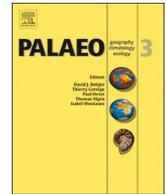




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# $\delta^{13}\text{C}$ records from fish fossils as paleo-indicators of ecosystem responses to lake levels in the Plio-Pleistocene lakes of Tugen Hills, Kenya

Anne L. Billingsley<sup>a,\*</sup>, Peter Reinthal<sup>b</sup>, David L. Dettman<sup>a</sup>, John D. Kingston<sup>c</sup>, Alan L. Deino<sup>d</sup>, Kevin Ortiz<sup>e</sup>, Benjamin Mohler<sup>a</sup>, Andrew S. Cohen<sup>a</sup>

<sup>a</sup> Department of Geosciences, University of Arizona, Tucson, AZ, United States of America

<sup>b</sup> Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, United States of America

<sup>c</sup> Department of Anthropology, University of Michigan, Ann Arbor, MI, United States of America

<sup>d</sup> Berkeley Geochronology Center, Berkeley, CA, United States of America

<sup>e</sup> Department of Earth and Environmental Sciences, University of Michigan, Ann Arbor, MI, United States of America

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## ABSTRACT

The carbon isotopic ratios of organic matter in fish fossils from diatomites and other lake beds in the HSPDP drill core from Tugen Hills, Kenya (2.56–3.29 Ma) reflect trophic resource uses and can indicate the dietary habitats of fish in the paleolake. This information offers insight into how fish communities responded to lake-level fluctuations during the Plio-Pleistocene in the East African Rift Valley. We have compared this record with fish fossil isotopes from both a previously published study of a Lake Malawi drill core (139 ka - present) and core top (modern ca 1978) samples collected at the water/sediment boundary from Lake Turkana (Kenya) of known environmental provenance. Both the Lake Malawi drill core fossils ( $-7.2\text{‰}$  to  $-27.5\text{‰}$  VPDB) and modern Lake Turkana samples ( $-16\text{‰}$  to  $-24.6\text{‰}$  VPDB) have  $\delta^{13}\text{C}$  values indicating a mix of near-shore and deep-water pelagic species. In contrast, the  $\delta^{13}\text{C}$  values for the Tugen Hills core fossils vary only between  $-20\text{‰}$  and  $-27\text{‰}$  VPDB. The absence of  $\delta^{13}\text{C}$  values greater than  $-19\text{‰}$  suggests none of these fossils are derived from near-shore benthic habitats. The lack of shallow water, benthic lacustrine fish fossils through the Tugen Hills lake cycles may indicate that the rate of change from low-lake stands to deeper lake phases was very rapid, and shallow water communities were not established for long enough to leave a fish fossil record at the core site. These results strongly suggest that lake-level responses to climate variability in the Baringo Basin of the East African Rift were very abrupt during the Plio-Pleistocene transition.

## 1. Introduction

Isotopic records from fish have been used to determine many aspects of the environment such as the source water of lacustrine systems, the functional redundancy and vulnerability of fish populations, the food partitioning within communities, and migration patterns (Bootsma et al., 1996; Zazzo et al., 2006; Joordens et al., 2011; Reinthal et al., 2011; Gownaris et al., 2015). The isotopic composition of both extant fish and fish fossils can offer insight into their ecological strategies and how they responded to climate and environmental changes. As the biological processes that control the isotopic values of fish communities operate similarly in most lacustrine environments, comparisons can be made between basins in different geographical locations as well as through time.

In 2013, a 228-meter core spanning the Plio-Pleistocene transition

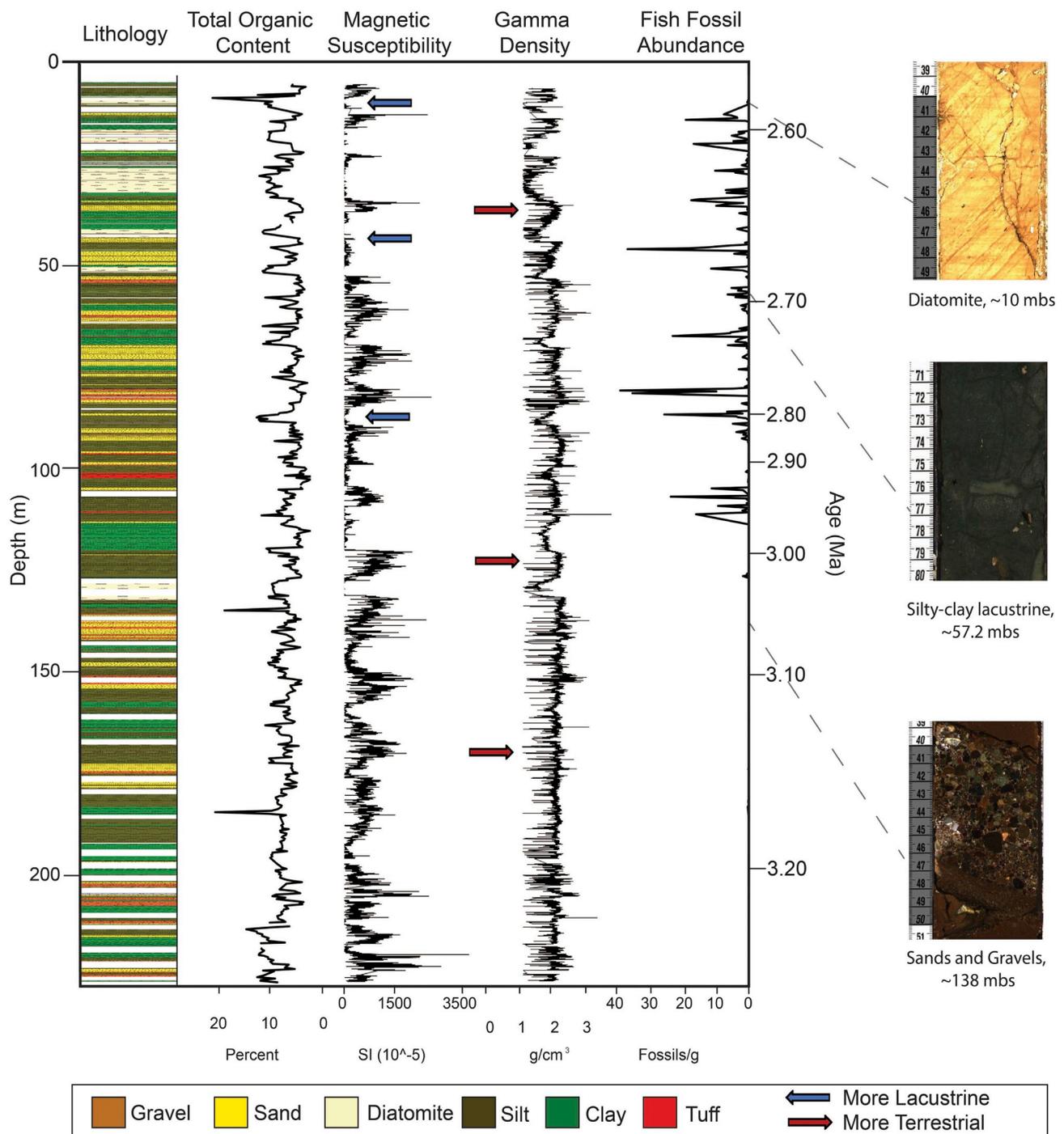
was taken from the Chemeron Formation of the Baringo Basin in the Tugen Hills region of Kenya as part of the Hominin Sites and Paleolakes Drilling Project (HSPDP-BTB13-1A, hereafter BTB13-1A) (Cohen et al., 2016). The drill site was chosen because of the paleoanthropological significance of the basin, which includes the recovery of several hominin specimens as well as relevant paleoenvironmental data (Cohen et al., 2016; Campisano et al., 2017). Prior detailed outcrop studies of lacustrine deposits provide a well dated context for the investigation of this core (Deino et al., 2006; Kingston, 2007; Wilson et al., 2014). This work had previously indicated a series of relatively large lakes occupying this portion of the central Kenyan rift during the Plio-Pleistocene, which underwent lake-level fluctuations driven by both precessional forcing and millennial-scale climate variability.  $^{40}\text{Ar}/^{39}\text{Ar}$  dating of BTB13-1A core shows that the core ranges in age from approximately 2.56–3.29 Ma (Deino et al., this issue), encompassing the Plio-

