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TANGANYIKA LAKE, MODELING THE ECO-HYDRODYNAMICS

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Introduction

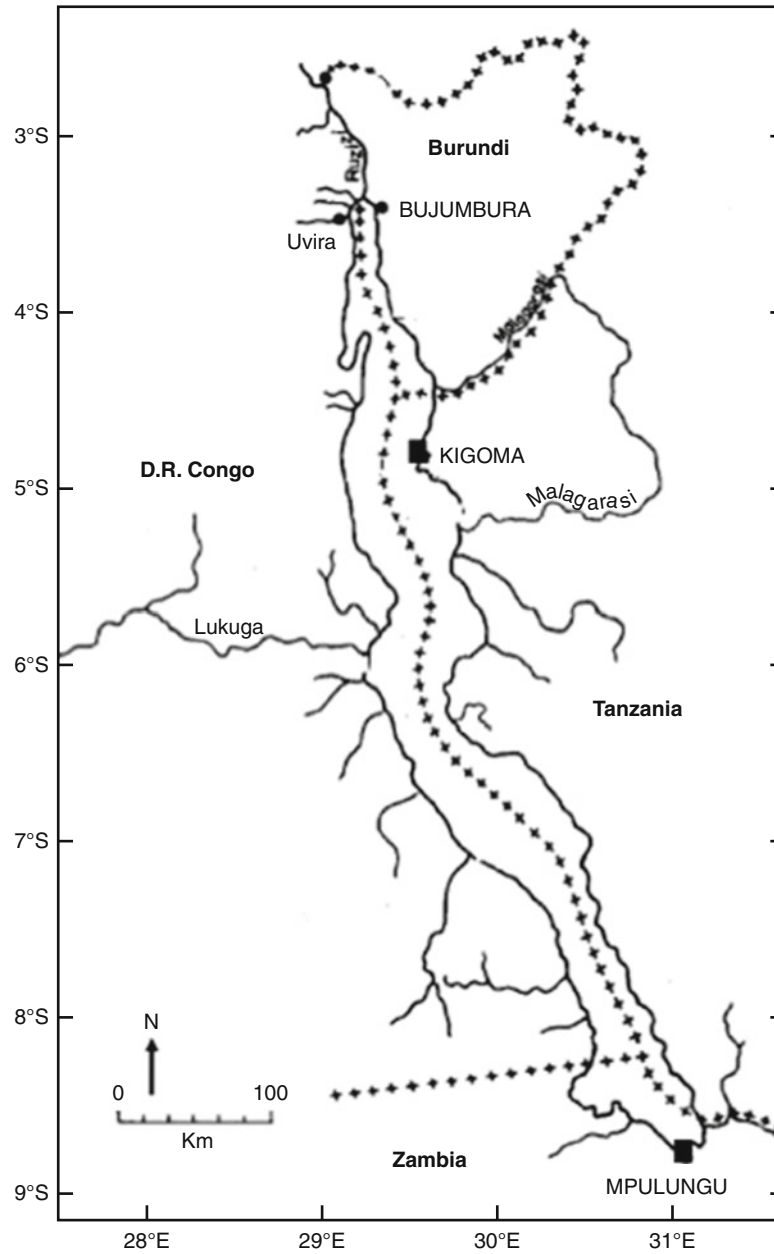
Lake Tanganyika is one of the Great Rift Valley Lakes of East Africa (Figure 1) and is situated between 3°S and 9°S. It is 650 km long with a mean width of around 50 km and an average depth of 570 m. It is a freshwater Lake characterized by a quasi-permanent thermocline. The Lake is meromictic – complete overturning of the water never takes place – and mixing occurs only partially. The epilimnion (surface layer) undergoes seasonal temperature change annually, while the hypolimnion is anoxic with an invariant temperature. The hypolimnion is a vast reservoir of nutrients largely isolated from surface influences (Hecky and Fee, 1981; Hecky et al., 1991). The average transparency of the Lake is close to 11 m. The solar radiation around the Lake varies very little in the year because of its closer proximity to the equator. The nutrients supplied to the mixed layer, where photosynthesis can occur, are mainly internal nutrients from within the Lake, whereas riverine and atmospheric input of nutrients is considered negligible for Lake Tanganyika (Hecky and Fee, 1981; Sarvala et al., 1999a; Langenberg et al., 2003a). Nutrients from the hypolimnion are supplied to the epilimnion mainly by wind-driven upwelling of the strong southeast winds during the dry season from March/April

