Palaeogeography, Palaeoclimatology, Palaeoecology 417 (2015) 467–475

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

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

Hydrological connectivity and mixing of Lake Towuti, Indonesia in response to paleoclimatic changes over the last 60,000 years

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ARTICLE INFO

Article history:
Received 28 July 2014
Received in revised form 2 October 2014
Accepted 8 October 2014
Available online 12 October 2014

Keywords:
Indonesia
Tropical paleoclimate
Redox
Sediment provenance

ABSTRACT

The Indo-Pacific Warm Pool (IPWP) is an important driver of global climate, but its response to and involvement in paleoclimate change is poorly constrained. We generated a new record of sediment geochemistry from Lake Towuti (2.5°S, 121.5°E), Indonesia, located in the heart of the IPWP, to investigate changes in hydrological connectivity with upstream lakes and the extent of lake mixing and oxygenation during paleoclimate changes over the last 60,000 years BP (60 ka). Lake Towuti is located at the downstream end of the Malili Lakes, a chain of large, ancient, and biologically diverse tectonic lakes occupying a geologically heterogeneous terrain in central Sulawesi, Indonesia. Major and trace element data from river and lake sediments suggest no changes in sediment provenance during the Last Glacial Maximum (LGM), indicating that some of the Malili Lakes remained hydrologically open despite a regionally drier climate. However, samples from the LGM are uniformly less enriched in trace elements than samples from the Holocene and Marine Isotope Stage 3 (MIS3), which suggests a decrease in weathering intensity during the LGM, likely in response to decreased precipitation and temperature. Changes in Fe and other redox-sensitive trace element concentrations indicate changes in water column oxygenation, with the highest oxygen availability occurring during the LGM (15–35 ka) likely due to more frequent and/or deeper mixing of Lake Towuti's water column. The glacial–interglacial trend in lake oxygenation corresponds with changes in regional precipitation and associated changes in the seasonal cycle. The high degree of faunal endemism in these lakes may be related to changes in the lake geochemistry associated with glacial–interglacial environmental variability driven by changing inputs and redox variability.

1. Introduction

The Indo-Pacific Warm Pool (IPWP) houses the largest region of high sea surface temperature (>28 °C) and strong atmospheric convective activity on Earth. It exerts significant control on the global atmospheric moisture budget, and thus it can influence climate on the global scale (Cane and Clement, 1999; Clement et al., 2001; Chiang and Koutavas, 2004; Broccoli et al., 2006; Fedorov et al., 2006; DiNezio and Tierney, 2013; Russell et al., 2014). Linked to Walker Circulation and the Inter-Tropical Convergence Zone (ITCZ), the IPWP drives heat and moisture exchange between the tropics and the mid-latitudes and between the Pacific and Indian Oceans.

The Malili Lakes (Matano, Mahalona, and Towuti) of Sulawesi, Indonesia are large tropical lakes that are both sensitive to and optimally located to record climate variability in the IPWP (Fig. 1). At present these lakes are hydrologically open, with outflow from the most upstream lake, Matano, draining into Lake Mahalona and then into Lake Towuti. These lakes contain exceptional faunal endemism and floral diversity that make them part of a unique tropical ecosystem that contains outstanding parallel adaptive radiations of gastropods (von Rintelen et al., 2004), parathelphusid crabs (Schubart et al., 2008), atyid shrimps (von Rintelen et al., 2010), telmatherinid fishes (Herder et al., 2006), and diatoms (Bramburger et al., 2008). In addition to the high rates of biological endemism across the Malili Lakes as a whole, each lake contains its own endemic fauna despite the existence of hydrological connections that could allow biological exchange between lakes. This might favor allopatric speciation during periodic hydrological separation of the lakes, which may occur when dry conditions cause lower lake levels. Such hydrological closure occurred during the extreme 1997–98 El Niño event when severe drought lowered lake levels by three meters at Towuti (Tauhid and Arifian, 2000). Prolonged dry conditions caused by large-scale climate changes within the IPWP may therefore be an important forcing by which biological endemism developed.

One such extended dry period in central Indonesia was the last glacial maximum (LGM), as suggested by terrestrial runoff (Russell

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http://dx.doi.org/10.1016/j.palaeo.2014.10.009
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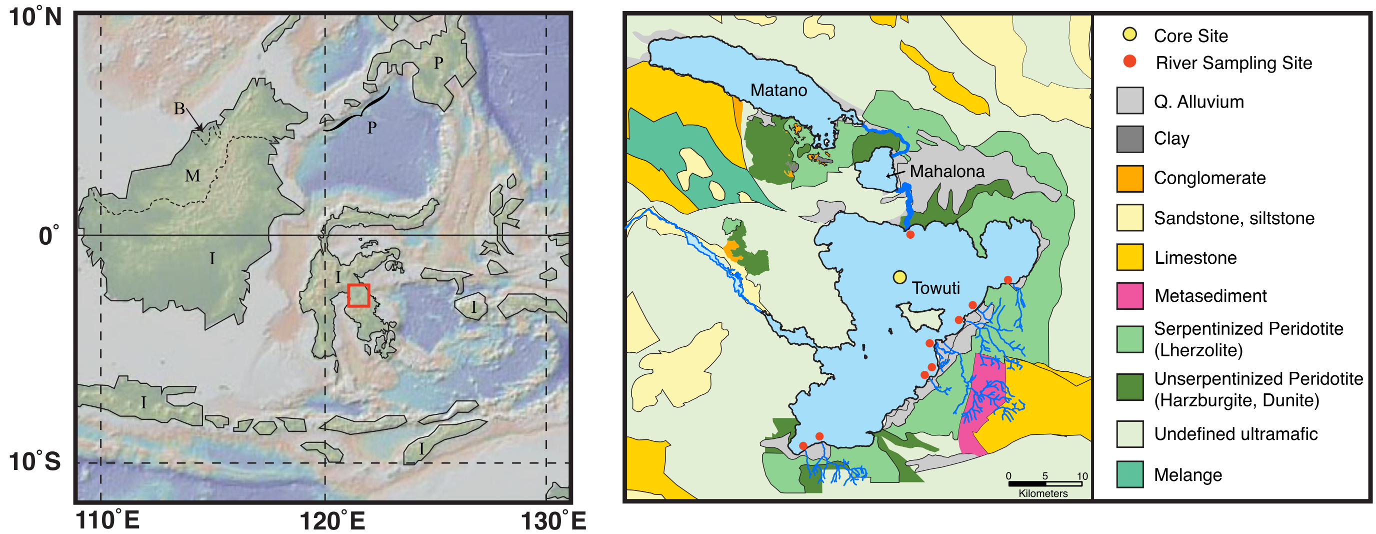

Fig. 1. *Left*: Map of the Indo-Pacific Warm Pool region. Red box indicates the location of the Malili Lakes on Sulawesi, Indonesia. Dashed lines reflect political boundaries. P: Philippines, M: Malaysia, B: Brunei, I: Indonesia. Unmarked islands are part of Indonesia. *Right*: Geological map of the Malili Lakes: Matano, Mahalona, and Towuti. Red dots indicate the locations of river sediment samples. Yellow dot indicates the location of the TOW9 piston core. Regional bedrock is based on surveys by PT VALE Indonesia (2008), a nickel mining company that operates in the region. The Malili Lakes are generally underlain by heavy-metal-rich, trace-metal-poor ultramafic rock, but notable exceptions include limestone partially underlying southwestern Matano and metasedimentary complex draining into southeastern Towuti.