\* Corresponding author.

E-mail address: [albillin@central.uh.edu](mailto:albillin@central.uh.edu) (A.L. Billingsley).

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**Fig. 1.** Summary stratigraphy, physical properties and fish fossil abundance from a portion of the Chemeron Formation recovered in the BTB13-1A drill core from the Tugen Hills, Kenya. Increased magnetic susceptibility and gamma density coincide with periods of increased terrestrially derived sediments, such as siliciclastic sands and gravels, whereas higher total organic content (mostly in fine-grained silts and clays) is associated with more lacustrine phases of the core record. Terrestrial and lacustrine depositional environments were determined using sediment and trace fossil analysis as well as other indicators such as diatoms (Scott et al., this issue; Westover et al., this issue).

Pleistocene climate transition and the apparent adaptive radiation in hominin evolution, including the emergence of the *Paranthropus* and *Homo* lineages. Further details on the coring, project objectives and core stratigraphic context can be found in Cohen et al. (2016). Various records suggest that prior to ~3.05 Ma the deposystem was dominated by wetland, fluvial, and small-lake deposystems, whereas lacustrine conditions became more prevalent after that time (Scott et al., this issue; Westover et al., this issue; Yost et al., this issue). Gamma density, magnetic susceptibility, and total organic matter content records from

the post 3.05 Ma part of the core show that the lake went through multiple transgressions and regressions, some of which were geologically rapid, interpreted to represent relative climate instability (Fig. 1).

One of these periods of instability is represented in the drill core by a series of five diatomaceous units between 10 mbs and 55 mbs (~2.70–2.58 Ma). Prior investigations indicated that these diatomites formed during deep lake phases, which were separated by fluvial deposits and paleosols deposited when the lake floor was exposed for extended periods during lake-level low stands (Deino et al., 2006;

Kingston et al., 2007; Wilson et al., 2014). The five diatomite layers are dominated by two planktonic diatom genera, *Stephanodiscus* and *Aulacoseira* (Kingston et al., 2007; Westover et al., this issue). The assemblages and the condition of the diatoms suggest the lake was at least 40 m deep during these periods (Kingston et al., 2007). However, sediments from these deep lake phases lack the abundance of fish bones seen within other depositional environments in outcrops, raising interesting questions about the responses of fish communities to the timing and extent of deep lake-level pulses.

For this study, we have investigated the record of  $\delta^{13}\text{C}$  changes in organic carbon isolated from fish fossils from the BTB13-1A core to determine the paleoenvironments that the fish inhabited in the Pliocene-Pleistocene lakes of the central Kenyan rift. Species or genus level identifications of fossil fish material preserved in the cores are generally impractical because most of the fossil remains are too small. Fish fossil isotopic compositions have previously proven useful in establishing ancient food web dynamics of aquatic environments (Bootsma et al., 1996; Genner et al., 1999; Reinthal et al., 2011). Fish communities of African rift valley lakes are often highly diverse, especially among members of the family Cichlidae, and have exhibited a remarkable capacity for speciation and adaptation to new ecological niches (Salzburger et al., 2014). These morphological and behavioral adaptations often reflect evolutionary convergence in feeding specializations between lake systems (Burress, 2014; Salzburger et al., 2014). A variety of fish taxa occupy both benthic (demersal) and pelagic environments. In large lakes comparable to the Tugen Hills paleolakes at their maximum extent, benthic algal production (i.e. algae growing on the bottom of the lake or on rock surfaces) is an important trophic resource for many cichlid and non-cichlid fish species from 0 to 30 m water depth, whereas many offshore species obtain their food either directly from planktonic algae (i.e. algae grown within the photic zone of the water column), or by feeding at higher trophic levels on planktivores (Reinthal, 1990; Duponchelle et al., 2005).

