Ecological Modelling 361 (2017) 66–73

Contents lists available at ScienceDirect

Ecological Modelling

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

Modeling the biogeochemical role of photosynthetic sulfur bacteria in phosphorus cycling in a managed eutrophic lake

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ARTICLE INFO

Article history:
Received 7 December 2016
Received in revised form 17 May 2017
Accepted 19 May 2017
Available online 10 August 2017

Keywords:
Phosphorus
Eutrophic
Sulfur bacteria
Management
Modeling

ABSTRACT

Vertical distributions of total dissolved phosphorus (TDP), sulfide, chlorophyll, and primary production produced by photosynthetic sulfur bacteria (PSB) were studied in a small stratified, highly productive, and dimictic lake, Linsley Pond, CT, USA. The goal was to understand and model the role of PSB in a lake undergoing trophic transformation as a result of lake management involving reduced phosphorus loading. High levels of sulfide developed in the anoxic hypolimnion, though a decrease was observed compared to earlier years, possibly as a result of lake management under a Total Maximum Daily Load (TMDL) process. A deep chlorophyll maximum was observed, and absorption spectra confirmed that it was the result of photosynthetic sulfur bacteria. The summer chlorophyll maximum occurred at an interface marked by high amounts of sulfide and low, but adequate, levels of light. Primary production by PSB was found at a depth of 7 m in July 2008, and thereafter extended slowly to 9 m until late fall overturn. PSB only contributed a minor portion of total primary production in Linsley Pond that year, but a straightforward biogeochemical phosphorus model reveals that the existence of PSB serves as a significant biological barrier for phosphorus being transported back into the upper mixing zone. A large amount of TDP was trapped in the hypolimnion, and upward transport of TDP from the upper boundary of the hypolimnion to the mixing zone was about 30% of external phosphorus loading from the only tributary during the summer stratification period. By comparison, the amount of TDP assimilated by PSB and settling back to the hypolimnion was comparable to external phosphorus loading to the lake from its tributary. As lake management reduces external P loading and productivity, bottom sulfide is likely to decrease, suppressing PSB activity and having the undesired effect of allowing more TDP to be transported upward to the epilimnion as this biological barrier is suppressed.

1. Introduction

Eutrophication, increased primary productivity induced by an increase in limiting nutrients, causes severe negative effects on aquatic ecosystems (Charlton and Milne, 2005; Kajino and Sakamoto, 1995; Karim et al., 2003; Shamsudin, 1999; Vanderploeg et al., 2009; Yu et al., 2010). Ever since phosphorus (P) was recognized as the main limiting nutrient in most lake ecosystems, tremendous efforts have been made to reduce its external loading into receiving water bodies (Lee et al., 1978; Pallesen et al., 1985). Although water quality for some lake ecosystems has been significantly improved after phosphorus reductions from external anthropogenic sources, the extent of improvement varies from case to case. Expected recoveries have not been experienced by all lake ecosystems, or showed a delayed effect after nutrient abatement (McCauley et al., 1989; Prairie et al., 1989; Sondergaard et al., 2003; Watson et al., 1992; Welch et al., 1980). Internal phosphorus loading from the hypolimnion during summer stratification periods is one of the major mechanisms that are responsible for this delay of eutrophication recovery (Mayer et al., 2005; Sondergaard et al., 1999). A recent study showed that the existence of photosynthetic sulfur bacteria (PSB) made eutrophication control even more complicated (Yekta and Rahm, 2011).

In contrast to other photosynthetic algae, PSB are mainly influenced by sulfide and light availability instead of phosphorus as a major limiting nutrient (Van Gemerden and Mas, 1995). Organic matter produced by PSB at the interface of the metalimnion and hypolimnion of stratified lakes can cause eutrophication management to be reevaluated (Fahnenstiel and Scavia, 1987; Gross et al., 1994; Ledwell et al., 2008; Wurtsbaugh et al., 2001). For example, the desired decrease in bottom water hypoxia caused by cultural eutrophication might be severely delayed because detritus from

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http://dx.doi.org/10.1016/j.ecolmodel.2017.05.016
0304-3800/© 2017 Published by Elsevier B.V.

PSB settling into the hypolimnion could consume all the oxygen in bottom water (Krstulovic and Solic, 2001).

Previous research on PSB has tended to focus on either quantification of organic matter production or limnological characteristics which determined PSB's existence (Arvola et al., 1992; Chapin et al., 2004; Christensen et al., 1993; Cloern et al., 1987; Rodrigo et al., 2000; Schanz et al., 1998). However, less attention has been paid to mutual impacts between PSB and biogeochemical cycles near the sulfide-oxygen interface. The existence of sulfur bacteria greatly changed nitrate cycling of coastal sediments (Sayama, 2001) and vertical distribution of zooplankton in the Gulf of Maine (Townsend et al., 1984). However, it remains unclear how phosphorus uptake by sulfur bacteria would affect cycling of phosphorus in the water column of a lake.

The present paper is a part of a series of studies carried out in Linsley Pond with the focus on:

1) phosphorus distribution over time and depth, and quantification of upward phosphorus transport from the hypolimnion to the mixed zone;
2) the existence of a deep chlorophyll maximum and active primary production produced by PSB;
3) development of a one dimensional biogeochemical model to study the significance of PSB's impact on internal phosphorus cycling;
4) discussion of lake management to reduce eutrophication and how it differs when PSB are present.