et al., 2014) and vegetation indicators such as pollen and carbon isotopes of leaf waxes (Dam et al., 2001; Hope, 2001; Russell et al., 2014). Carbon isotopes of terrestrial leaf waxes ($\delta^{13}C_{wax}$) imply that the vegetation surrounding Lake Towuti varied from the closed-canopy rainforest, present during the Holocene and Marine Isotope Stage 3 (MIS3), to a more open forest ecosystem with dry-adapted C_4 grasses during the LGM (Russell et al., 2014). These ecological shifts suggest reduced precipitation during the LGM, consistent with regional pollen and lake level records from Lake Tondano (Dam et al., 2001) and Wanda Swamp (Hope, 2001). Lakes Matano, Mahalona, and Towuti occupy geologically heterogeneous catchments, and if dry conditions lowered the lake levels of Matano and Mahalona, the chemical composition of sediment in Lake Towuti would shift towards that of the sediment from the surrounding catchment areas rather than that coming from the upstream lakes, providing a tracer of regional lake levels and hydrological connectivity. Furthermore, drier and colder conditions may result in increased lake mixing due to decreased thermal stratification, which would increase oxygen availability in the lakes' hypolimnia. Changes in oxidation state and the resulting impacts on nutrient (e.g. P) cycling may also play a role in the development of faunal endemism (von Rintelen et al., 2012). These changes in oxidation state will be recorded in the sediment by changes in the concentration of oxygen-sensitive (redox) elements, like Fe and Cr (Brown et al., 2000). Lake Towuti is rich in these redox elements because of the heavy-metal-rich ultramafic bedrock (Monnier et al., 1995; Kadarusman et al., 2004), and thus the lake should retain a robust record of changes in redox conditions over time. This paper will utilize major and trace element data from sediment in Lake Towuti to investigate changes in the lakes' hydrological connectivity and redox variability and the consequent implications for regional climate in the IPWP over the past 60,000 years.

2. Site information/geological background

Sulawesi, Indonesia is located at the junction of the Australian, Pacific, and Eurasian tectonic plates (Monnier et al., 1995). Formed from the collision and accretion of island arcs and the obduction of oceanic crust on the Eurasian margin, the island is a bedrock collage that includes one of the three largest ophiolites in the world (Monnier et al., 1995; Hope, 2001; Kadarusman et al., 2004). While the exact age of the Malili Lakes is poorly known, they are thought to have formed between 1 and 2 Ma as a result of extensional tectonics associated with the Matano Fault, a major regional strike-slip fault. The region remains tectonically active with slip rates in the Malili Lakes region on the order of tens of mm/year. The dominant bedrock is peridotite, likely obducted during the Miocene (Kadarusman et al., 2004), which outcrops primarily as serpentinized lherzolite around Lake Towuti, with harzburgite and dunite outcropping near Lake Matano and Mahalona.

Lake Towuti (2.5°S, 121.5°E, 560 km^2 surface area, 318 m above sea level) is the largest of the Malili Lakes, with a catchment area of ~1600 km^2 and maximum depth of 205 m (Russell et al., 2014). The lake is relatively dilute (210 μS/cm) with a chemistry dominated by Mg^{2+} and HCO_3^- (Lehmusluoto et al., 1995; Haffner et al., 2001). Biological alteration and authigenic mineralization are minimal in the neutral (pH = 7.3–7.7), hyposulfidic (SO_4^{2-} = 1.5–2 ppm) and ultra-oligotrophic lake waters. Because the lakes are removed from major volcanic centers and the prevailing winds would carry Asian and Australian dust away from the region, we assume that aeolian and volcanic input is minimal over the investigated time period. Therefore, the chemical composition of sediment in Lake Towuti should primarily reflect changes in the relative contributions of the three distinct sediment sources and changes in the redox state of the lake bottom waters. Lake Towuti receives inflow from three sources: 1) the Mahalona River, which drains Lake Mahalona, 2) smaller drainages from the surrounding peridotite, and 3) drainage of a small metasedimentary complex to the southeast of the lake (Fig. 2). The Mahalona River encompasses approximately half of Towuti's drainage area and is by far the most important river delivering water and sediment. Although the Mahalona River catchment area includes drainage into Lakes Mahalona and Matano, much of the sediment from these upstream catchments is trapped in those lakes before reaching Lake Towuti.

The Malili Lakes region is located at the heart of the IPWP, and its climate is controlled by a complex interplay of the Walker Circulation, Austral-Indonesian Summer Monsoon, long term ITCZ migration, and El Nino-Southern Oscillation (Aldrian and Susanto, 2003; Hendon, 2003). Located just south of the equator, the region is hot (monthly temperatures 26 ± 1 °C) and humid (average precipitation 2900 mm/year; Hope, 2001). During the rainy season, from November to May, precipitation >250 mm/month is sustained by the northern monsoon,

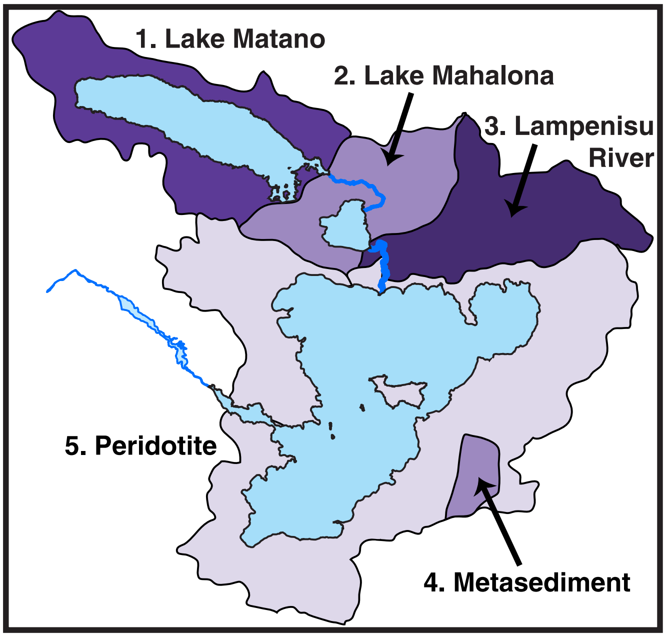

Fig. 2. Hydrological map of the catchment basins draining into the Malili Lakes. 1) Lake Matano catchment. 2) Lake Mahalona catchment. 3) Lampenisu River catchment. 4) Lake Towuti metasedimentary catchment. 5) Lake Towuti perioditic catchment. The total catchment of the Mahalona River encompasses catchments 1, 2, and 3.

warm sea surface temperatures (SSTs), and strong local convection within the ITZC (Hendon, 2003; Russell et al., 2014). The dry season occurs in July–October when the southeastern monsoon and cooler SSTs dampen local convection, causing precipitation to fall below 200 mm/month (Aldrian and Susanto, 2003; Hendon, 2003). The combination of heavy rainfall and ultramafic bedrock results in intense weathering that generates several meter thick lateritic soil horizons composed of as much as 60% iron oxide (Hope, 2001).

