Effects of internal phosphorus loadings and food-web structure on the recovery of a deep lake from eutrophication

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A B S T R A C T

We used monitoring data from Lake Lugano (Switzerland and Italy) to assess key ecosystem responses to three decades of nutrient management (1983–2014). We investigated whether reductions in external phosphorus loadings (L_{ext}) caused declines in lake phosphorus concentrations (P) and phytoplankton biomass (Chl a), as assumed by the predictive models that underpinned the management plan. Additionally, we examined the hypothesis that deep lakes respond quickly to L_{ext} reductions. During the study period, nutrient management reduced L_{ext} by approximately a half. However, the effects of such reduction on P and Chl a were complex. Far from the scenarios predicted by classic nutrient-management approaches, the responses of P and Chl a did not only reflect changes in L_{ext}, but also variation in internal P loadings (L_{int}) and food-web structure. In turn, L_{int} varied depending on basin morphometry and climatic effects, whereas food-web structure varied due to apparently stochastic events of colonization and near-extinction of key species. Our results highlight the complexity of the trajectory of deep-lake ecosystems undergoing nutrient management. From an applied standpoint, they also suggest that [*i*] the recovery of warm monomictic lakes may be slower than expected due to the development of L_{int}, and that [*ii*] classic P and Chl a models based on L_{ext} may be useful in nutrient management programs only if their predictions are used as starting points within adaptive frameworks.

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Introduction

Eutrophication, or excessive nutrient enrichment, is among the most widespread human impacts on lakes worldwide (Carpenter et al., 1998; Smith et al., 1999; Smith, 2003). Through symptoms such as the proliferation of phytoplankton, eutrophication affects several of the ecosystem goods and services provided by lakes, including clean water, fisheries, and recreation (Smith et al., 1999; Pretty et al., 2003; Dodds et al., 2008). Consequently, during the last decades, governmental agencies have invested considerable resources to control nutrient inputs and restore lake ecosystems (Smith et al., 1999). At the same time, monitoring programs have been established to assess the effects of the management actions undertaken. The results of these programs, which can now include several decades of data, offer valuable opportunities to assess the outcome of eutrophication management and the strength of its underlying assumptions.

Traditionally, efforts to manage eutrophication have focussed on the reduction of the external loadings of nutrients, especially phosphorus (Vollenweider, 1968; Dillon and Rigler, 1975; Smith et al., 1999). This approach is based on the assumptions that [*i*] phytoplankton biomass

is proportional to the concentration of total phosphorus (TP) within the photic zone of the lake, and [*ii*] phosphorus concentration is proportional to the external loadings of this nutrient (L_{ext}). In other words, L_{ext} is assumed to control phytoplankton biomass through the two-link pathway $L_{ext} \rightarrow TP \rightarrow$ biomass, so that a reduction in L_{ext} would cause a proportional decline in phytoplankton biomass. These links are supported by considerable empirical evidence, and have formed the basis for classic predictive models including the P model of Vollenweider (1968) and the phytoplankton biomass (Chl a) model of Dillon and Rigler (1974a). In a typical application of the nutrient-loading reduction approach, environmental managers identify the level of phytoplankton biomass that would be acceptable in a lake, and use these (or similar) models to predict the reduction in L_{ext} that would be necessary to achieve such an objective (Dillon and Rigler, 1975). However, despite the support for the underlying assumptions, evidence so far indicates that reductions in L_{ext} do not always lead to changes in surface-water P concentrations and phytoplankton biomass predicted by these models (Smith et al., 1999; Scavia et al., 2014).

Deviations from predicted results have two main causes, i.e., the development of internal loadings of TP (L_{int}), and top-down control by grazers (Smith et al., 1999). Internal loadings occur in lakes with a long history of nutrient pollution, where sediments have accumulated high reserves of TP. Where anoxic conditions develop in deep waters,

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Table 1

Morphometric and hydraulic characteristics of the two basins of Lake Lugano, Switzerland and Italy. All data except Osgood Index and % of littoral area from Barbieri and Mosello (1992).

	North basin	South basin
Watershed area [km^2]	269.7	290.3
Lake area [km^2]	27.5	21.4
Lake volume [km^3]	4.69	1.14
Z_{max} [m]	288	95
$\bar{Z}$ [m]	171 (0–288 m layer)	55
	86 (0–100 m layer)	
Osgood Index	32.6	12.2
Littoral[a] area (%)	4%	12%
Residence time [yr]	12.3 (0–288 m layer)	1.5
	6.2 (0–100 m layer)	
Flow out [km^3 yr^{-1}]	0.38	0.77

[a] The littoral was defined as the lake area with depth ≤ 10 m.

these reserves are released from the sediments over several years or decades, primarily through anaerobic release of iron-bound phosphorus (Pettersson, 1998). This release may delay the response of in-lake TP concentrations to any reductions in L_{ext} (Nürnberg and Peters, 1984; Søndergaard et al., 2001). Top-down control implies that phytoplankton biomass is determined by grazer consumption, rather than nutrient availability. Although not explicitly considered by the nutrient-reduction approach, top down control is common in lakes worldwide (Hrbáĉek et al., 1961; Carpenter et al., 1985) and appears to be associated with high densities of large-bodied zooplanktonic grazers, such as *Daphnia* (McQueen et al., 1986; Schindler, 2006).

