Ecosystem of Lake Tanganyika

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Abstract

The ecosystem response of Lake Tanganyika is studied using a four-component (Nutrient Phytoplankton Zooplankton Detritus, NPZD) phosphorus-based ecosystem model coupled to a non-linear reduced-gravity circulation model. The ecosystem model estimates the annual primary production of Lake Tanganyika and its spatial and temporal variability. The simulations are driven with the National Centres for Environmental Protection (NCEP) model’s wind and solar radiation forcing. The simulated annual cycles of the four ecosystem variables and the daily net primary production are compared with the observations. The comparisons show that simulations reproduce realistically the general features of the annual cycles of upper layer depth, phosphate, net primary production and plankton dynamics. The climatic simulations for the years 1970 through 2004 yield an integrated upper layer net production ranging from 317 and 432 g C m⁻² yr⁻¹ (0.87-1.18 g C m⁻² d⁻¹). The simulated mean net primary production for Lake Tanganyika for the whole period is 366.43 g C m⁻² yr⁻¹ (1.09 g C m⁻² d⁻¹). Although the nutrient levels in the epilimnion during the strong wind years are high, the net production is low which is partly because of the greater vertical mixing, produced by strong winds, exposing the phytoplankton to low light conditions at deeper waters. The simulated annual net production agrees quite well with observed production available in the literature. It is envisaged to use this model to predict the future scenarios of primary productivity of the lake.

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° to 9°S (Figure 1). It plays a vital role in the economy and food source of the surrounding riparian nations. 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 and Spigel, 1991]. The water temperature in the lake varies from 24-28°C in the surface layer to around 23.5°C in the bottom layer. The main seasons around the lake are a four-month long 'dry season', characterised by cooler dry weather and fairly constant southeasterly (trade) winds from around May to September, and a 'wet season' during the rest of the year, during which the winds are weaker and mainly from northeaster (Coulter and Spigel, 1991). Wind speed during the dry season reaches 7-9 m/sec with gusts of 10-12 m/sec. The wind stress pushes the warmer surface water away from the southern end of the lake towards the northern end and an upwelling occurs to replace the loss of water at the south.

Lake Tanganyika is long been recognized for its southern upwelling in direct response to the prevailing southeast winds of the dry season. In Lake Tanganyika the growth of phytoplankton is generally nutrient limited. It is like the ocean where most of the nutrients are in the deep water, and nutrient supply to the mixed layer, where photosynthesis can occur, is dependent on vertical mixing processes (Coulter and Spigel, 1991). The physical process mainly responsible for injecting nutrients into the upper layer from below is the vertical mixing processes caused by high winds. The entrainment of nutrient rich cold bottom water, during upwellings, into the upper layer generates phytoplankton bloom. Climate warming, through increased water density gradients, has apparently slowed vertical mixing, reduced exchange rates between shallow and deep water and reduced primary production in Lake Tanganyika (Verburg et al., 2003). Knowledge of primary productivity from the lake 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 and Kling, 1981; Langenberg, 1996; Salonen et al., 1999; Sarvala et al., 1999; Cocquyt and
Vyverman, 2005; Descy et al. 2005). Use of numerical modelling will improve the understanding of the spatial and temporal distribution of nutrients and primary productivity of the Lake.

The aim of this research is to simulate the biological and chemical processes of the plankton system that are important to understand the estimates of annual primary productivity of the lake and the amount of carbon that will be available to higher trophic levels in the lake. The carbon transfer efficiency of Lake Tanganyika from primary production to fish production is as high as the most efficient marine fisheries (Hecky et al., 1981). These estimates can further be used to study the sensitivity of lake ecosystem to past and future climate variability and change.