3. Materials and methods

Major and trace elements were analyzed on sediment from piston core TOW9, which was taken from Lake Towuti in March 2010 at 154 m water depth (Russell et al., 2014). The age model for this core is based on 23 AMS ^{14}C dates on bulk organic carbon (n = 20) and terrestrial macrofossils (n = 3) interpolated using a mixed effect regression (Russell et al., 2014).

Major (Al, Ca, Mg, Fe, K, Na, Si) and select trace (Cr, Mn, Ni, Sr, Ti) elements were analyzed in sediment following the procedure in Murray et al. (2000). The samples were combined with lithium metaborate flux in graphite crucibles and fused at 1050 °C for 10–12 min. The fused bead was dissolved in 10% HNO_3, agitated for at least 30 min, and then filtered and diluted for analysis. Samples were analyzed on a Jobin Yvon JY2000 Inductively Coupled Plasma Atomic Emission Spectrometer (ICP-AES) at Brown University. Concentration data are calibrated to fluxed standard reference materials (NIST1646a, BIR-1, MESS-3, DTS-2B, SGR-1, NIST2702, MAG-1, SDO-1, NIST2711, BHVO-2). Standard deviations are based on six analyses of an internal sediment standard.

A subset of samples was also analyzed for trace elements following acid digestion (concentrated HNO_3 and HF) at 260 °C and 100 bar in an UltraWave Microwave Digestion system. Samples were analyzed on a Thermo X Series II Inductively Coupled Plasma Mass Spectrometer (ICP-MS) at the University of Rhode Island. Each sample was analyzed in duplicate, with each run consisting of 3 sweeps across the entire mass range. Count data are calibrated to the same standard reference materials used for ICP-AES (see above). Standard deviations are based on six analyses of an internal sediment standard.

To characterize the three sediment sources, major and trace elements were analyzed on river bedload sediments collected in March 2013 following the procedures outlined above. Fe concentrations were directly analyzed in acidified, filtered lake water (collected in March–July 2013) on the ICP-AES.

High-resolution Fe and Cr count rate intensities were analyzed on u-channel core sections with an X-ray fluorescence (XRF) core scanner at the University of Cologne using a Mo-tube at 30 kV and 30 mA, scanning at 2 mm resolution, and integrating over 10 s per measurement. XRF counts were calibrated to weight percent using the ICP-AES measurements and the procedure outlined by Russell et al. (2014). Lake water temperatures were monitored over 2012–2013 with Onset® Hobo® Tidbit loggers deployed at 15-m depth intervals through the lake water column at 2.72002°S, 121.52665°E. Synchronized measurements were taken every two hours from 5 August 2012–14 July 2013.

4. Results

The river sediments can be separated into three groups based on their geochemistry. The first group is defined by relatively high Sr (69.2–73.2 ppm), Al (6.05–7.24 wt.%), Ca (3.06–6.57 wt.%), K (1.52–1.57 wt.%), Na (0.21–0.42 wt.%) and Ti (0.48–0.54 wt.%), low heavy metal content, with Fe (6.45–7.33 wt.%), Mg (2.76–5.77 wt.%), Cr (0.10–0.32 wt.%), and generally high concentrations of trace elements (Rb, Y, Zr, Cs, Ba, La, Pr, Nd, Sm, Eu, Tb, Gd, Dy, Ho, Er, Tm, Yb, Lu, Hf, Pb, Th), with the sum of trace elements (ΣTE) ranging from 369–483 ppm. The second group is defined by relatively high heavy metal concentrations, with Fe (15.3–28.9%), Mg (6.36–15.9%), Cr (1.00–2.38 wt.%). It is relatively depleted in Sr (0.54–5.75 ppm), Al (2.32–5.93 wt.%), Ca (0.42–1.44 wt.%), K (0–0.09 wt.%), Na (0–0.04 wt.%) and Ti (0.03–0.31 wt.%), as well as in trace elements with ΣTE ranging from 14.5 to 91.3 ppm. The third group is defined mainly by high Mg content (21.3 wt.%), and it is intermediate between Groups 1 and 2 in most other elements: Fe (10.8 wt.%), Cr (0.93 wt.%), Sr (14.7 ppm), Al (3.22 wt.%), Ca (1.31 wt.%), K (0.14 wt.%), Na (0.09 wt.%) and Ti (0.15 wt.%), as well as in trace elements (ΣTE of 100 ppm).

Elemental data show distinct and coherent variations over the 60,000 years covered by core TOW9. Al (3.06–6.51 wt.%), Ti (0.13–0.30 wt.%), and K (0.19–0.99 wt.%) generally have high concentrations from 60 to 38 ka, low concentrations from 35 to 15 ka, and high concentrations from 12 ka to the present (Fig. 3). The transitions between these intervals appear fairly abrupt. One exception to this general pattern is

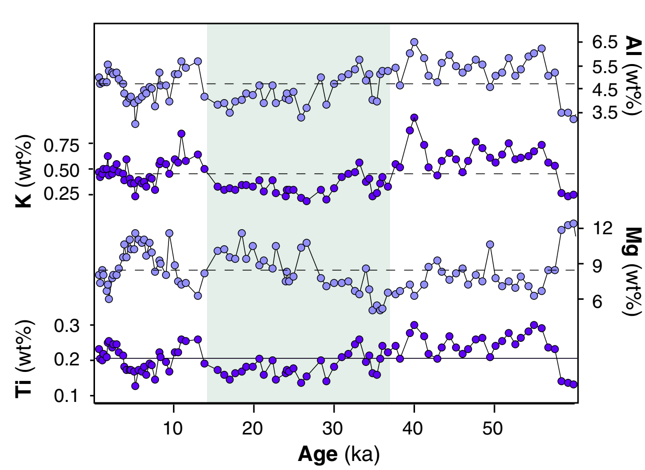

Fig. 3. Downcore profiles of major ion concentrations: Al, Mg, K, and Ti. The green band highlights the dry LGM period. There is a clear decrease in Al, K, and Ti concentrations during the dry LGM, but there is no distinct shift in Mg concentrations.

Mg, which shows no clear change corresponding to the LGM. The sediment from the LGM contains 8.12 ± 1.80 wt.% Mg, which is statistically equivalent ($p = 0.84$) to sediment deposited during the wet periods (8.65 ± 1.80 wt.% Mg).

Fe concentrations range between 7 wt.% and 23.5 wt.% during the past 60 ka (Fig. 4), with low concentrations from ca. 60 to 38 ka (average 13.7 wt.%), high concentrations from 38 to 12 ka (average 16.9 wt.%), and a return to low concentrations from ~12 ka to the present (average 13.4 wt.%). The transition from low Fe concentration to high Fe concentration appears abrupt, beginning ca. 38 ka, and Fe concentrations remain high until ~20 ka, when they start to gradually decrease into the Holocene. Heavy trace metals like Cr (0.29–0.37 wt.%) and Co (160–215 ppm) mirror the trend in Fe, while U (0.54–0.80 ppm) and V (131–135 ppm) decrease during the LGM, similar to the major elements.