Benthic and pelagic algae typically differ in their  $\delta^{13}\text{C}$  compositions. Carbon in lakes is limited, and algae preferentially incorporate  $^{12}\text{C}$  during photosynthesis compared to  $^{13}\text{C}$  (Pardue et al., 1976). The amount of carbon available is influenced by the boundary layer of the algae. Pelagic algae have a smaller boundary layer and much more carbon available because of their smaller size and larger surface area/volume ratio, and grow in zones of the lake most influenced by surface water/atmosphere interactions. Benthic algae grow on the bottom of the lake where the influence of atmospheric carbon dioxide is more limited. Benthic algae also preferentially take up  $^{12}\text{C}$ , but  $^{12}\text{C}$  becomes proportionately depleted within the boundary layer through its uptake. As time progresses,  $^{13}\text{C}$  is increasingly included in the photosynthetic process and benthic algae becomes enriched in  $^{13}\text{C}$  relative to pelagic algae (Bootsma et al., 1996). The difference between the two is substantial. Modern studies from Lake Malawi, a large Afrotropical lake, show  $\delta^{13}\text{C}$  values of benthic algae as positive as  $-6\text{‰}$  whereas planktonic species may be as negative as  $-26\text{‰}$  (Fig. 2) (Bootsma et al., 2016).

There is little fractionation of carbon isotope values within a food chain and thus, isotopic values of higher trophic levels are reflective of the original autotrophic food source (Reinthal, 1990; Bootsma et al., 1996). The difference in carbon uptake between pelagic and benthic algae allows for a spatial determination of the living environment of the fish (Melville and Connolly, 2003; Devlin et al., 2013). Benthic algae are restricted by available light and relegated to the shallower portions of the lake, a pattern that is accentuated in more turbid lakes. Higher (less negative)  $\delta^{13}\text{C}$  values in fish fossils would suggest a benthic resource and a shallow habitat. Lower (more negative)  $\delta^{13}\text{C}$  values would suggest a phytoplankton resource and relatively deeper-water habitat (Fig. 2). Lake depth fluctuations through time would cause a migration of the benthic/pelagic boundary through the BTB13-1A core site. These migrations would then be recorded by the  $\delta^{13}\text{C}$  values of fish communities represented in the core. As the lake gets deeper, the food

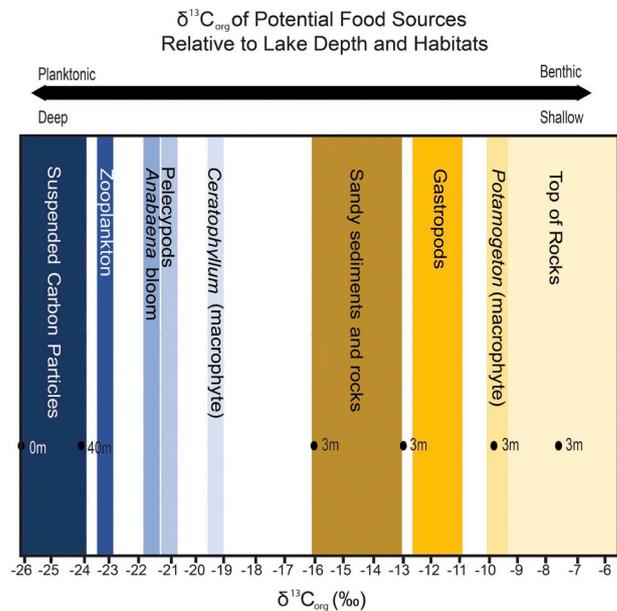


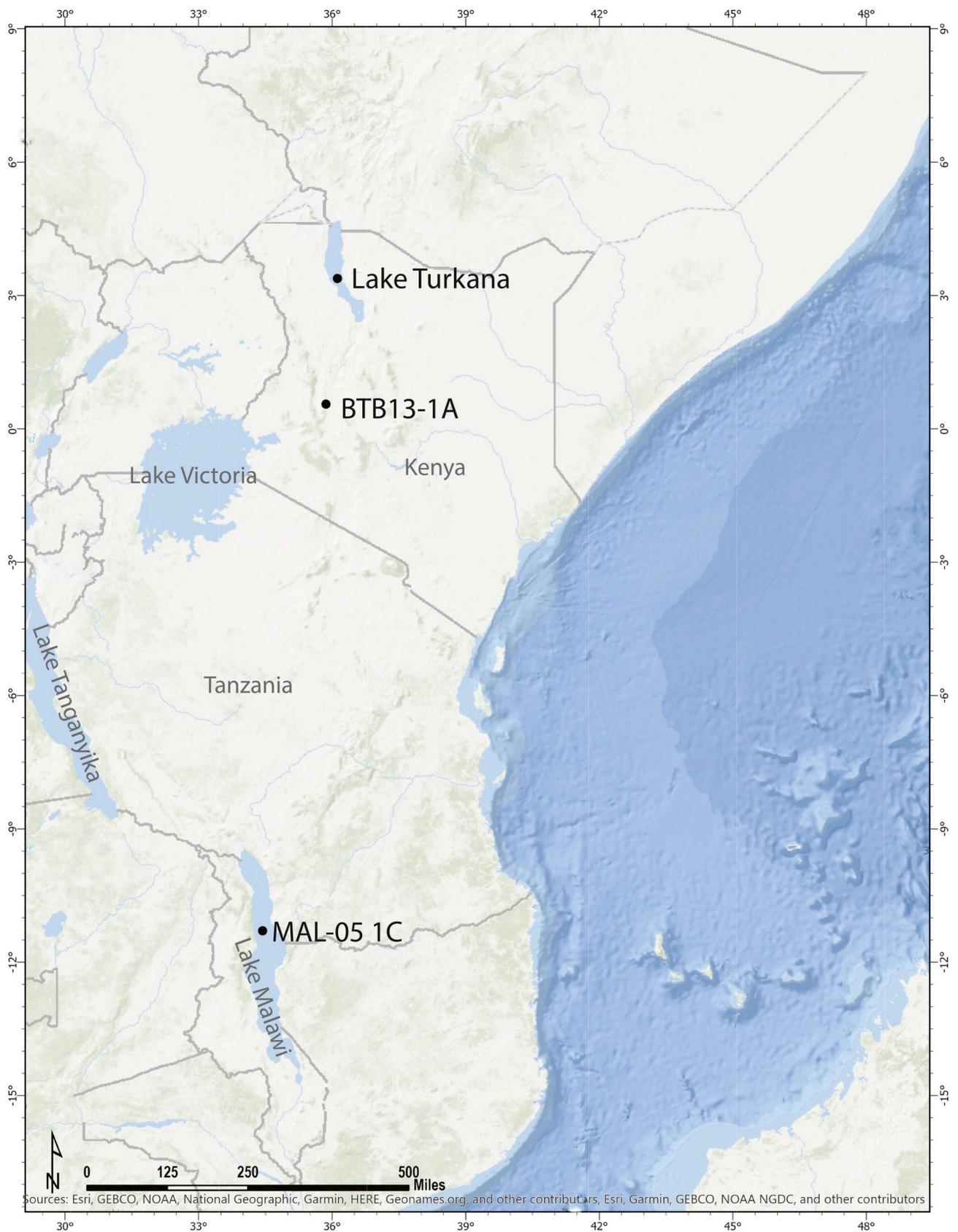
Fig. 2.  $\delta^{13}\text{C}$  values of potential food sources for fish. (Modified from Bootsma et al., 1996).