Modelling of Lake Tanganyika ecosystem has been previously reported using a three-component Nutrient Phytoplankton Zooplankton (NPZ) model coupled to a hydrodynamic model –ECOH model (Naithani et al., 2006). The hydrodynamic model is based on non-linear reduced-gravity equations with entrainment included. In this work the model is improved by incorporating a detritus pool and better parameterization of ecosystem processes. Theoretically the ecosystem model can be further improved by the addition of several species of phytoplankton and zooplankton, and by including a complete microbial loop. However, all this complexity and increasing number of components will require increasing number of model parameters needed to describe the ecosystem. For Lake Tanganyika the knowledge of most of these parameters is poor and specifying appropriate value is a difficult task. This would also increase the number of observations and measurements needed to properly calibrate the model. For this reason the model is kept as simple as possible. The river inputs have not been considered in the present ecosystem model. In Lake Tanganyika pelagic ecosystem accounts for most of the production of organic Carbon in the lake (Hecky and Fee, 1981). The great volume of Tanganyika together with its relatively arid climate limits the direct effect that river inflows can have on the pelagic system as the water turnover time based on river inflows is about 1000 years (Hecky, 1978). This reduces the immediate influence of the watershed just as the pelagic ocean is little affected by annual riverine inputs (Coulter and Spigel, 1991 page 90).

The aim of this paper is to simulate the annual primary productivity of the Lake under actual circulation and solar radiation and to compare model generated regional patterns to observations, and to study the climatic influences on lake ecosystem since the year 1970.

The model
The circulation model is the modified version of the non-linear, two-layer, reduced-gravity model developed for Lake Tanganyika and used in earlier studies (Naithani et al. 2002; 2003; Naithani and Deleersnijder, 2004). The complete model is described in Naithani et al., 2006 and Naithani, Plisnier and Deleersnijder, 2006). The phytoplankton and zooplankton are represented by one state variable each. Phosphorus is the only nutrient to trigger phytoplankton bloom. The water column dynamics is implemented so that the ecosystem variables are transported by advection and diffusion. The model includes the primary production, remineralization within the upper layer, and sedimentation of detritus. Phytoplankton is utilised by copepods, settles slowly ($1 m/d$) or die out (Figure 2). Grazing is divided into copepod growth, fecal pellet egestion, mortality and excretion. A small percentage of feces, 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 is closed by predation from zooplanktivorous fish and settling of detritus out of the surface layer. The parameters for the ecosystem model are defined in Table I of Naithani, Plisnier and Deleersnijder, 2006. The circulation model is discretized on a 20 km x 6 km grid along y- and x-direction of the Lake, respectively. The atmospheric forcing is uniform in space but vary in time. The wind and solar insolation used to initialize the circulation model are from the NCEP reanalyses data. The wind-stress is 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 are assumed to be zero. The model is run for 1 year before the actual simulation period and therefore, the simulation of the model parameters are not sensitive to their initial concentrations/values.
Model Results and Discussion

Simulations were carried out since 1970 until 2004 using NCEP data in order to study the influence of climatic variability on the net productivity of Lake Tanganyika. This period was chosen as it includes the year 1975 when measurements of primary production were carried out rather intensively for the first time and are reported in the literature (Hecky and Kling, 1981; Hecky and Fee, 1981; Hecky et al., 1981). Climatological model run are given in Figures 5 and 6 showing the daily averages (left y-axis) and yearly averages (right y-axis) of model forcing and simulated ecosystem parameters. The average yearly winds (Figure 3a) during this period varied between 2 and 4 ms\(^{-1}\) being on average around 3 m s\(^{-1}\) except during the years 1984-1992 and 2001 and 2002, when they exceeded 3.5 m s\(^{-1}\). The average yearly winds were lowest in the year 1974 (2.5 m s\(^{-1}\)). The average yearly air temperature (Figure 3b) increased more or less steadily during all these years from 21.5 °C to 22 °C. In 1974 low winds were accompanied by low air temperature (21.3 °C). Similar air temperatures were observed during the years 1984 and 1985 but with high winds (>3.6 m s\(^{-1}\)). The highest average yearly air temperatures (>22.2 °C) were observed during 1987-1988 with winds around 3.5 m s\(^{-1}\). This reflects that high winds were not necessarily observed with lower air temperatures. The average yearly PAR (Figure 3c) also increased steadily. The increasing trend was seen mostly between 1970 and 1986 and from 1998 until 2004, while during 1987 to 1997 it remained more or less constant being slightly low during 1995-1997. The increase is rather sharp from the year 2000 onwards.