until August/September (Hecky et al., 1991; Plisnier et al., 1999; Langenberg et al., 2003b). The wind stress pushes the warmer surface water away from the southern end of the Lake toward the northern end, resulting in a well-known compensating upwelling in the south. This upwelling results in the seasonal enhancement of the nutrients in the euphotic layer initiating phytoplankton blooms. Apart from this major wind-induced southern upwelling, small coastal upwellings can also be seen from time to time propagating clockwise around the western boundaries of the lake, which are the internal Kelvin wave packets (Naithani and Deleersnijder, 2004). During the wet season, the primary production is less important and is primarily dependent on the nutrients regenerated within the epilimnion (Coulter and Spigel, 1991).

The above mentioned thermodynamic, hydrodynamic, and ecological characteristics are incorporated into an eco-hydrodynamic model to study the primary food web of Lake Tanganyika. The hydrodynamic model comprises nonlinear, reduced-gravity equations (Naithani et al., 2002, 2003). The ecological model components include one nutrient, phytoplankton biomass, zooplankton biomass, and detritus (Naithani et al., 2007a, b, 2011).

Materials and method

The model consists of a four-component ecosystem model, coupled to a hydrodynamic model. The hydrodynamic model considers the Lake as two homogeneous layers of different density lying above each other, 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. Studies using the hydrodynamic model have shown that in the motion of water there are internal waves with oscillations similar to that in the forcing



Tanganyika Lake, Modeling the Eco-hydrodynamics, Figure 1 Geographic map of Lake Tanganyika.

winds (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 hydrodynamic model equations are:

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

$$w_e = \left(\frac{3}{20}\right)^{1/2} \frac{(\tau_x^2 + \tau_y^2)^{1/2}}{(\varepsilon g H)^{1/2}} - w_d - \frac{\zeta}{r_u} \quad (2)$$

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

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

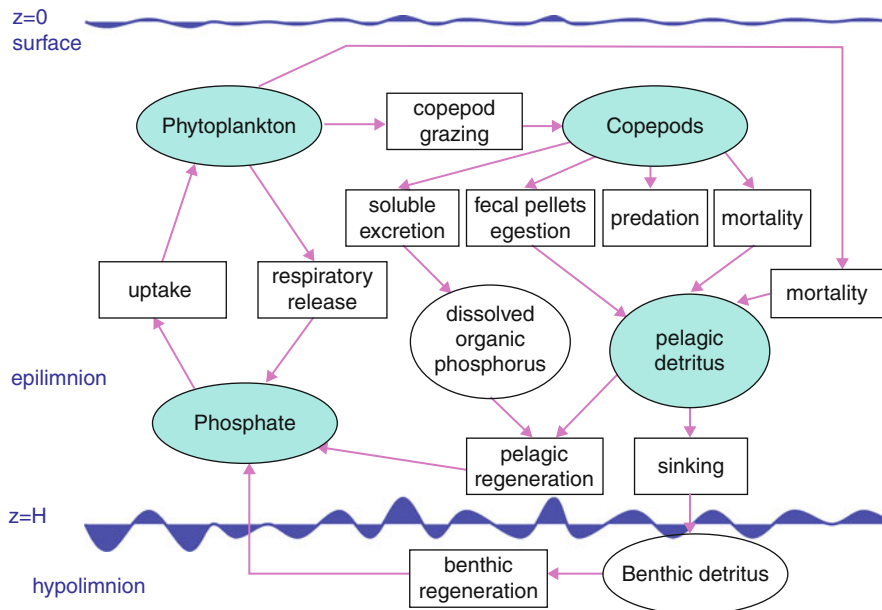
where x and y are horizontal axes, u and v are the depth-integrated velocity components in the surface layer in the x and y directions, t is the time, x is the downward displacement of the thermocline, $H = h + \xi$ is the thickness of the epilimnion (the surface, well-mixed layer), h is the reference depth of the surface layer (m), and w_e is the entrainment velocity (ms^{-1}). The first term on the right hand side of Equation 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^2s^{-2}), and $\varepsilon = (\rho_b - \rho_s)/\rho_b$ 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 (ms^{-1}), 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. f is the Coriolis factor (<0 in the southern hemisphere), and A_s is the horizontal eddy viscosity in the $s (=x,y)$ direction.