resources would become more pelagic with lower  $\delta^{13}\text{C}$  values. As the lake regresses and becomes shallower, the food resources become more benthic, reflected in higher  $\delta^{13}\text{C}$  (Reinthal, 1990; Bootsma et al., 1996).

If the diatomites were deposited rapidly, we hypothesize that they would overwhelm the fossil record, producing fish fossil isotopes with similar values before and after deposition, most likely reflecting the lower values of pelagic food sources. If the diatomites were deposited in a series of algal blooms, similarly we would expect to observe lower  $\delta^{13}\text{C}$  values both before and after the diatomites; however, we would expect to observe an increase in abundance of fish fossil prior to deposition. If the fish community did not have time to respond to the lake level pulses, then there would only be a small range in  $\delta^{13}\text{C}$  values representing one preferred habitat type.

For this study, we have compared  $\delta^{13}\text{C}_{\text{org}}$  values of fish fossils (bones, teeth and scales) from the BTB13-1A core with bones, teeth, scales, and flesh of modern fish samples as well as core top fish bones from Lake Turkana (northern Kenya) and Pleistocene samples from a Lake Malawi drill core (Fig. 3). Lake Turkana is a potential modern analog for the Chemeron Formation paleolakes, given its proximity and possible similar range of ecological conditions. Lake Turkana has experienced large-scale fluctuations in lake levels, with approximately 100 m difference between high- and low-stands during the Quaternary (Owen and Renaut, 1986; Garcin et al., 2009). Modern trophic studies from Lake Turkana show some functional redundancy in the fish communities, but most species have relatively low isotopic overlap (Gownaris et al., 2015). The lake is also turbid, which controls the depth of the photic zone, and therefore, may shift the  $\delta^{13}\text{C}$  boundary to shallower and more nearshore positions.

In 2005, core MAL-05 1C, was collected from Lake Malawi. This drill core, which penetrated to 89.9 mblf (6.51 m overpenetration) contains numerous fish fossils at all depths and spans from  $\sim 139\text{--}10\text{ ka}$  (Scholz et al., 2011; Ivory et al., 2016). Lake Malawi has the most diverse freshwater fish fauna of any lake in the world, overwhelmingly dominated by cichlid species. Many studies have focused on habitat and food partitioning in Lake Malawi, which has generated an extensive data set relating  $\delta^{13}\text{C}$  values from its fish and their associated habitats and food webs (Reinthal, 1990; Bootsma et al., 1996).  $\delta^{13}\text{C}$  values of fish bones from the Lake Malawi drill core show that lower values are associated with deeper lake phases through the late Pleistocene, as would be predicted from modern habitat and trophic relationships



**Fig. 3.** Lake Turkana (3.3830 N; 36.1167 E) and Lake Malawi (11.2933 S; 34.4358 E) are both positioned in the African rift system allowing for a good comparison between the Plio-Pleistocene record of BTB13-1A (0.5546 N; 35.9375 E) and modern lacustrine systems.

(Source: Esri, DigitalGlobe, Geoeye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN and the GIS User Community).

(Reinthal et al., 2011). This Malawi study indicates that despite their small size and thus our inability to precisely identify the BTB13-1A fish bones, the isotopic record can potentially provide insight into the rate of ecological and depositional changes within the paleolake's history.

## 2. Methods

Magnetic susceptibility and gamma density were determined using a GEOTEK multi-sensor core logger (MSCL) at the National Lacustrine Core Facility, University of Minnesota (LacCore). Gamma density data were screened to remove spurious low values caused by core voids (densities < 1.0 g/cm<sup>3</sup>). Subzero MS values were also removed from that dataset because of the difficulty in distinguishing if these points represent drill water, organic material or a void in the core. Total organic carbon was determined using standard loss-on-ignition techniques at the University of Arizona (Bengtsson and Enell, 1986).

The BTB13-1A core was sampled every 32 cm. The samples were then disaggregated by freezing and thawing or by using a kerosene treatment. There is no indication that the kerosene treatment influences the outcome of the isotopic analysis. The samples were screen washed using distilled water on a 120-micron sieve, and then examined using a Leica M165 stereomicroscope. Fish bones, teeth and scales were counted and calculated per dry gram weight. Close examination of the fossils showed that there was no apparent overgrowth or contamination of the bone structure. The fossils were selected for isotope analyses from different sediment compositions ranging from clays to coarse-grained sandstone to ensure that all possible environments were tested. The fossils were mainly bone fragments, but some teeth and complete vertebrae were also processed. Multiple fish fossils were run for three horizons (13.02 mbs, 13.65 mbs, and 17.37 mbs) in order to determine homogeneity of the  $\delta^{13}\text{C}$  values (Table 1).