**Figure 1.** Map of Lake Tanganyika and the model domain, respectively.
Figures 3e-3i and Figures 3j-3n show the upper layer depth and depth-averaged values of ecosystem variables off Kigoma and Mpulungu, respectively for the years 1970 to 2004. Epilimnion depth (Figures 3e and 3j) followed more or less the trend in the winds, being shallow during low wind years and deeper during high wind years off both stations. Shallow upper layer depth resulted in the entrainment of water with lesser nutrients while deeper mixing resulted in bottom water richer in nutrients (Figures 3f-3k). Net primary productivity of the lake was higher during shallow mixing periods and low during deep mixing periods, implying more time spent by the phytoplankton in the euphotic layer. Surprisingly, in the year 1974, when the winds were very low resulting in shallower upper layer depth (Figures 3e-3j) and the nutrient level too was low, the NP was high off both stations (Figures 3f-3k). During this year phytoplankton biomass was high off Mpulungu (Figure 3m). Lower winds might have caused lesser horizontal diffusion of phytoplankton biomass. During the years 1984 to 1986, when phosphorus level in the lake is high and the upper layer depth is deeper, the phytoplankton biomass is low implying more time spent by the cells in the light limited deeper waters. Such negative effects of deep mixing were also considered by Sarvala et al. (1999b). In the year 1996, when the winds were low, the phosphate level and phytoplankton biomass off Mpulungu were low. Similarly, lower phosphate levels during 2000-2001 and 2003 were accompanied by lower phytoplankton biomass. The highest phytoplankton biomass off Mpulungu during the period of study was obtained in the years 1991-1992, followed by 1987, 1998-1999 and 2002. The maximum NP was observed during the years 1974, 1998 and 2004. Figure 4 shows the NCEP wind, simulated upper layer depth and lake averaged values of ecosystem parameters. The lake averaged phosphate level (Figure 4c) follows the winds (Figure 4a), while the NP (Figure 4d) shows an inverse relationship with phosphate level. The highest lake averaged phytoplankton biomass (Figure 4e) was obtained in the year 1999. The enhancement of nutrients in the upper layer followed systematically the winds. The lake averaged NP show an inverse relationship with the winds, being high for low wind years and vice versa. In 80’s and early 90’s the average yearly winds were stronger and the lake average NP and
chlorophyll a were relatively low. This was also the case for NP off Kigoma and off Mpulungu, while off Mpulungu the phytoplankton biomass was rather high in the years 1987 and 1991-92 (Figure 5m).

Figure 3. Time series of daily and yearly averaged values of the NCEP reanalysed horizontal wind speed (a), air temperature (b), photosynthetically active radiation, PAR (c) and the y-component of wind-stress (d), model simulated epilimnion depth (e), depth averaged values of phosphate (f), net primary productivity- NP (g), phytoplankton biomass (h) and zooplankton biomass (i) off Kigoma, and model simulated epilimnion depth (j), depth averaged values of phosphate (k), net primary productivity- NP (l), phytoplankton biomass (m) and zooplankton biomass (n) off Mpulungu during the years 1970-2004. The yearly averaged values are shown on the right hand side of the y-axis.
Figure 4. Time series of daily and yearly averaged values of the NCEP reanalysed horizontal wind speed (a), air temperature (b), depth-averaged values of phosphate (c), net primary productivity- NP (d), phytoplankton biomass (e) and zooplankton biomass (f) averaged over the whole lake during the years 1970-2004. The yearly averaged values are shown on the right hand side of the y-axis.

Comparison with observations from literature

According to Hecky (Coulter and Spigel, 1991 page 92) observations and measurements on plankton and primary productivity of the lake are short term, i.e. less than a year, and partial in their spatial coverage. Hecky and Fee (1981) reported the annual net primary production of 290 g C m$^{-2}$ yr$^{-1}$ (0.8 g C m$^{-2}$ d$^{-1}$) for the year 1975. Melack (1980) reported a single pelagic measurement of 0.5 g C m$^{-2}$ d$^{-1}$ in April 1971. Our simulated value of annual net primary productivity for the year 1975 is 359.9 g C m$^{-2}$ yr$^{-1}$ (0.98 g C m$^{-2}$ d$^{-1}$). It should be observed that Hecky and Fee (1981) measured chlorophyll concentration on two whole lake transects, which traversed Lake Tanganyika from north to south and back. Each of these transects were completed within three weeks in April-May and October-November 1975. They chose these two periods to coincide with periods of low algal abundance at the end of the prolonged wet season and high algal abundance after dry season mixing. Also it was assumed that the mean chlorophyll concentrations in April-May and September-October each were representatives of six-month periods of low photosynthesis during stratification, January-June, and high photosynthesis during mixing and re-stratification, June through December (Coulter and Spigel, 1991 page 100). While model simulations are for the whole year over the whole lake area. Hecky and Kling (1981) observed the minimum phytoplankton biomass, as low as 60 mg m$^{-3}$, during the phase of stable stratification and maximal, as high as 930 mg m$^{-3}$, at the end of the deep mixing period. Their estimate of chlorophyll $a$ 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 chlorophyll $a$ of 0.82 mg m$^{-3}$ averaged in the upper layer. The lower value might be because we took the average over the upper layer while Hecky and Kling (1981) reported the average over the euphotic layer. The depth profiles of observed chlorophyll $a$ show that the maximum chlorophyll $a$ is often observed around 20-30 m depth (Salonen et al., 1999; Descy and Gosselain, 2004; Plisnier et Descy, 2005).