5. Discussion

5.1. Sedimentary records of hydrological connectivity

Climate-driven lake level fluctuations could alter the hydrological connectivity between Lakes Towuti, Matano, and Mahalona, providing barriers to species exchange and potentially promoting biological diversification and endemism. While many of the endemic species in these lakes may be limited in their ability to migrate along the Mahalona River due to their specializations to muddy or rocky substrates, many of the Malili Lake taxa are thought to have evolved from riverine ancestors (von Rintelen et al., 2012). The presence or absence of this river should play a critical role in population connectivity and determine the potential for allopatric speciation within this system. The drier climate of the LGM reduced surface water availability (Russell et al., 2014) and may have turned the Malili Lakes into closed basins, although currently available data do not constrain past lake level changes. Without overflow from Lake Matano and Lake Mahalona, the Mahalona River flow would be significantly reduced as its flow would be limited to the Lampenisu River catchment, to the northeast of Lake Towuti. Because the Mahalona River is the dominant source of sediment to the TOW9 core site, changes in its discharge rate should impart substantial geochemical shifts in Lake Towuti sediment.

In this context the two largest of the Malili lakes, Matano and Towuti, are particularly important as they have the highest rates of biological endemism and diversity in the region (von Rintelen et al., 2012). To reconstruct the hydrological connectivity from Lake Matano to Towuti and the intensity of the Mahalona River flow, we investigated the geochemistry of Lake Towuti's sediment sources to identify distinguishing characteristics. The Mahalona River sediment signature is defined by harzburgite and dunite regions between Lake Mahalona and Lake Towuti, and so it is expected to be lower in Si, Ca, Al, and Ti and higher in Mg, Ni, and Cr than the more lherzolitic signature of sediment sourced from drainage of the surrounding peridotite (Monnier et al., 1995; Kadarusman et al., 2004). Sediment derived from the metasedimentary complex is expected to be much higher in Ca, Al, K, and Na and much lower in Mg, Ni, and Cr than both the Mahalona-sourced and surrounding peridotite-sourced sediments. Major element analyses of river sediments support these predictions and highlight the utility of Mg and K in particular in distinguishing the three sediment sources (Fig. 5a). The peridotite rivers have very low K concentrations (<0.09 wt.%) as does the Mahalona River (0.14 wt.%) while the metasedimentary rivers contain an order of magnitude more K (1.52–1.57 wt.%). The Mahalona River is distinctive in its high Mg concentration (21.3 wt.%) compared to the other peridotite rivers (8.64–15.9 wt.%), but its major element signature is otherwise intermediary between those of the metasedimentary complex and the general peridotite drainage. Without using Mg, it would be difficult to unambiguously distinguish the Mahalona River from a mixture of metasediment and peridotite (Fig. 6).

While these data suggest that changes in the Mahalona River input should be detectable in Towuti sediments, analysis of Mg and K in core TOW9 reveals no apparent shift in input from the Mahalona River relative to other sediment sources between the dry LGM (15–35 ka) and wet Holocene and MIS 3 (0–15 ka and 35–60 ka). The compositional fields for these time periods overlap significantly within a three endmember mixing model (Fig. 5a). While the relatively constant Mg content in the lake sediment suggests a stable relationship between the Mahalona River and the other river sources, and therefore continued flow from the upstream lakes to Lake Towuti, K content in the lake sediment decreases significantly ($p > 0.999$) from the wet periods to the dry period. Lowered K concentrations imply that sediment input from the metasedimentary source decreased relative to peridotite sources and the Mahalona River. Decreased precipitation during the dry period would decrease the flow from the metasedimentary rivers, but it would simultaneously reduce the flow from all river sources. There are no morphological constraints (e.g., river sills or active fault) to explain how the metasedimentary source input into the lake could be reduced relative to that of the other sources based solely on hydrological changes during the dry period.

While the major element composition of river sediment appears to distinguish major sediment sources in the present, Mg and K concentrations may not be a reliable method of tracking changes in river input over time. This is because the lake sediment composition convolves source rock composition with the chemical environment of weathering, transport, and deposition. Increasing the degree of chemical weathering will solubilize major elements (e.g., Ca, Mg) so that their concentrations in the lake sediments vary independently from hydrological changes affecting sediment provenance and the volume transport of the rivers. Furthermore, authigenic mineralization of carbonates, although expected to be small in Lake Towuti, will interfere with the ability of the lake sediments to provide a sound record of detrital input from sediment sources (Muller et al., 1972). Changes in erosion intensity can also alter the major element concentration of sediment delivered to Lake Towuti. The thick laterite soils in this region are formed by the

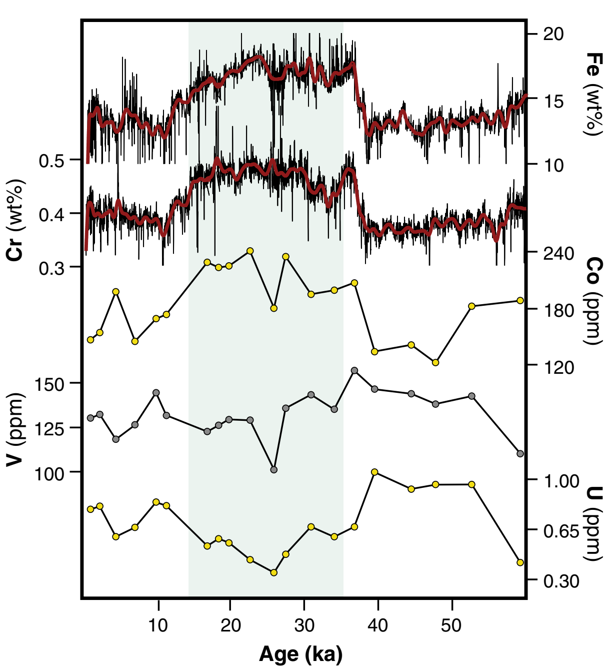

Fig. 4. Downcore profiles of redox-sensitive elements: Fe, Cr, Co, V, and U. Fe and Cr concentrations from ICP-AES calibrated XRF counts, following the procedure described in Russell et al. (2014). Red lines are filtered at 1kyr. The green band highlights the dry, more oxygenated LGM period. A shift to more oxygenated conditions increases Fe, Cr, and Co concentrations and decreases U and V concentrations in the sediment.