2. Materials and methods

2.1. Study site

Linsley Pond (0.09 km^2, 6 m mean depth, 14 m maximum depth), located in the town of North Branford, Connecticut, USA, generally stratifies from April through November each year. During summer stratification, the hypolimnion becomes anoxic and significant amounts of dissolved phosphorus and bisulfide (HS^-) accumulate (Hu et al., 2006; Mylon and Benoit, 2001). Linsley Pond's rural watershed underwent rapid development beginning in the 1930s. As a consequence, Linsley Pond was included on the *List of Connecticut Waterbodies Not Meeting Water Quality Standards* (Protection, 2004) in 2004, due to the degradation of water quality and recreational use by cultural eutrophication in the summer. A TMDL (Total Maximum Daily Load) for phosphorus regulation was developed by the CT DEEP (Connecticut, Department of Energy and Environmental Protection), as it was determined that excessive phosphorus loading was responsible for current degraded conditions (Stahl and Bolton, 2005). The pond is famous because it was a key study site for G. Evelyn Hutchinson and his students in their seminal work that helped establish the science of aquatic ecology (Hutchinson, 1975).

2.2. Sampling and analysis methods

The current study was predicated on our measurements in July 2007, which indicated the existence of PSB (photosynthetic sulfur bacteria) at the location of a deep chlorophyll maximum. Water samples from depths of 1 m and 8 m were taken at that time and extracted in the laboratory (Franson, 2005) to measure absorption spectra of different algal pigments. The existence of PSB in Linsley Pond, which was responsible for the deep chlorophyll maximum in other lakes (Baneras et al., 2001; Schanz et al., 1998; Takahash and Ichimura, 1970), was verified by the absorption spectra of unique PSB pigments (Fig. 1). The curve of the absorption spectra from the surface sample showed a maximum absorption at around 663 nm,

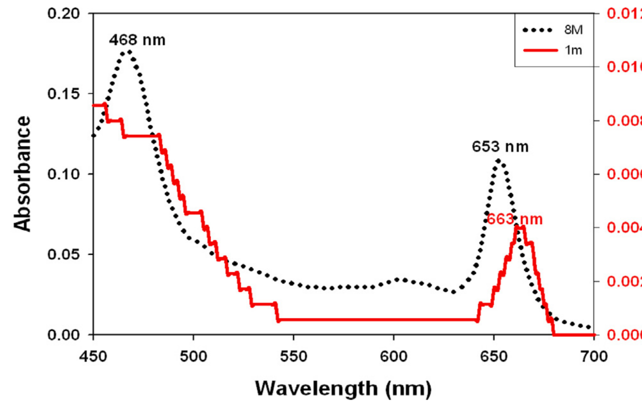

Fig. 1. Absorption spectra of pigments in 90% acetone crude extract at two depths in Linsley Pond in late July 2007. (Solid and dotted lines represent depths of 1 and 8 m, respectively). The very low levels of pigment at 1 m cause the stepped appearance of this curve.

coinciding with that in green algae (Jeffrey and Humphrey, 1975). The curve generated from deep water (8 m) displayed two absorption peaks at 468 nm and 653 nm. Multiple peaks occurring on this absorption spectrum support the existence of PSB in the deep water (Czeczuga, 1965; Czeczuga, 1968).

In 2008 and 2009, we conducted a series of analyses to determine how PSB identified in 2007 were contributing to phosphorus mass transport in the lake. This involved *in situ* incubations to measure PSB productivity as well as detailed profiles of several other characteristics that can influence PSB growth or whose cycles they might affect. In the current study, extensive samples were collected and were compared to results for 2003 by Hu et al. (2006) for the same lake. In the current paper we focus on results from 2008, but measurements from 2009 were very similar, while suggestive of continued declining productivity overall.

From Feb to December 2008 and again in 2009, lake water samples were taken at 1-m intervals from surface to bottom at the point of maximum depth in Linsley Pond (13 m) to characterize variations in space and time of a number of chemical and physical parameters. These included temperature, dissolved oxygen, conductivity, dissolved phosphorus, sulfide, and sulfate. For most characteristics, patterns were similar to results documented by Hu et al. (2006, 2007), though important differences are described later.

Light is one factor that can limit PSB, especially because they occur primarily at deeper, darker depths. Light intensity was profiled in June 2008, decreasing to 10% of surface intensity at a depth of 2.8 m and to 1% at 6.6 m. The Secchi depth measured at the same time was 2.5 m and served as an indicator of 10% surface light intensity in our study as in previous research (Bukata et al., 1988). Although no further light intensity measurements were made with a photometer, Secchi depth was measured monthly in the stratification period of 2008 and was close to 3.3 ± 0.5 m (ave ± s.d.). Secchi depths in 2009 were similar, but more variable (3.4 ± 1.9 m).

We measured phosphorus in 2008 and 2009 because of its critical role in limiting primary productivity both of PSB and green algae. For dissolved phosphorus analysis, water from each 1 m sample interval was pumped into previously cleaned 30 ml HDPE (high density polyethylene) bottles (Nalgene) through FEP-lined tubing (Tygon SE-200, ColePalmer) with a peristaltic pump. For water samples from the hypolimnion, extra attention was given to preserving the redox conditions by allowing the water to overflow from the bottles for several replacement volumes and eliminating the headspace. Filtration through Millipore^{TM} membrane filters (Durapore^{TM} 0.45 μm pore size) was carried out during sample collection to later determine total dissolved phosphorus (TDP) by the