We determined  $\delta^{13}\text{C}$  values of modern fish bones from 12 samples taken along three water-depth transects in Lake Turkana, Kenya. The

**Table 2**

$\delta^{13}\text{C}$  VPBD values were determined for 12 samples from Lake Turkana.

Sample	Depth of water (m)	Distance from shore (m)	$\delta^{13}\text{C}_{\text{org}}$ (‰)
11	5.6	600	-20.9
12	11.5	50	-24.6
13	22	500	-20.8
14	25	800	-20.4
15	2.5	150	-19.5
19	2.5	200	-22.1
20	2	400	-16.8
21	2	100	-17.6
27	38		-21.6
28	18	200	-21.2
32	32		-20.1
33	28		-21.5

samples were taken from modern core tops (collected in 1978), sampling the water/sediment interface. The shallowest depth is 2 m whereas the deepest is 38 m (Table 2). The samples were processed using the same procedures used for the BTB13-1A samples.

Modern fish samples of *Oreochromis niloticus* (Nile tilapia) were raised in common culture at the University of Arizona Aquaponics Greenhouse. This modern analog was chosen because *Oreochromis niloticus baringoensis* is an endemic subspecies found in Lake Baringo, a freshwater lake with seven fish species near the core site. Bones, teeth, scales and flesh were removed and pretreated twice with a 2:1 chloroform/methanol solution in order to remove excess lipids which would influence the  $\delta^{13}\text{C}$  values.

Stable isotope data were collected on a continuous-flow gas-ratio spectrometer (Finnigan Delta PlusXL). Samples were combusted using an elemental analyzer (Costech) coupled to the mass spectrometer. Standardization is based on acetanilide for elemental content and NBS-22 and USGS-24 for  $\delta^{13}\text{C}$ . The following isotope ratios are assigned to

**Table 1**

$\delta^{13}\text{C}$  VPBD data from fish fossils from the HSPDP-BTB13-1A core.

Section ID	Depth range in section (cm)	Age (Ma)	$\delta^{13}\text{C}_{\text{org}}$ (‰)
HSPDP-BTB13-1A-4Q-1	32–34	2.59	-23.5
HSPDP-BTB13-1A-4Q-1	95–97	2.6	-24.6
HSPDP-BTB13-1A-4Q-2	31–33	2.6	-24.2
HSPDP-BTB13-1A-5Q-2	51–53	2.6	-23.7
HSPDP-BTB13-1A-8Y-1	38.5–40.5	2.62	-24.7
HSPDP-BTB13-1A-11Y-2	120.5–122.5	2.64	-26
HSPDP-BTB13-1A-20Q-2	72–74	2.69	-24
HSPDP-BTB13-1A-20Q-2	97–99	2.69	-25.2
HSPDP-BTB13-1A-24Q-1	115.5–117.5	2.71	-24.3
HSPDP-BTB13-1A-28Q-2	29–31	2.76	-24.2
HSPDP-BTB13-1A-31Q-1	33–35	2.8	-25.7
HSPDP-BTB13-1A-31Q-1	66–68	2.8	-26.2
HSPDP-BTB13-1A-31Q-1	98.5–100.5	2.8	-26.5
HSPDP-BTB13-1A-31Q-1	131.5–133.5	2.8	-26.7
HSPDP-BTB13-1A-32Q-2	73–75	2.83	-26.1
HSPDP-BTB13-1A-33Q-1	50–52	2.84	-21.4
HSPDP-BTB13-1A-33Q-1	83–85	2.84	-26.2
HSPDP-BTB13-1A-33Q-1	147–149	2.85	-26
HSPDP-BTB13-1A-33Q-2	32.5–34.5	2.85	-26.5
HSPDP-BTB13-1A-35Q-3	4-Feb	2.92	-27
HSPDP-BTB13-1A-37Q-1	101–103	2.94	-26.8
HSPDP-BTB13-1A-37Q-1	136–138	2.94	-20.1
HSPDP-BTB13-1A-37Q-2	90.5–92.5	2.94	-22.5
HSPDP-BTB13-1A-37Q-3	10-Aug	2.95	-27.5
HSPDP-BTB13-1A-38Q-1	58.5–60.5	2.95	-24.8
HSPDP-BTB13-1A-39Q-1	17–19	2.96	-24.6
HSPDP-BTB13-1A-44Q-1	66.5–68.5	3.03	-25.7
HSPDP-BTB13-1A-44Q-1	132.5–134.5	3.03	-26.1
HSPDP-BTB13-1A-61Q-1	3.5–5.5	3.15	-25.9
HSPDP-BTB13-1A-63Q-2	36–38	3.18	-25.8
HSPDP-BTB13-1A-63Q-2	102–104	3.18	-26.4
HSPDP-BTB13-1A-63Q-3	7.5–9.5	3.18	-26
HSPDP-BTB13-1A-64Q-1	22–24	3.18	-26.3

these standards ( $\delta^{13}\text{C}$  VPDB): USGS24,  $-16.05\text{‰}$ ; NBS 22,  $-30.03\text{‰}$ . Analytical precision is better than  $\pm 0.08$  for  $\delta^{13}\text{C}$  ( $1\sigma$ ), based on repeated internal standards. Samples that were extremely small have a higher uncertainty: standards of equivalent size had a variability of  $\pm 0.25\text{‰}$  ( $1\sigma$ ). Because the amount of organic carbon in these samples was extremely small, extra care was taken to eliminate inorganic carbon contamination. On average, fossilized fish material contains 0.25–0.5 times the amount of organic carbon as modern samples of similar size. Bone and tooth samples were acidified with sulfurous acid ( $\text{H}_2\text{SO}_3$ ) in silver foil capsules to remove structural carbonate from the bone apatite. Two drops of acid were used followed by overnight drying in  $60^\circ\text{C}$  oven. This procedure was repeated once. The silver foil capsules were heated to  $\sim 500^\circ\text{C}$ .

