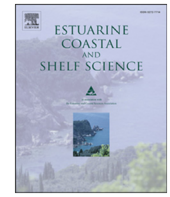
Estuarine, Coastal and Shelf Science xxx (2014) 1–17

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss



Influence of variable water depth and turbidity on microalgae production in a shallow estuarine lake system — A modelling study

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ARTICLE INFO

Article history:
Received 19 December 2013
Accepted 20 May 2014
Available online xxx

Keywords:
light limitation
primary production
mathematical model
environmental variability
St. Lucia
South Africa

ABSTRACT

Strongly varying water levels and turbidities are typical characteristics of the large shallow estuarine lake system of St. Lucia, one of the largest on the African continent. This theoretical study investigated the combined effects of variable water depth and turbidity on seasonal pelagic and benthic microalgae production using a mathematical model, in order to ascertain productivity levels during variable and extreme conditions. Simulated pelagic and benthic net production varied between 0.3 and 180 g C m^{-2} $year^{-1}$ and 0 and 220 g C m^{-2} $year^{-1}$, respectively, dependent on depth, turbidity, and variability in turbidity. Although not surprising production and biomass decreased with increasing turbidity and depth. A high variability in turbidity, i.e. an alteration of calm and windy days, could reduce or enhance the seasonal pelagic and benthic production by more than 30% compared to a low variability. The day-to-day variability in wind-induced turbidity therefore influences production in the long term. On the other hand, varying water depth within a year did not significantly influence the seasonal production for turbidities representative of Lake St. Lucia. Reduced lake area and volume as observed during dry periods in Lake St. Lucia did not reduce primary production of the entire system since desiccation resulted in lower water depth and thus increased light availability. This agrees with field observations suggesting little light limitation and high areal microalgal biomass during a period with below average rainfall (2005–2011). Thus, microalgae potentially fulfil their function in the lake food-web even under extreme drought conditions. We believe that these results are of general interest to shallow aquatic ecosystems that are sensitive to drought periods due to either human or natural causes.

1. Introduction

Microalgae productivity contributes significantly to the total production of aquatic systems (MacIntyre and Cullen, 1996; Adams and Bate, 1999). Microalgae, both in the water column and in the sediment (benthos) are important primary producers and provide the nutritional basis for pelagic and benthic invertebrates and higher organisms (fish, birds). In estuarine systems, microalgae productivity is often limited by low light availability due to high turbidity originating from high suspended sediment concentrations (Cloern, 1987; Scheffer, 1998). Reasons for such high sediment concentrations in estuaries and shallow lakes are sediment transport from catchment areas, tidal activities and wind induced sediment resuspension (Winter, 1999; Dyer, 2000). The effect of turbidity on microalgae productivity is closely related to the mixing depth in stratified systems or to the total water depth in non stratified systems (Cloern, 1987). A low water depth or a low ratio of mixing to total depth generally increases the average underwater light availability reducing the negative effect of a high turbidity for primary production.

Estuaries being influenced by ocean tides as well as river runoffs are generally highly dynamic systems experiencing a high variability in their environmental parameters including salinity, temperature, depth and turbidity (e. g. Potter et al., 2010). Estuarine systems that can loose their connection to the sea (temporarily open-closed estuaries, Whitfield, 1992) and shallow lakes prone to evaporation and rainfall can strongly vary in their depth, particularly in climatic areas that experience distinct dry and wet seasons (tropics and subtropics) or dry and wet periods on longer time scales. Further, resuspension of sediment due to tidal activities or wind leads to variability in underwater light availability on time scales of hours (tides) and days (e. g. alternation of calm and windy days). In systems where both the water depth and turbidity vary in time or space primary production may be highly variable (e. g.

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http://dx.doi.org/10.1016/j.ecss.2014.05.011
0272-7714/

Please cite this article in press as: Tirok, K., Scharler, U.M., Influence of variable water depth and turbidity on microalgae production in a shallow estuarine lake system — A modelling study, Estuarine, Coastal and Shelf Science (2014), http://dx.doi.org/10.1016/j.ecss.2014.05.011

MacIntyre and Cullen, 1996) influencing food availability for higher trophic levels. Understanding what drives different patterns in primary production is important to understand the flow of energy through food webs and the dynamics of food webs (Miller et al., 1996; Jassby et al., 2002).

It is well known that primary production varies seasonally and spatially (e. g. Jassby et al., 2002; Perissinotto et al., 2010), however short term variability was identified to be important as well and there are still open questions in particular on the role of short-term variability on primary production at larger time scales, e. g. seasonal or annual production (Desmit et al., 2005; Canion et al., 2013). Long-term data sets often arise from monitoring schemes where samples are taken on bi-weekly to monthly or even less frequent time steps. While such data are invaluable for our understanding of primary production in aquatic systems, they do not allow for resolution of short-term variability. In addition to experiments at different time scales, mathematical models are useful tools for developing frame works and explore different scenarios. In this study we investigate the effect of the variability in both water depth and turbidity on primary production in a shallow coastal system with the aid of a dynamic simulation model, motivated by observations from an estuarine lake system, Lake St. Lucia (South Africa).

