



Evolution of the Lake Titicaca basin and its diatom flora over the last ~370,000 years

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ABSTRACT

In recent years, deep drilling undertaken as part of the International Continental Drilling Program has generated multiple long lacustrine sedimentary records to reconstruct continental paleoclimate. In many cases, the tectonic and geomorphic history of these basins is under-constrained and poorly known, which affects the interpretation of climate history from geophysical, geochemical, and paleobiotic proxies in the sedimentary record. In addition, non-analog biotic assemblages that reflect evolutionary processes may constrain the reconstruction of past environments. In the drill-core record of Lake Titicaca, spanning the last ~370 ka, the diatom stratigraphy reflects both the influence of climate and the long-term evolution of the lake basin and its biota. In the upper part of the drill-core sequence, glacial intervals were deep and dominated by freshwater planktic taxa, and peak interglacial intervals were shallow and dominated by benthic species, some with saline affinities. In the basal sections of the drill-core record, benthic diatoms are dominant in both glacial and interglacial units, with freshwater taxa dominating the glacial strata. This suggests that the ancient lake basin was shallower during intervals of both wet and dry climate, and that the modern deep lake may result from a progressive subsidence and deepening of the basin over time. In addition, morphological evolution in one of the major lineages of planktic diatoms, *Cyclotriophanos*, indicates substantial change in the limnological environment that affected species morphology and may have driven speciation.

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1. Introduction

Large long-lived lakes have the potential to produce archives of environmental dynamics spanning hundreds of thousands to millions of years. As a result, many of these systems have been the targets of recent lake drilling projects, because they can elucidate climatic processes operating at these long temporal scales (Williams et al., 2001; Fritz et al., 2007; Scholz et al., 2007). Long-lived lakes also have the potential to reveal evolutionary processes, including diversification, speciation, and extinction of aquatic biota (Khursevich et al., 2001; Williams et al., 2001), as well as the long-term ontogeny of the lake basin itself.

A number of the large lakes that have been targeted for drilling are located in tectonically active settings (e.g. Lake Titicaca, Bear Lake, Lake Qinghai, Lake Van, and the Dead Sea), and it is likely, especially on longer timescales, that some of these lacustrine sedimentary sequences were impacted by structural and geomorphic processes that affected the watershed and the lake basin itself, including its hydrologic thresholds (both inlets and outlets). These factors can affect the physical, chemical, and biological dynamics of the lake and in turn the lake's water balance and rate and style of sedimentation. In cases

where the tectonic or hydrogeomorphic setting has been altered, the response of the ancient lake and landscape to climate may be different from the system of recent times (Bradbury, 1997; Colman, 1998; Kowalewska and Cohen, 1998). As a result, "correct" interpretation of climate history from long sedimentary sequences can be challenging without *a priori* knowledge of geomorphic and tectonic history.

Many large long-lived lakes are known for their high degree of endemism, and the sedimentary record can reveal the conditions associated with the diversification of aquatic biota and hence the potential drivers of evolutionary change (Brooks, 1950; Johnson et al., 1996; Theriot et al., 2006). At the same time, ancient organisms may have gone extinct (Khursevich et al., 2001; Williams et al., 2001), and hence their ecology cannot be determined from modern analogs. In such cases, ecological tolerances can only be inferred from generic analogs, morphological characteristics, or the co-occurrence of extinct taxa with assemblages of other organisms with known ecological affinities or with distinctive geochemical or sedimentary features.

Lake Titicaca (14°09'–17°08' S, 68°03'–71°04' W) is a large high-elevation (3812 m) lake in the tropical Andes (Fig. 1). The lake has been the focus of several decades of paleoclimatic study (Servant and Fontes, 1978; Wirmann and Mourguiart, 1995; Abbott et al., 1997; Baker et al., 2001a), because of its potential for reconstructing the long-term history of precipitation variation in tropical South America, for understanding the factors that force tropical climate variability on paleoclimatic time scales, and for evaluating the impact