### 3. Results

#### 3.1. BTB13-1A core samples

Approximately 1200 fish scales, teeth, and bone were counted from 592 samples taken throughout the BTB13-1A core. Most of the material is unidentifiable fragments; however, the fossils that can be identified come from the families Cichlidae and Cyprinidae. There are very few fish bones in the dominantly fluvial-wetland-shallow pond deposits in the lower portions of the core, below 132 mbs (3.04 Ma) (Fig. 1). Only two segments in the lower portion, at 183.6–181.9 mbs and 174.6 mbs (3.17 Ma and 3.15 Ma respectively), contain fish material. Above 132 mbs, the samples that contain an abundance of fish fossils coincide with higher percentages of total organic content and lower values for gamma density and magnetic susceptibility. These intervals of the core are often clayey or silty, and are associated with lacustrine phases as inferred from both litho- and bio-facies analysis. A few samples towards the top are associated with sands which have been interpreted as being deposited in a delta front within the lake (Scott et al., this issue) (Fig. 1).

$\delta^{13}\text{C}$  values were determined for 36 fish fossils throughout the Tugen Hills drill core (Table 1). Values range between  $-20\text{‰}$  to  $-27\text{‰}$ . The low  $\delta^{13}\text{C}$  values correlate with zones of low magnetic susceptibility and deeper water environments (Fig. 4).

#### 3.2. Carbon isotopic fractionation in modern fish

To supplement the interpretive isotopic framework for the fossil fish analyses,  $\delta^{13}\text{C}$  values for scales, bones, oral teeth and muscle (flesh) from the cichlid, *Oreochromis niloticus* (Nile tilapia) raised in common culture at the University of Arizona Aquaponics Greenhouse were determined. Four specimens were raised in the same habitat. Fish 1 and 2 are juveniles whereas fish 3 and 4 are adults. The  $\delta^{13}\text{C}$  values ranged from  $-17.0\text{‰}$  to  $-23.1\text{‰}$ , with an uncertainty of  $\pm 0.33\text{‰}$  for all samples but the flesh from fishes 2, 3, and 4 have an uncertainty of  $\pm 0.10\text{‰}$ . Fractionation seems to occur in individual specimens as well as different sample types. However, the range of  $\delta^{13}\text{C}$  average values between the four specimens are similar to ranges observed among modern cichlids from Lake Malawi, where fish populations can vary by approximately  $1.5\text{‰}$  (Bootsma et al., 1996) (Fig. 5). The fish flesh is significantly more negative than bone, teeth and scales because fish oils are depleted in carbon-13.

#### 3.3. Modern Lake Turkana

$\delta^{13}\text{C}$  values of core top samples range from  $-24.6\text{‰}$  to  $-16.8\text{‰}$ . Higher values are found in samples from water depths shallower than 5 m. The lowest value occurs at 11.5 m ( $-24.6\text{‰}$ ), but this sample was collected relatively close to the shore, which may indicate it was reworked from previously deposited sediments from the nearby and much higher Early Holocene lake stand terraces that surround the lake today (Owen and Renaut, 1986; Garcin et al., 2009) (Fig. 6).  $\delta^{13}\text{C}$  values of

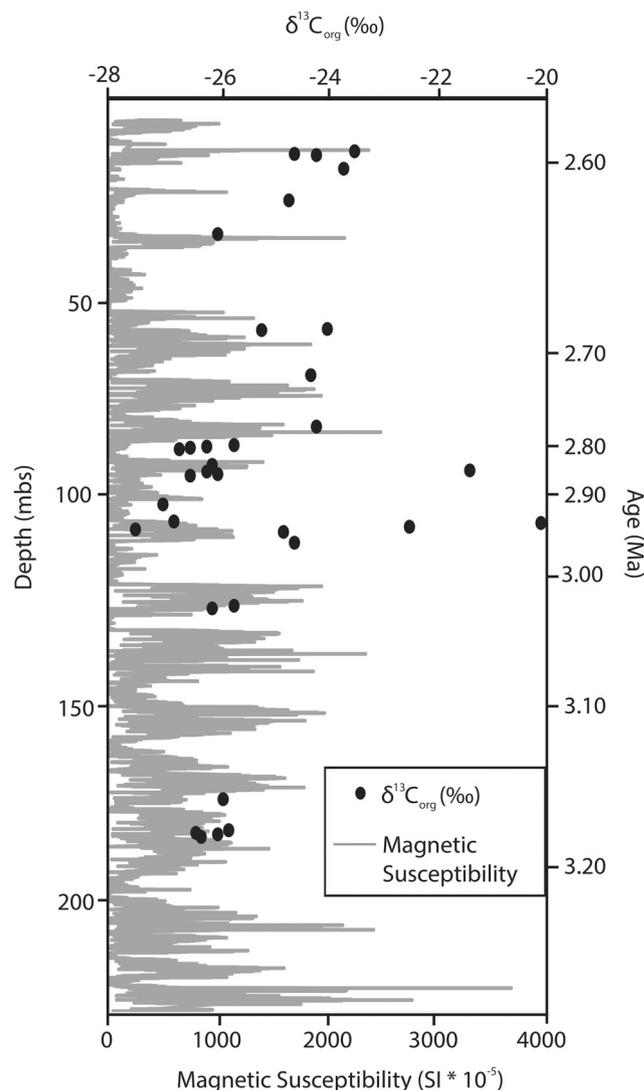


Fig. 4.  $\delta^{13}\text{C}$  values of fish fossils from the BTB13-1A plotted along with magnetic susceptibility. 63% of our isotope values are at depths where the magnetic susceptibility falls below the mean (377.65) for the whole record.

samples from sediments deposited in deeper water are between  $-20.1\text{‰}$  and  $-21.6\text{‰}$ , which suggest a more planktonic food source than found at shallower water depths. The isotope values from this study are similar to those found in the living fish species of Lake Turkana, which range between  $-20.18\text{‰}$  to  $-16.88\text{‰}$  (Gownaris et al., 2015).

