nature, the nutrients lie mainly in greater depths. Primary production in the nutrient depleted surface layer depends upon the recycling of nutrients by wind-induced vertical mixing. High temperatures will lead to shallow thermocline depths, thereby

decreasing the mixing probabilities with the nutrient rich bottom water (Schindler et al., 1990; Hondzo and Stefan, 1991, 1993; Stefan et al., 1993; De Stasio et al., 1996; Livingstone, 2003; Verburg et al., 2003; Verburg & Hecky, 2009; Adrian et al., 2009). We can also suppose that the nutrient-rich layer would move together with thermocline. If the latter is shallower, the nutrient rich layer is shallower too and likewise. This is not tested in this study. Since the entrainment of phosphate from the hypolimnion was extrapolated exponentially considering its concentration to be 45 μg P l^{-1} below 60 m depth and 1 μg P l^{-1} near the surface. According to Verburg et al. (2003), the increased density gradient in the water column combined with the extreme depth of the Lake impedes vertical mixing. Lower temperature will lead to deeper lying thermocline thereby forcing the algal community to spend more time in the low light conditions at greater depths.

Fig. 7 Lake averaged parameters for wind stress varying by the factor indicated in the ordinate and temperature of the surface layer, at reference thermocline depth = 30 m. In the surface layer depth, the depth contours at 40, 50, and 60 m are marked

The behaviour of the model-simulated parameters reflects that the dominant components responsible for the phytoplankton biomass in the lake are temperature stratification, availability of light and nutrients. Increasing stratification decreases mixing and entrainment of nutrients from the hypolimnion. At too high light conditions at shallower depths, linked to higher surface layer temperature, the phytoplankton growth was limited by nutrients. At higher nutrient levels at deeper depth, associated with low surface layer temperature, phytoplankton production was limited by light. The most favouring surface layer depth for the biomass production is found to be between 40 and 60 m. This depth seems to be linked to optimal light and nutrients conditions allowing phytoplankton production and an increase in biomass. High winds are important for the supply of nutrients to the euphotic zone in the Lake. They are also linked with increased

internal wave activities and turbulence. This could induce an increased temporal patchiness in the primary production around the shores (short moments when primary production could be very high). So the average seasonal condition should not be considered when investigating phytoplankton growth. But short-term strong wind events could also be important for local blooms in phytoplankton.