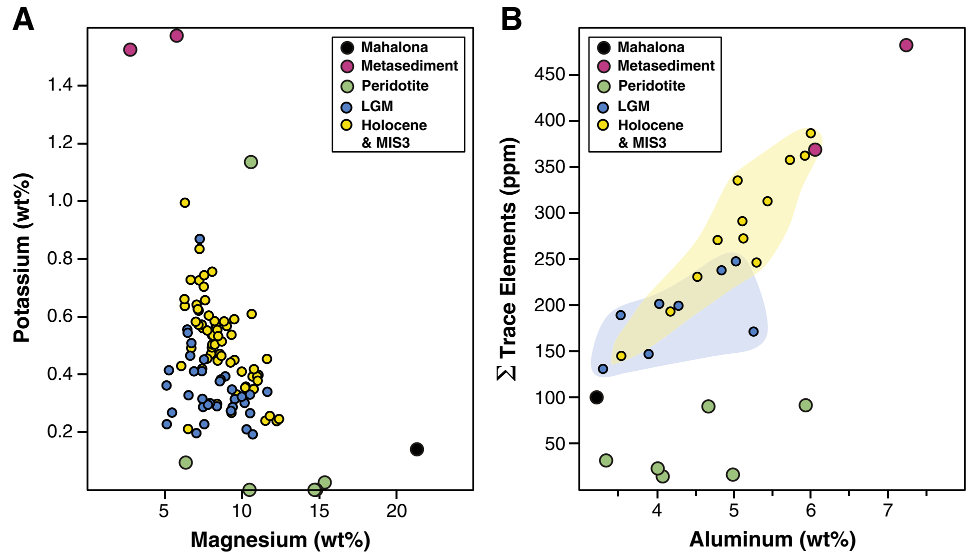

Fig. 5. A) Potassium and magnesium concentrations for the rivers and the TOW9 lake sediment. LGM (15–35 ka, blue) and Holocene & MIS3 (0–15 ka and 35–60 ka, yellow) periods are segregated based on $\delta^{13}C$ of terrestrial leaf waxes (Russell et al., 2014). There is no statistically significant shift in the Mg content of the lake sediment during the dry LGM, which suggests that the Mahalona River flow was not impacted by loss of upstream overflow from Lake Matano and Lake Mahalona. The decrease in K during the dry LGM suggests a reduction in input from the metasedimentary source. B) Aluminum and total trace element concentrations for the rivers and the TOW9 lake sediment. The sediments from the wet Holocene and MIS3 show 2-endmember, linear mixing between the Mahalona River and the metasedimentary source. The sediments from the dry LGM reflect 3-endmember mixing, in which the peridotite rivers have more influence due to a reduction in the metasedimentary input.

progressive chemical and physical weathering of the ultramafic bedrock, leaching Mg, Ca, and Si and residually concentrating Fe, Al, and Ti (Brand et al., 1998). The garnierite horizon, directly above the bedrock, is the least weathered, and thus it contains more primary, Mg-rich minerals, fewer secondary Al- and K-rich clays, and coarser grains than the surface limonite horizon (Brand et al., 1998). Increased incision into the soil horizons would shift the sediment composition from the K-rich surface clays and towards the deeper Mg-rich primary minerals. Such a shift to deeper erosion during the LGM may explain the relatively constant Mg concentration at TOW9 over time: a decrease in the Mg-rich Mahalona River sediment may have been compensated by deeper erosion into the Mg-rich garnierite soil horizon. The combination of these processes can result in lake sediment so overwritten by chemical processes that major element concentrations fail to reconstruct the sediment provenance (Weltje and von Eynatten, 2004).

Because the trace elements selected for this study are negligibly soluble in freshwater, they are generally more faithful recorders of the provenance of detrital input. Peridotites range from depleted to slightly enriched in trace elements relative to bulk silicate earth (Mcdonough and Sun, 1995), and trace element concentrations in peridotites in the

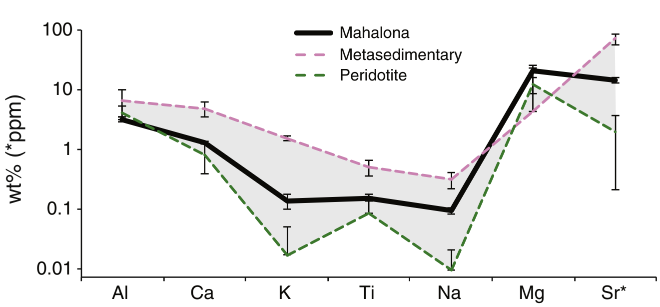

Fig. 6. Average major ion concentrations for the three river groups: the Mahalona River (2 samples), metasedimentary drainage (2 rivers), and peridotite drainage (6 rivers). All elements except Mg are more concentrated in the metasedimentary rivers than the peridotite rivers. The Mahalona River is indistinguishable from a mixture of peridotite and metasedimentary rivers for all major elements except Mg.

Malili Lakes region are below detection limits (Kadarusman et al., 2004). Because the trace elements are negligible in peridotites, we would not expect their concentrations to be influenced by changes in erosional intensity. In comparison, sediment sourced from the metasedimentary complex should be relatively enriched in trace elements, and, like potassium, the summed concentration of trace elements (ΣTE) in the lake sediments should reflect drainage directly into Lake Towuti from the metasedimentary complex. Indeed, variations in total trace element concentrations relative to Al distinguishes the three sediment sources (Fig. 5b). The peridotite rivers subdivide into a source with extremely low ΣTE (14.5–31.9 ppm) and another with low ΣTE (90.2–100 ppm). The Mahalona River belongs to the latter, although its Al concentration (3.22 wt.%) is low relative to most other peridotite rivers. As expected, the metasedimentary river sediments are relatively enriched in trace elements (ΣTE = 369–483 ppm), contributing up to four times as much as the peridotite rivers and making them the dominant source of trace elements to Lake Towuti.

With these tracers, changes in sediment source and inferred hydrological changes in Lake Towuti can be reconstructed over time. The data show a marked shift in lake sediment geochemistry between dry (15–35 ka) and wet (0–15 ka and 35–60 ka) time periods. During the wet periods, the lake sediment composition varies in a roughly linear manner between the high Al, high ΣTE metasedimentary rivers and the low Al, low ΣTE peridotite rivers, with the Mahalona River as a low Al endmember. The predominance of these two endmembers stems from the large sediment input of the Mahalona River versus the high trace element concentration of the metasedimentary rivers; the low volume, trace-element-poor peridotite rivers have a limited impact on the lake sediment composition during the wet period. During the dry period, however, the lake sediments become more depleted in trace elements and slightly less Al-rich. The Mahalona River remains the depleted endmember in the mixing model, but the second endmember rotates from the high Al, high ΣTE metasediment source towards the high Al, low ΣTE peridotite sources. The rotation of this mixing regime suggests relatively diminished input from the metasedimentary source during the dry period, confirming the findings from Mg and K concentrations.

This shift in sediment source indicated by trace element concentrations is not easily explained by regional changes in hydrological connectivity linked to variations in the flow of the Mahalona River. If dry conditions during the LGM lowered lake levels enough to close the Malili Lakes, the Mahalona River flow would have been severely reduced relative to that of other rivers. Assuming that water flow is proportional to catchment area, outflow from Lake Matano (catchment area, including lake surface: 440 km^2) currently supplies ~49% of the Mahalona River water entering Lake Towuti, outflow from Lake Mahalona supplies ~22% of the Mahalona River water due to its slightly smaller catchment area (208 km^2), and the Lampenisu River to the northeast of Lake Towuti contributes ~29% of the Mahalona River water because of its catchment area of 259 km^2. The total Mahalona River catchment area (907 km^2) is considerably larger than that of the general peridotite drainage into Lake Towuti (805 km^2) and an order of magnitude larger than the metasedimentary drainage (35 km^2). In the present, the Mahalona River contributes ~52% of all river water delivered to Lake Towuti, making it the single dominant river for geochemical input in northern Lake Towuti.