The ecosystem model (Figure 2) consists of dissolved phosphorus (*Phos*), phytoplankton (*Phyto*), zooplankton (*Zoo*), and detritus (*Detr*) (Naithani et al., 2007b). Phosphorus was the only nutrient simulated in the model to trigger phytoplankton growth (Järvinen et al., 1999). The phytoplankton processes include primary production (*PROD*), respiration (*RESP*), and mortality (*MORT_d*). The processes concerning the zooplankton are grazing (*GRAZ*), fecal pellet (*FEC*) egestion, excretion (*EXC*), and mortality (*MORT_z*). Phytoplankton respiratory release and the excretion from zooplankton are directly remineralized in the surface layer. A small percentage of feces, dead phytoplankton, and zooplankton are also remineralized into phosphate in the surface layer whereas the rest contributes to the detritus pool, which sediments fast. The regeneration/remineralization within the surface layer represents the effect of the microbial food web and also represents the pelagic regeneration. The model is closed by predation (*PRED*) from zooplanktivorous fish and sinking of detritus out of the surface layer. The zooplanktivorous fish biomass is assumed equal to that of zooplankton biomass (Sarvala et al. 1999a).

The ecosystem model equations are:

$$\begin{aligned} \frac{\partial(HPhyto)}{\partial t} = & -\frac{\partial(HuPhyto)}{\partial x} - \frac{\partial(HvPhyto)}{\partial y} \\ & + \frac{\partial}{\partial x} \left(HK_x \frac{\partial Phyto}{\partial x} \right) + \frac{\partial}{\partial y} \left(HK_y \frac{\partial Phyto}{\partial y} \right) + \phi_{he} \\ & + H\{PROD - RESP - MORT - GRAZ\} \end{aligned} \quad (6)$$

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



Tanganyika Lake, Modeling the Eco-hydrodynamics, Figure 2 Flow diagram of the ecological parameters considered in the model.

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

$$MORT_a = m_a Phyto \quad (9)$$

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

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

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

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

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

$$\begin{aligned} \frac{\partial(HZoo)}{\partial t} = & -\frac{\partial(HuZoo)}{\partial x} - \frac{\partial(HvZoo)}{\partial y} \\ & + \frac{\partial}{\partial x} \left(HK_x \frac{\partial Zoo}{\partial x} \right) + \frac{\partial}{\partial y} \left(HK_y \frac{\partial Zoo}{\partial y} \right) + \phi_{he} \\ & + H \{ GRAZ - EXC - FEC - MORT_z - PRED \} \end{aligned} \quad (15)$$

$$EXC = n_e GRAZ \quad (16)$$

$$FEC = n_f GRAZ \quad (17)$$

$$MORT_z = m_z GRAZ \quad (18)$$

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

$$\begin{aligned} \frac{\partial(HPhos)}{\partial t} = & -\frac{\partial(HuPhos)}{\partial x} - \frac{\partial(HvPhos)}{\partial y} \\ & + \frac{\partial}{\partial x} \left(HK_x \frac{\partial Phos}{\partial x} \right) + \frac{\partial}{\partial y} \left(HK_y \frac{\partial Phos}{\partial y} \right) \\ & + \phi_{he} + H \left\{ \frac{-(PROD - RESP)}{CP_a} + \left(\frac{p_a MORT_a}{CP_a} \right. \right. \\ & \left. \left. + \frac{(p_f FEC + p_z MORT_z + EXC)}{CP_z} \right) \right\} \end{aligned} \quad (20)$$

$$\begin{aligned} \frac{\partial(HDetr)}{\partial t} = & -\frac{\partial(HuDetr)}{\partial x} - \frac{\partial(HvDetr)}{\partial y} \\ & + \frac{\partial}{\partial x} \left(HK_x \frac{\partial Detr}{\partial x} \right) + \frac{\partial}{\partial y} \left(HK_y \frac{\partial Detr}{\partial y} \right) + \phi_{he} \\ & + H \{ (1 - m_p) MORT_a + (1 - p_f) FEC \\ & + (1 - p_z) MORT_z - r_d Detr \} - w_d Detr \end{aligned} \quad (21)$$