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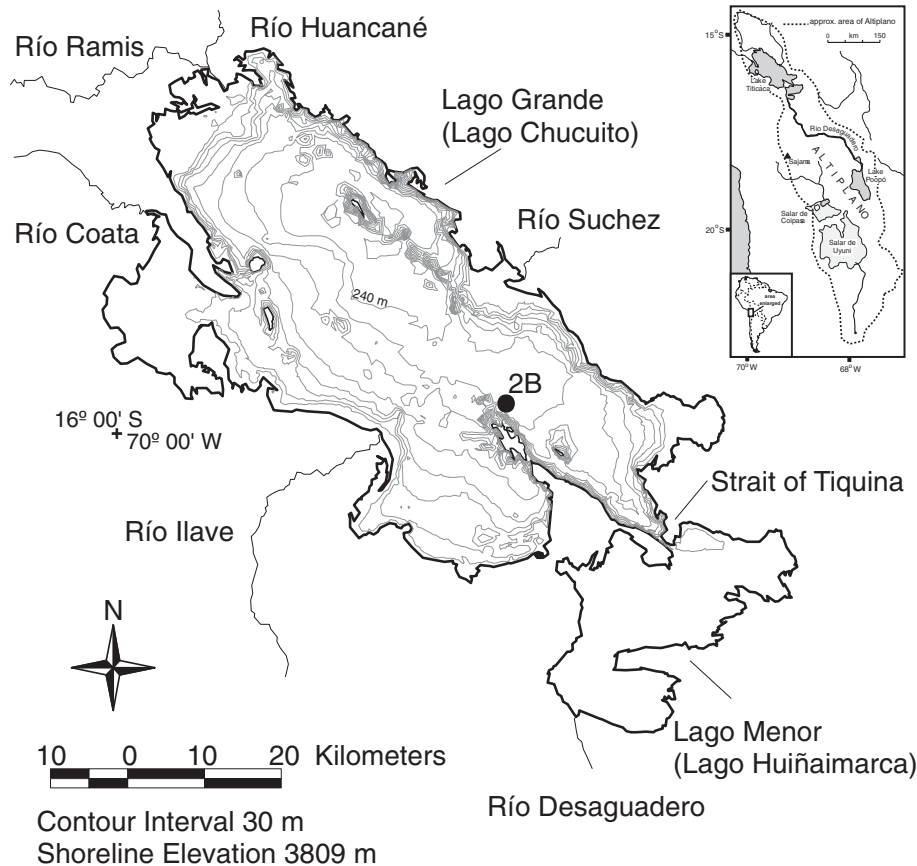


Fig. 1. Map of Lake Titicaca showing the LT01-2B drill core site (marked by a filled circle). Inset map shows the location of the outlet, the Río Desaguadero, and other large lake basins in the Bolivian Altiplano that have been hydrologically connected to Lake Titicaca at times in the past.

of climate on the evolution of high tropical biodiversity. In 2001 we drilled the sediments of Lake Titicaca to obtain a paleoclimatic record that extended to periods prior to the Last Glacial Maximum (LGM). Here, we use the detailed diatom stratigraphy of one of those cores to interpret the lake-level history of Lake Titicaca, to evaluate the role of climate relative to basin alteration in affecting lake-level change, and to document morphological change in a major lineage of planktic diatoms. A synthesis of the biotic and geochemical data and a detailed discussion of the climatic context for our studies are contained in prior papers (Fritz et al., 2007, 2010).

1.1. Site description

Lake Titicaca (Fig. 1) consists of a large (7131 km²) deep (max depth 284 m, mean depth 125 m) main basin (Lago Grande) and a smaller (1428 km²) shallower (max depth 42 m, mean depth 9 m) basin (Lago Huiñaimarca), which are connected at the Straits of Tiquina by a sill at 25 m depth. In the contemporary lake, inter-annual variation in lake level is most strongly influenced by precipitation (Baker et al., 2001a), which enters the lake in both direct rainfall (~47%) and inflow (~53%) from six major rivers. In the 20th century, water loss via evaporation (~91% of total losses) is less variable from year to year than precipitation over the lake. Less than 9% of water is lost via the sole surface outlet, the Río Desaguadero (3804 m elevation) (Roche et al., 1992). Thus, the lake is effectively a closed basin and has moderately elevated salinity (~1 g L⁻¹). Waters are of the NaCl(SO₄) type.

Lake Titicaca is a warm monomictic lake, and the water column is commonly stratified between October and June. Stratification is usually relatively weak, with a temperature difference between the epilimnion and hypolimnion of <5 °C (Kittel and Richerson, 1978).

In many years, winter mixing is incomplete, particularly in years of high winter temperatures (Richerson et al., 1992). The lake is nitrogen-limited (Wurtsbaugh et al., 1985, 1992), with a dissolved inorganic nitrogen to soluble reactive phosphorus ratio of <3:1. The major source of nitrogen is nitrogen fixation; most external nitrogen and phosphorus loading occurs in stream flow during summer months. Silica concentrations in the epilimnion (0.5–1.8 mg L⁻¹) (Iltis et al., 1992) are frequently below concentrations limiting for diatom growth (Wurtsbaugh et al., 1985). The contemporary algal flora is composed primarily of chlorophytes (43–57%), cyanophytes (10–12%), and diatoms (27–39%) (Iltis, 1992). Diatoms bloom primarily during isothermal mixing; during years when mixing is not as deep, diatom biomass is greatly reduced (Richerson et al., 1992).

2. Methods

Overlapping drill cores were obtained in 2001 from three locations in Lake Titicaca, using the GLAD 800 drilling platform and coring system. The analyses reported here are from site LT01-2B (Fig. 1) to the east of Isla del Sol in 235 m water depth. The site was drilled to a total depth of 136 meters below the sediment floor of the lake (mblf). The cores were shipped back to the U.S. and are stored at the University of Minnesota Lacustrine Core Repository (LacCore).

Photographs and detailed sedimentological descriptions were made of the core, which was sub-sampled at a resolution of 10 cm in units of apparently uniform lithology and at 2-cm intervals in units of more variable lithology. Diatom species composition was determined at 20-cm intervals (~700 samples) throughout the drill-core sequence. Samples for diatom analysis were treated with 10% hydrochloric acid to remove carbonates and cold hydrogen peroxide to oxidize organic matter and then were rinsed to remove

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