Sarvala et al. (1999) reported the estimates of primary production of 426-662 g C m$^{-2}$ yr$^{-1}$ for the period July 1993 – June 1996. Model prediction of net primary production for this period is around 359.9 g C m$^{-2}$ yr$^{-1}$. Salonen et al. (1999) reported the mean chlorophyll $a$ concentration of 1.4 mg m$^{-3}$ in surface water for the whole lake during the cruise of April-May 1995. Their estimate was 1.0 mg m$^{-3}$ for the first 40 m for 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 0.6–1.6 mg m^{-3} during August-December 1995. Our model predictions of the upper layer depth averaged values for the whole lake for these periods are 0.72 (April-May 1995), 1.56 (October-November 1995), 1.22 (November 1996) and 1.0 mg m^{-3} (August-December 1995), respectively. Model predictions are not very different from the observed estimates, keeping in mind once again that model predicts over the whole lake and predicts an average over the surface layer.

In order to see the bias in the simulated annual production because of NCEP wind forcing, we did the simulations using the winds observed at Mbulungu 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 I). The annual simulations with NCEP wind forcing show higher estimates over the whole lake and off Kigoma by around 3 and 5 percent, respectively, while the simulations off Mbulungu remained more or less similar. The winds off Mbulungu are representative of the winds in the southern parts of the lake and cannot be fully considered to represent winds over the northern regions of the lake. The northern region experiences occasionally strong winds during the wet season from the north. These small strong wind pulses cannot be adequately represented by the winds observed off Mbulungu and to some extent by NCEP winds. It is seen that with NCEP wind forcing the x component of wind stress increases, which is giving 5 percent more productivity in the northern regions of the lake. This is to say that if the wind forcing can fully represent the whole lake the estimates of primary productivity of the lake will further increase.

<table>
<thead>
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<th>g C m^{-2} yr^{-1}</th>
<th>Observations</th>
<th>NCEP</th>
<th>percent difference</th>
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<tr>
<td>Lake av. NP</td>
<td>333.37</td>
<td>342.18</td>
<td>2.6</td>
</tr>
<tr>
<td>Mbulungu NP</td>
<td>375.15</td>
<td>369.40</td>
<td>-1.5</td>
</tr>
<tr>
<td>Kigoma NP</td>
<td>317.35</td>
<td>329.88</td>
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**Conclusions**
In the absence of sufficient regional, spatial and temporal measurements carried out in Lake Tanganyika, the model provides an easy simplified tool to study the lake hydrodynamics and ecosystem functioning. ECOH-II model based on a simplified phosphorus cycle and only three prognostic pelagic variables is able to predict the net primary productivity of the lake. The model simulations successively predicted the present as well as the past primary productivity of Lake Tanganyika. The comparison with observations establishes confidence in predicted mean net production of the Lake. Our simulations clearly confirm the finding from previous observations (Langenberg et al., 2003) that the relationship between mixing depth changes (due to warming) and lake productivity is not simple and straightforward. Long term climatic simulations are in agreement to Sarvala et al. (1999b) that at least phytoplankton chlorophyll concentrations seem to have remained largely similar from 1970’s to the present except for some year to year fluctuations because of very strong or very weak winds. In future it is envisaged to use this model to predict the future scenarios of primary productivity of the lake and to be able to predict the fish production. Comparison of primary production with fish statistics will be discussed at the symposium.

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