The first four terms on the right hand side of Equations 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, and K_x and K_y are the horizontal

diffusion coefficients. The fifth term represents entrainment from hypolimnion. Entrainment of phosphate from the hypolimnion was extrapolated exponentially from $45 \mu\text{gPL}^{-1}$ below 60 m depth to $1 \mu\text{gPL}^{-1}$ near the surface (Coulter and Spigel, 1991; Plisnier et al., 1996; Plisnier and Descy, 2005). This ensured that the water is richer in nutrients if upwelling occurs from deeper depths. The definition of the parameters and their values are given in Table 1. Model was run with the thermocline at 30 m and the temperature of the surface and lower layers as 27°C and 24.5°C , respectively for the years 2002–2009.

Results and discussion

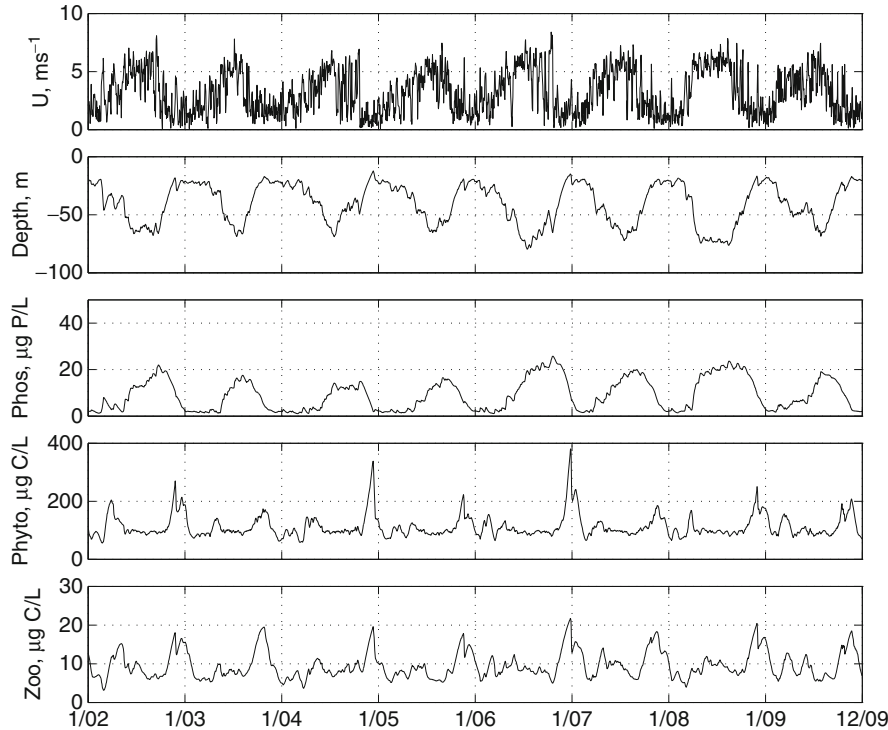
Figure 3 shows the time series of wind speed, model predicted surface layer (epilimnion) depth, and the depth-averaged concentration in the surface layer of phosphate, phytoplankton biomass, and zooplankton biomass. The surface layer depth increases at the beginning of the dry season because of wind driven mixing and remains at greater depth during the whole season. It decreases at the end of the dry season and remains more or less at this depth during the wet season until the beginning of the next dry season. Phosphate concentration closely follows the mixed layer depth. It increases because of entrainment associated to the upwelling of nutrients from below and remains high for the rest of the dry season, because of almost continuous upwelling, and decreases at the end of the dry season. Increase in the biomass of phytoplankton at the beginning of the dry season is natural because of the input of nutrients in the surface layer. However, the phytoplankton biomass cannot sustain at this high value and decreases in spite of the continuous abundance of nutrients. 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. Phytoplankton biomass shows another bloom 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 (Plisnier et al., 1999). Phytoplankton biomass in effect showed a trade-off between the availability of nutrients and light. Negative effects of deep mixing on the phytoplankton biomass were also considered by Sarvala et al. (1999b).