### 4. Discussion

There are no  $\delta^{13}\text{C}$  values for fossil fish from the BTB13-1A core within the range of shallow lacustrine environments (i.e. benthic algae) determined through modern fish  $\delta^{13}\text{C}$  ranges ( $-7.0\text{‰}$  to  $-19\text{‰}$  VPDB) (Fig. 2) (Bootsma et al., 1996; Reintal et al., 2011). It is possible, although unlikely, that this uniformity of results is a consequence of low sampling frequency in this study, meaning that not all environments were tested. Higher resolution sampling is needed to determine if benthic species are in other sedimentary units. However, it is probable that the lake-level fluctuations between exposure surfaces and deep lake phases were quick enough to prevent shallow water, benthic species to become established at the core site. This may be consistent with the observation that exposure surfaces with pedogenesis throughout the core typically lie directly below silty-clay profundal lacustrine flooding

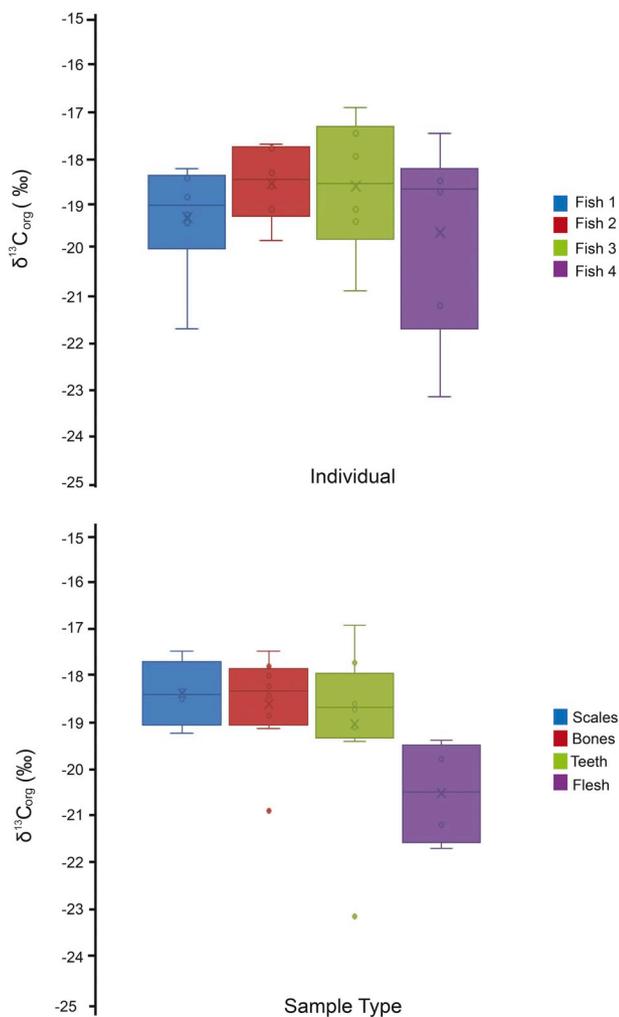


Fig. 5.  $\delta^{13}\text{C}_{\text{org}}$  values, with a mean of  $-19.05\text{‰} \pm 1.12$ , from four living, tank reared *Oreochromis niloticus* reveal that the isotopic values of material can vary over both individual specimens and sample types. The dark line represents median value, boxes represent the upper and lower quartiles, and whiskers represent the upper and lower values of each data set excluding outliers.

surfaces (Scott et al., this issue).

When compared with the diatom record from the core, we see that fish fossils are present in five horizons with an abundance of diatoms: 8.5–10.95 mbs, 17.08–22 mbs, 25.29–39.27 mbs, 40.98–43.48 mbs and 50.67–52.29 mbs (Westover et al., this issue). However, the abundance of fish fossils is not consistent throughout the diatomaceous units within the core, and often large segments within these units have no fish material. This may suggest that the lack of fish fossils in the diatomaceous units of the outcrop may have resulted from an increased sedimentation rates of diatoms overwhelming the deposition of fish material.

The range of  $\delta^{13}\text{C}$  values found in the fish fossils from BTB13-1A are within the range of values seen in modern fish communities seen at Lake Malawi (Bootsma et al., 1996) (Fig. 7). The BTB13-1A values, when compared to modern fish communities studied in Lake Malawi, indicate pelagic food sources, suggesting that even during low-lake stands, the lake was deep enough to preclude benthic algae as a significant food resource or a benthic fish community. However, published modern fish values were obtained from analysis of tissue rather than bone, and a number of factors could have influenced these values such as water chemistry, terrestrial input, post-depositional alteration, and life-cycles (Genner et al., 1999; Wurster and Patterson, 2001; Bootsma et al., 2016). Reinthal et al. (2011) demonstrate  $\delta^{13}\text{C}$  isotope values in

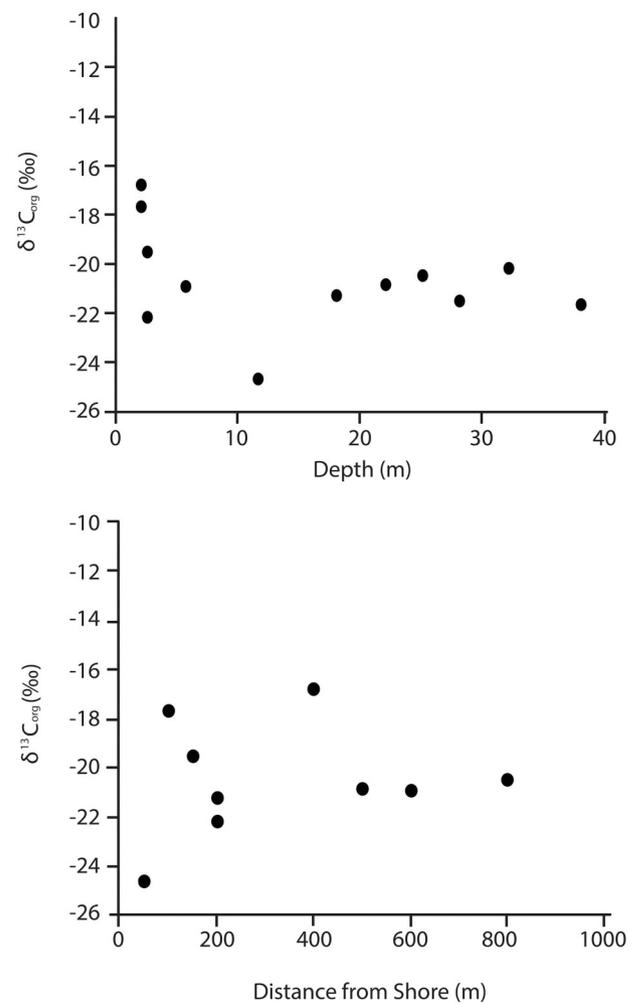


Fig. 6.  $\delta^{13}\text{C}_{\text{org}}$  values relative to VPDB for modern Lake Turkana fish bones are plotted against lake depth (top) and distance from shore (bottom).