Lake St. Lucia, South Africa's first World Heritage Site, is a shallow and turbid estuarine lake system situated on the East Coast of South Africa (Cyrus, 1988) providing 80% of the estuarine area in KwaZulu-Natal and 50% of that in South Africa. Wet and dry periods occur on decadal time scales, therefore periods with low rainfall spanning several consecutive years are common for the St. Lucia catchment (Lawrie and Stretch, 2011). During the last decade, between 2002 and 2011, below average rainfalls led to drastically reduced water levels and desiccation of the lake of up to 90% was observed in some years (Whitfield and Taylor, 2009; Cyrus et al., 2010). The lack of freshwater entering the system was also intensified by the artificial separation of the Mfolozi river from the St. Lucia inlet which took place in the early 1950s to prevent increasing silt loads reaching the lake system (Day et al., 1952; Taylor, 1982). Lake St. Lucia is classified as highly turbid with turbidities >80 NTU (Cyrus, 1988). Wind is the driving force leading to resuspension of sediment and thus high turbidities in the large and shallow lake (Cyrus, 1988; Pringle, 2011). Turbidity is highly variable from day to day, and between seasons due to variable wind conditions (Cyrus, 1988). Perissinotto et al. (2010) suggest that primary production in Lake St. Lucia is mainly light limited given high turbidities, but high algae biomasses in certain areas might result from shallow water depths. It is unlikely that nutrient limitation inhibits algae growth since low nutrient levels were rarely observed (Perissinotto et al., 2010; Van der Molen and Perissinotto, 2011). Van der Molen and Perissinotto (2011) showed that microalgae production in Lake St. Lucia is mainly influenced by salinity, irradiance (as photosynthetic active radiation close to the bottom of the water column), and temperature. Their results indicate that light availability in the water column and thus turbidity plays an important role in influencing the dynamics of primary production in Lake St. Lucia which motivated our theoretical study on the effects of variable turbidities in connection with variable water depths on seasonal primary production of microalgae.

This theoretical study aimed to investigate the interrelated effects of water depth and turbidity on seasonal microalgae production in very shallow and turbid systems such as Lake St. Lucia. We emphasise the temporal variability of water depth and turbidity to provide a framework for present and future studies and inform management decisions. First, we investigated field data of turbidity and water depth from Lake St. Lucia from 2005 to 2011 to establish empirical ranges of these variables and their variability and calculated the relative light availability in the water column and at the bottom of the water column. Second, we used a mathematical model to simulate the dynamics of microalgae in relation to light availability (global irradiance, water depth, turbidity/light attenuation), nutrients, salinity, and temperature. We ran a set of simulations with different water depths and turbidity distributions, then compared the seasonal microalgae production of the different scenarios.

2. Methods

2.1. Study site and field data

The St. Lucia estuarine lake system is situated on the northern east coast of South Africa between 27° 52′–28° 24′ S and 32° 21′–32° 34′ E. The system consists of three shallow interconnected lake basins (South Lake, North Lake, False Bay) linked to the Indian Ocean via a 21 km long natural channel, the Narrows (Fig. 1). The system covers an estimated 300–350 km^2, depending on water levels (Cyrus, 1989; Taylor, 2006) and has an average depth of 1 m. Thus the lake is sensitive to direct rainfall inputs and evaporative losses. In times of very low rainfall, losses from the system exceed inputs.

Water depth and turbidity were measured quarterly as part of a basic monitoring program, at 5 different stations in the lake (Fig. 1) — the Estuary Mouth (MT), the Narrows (ES), Catalina Bay on the eastern shores (CB) and Charters Creek on the western shores of South Lake (CC), as well as Listers Point at False Bay (LP) from August 2005 until May 2011. Turbidity (NTU) was measured using either a YSI 556 or YSI 6920 Multiprobe system, in the top 20 cm of the water column and at the bottom of the water column at sites deeper than 50 cm. Depth averaged values were used for further calculations. Stratification was not observed due to vertical mixing driven by wind-wave generated turbulence. Depth was measured with a ruler when very shallow (<0.5 m), otherwise it was taken from YSI readings. Depth was measured approximately 50–100 m from the shore at CC, CB, and LP, and from the boat in the middle of the Narrows at ES. These depth measurements represent the water depth at each sampling site, but do not represent the mean water level of the subsystem. However, they represented changes in the water level at each site and served as a proxy for the entire lake area. Their representativeness was assumed due to the shallow depths throughout the lake basins (e. g. MacKay et al., 2010). There are no representative depth measurements for the Mouth because sampling was conducted from the shore, but total depth usually exceeds 2 m (e. g. MacKay et al., 2010). Photosynthetic active radiation (PAR, 400–700 nm) and turbidity were additionally measured at CC, LP, and MT biweekly from October 2010 until July 2011 to establish a relationship between turbidity and light attenuation in the lake system. Surface and bottom PAR were measured using an LI-COR light meter, fitted with an LI-193SA spherical quantum sensor. These measurements were used to calculate the diffusive light attenuation coefficient (κ, Kirk, 1994), using the following equation: $\kappa = -ln(I_{z2}/I_{z1})/(z2 - z1)$, where I_{z2} is radiation (μmol photons m^{-2} s^{-1}) at depth $z2$ (m) and I_{z1} is radiation at depth $z1$. A linear regression model between log transformed turbidities and log transformed light attenuation coefficients resulted in: $log(\kappa) = 0.78 \cdot log(turb) - 0.72$, $r^2 = 0.82$, $p < 0.01$ (Fig. 2 D). This model was used to estimate κ from measured or simulated turbidities, which was subsequently used in the calculations of light availability and primary production.

2.2. Relative light availability

To obtain information on potential light limitation or photoinhibition of microalgae production in Lake St. Lucia, the relative

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