If Lake Matano closed but Lake Mahalona remained open, the Mahalona River flow volume would reduce by about 50%, but it would still remain an important water and sediment source by contributing 36% of the river water delivered to Lake Towuti, far more than any other river. While this somewhat limits the sensitivity of our approach to detecting Lake Matano closure and possible inter-basin isolation, a 50% reduction in Mahalona River flow relative to the other rivers should still be detectable as reduced inputs of Mg and increased ΣTE and Al. If Lake Mahalona also closed, the Mahalona River flow volume would reduce by 70%, decreasing its contribution of water delivered to Lake Towuti to 24%. This reduction in Mahalona River input would impart a strong reduction in Mg and increase in Al and a shift of the geochemical signature towards that of the surrounding peridotite, and rotate the two-endmember mixing model from a Mahalona River-metasedimentary mixing regime to peridotite-metasedimentary mixing regime.

Instead, during the LGM we observe no loss of the Mg-rich Mahalona River material in the mixing model, which strongly suggests maintenance of the connection at least between Lake Mahalona and Lake Towuti, and likely Matano, Mahalona, and Towuti. Without upstream basin closure, the relative differences in sediment inputs of the sources are likely to remain similar to the modern (e.g., Talbot et al., 2000). This occurs despite strong evidence for regionally dry conditions, yet recent $\delta^{13}C$-based hydrological evidence suggests that dry conditions during the LGM were less severe at Lake Matano than at Lake Towuti (Wicaksono et al., in revision). This is likely due to wetter conditions persisting in the higher elevation catchment of Lake Matano. Our geochemical data supports this scenario and suggests that Lake Matano is likely to have remained hydrologically open during this time.

Instead the apparent decrease in the metasedimentary source may be related to glacial–interglacial changes in erosion and the rates of chemical weathering. Changes in weathering affect parent rocks to different degrees depending on their mineralogy: feldspars, zircons, quartz, and other metasedimentary minerals are much more resilient than olivine and pyroxenes in peridotite (Weltje and von Eynatten, 2004). During the LGM, a decrease in weathering intensity, consistent with lowered precipitation (Russell et al., 2014) and temperature (inferred from SST, Reeves et al., 2013 and references therein), would result in a greater reduction in weathering of the more resistant metasedimentary bedrock than the peridotite bedrock. Because the metasediment is the predominant source for trace elements, decreased chemical weathering will bias the lake sediment composition towards the peridotite sources independent of hydrological shifts. Furthermore, trace elements are not entirely immune to changes in chemical weathering (Cullers et al., 1987). The fractionation of light and heavy rare earth elements may vary in response to weathering intensity (Balashov et al., 1964), and increased fractionation during the drier glacial period would be recorded in the sediment as an overall decrease in trace element concentrations. Lastly, the drier climate around Lake Towuti, and likely lower lake levels, should result in river incision, shifting the sediment supply towards less weathered, Mg-rich primary minerals. Thus, the most likely cause for the shift in the lake sediment geochemistry from the wet to the dry periods is a change in weathering intensity rather than a change in the hydrological regime of the Malili Lake system. With no evidence for upstream basin closure in the past 60 ka, intralake endemism, if caused by physical isolation, may have developed prior to this time or via sympatric speciation within each lake.

5.2. Redox variability

The solubility of many elements is dependent on both the oxygen availability (redox potential) and acidity (pH) of the lake waters, particularly at the sediment–water interface. Most redox sensitive elements (Fe, Cr, Co) are more soluble under reducing conditions (low oxygen availability), while a select few (U, V) are more soluble under oxidizing conditions (high oxygen availability). In general, the sedimentary concentration of a redox-sensitive element responds inversely to its solubility, so that high concentrations in the sediment reflect periods of low solubility. However, redox-sensitive elements can also be affected by processes independent of changes in oxygen availability including adsorption onto particulate matter (reduces soluble phase concentration), complexation with water and other ligands (enhances solubility), redissolution during diagenesis (distorts time series and signal amplitude), reaction kinetics (determines resolution), and changes in pH (may alter solubility) (Delfino and Lee, 1968; Tipping, 1998; Brown et al., 2000; Boyle, 2001). As different elements have different sensitivities to these processes, examining a suite of redox-sensitive elements (Fe, Cr, Co, U, V) that respond to different degrees to these non-redox effects provides insight into the redox conditions during sediment deposition (Brown et al., 2000) and can inform us about the distribution and availability of many biologically important trace elements (Buffle and Stumm, 1994; Hamilton-Taylor and Davison, 1995; S.A. Crowe et al., 2008).

The heavy-metal-rich ophiolitic bedrock makes Lake Towuti a unique environment to investigate changes in lake oxygenation and its effects on sediment chemistry. Sediment sourced from the peridotite contains as much as 28.9 wt.% Fe and 2.38 wt.% Cr, so that a shift in oxygen concentration in Towuti's water column would have a major impact on the lake sediment composition. Additionally, hyposulfidic Lake Towuti presents a novel context to study the effects of changing oxidation state on sediment geochemistry. Previous work on the metal geochemistry of large lake basins has been conducted primarily in sulfidic environments, such as Tanganyika (Brucker et al., 2011), Malawi (Brown et al., 2000), the Black Sea (Oguz et al., 2001), and Thau Lagoon (Elbaz-Poulichet et al., 2005), where concentrations of Fe and Cr are strongly affected by burial as sulfides under anoxic conditions. Lake Towuti provides the opportunity to investigate the behaviors of major (Fe, Cr) and trace (Co, U, V) elements in response to changes in oxygen availability with only negligible contribution of sulfur species.

Modern Lake Towuti is stratified, with nearly constant bottom water temperatures of 28.4 °C. Temperatures in the upper 90 m vary seasonally in response to changes in the lakes' heat budget and mixing, with lower temperatures and increased mixing of the lake during the dry season (July-Sept) due to evaporative cooling at the lake surface, enhanced long-wave heat loss due to reduced cloud cover, and reduced shortwave heat input (Fig. 7). The cooler and invariant temperatures below 90 m indicate that the bottom waters do not mix annually, and dissolved oxygen concentrations demonstrate anoxic conditions below ~140 m depth (S. Crowe, pers. comm.). Bottom water anoxia and its effects on metal solubility are corroborated by dissolved Fe profiles (sampled monthly at 10, 80, and 150 m depth) that illustrate elevated metal concentrations in Towuti's bottom waters. Hence, the temperature and chemical profiles show that 1) the modern climate does not fully