Effect of changing the model ecological parameters

Increasing (decreasing) the half-saturation constant for grazing decreased (increased) the zooplankton biomass and increased (decreased) phytoplankton biomass (Naithani et al., 2007a). The change in the phytoplankton biomass is almost half the change in the zooplankton biomass. Decreasing the predator population increases the zooplankton biomass and vice versa. For these tests with the predator population the change in the phytoplankton biomass is much less than the change in the zooplankton biomass. It is seen that the primary production, which

Tanganyika Lake, Modeling the Eco-hydrodynamics, Table 1 Governing parameters, their description, value, and units used in the model

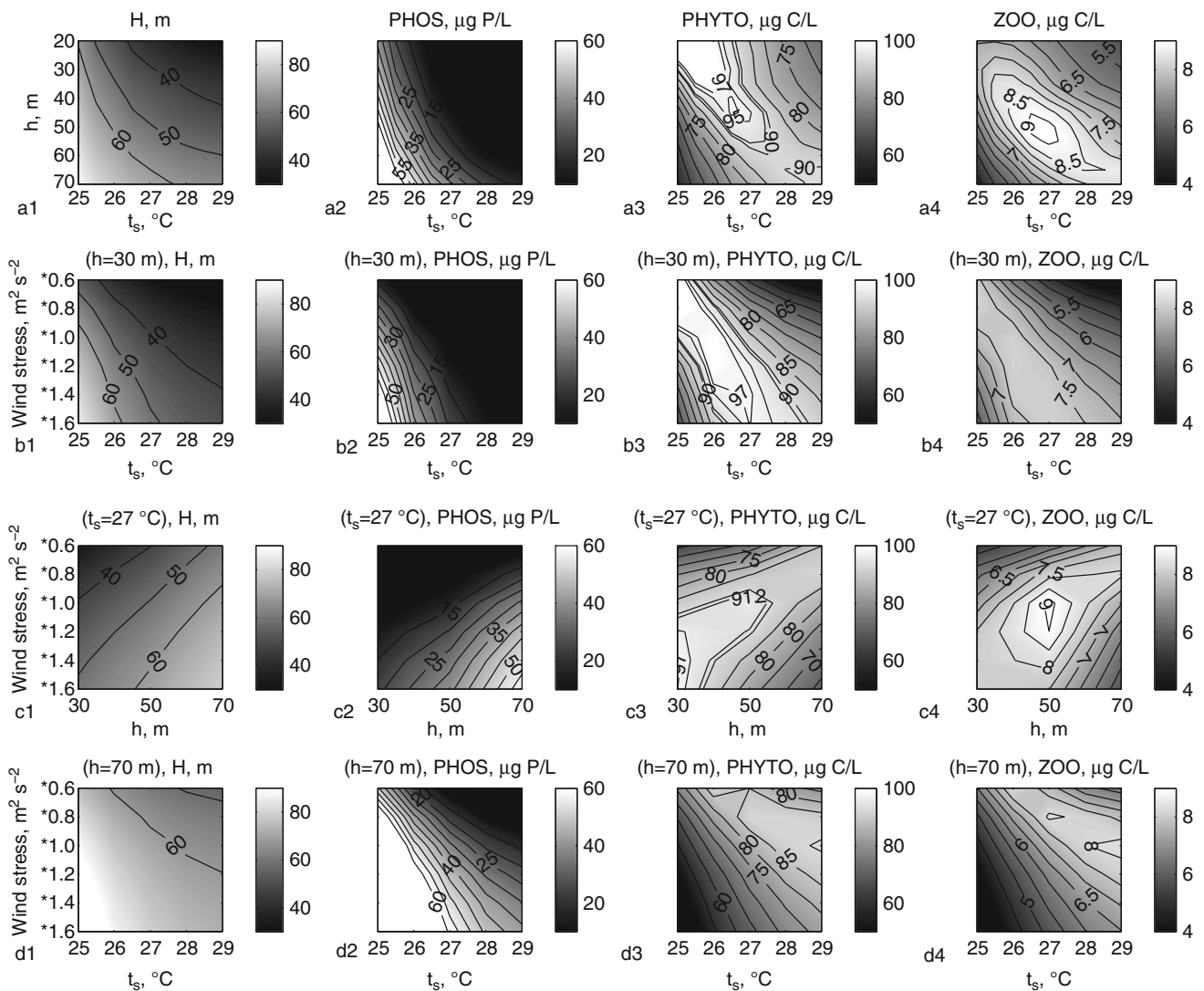
Symbol	Parameter	Value	Unit
α	Coefficient accounting for the photosynthetic activity	0.56	–
CP_a	C/P ratio of phytoplankton	58.1	–
CP_z	C/P ratio of zooplankton	77.42	–
I_o	Incident light radiation at the air-water interface	Variable	$\mu\text{E m}^{-2}\text{s}^{-1}$
I_k	Light saturation constant	375	$\mu\text{E m}^{-2}\text{s}^{-1}$
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/Chla 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 sec^{-1}
ZOO_{min}	Zooplankton threshold for grazing	2.0	$\mu\text{g C L}^{-1}$