It is inferred that a slight increase in temperature will still be bearable for Lake Tanganyika ecosystem and algal production, as long as the wind is strong enough to mix water and bring nutrients from the hypolimnion to the epilimnion. Otherwise, the primary production will decrease. The impact of climate change on the lake is thus not simple and straightforward but rater depends upon the combination of climatic parameters, leading to variable productivity responses by the Lake.
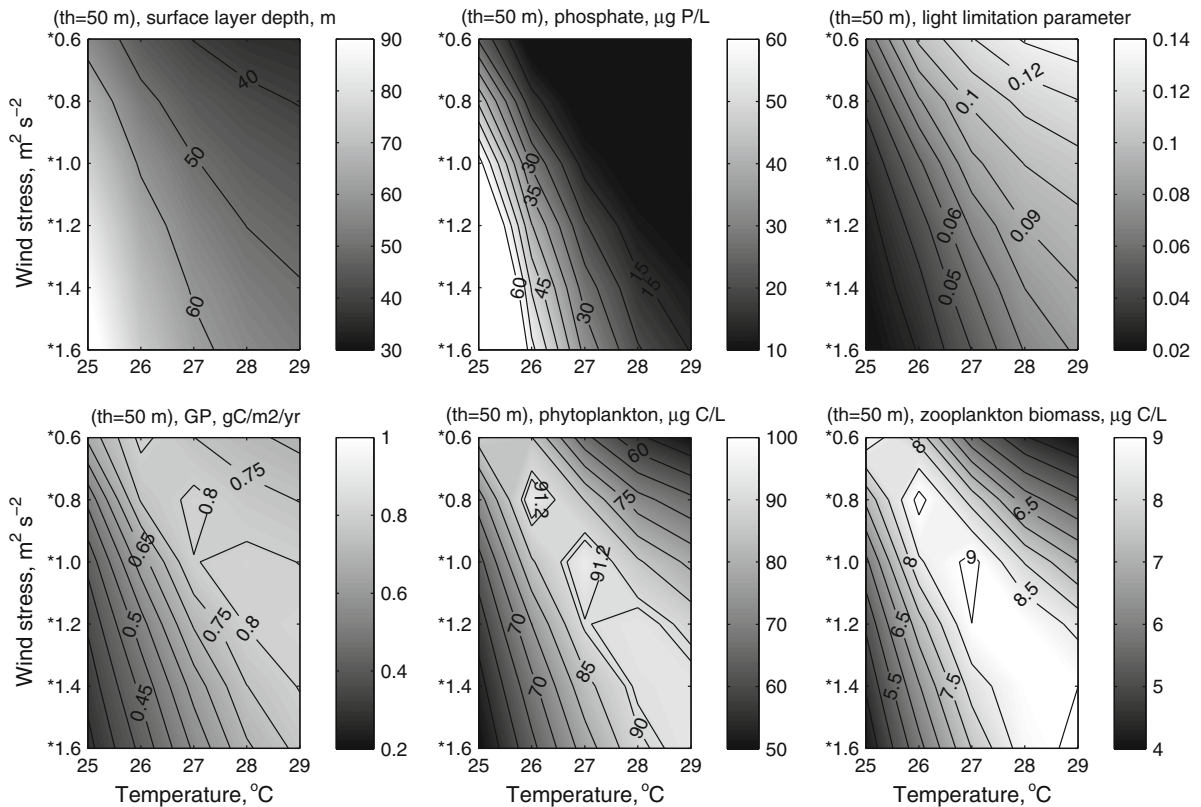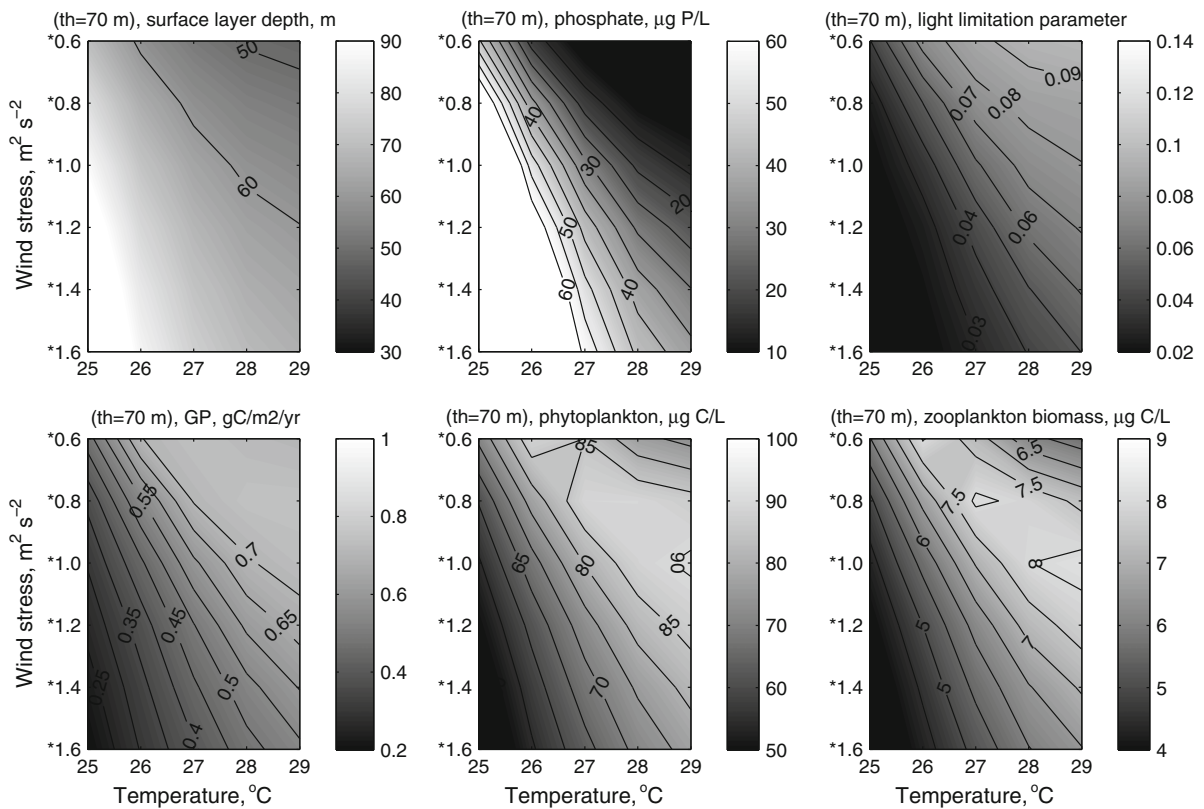
Fig. 8 Same as Fig. 7 for reference thermocline depth = 50 m

Conclusions

This study confirms that the hydrodynamical processes to which the lake ecosystem responds are mainly induced by predominant southeast winds of the dry season and temperature stratification. The transport and mixing events are critical for the re-supply of nutrients for the primary productivity and biogeochemical processes in the stratified lake.