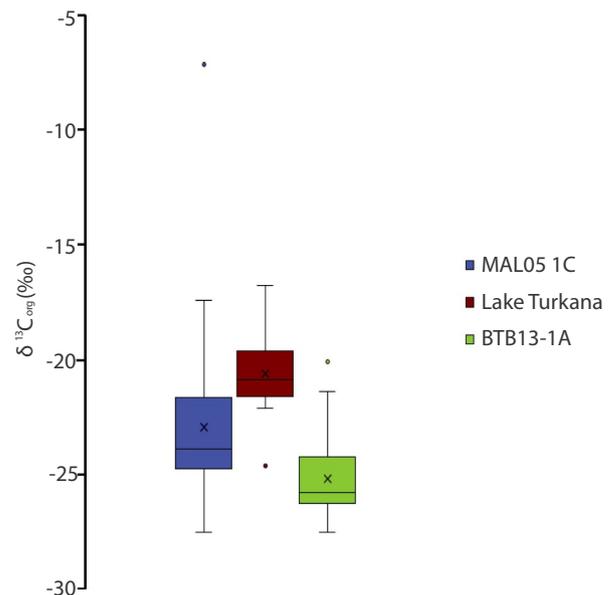


Fig. 7. Summary plot of all  $\delta^{13}\text{C}_{\text{org}}$  values determined for the three lake/paleolake data sets: MAL-05 1C (Reinthal et al., 2011), Lake Turkana and the Plio-Pleistocene lakes of BTB13-1A. The dark line represents median value, boxes represent the upper and lower quartile, and whiskers represent the upper and lower values of each data set excluding outliers.

MAL 05-1C follow the trend of modern fish communities of lower values coinciding with deeper lakes and higher values coinciding with shallower lakes despite the difference in material used. Our modern fish samples showed that a range of  $\delta^{13}\text{C}$  values can occur not only throughout fish communities but within different tissue types from individual specimens as well. However, the flesh exhibits significantly lower  $\delta^{13}\text{C}$  values than either the bone or the teeth. This means that the bone and teeth of the BTB13-1A fossil fish represent the highest  $\delta^{13}\text{C}$  values of the fish communities. Furthermore, there is little overlap between the  $\delta^{13}\text{C}$  values of the BTB13-1A samples and those from modern Lake Turkana (a *t*-test shows no substantial overlap,  $p = 7.96 \times 10^{-10}$ ). This indicates that the fish living in the Tugen Hills paleolakes were more dependent on pelagic food sources than those currently living in Lake Turkana (Fig. 7).

Environmental interpretations can become further complicated in situations where sediment and terrestrial carbon may be transported into the system from elsewhere. This can be seen in one of our Lake Turkana samples, where a nearshore, shallow environments contained a bone most likely deposited from the shoreline where fossils from an older, deeper lake can be found. However, our study does show that even in an environment such as Lake Turkana where the photic zone may be restricted in depth by increased turbidity, there is still a pattern of higher  $\delta^{13}\text{C}$  values in environment shallower than 5 m and lower values in deeper waters (Table 2; Fig. 6).

Fluvial systems may be difficult to differentiate from deep-water habitats solely on the  $\delta^{13}\text{C}$  values of fish fossils. In a fluvial or deltaic system, the water is usually turbulent, and both pelagic and benthic algae would have their boundary layer continuously replenished in carbon. Fish living in a river or near a delta environment have lower  $\delta^{13}\text{C}$  values than shallow lacustrine species at the same depth (Hoffman et al., 2010). Significant fluvial inputs from a nearby delta may explain the anomalous combination of low  $\delta^{13}\text{C}$  values and relatively high MS values for sediment horizon HSPDP-BTB13-1A-4Q-1, 32–34 cm (13.02 mbs). The sample is from a relatively coarse-grained sandy unit, which has been interpreted as a deltaic deposit (Scott et al., this issue).

## 5. Conclusions

The isotopic analysis of fish fossils can be an important tool when determining how fish communities respond to climate and environmental variability, especially when the changes are dramatic and quick. We have investigated fossil fish abundances and carbon isotopes from a drill core record of paleolakes that occupied the central Kenya Rift Valley during the late Pliocene-early Pleistocene. This study of the HSPDP-BTB13-1A fossil record is the first application of  $\delta^{13}\text{C}$  analyses to fish fossils of this age in East Africa. The  $\delta^{13}\text{C}$  values are within the range of those seen in both modern fish community assemblages and fish fossils of Lake Malawi. The BTB13-1A values, however, are lower than those of modern Lake Turkana, which suggests that the fish of the paleolake were more dependent on pelagic food sources than those currently present in Lake Turkana. The lack of shallow benthic  $\delta^{13}\text{C}$  values for the fish fossils indicates that the transitions between shallow and deep lake conditions were abrupt. The narrow range in  $\delta^{13}\text{C}$  values also suggests high dependency on a phytoplanktonic food source that would make the fish communities more vulnerable to sudden changes in the pelagic community. This study shows that the  $\delta^{13}\text{C}$  of fish fossils may be used in tandem with other environmental indicators as a tool to better understand the timing and extent of lake-level pulses as East African climate became more highly variable during the Pliocene-Pleistocene transition.

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