**Tanganyika Lake, Modeling the Eco-hydrodynamics, Figure 3** Time variation of the Lake averaged parameters over a period of 8 years, from 2002 until 2009.

strongly depends upon the light in the water column and entrainment of nutrients, is bottom-up controlled, while it seems that predator abundance strongly controls zooplankton biomass (top-down control, Naithani et al., 2007a). By contrast, fish predation influence seems reduced on the phytoplankton level. In other words, any change in predator biomass significantly affects the herbivore biomass, but has little influence on phytoplankton biomass. Indeed, in our simulations, reduced grazing pressure from top-down control of mesozooplankton did not increase phytoplankton abundance considerably. In planktivore-dominated Lake Tanganyika, zooplankton are not able to control phytoplankton, and therefore, light or nutrient limitation and resource competition seem to be common among the latter (Järvinen et al., 1999).

Effect of changing the physical parameters

Various tests of the model using different physical parameters (thermocline depth, surface layer temperature, and wind velocity) are summarized in Figure 4. Any change in these physical forcing parameters modifies the timing and intensity of the dry season blooms of the biogeochemical parameters (Naithani et al., 2011). Increasing t_s or the wind stress delays the phytoplankton peak. Increasing the reference thermocline depth (h) increases the entrainment of phosphate from below and decreases the phytoplankton biomass. Increasing/decreasing the surface layer temperature decreases/increases the depth of the upper mixed layer and the entrainment of phosphate (Naithani et al., 2011). This decreases the phytoplankton biomass. The phytoplankton growth is favored at low t_s for a shallower



Tanganyika Lake, Modeling the Eco-hydrodynamics, Figure 4 Lake averaged parameters for various h and t_s (a1–a4), for wind stress varying by the factor indicated in the ordinate and t_s , at $h = 30$ m (b1–b4), for various wind stress and h (c1–c4), and for various wind stress and t_s , at $h = 70$ m (d1–d4).

thermocline and high t_s at a deeper thermocline. Increasing wind stress favors phytoplankton production because of deeper mixing.

An increase in temperature will decrease the phytoplankton and zooplankton biomass. This is because high temperature will result in shallower thermoclines, thereby decreasing the mixing probabilities with the nutrient-rich bottom water (Livingstone, 2003; Verburg et al., 2003; Verburg and Hecky, 2009). 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. Decreasing wind stress also has a negative effect on the growth. However, if these high temperatures are accompanied by stronger winds, the resulting wind mixing will bring the nutrients up to the euphotic zone allowing a greater primary production.

Conclusions

The behavior 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. Primary production in the nutrient-depleted surface layer depends upon the recycling of nutrients by wind-induced vertical mixing. The transport and mixing events are critical for the resupply of nutrients for the primary productivity and biogeochemical processes in the stratified lake. 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. Inversely, at higher nutrient levels at deeper depth, associated with low surface layer temperature, phytoplankton production was limited by light. The most favoring surface layer depth for the biomass production was found to be between 40 and 60 m (Figure 4). This depth seems to be linked to optimal light and nutrient conditions allowing phytoplankton production and an increase in its 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 (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 can be inferred that a slight increase in temperature will still be bearable for Lake Tanganyika ecosystem, 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.