The lake's role in supporting nutritional welfare is critical in a region where fish are estimated to account for up to 40% of total protein supply. According to O'Reilly et al. (2003), Verburg et al. (2003), Verburg & Hecky (2009), and Tierney et al. (2010), there is no doubt that climate changes play a major role in the dynamics and ecosystem of the Lake. O'Reilly et al. (2003) have suggested that the fish yields could decrease by 30% if the primary production decreases by 20%. But is it solely due to climate change or increased pressure from the human population? The question remains in relation to the impact of climate change versus the possible impact of overfishing.

How much is the contribution of each? Lakes can be extremely sensitive to short- and long-term changes in the weather and to the processes that take place in the catchment (Adrian et al., 2009; Carpenter et al., 2007; Pham et al., 2008). According to some other studies, the lake and its resources are seriously threatened by constantly increasing pressure from the human population residing around the lake and its watershed, and from unsustainable aquatic and terrestrial resource exploitation practices (Caljon, 1992; Cohen et al., 1993; Alin et al., 1999; Reynolds & Molsa, 2000; Sarvala et al., 2006; Jorgensen et al., 2006; Kamenya et al., 2008). Jorgensen et al. (2006) has summarized the roles of over-exploitation of the biological resources (because of high fishing pressure and the use of destructive methods), siltation (due to erosion in the drainage area as a result of increased deforestation), untreated wastewater discharges, agricultural runoff, increased population, urbanization and industrialization and global climate change on the Lake. According to them, of the first two threats, over-exploitation is thought to be the most acute for

Fig. 9 Same as Fig. 7 for reference thermocline depth = 70 m

Table 2 Percentage change in lake averaged ecological parameters because of changing surface layer temperature (t_s)

t_s (°C)	26	27	28
Phyto (μg C l^{-1})	15.0	–	−12.5
Zoo (μg C l^{-1})	15.2	–	−12.3

The percentage change in the parameters is calculated as compared to the control run parameters using th = 30 m, t_s = 27°C and NCEP wind stress

Table 3 Percentage change in lake averaged ecological parameters because of changing reference thermocline depth (th)

th (m)	20	30	40	50
Phyto (μg C l^{-1})	−4.0	–	4.4	7.3
Zoo (μg C l^{-1})	−10.0	–	18.0	34.0

Table 4 Percentage change in lake averaged ecological parameters because of changing wind stress by a certain fraction given above

t_s = 27°C, th = 30 m

τ (m^2 s^{-2})	*0.6	*1.0	*1.4
Phyto (μg C l^{-1})	−27.7	–	11.8
Zoo (μg C l^{-1})	−23.1	–	12.9

Table 5 Percentage change in lake averaged ecological parameters because of changing wind stress and increased temperature

t_s = 28°C, th = 30 m

τ (m^2 s^{-2})	*0.6	*1.0	*1.4
Phyto (μg C l^{-1})	−40	−14.0	2.0
Zoo (μg C l^{-1})	−34	−12.5	−0.2

short-term fishery potential, while siltation is the most detrimental factor affecting the lake's biodiversity and long-term potential. Ogutu-Ohwayo et al. (1997) have documented similar human impacts on

the African Great Lakes. Sarvala et al. (2006) reported that the purse seine fishery catch per unit effort in Lake Tanganyika has declined steeply since

Table 6 Percentage change in lake averaged ecological parameters because of changing wind stress along with increased temperature and reference thermocline depth

$t_s = 28°C$, th $= 50$ m			
τ (m^2 s^{-2})	*0.6	*1.0	*1.4
Phyto (μg C l^{-1})	−29.55	0.02	1.32
Zoo (μg C l^{-1})	−18.9	24.8	21.9

1985 (possibly) as the result of an increase in fishing effort by other fishing technologies, and, thus, high fishing pressure.

A change in the climate can certainly effect the production of the Lake, as can increasing the human population, which depends on the Lake for many of its activities (food, water, transport, etc.). Whatever the cause, the situation should not be allowed to deteriorate further. Better ways and means should be devised for the sustainable use of its resources for the benefit of the population depending directly upon it. The new Lake Tanganyika Authority will require increased information in this field to allow it to take appropriate measures for the sustainable management of Lake Tanganyika resources for the people as well as for the preservation of this important site of the world for the bio-diversity.

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