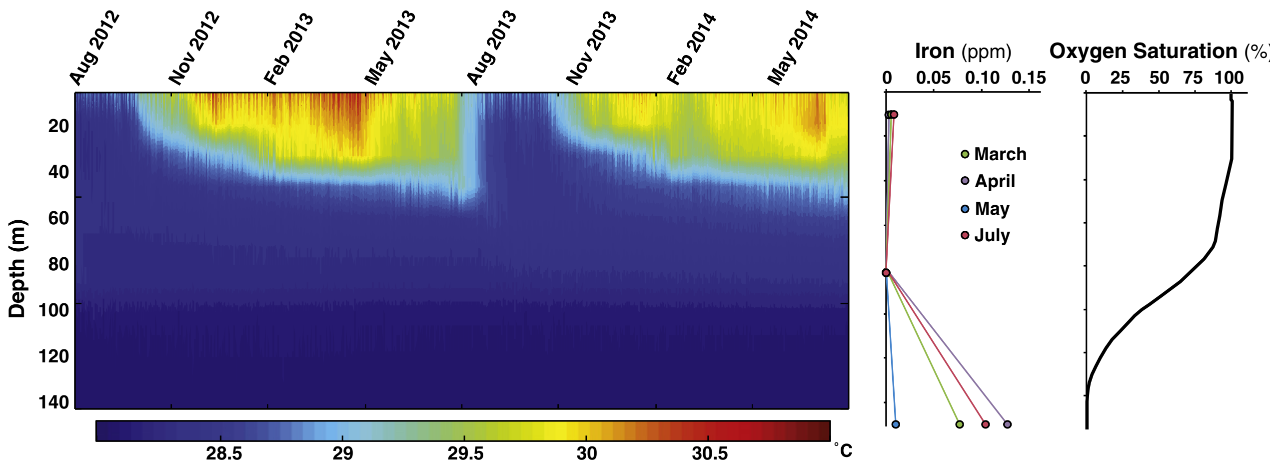

Fig. 7. (Left) Daily temperature profile of Lake Towuti, measured from August 2012 to June 2014 at 2.72002°S, 121.52665°E. Relatively constant temperatures below ~90 m suggest that the lake did not mix below that depth during the observational period. (Center) Dissolved Fe concentration profiles in March–July 2013 lakewater samples (June samples not available). Concentrations for 10 m and 80 m are nominally zero for all four months, indicating oxidizing conditions under which Fe is predominantly in solid phase. Measurable dissolved Fe in the deepest water samples suggests reducing conditions in the unmixed bottom layer. (Right) Oxygen saturation profile for Lake Towuti's deep basin, measured in 2013 (S. Crowe, *pers. comm.*).

mix Lake Towuti, 2) an oxycline exists between 70 and 140 m depth at present, and 3) the modern bottom waters are anoxic and enriched in dissolved heavy metals. Past climates with more vigorous mixing of the lake could increase the oxygen availability in these bottom waters, resulting in higher Fe concentrations deposited in the lake sediments.

Such an increase in Fe concentrations is observed in Lake Towuti during the last glacial period (Fig. 5). The ~25% increase in Fe concentrations during the LGM cannot be attributed to changes in erosion, as the changes in Mg imply, if anything, deeper erosion, while Fe is concentrated at the surface in lateritic soils. Rather, because the relative inputs of the rivers do not vary substantially with time, variability in heavy metal concentrations in the lake sediment should primarily reflect changes in the mixing regime and oxidation state of the lake bottom. Thus, these data suggest that the lake bottom waters were more oxygenated, an inference that is corroborated by corresponding increases in Cr and Co. Increased lake mixing and oxygenation during the LGM are further suggested by decreases in U concentrations and, to some extent, V concentrations , which both decrease due to the solubility of these elements in oxygenated water.

The redox conditions at the lake floor are directly dependent on the extent of mixing between oxygenated surface waters and the bottom waters in contact with the sediment. Since the extent of mixing responds to a complex interplay between surface wind stress, lake level, and lake temperature and density structure (Lewis, 1983), a substantial shift in climate would be required to change the oxygen concentration of Lake Towuti bottom waters (Fig. 8). Regional wind fields during the LGM are unknown, but increased wind strength during the LGM could have enhanced lake mixing. Lake Towuti is located within the Austral-Indonesian monsoon system, and grain size on the Chinese Loess Plateau, which positively correlates with the monsoon strength, indicates a strengthening of the winds during the last glaciation (Sun et al., 2011). However, thermally-driven density inversions are the dominant mechanism for mixing in this lake (Katsev et al., 2010), as they are in many tropical lakes (Lewis, 1983). In the present, this mixing is not strongly related to the wind regime, as the strongest winds occur during storms over the lake during the wet season, when the lake is stratified. Changes in the regional temperature may also have had an impact in the oxygenation of Lake Towuti. Colder air temperatures during the glacial in the IPWP (1–5 °C, Rosenthal et al., 2003; Garidel-Thoron et al., 2005; Stott et al., 2007; Reeves et al., 2013 and references therein) may have cooled the lake surface by increasing the sensible heat exchange between lake water and the air. However, sensible heat exchange is generally a small component of lake energy budgets compared to latent and longwave heat loss (Lewis, 1983). Moreover, both monsoon wind and regional temperature records suggest the windy and cool conditions during the LGM also characterized MIS3,

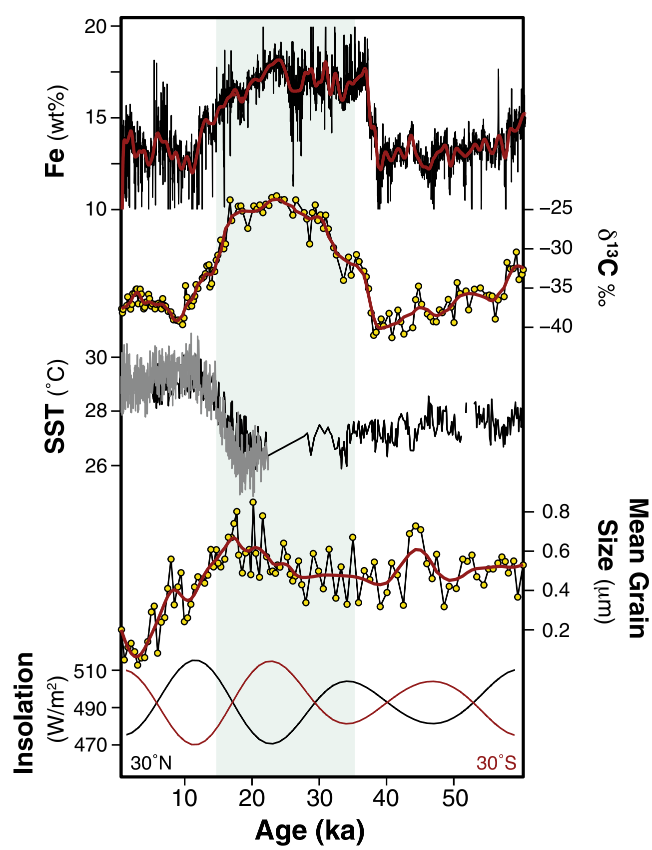

Fig. 8. Fe concentrations, reflecting oxygen availability, compared to proxies for possible forcings. The green band highlights the dry, more oxygenated LGM period. The redox signal is most coherent with changes in precipitation, which is inferred from $\delta^{13}C$ of terrestrial leaf waxes (Russell et al., 2014). More enriched carbon isotopes indicate drier conditions. Regional temperature, from Mg/Ca in foraminifera (Rosenthal et al., 2003; Stott et al., 2007), and wind stress, from mean grain size on the Chinese Loess Plateau (Sun et al., 2011), are consistent with oxygenated conditions during the glacial but do not replicate the abrupt changes observed in oxidation state.

when our data suggest strong stratification in Lake Towuti. Our redox signal also does not correlate with variations in northern or southern hemisphere summer insolation, regulated by orbital precession, so other processes seem likely to determine the changes in lake mixing that we observe.