Although the occurrence of L_{int} and top-down control in lakes is well known, the factors that govern their importance relative to L_{ext} and TP limitation remain uncertain. For example, does their effect depend on lake morphometry? As a starting point, we suggest that deep lakes should be less affected by internal loadings than shallow lakes, because deep lakes dilute the P released from the sediments into relatively larger volumes of water (Jacoby and Welch, 2004). Grazing pressure may also differ between deep and shallow lakes. All else being equal, large grazers, including *Daphnia*, tend to be more abundant in deep lakes, where fish predation is partly avoided through diel vertical migrations into deep-water refuges (Jeppesen et al., 2003). In turn, a greater abundance of large grazers is expected to result in stronger top-down control

of phytoplankton (Pace, 1984; McQueen et al., 1986). Taken together, the hypothesized low susceptibility toward developing internal loads and high grazing pressure suggest that deep lakes should respond quickly to reductions in L_{ext}. However, with notable exceptions, the recovery of deep lakes from eutrophication is poorly understood (but see the international P management plan and long-term monitoring of the North American Great Lakes; Evans et al., 2011; Dove and Chapra, 2015), partly because most assessments so far have focussed on a limited range of trophic states (usually between oligotrophic and mesotrophic) and climatic conditions (usually cold temperate; Jeppesen et al., 2005).

In this study, we examined the effects of nutrient reduction on Lake Lugano (Switzerland and Italy). This deep (maximum depth Z_{max} = 288 m), warm monomictic lake became eutrophic between the 1940s and the 1970s (Barbieri and Mosello, 1992). After the 1970s, external nutrient loadings were reduced through sewage management and a ban on the use of phosphate detergents. Using three decades of monitoring data (1983–2014), we examined the responses of P concentrations, L_{int}, phytoplankton biomass, zooplankton grazing, and the factors controlling phytoplankton biomass to the reduced P loadings. These responses were examined separately for basins of the lake, the deeper (288 m) north basin, and the shallower south basin (95 m), which have different morphometric and hydraulic characteristics (e.g., depth, volume, and water residence time; Table 1). We addressed four main questions: [*i*] Did the responses of P concentration and phytoplankton biomass in Lake Lugano support the predictions of the nutrient-loading reduction approach? [*ii*] Alternatively, did the response deviate owing to the development of internal loadings and/or top-down control? [*iii*] Was the response consistent with the patterns hypothesized for deep lakes (i.e., weak effects of L_{int}, strong effects of top-down control)? [*iv*] Was the response influenced by the different morphometric characteristics of the north and south basins?

Methods

Study lake

Lake Lugano (E 9° 0′ 56.35″, N 46° 0′ 23.77″, altitude 271 m) is a relatively large (surface area = 49 km^2), deep (Z_{max} = 288 m) peri-Alpine lake, shared between Switzerland and Italy (Table 1, Fig. 1). The two
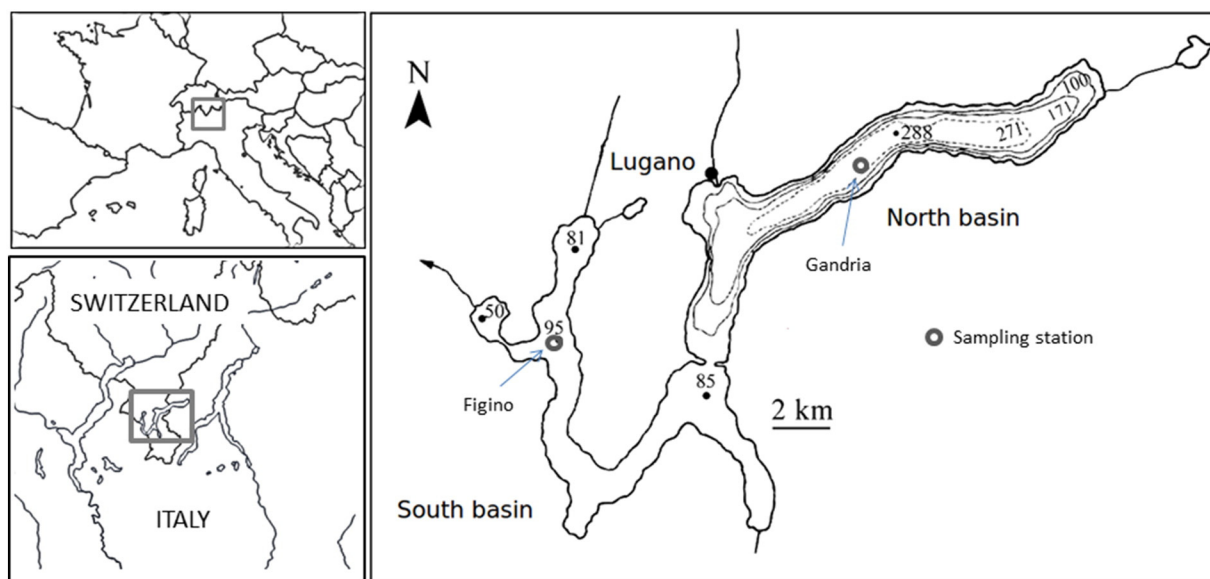

Fig. 1. Location of Lake Lugano and the sampling stations considered in this study. Upper left corner: position within Central-Southern Europe; lower left corner: position within southern Switzerland-northern Italy and bathymetry (map adapted from Barbieri and Polli, 1992). The bathymetry is represented by the depth of individual sub-basins and selected depth contours (the 100 m and 200 m depth contours are represented using solid lines, the 250 m depth contour is represented using a dotted line).