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TANGANYIKA LAKE: STRONG IN HYDRODYNAMICS, DIVERSE IN ECOLOGY

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Introduction

Lake Tanganyika (Figure 1) is one of the few ancient lakes in the world (estimated age 9–12 million years; Cohen et al., 1993). It is the second in size of the African Great Lakes and also second in depth among lakes in the world. It locates at an altitude of 773 m above m.sl. The drainage area is 263 000 km². The lake is 650 km long and 50 km wide in average. It has three main basins. In the north, the Kigoma basin extends to the depth of 1,310 m. The middle basin is separated from the Kigoma basin by a broad sill with a depth of 655 m, and in the south, from the Kipili basin by another sill with a depth of 700 m. The basin near Kipili is the deepest of the three basins, its maximum depth being 1,470 m. The lake is meromictic with stable hypolimnetic waters, and the salt content is low for this type of lake (Coulter, 1991).

The early studies from the beginning of the last century have been summarized by Coulter (1991). Later, a Belgian exploration in 1946–1947 proved the existence of internal waves in the thermocline as they measured the lake water temperature. Another result of the same expedition was the first bathymetric chart of the lake by Figure 1. In the late 1950s, Dubois collected the first depth-time series of temperature and oxygen data. In the early 1960s, Coulter (1963) continued the studies in the south, and later on, in 1973–1975, in the northern part of the lake.

Lake Tanganyika was studied intensively during 1990s as part of the Lake Tanganyika Research for the Management of Fisheries (LTR) by FAO and also as part of Lake

Tanganyika Biodiversity Project/LTBP by UNDP/GEF (www.fao.org/fi/ltr (LTR) and <http://www.ltbp.org/> (LTBP)). Water level fluctuations and meteorological data were collected at Bujumbura (Burundi), Kigoma (Tanzania), and Mpulungu (Zambia). Limited meteorological observations were conducted also in Uvira (DR Congo), Kalemie (DR Congo), and Kipili (Tanzania). Data on the thermal regime of the lake waters were collected with two moored buoy stations and also with a CTD-profiler near field stations, as well as from the research vessel during the expeditions. Data on water currents were collected with flow cylinders, which were used intensively near the field stations and also on lake-wide expeditions. During LTBP, also acoustic Doppler current profilers (ADCP) were used both on board and at moored stations.

Later four Finnish universities have arranged several field courses in Kigoma, Tanzania.

The CLIMLAKE “Climate Variability as Recorded by Lake Tanganyika,” funded by the Belgian Science Policy, included a 3-year survey of the lake over the period 2002–2004. Also hydrodynamic and ecological models were developed for the lake. The aim of the project was to understand the Lake Tanganyika variability and sensitivity to climate change. Another Belgian project, CLIMFISH was active in years 2004–2006.

Meteorological conditions

There are two main seasons with different weather conditions within the yearly cycle in the Lake Tanganyika region. The wet season from October to April is characterized by weak winds over the lake, high humidity, considerable precipitation, and frequent thunderstorms (Figure 2). The dry season from May until the end of August is characterized by little precipitation and strong, regular southerly winds. The seasonal changes of weather and winds result from large-scale atmospheric processes, especially of the position of the global tropical wind convergence zone.

The diurnal cycle of winds is also well developed in Tanganyika region. The studies of Savijärvi (1995 and 1997) and Podsetchine et al. (1999) revealed that the mountain slopes contributed about 50% and the trade winds 25% to the diurnal variation of winds. The rest 25% of the wind variation was due to the lake effect. The SE trade wind enhances the lake breeze considerably at daytime and adds on the downslope winds at nighttime.

Thermal regime

The seasonal thermal regime of the lake has been discussed by Capart (1952), Coulter (1963, 1991), Huttula (1997), Plisnier et al. (1999), Langenberg et al. (2002), Verburg et al. (2003), and Verburg and Hecky (2009).

Heating of the lake takes place mainly in the beginning of the wet season in October–November (Coulter, 1991; Huttula, 1997). Thermal stratification prevails all over the lake. The thermocline is situated at the depth of