The coherency between the redox signal and $\delta^{13}C_{wax}$ at Lake Towuti strongly suggests that changes in the extent of lake mixing were associated with changes in the regional hydrological cycle. In the present, reduced southern hemisphere insolation and increased evaporative cooling drive deeper seasonal mixing in Lake Towuti during the southern hemisphere winter, and thus, complete mixing of the lake is likely to result from an increase in the duration or intensity of the dry season. Interestingly, recent work has shown that regional vegetation, as reconstructed from $\delta^{13}C_{wax}$, is strongly sensitive to precipitation seasonality (Dubois et al., 2014). If so, a prolonged and more extreme dry season seem likely to have caused the changes in lake mixing and oxygen availability. The depth of lake mixing does not respond directly to precipitation or its seasonality, yet other climate variables that accompany seasonal changes in precipitation, such as humidity and cloud cover, do strongly affect lake heat budgets and therefore mixing. Thus, our data suggest that the interval from ~35 to 14 ka was characterized by increased seasonality, and particularly a more extreme and extended dry period with reduced humidity and cloud cover. These conditions lead to increased evaporation and long-wave heat loss from the lake surface, which cooled the lake and weakened the thermally-derived pycnocline, allowing for complete lake mixing. Thermal stratification may have still developed during the wet season, but the net increase in oxygen availability suggests that the duration of stratification was too short to fully deplete the oxygen from the hypolimnion. Thus, regionally cool and dry conditions enhanced mixing of Lake Towuti during the LGM, pushed the oxycline below the sediment–water interface, and resulted in increased deposition of Fe.

Stronger thermal stratification and weaker or more infrequent mixing would combine to reduce oxygen availability in the deep waters by 1) allowing greater consumption of bottom water oxygen and 2) reducing the mixing efficiency and thus the replenishment of the bottom water oxygen. The gradual return to anoxic bottom water conditions more or less follows the rise in regional sea surface temperatures (Fig. 8). Investigation into local changes in temperature and wind stress may provide valuable insight into how these forcings may or may not influence the redox state of Lake Towuti.

5.3. Paleobiological implications

The distribution and origin of Earth's amazing biodiversity is perhaps the major issue in evolutionary biology, ecology and conservation. Studies on the evolution of ancient lake organisms have continuously resulted in important insights into these issues (e.g. Brooks, 1950; Cohen, 2011). The Malili Lakes are an extraordinary example of intralake faunal endemism, with species flocks of fish, snails, shrimp, crabs, and other organisms. Genetic data indicate multiple colonizations of each lake by lacustrine as well as riverine ancestors, followed by intralacustrine diversification in response to alternative modes of resource use by trophic adaptations suggesting ecological speciation once the flocks are isolated (von Rintelen et al., 2012). This isolation and subsequent diversification may occur during hydrological closure of the lake basins, which results from regional drying as well as tectonic activity.

Here we present evidence for open hydrological exchange over the past 60 ka, at least between Lake Mahalona and Lake Towuti, despite a shift to drier conditions during the LGM (see Section 5.1). These data thus do not support recent (<60 ka) allopatric speciation as the cause of intralake endemism. Instead, endemism may have developed from much earlier (>60 ka) basin closure. Longer records of $\delta^{13}C$ of terrestrial leaf waxes as well as major and trace elements would provide insight into the timing of basin closures that may be important times of species diversification.

Alternatively, faunal endemism may have developed sympatrically due to 'ecological speciation' as taxa specialized to particular substrates or food sources. In this light, our data indicate large changes in Lake Towuti's geochemistry and nutrient availability, both of which accompany changes in weathering and redox conditions. The sulfur-poor, iron-rich environment of Lake Towuti, in combination with anoxic conditions has created new microbial niches (S. Crowe et al., 2008; Sabo et al., 2008), and many higher taxa may have developed sensitivities to trace element inputs. For example, the snail *T. kristinae* is found only on Loeha Island (Glaubrecht and von Rintelen, 2008), near the influx of trace element rich sediment from the metasedimentary complex. Lower weathering rates during the LGM could have favored those species adapted to low trace element conditions.

Furthermore, Fe cycling is a critical component of nutrient dynamics, especially in metal rich lakes like Lake Matano and Lake Towuti (Holtan et al., 1988). High concentrations of Fe may affect the bioavailability of nutrients and phosphorus in particular, by, on the one hand exerting toxicological stress, but on the other hand catalyzing biogeochemical reactions in a diverse microbial community. High concentrations of Fe also have secondary effects on other biologically important trace elements and nutrients (e.g., P), which react with and adsorb onto Fe oxides. Changes in the redox state of the bottom waters can release or sequester these nutrients in the sediment, and this resource partitioning may be important for regulating the composition and relative abundance of species in nutrient-poor Lake Towuti. As these lakes are already ultraoligotrophic in the present, a shift towards a more Fe-rich environment with even lower biological productivity during the LGM may have forced species adaptations and specializations to resource limitation (Brucker et al., 2011), favoring those species adapted for low food availability.

6. Conclusions

We generated a new record of sediment geochemistry from Lake Towuti to investigate the changes in hydrological connectivity and redox variability in response to climate change in the IPWP over the last 60 ka. Major and trace element data from the river sediments confirm the presence of three geochemically distinctive sediment sources, but they suggest almost no provenance shift during the dry LGM (15–35 ka), indicating that hydrological connectivity between the Malili Lakes was maintained throughout this time. However, the LGM samples are uniformly less enriched in trace elements than the wet period samples, which suggests a decrease in weathering intensity during the LGM, likely in response to decreased precipitation and temperature. The observed trends in Fe and redox-sensitive trace elements support a redox-driven change in sediment geochemistry during the dry period, with the highest oxygen availability occurring in the LGM. The high degree of faunal endemism in these lakes may have been influenced by these changes in the lake geochemistry during the LGM.

The long term (glacial–interglacial) trend in lake oxygenation corresponds to changes in the regional hydrological cycle (Russell et al., 2014) and likely seasonality that lead to prolonged, amplified dry periods with more efficient lake mixing. Regional cooling and increased wind stress may also impact the redox state of the lake, but their local effects on Lake Towuti are poorly constrained.

Acknowledgments

The authors thank Gerald Tamuntuan, Satrio Wicaksono, and Vale Base Metals for field assistance, David Murray and Joe Orchardo for laboratory assistance, and Sean Crowe for oxygen saturation data. We thank two anonymous reviewers for constructive feedback on this manuscript. This research was funded by NSF-EAR-1144623 to JMR.

Research permits for this work were granted by the Indonesian Ministry of Research and Technology (RISTEK).

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