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Original Article

Daily vertical distribution of zooplankton in two oligo-mesotrophic north Patagonian lakes (39° S, Chile).

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(With 3 figures)

Abstract

The zooplankton communities often exhibit daily vertical migrations to avoid natural ultraviolet radiation and/or fish predation. However there is no information on this topic in Chilean North Patagonian lakes up to date. Therefore, this study deals with a first characterization of plankton crustacean daily vertical migration in two temperate, oligotrophic lakes (Villarrica and Panguipulli lakes, 39°S) in Southern Chile. Zooplankton were collected at different depths intervals (0-10m, 10-20 m, 20-30m, 30-40m) at early morning, middle day, evening and night in the studied site. The results revealed that zooplankton species (*Daphnia pulex, Ceriodaphnia dubia, Neobosmina chilensis, Mesocyclops araucanus,* and *Tropocyclops prasinus*) are abundant in surface zones at night, early morning and evening, whereas at middle day the zooplankton abundances are high at deep zones. The results agree with observations for Argentinean and North American lakes where these daily migration patterns in crustacean zooplankton species were reported due mainly natural ultraviolet radiation exposure, whereas for northern hemisphere lakes the vertical migration is due to combined effect of natural ultraviolet radiation and fish predation exposure.

Keywords: zooplankton, daily vertical migration, Patagonian lakes, cladocera, copepod.

Distribuição vertical diária do zooplâncton em dois lagos oligo-mesotróficos ao norte da Patagônia (39º S, Chile)

Resumo

As comunidades zooplanctônicas frequentemente exibem migrações verticais diárias para evitar a radiação ultravioleta natural e/ou a predação de peixes. No entanto, não há informações sobre esse tema em lagos chilenos no norte da Patagônia até a presente data. Portanto, este estudo trata de uma primeira caracterização da migração vertical diária de crustáceo planctônico em dois lagos temperados e oligotróficos (lagos Villarrica e Panguipulli, 39º S) no sul do Chile. O zooplâncton foi coletado em diferentes profundidades (0-10 m, 10-20 m, 20-30 m e 30-40 m) no início da manhã, ao meio-dia, à tarde e à noite no local estudado. Os resultados revelaram que as espécies de zooplâncton (*Daphnia pulex, Ceriodaphnia dubia, Neobosmina chilensis, Mesocyclops araucanus* e *Tropocyclops prasinus*) são abundantes nas zonas de superfície à noite, de manhã cedo e à tarde, enquanto, ao meio-dia, as abundâncias do zooplâncton são altas nas zonas de profundidade. Os resultados expostos corroboram as observações para outros lagos argentinos e da América do Norte, onde foram reportados esses padrões de migração diária em espécies crustáceas de zooplâncton por causa, principalmente, da exposição à radiação ultravioleta natural, enquanto, para lagos do hemisfério norte, a migração vertical se dá em razão do efeito combinado da radiação ultravioleta natural e exposição à predação.

Palavras-chave: zooplâncton, migração vertical diária, lagos patagônicos, cladóceros, copépodes.

1. Introduction

In southern Chile and Argentina there is an area called NordPatagonian lakes (39-41°S). These lakes share different features: they are temperate, deep lakes (Zmax≥ 100m), transparent, ultra/oligotrophic, monomictic, of glacial origin, and have low salt and nutrient concentration (Campos, 1984; Pérez et al., 2002; Queimaliños, 2002;

Woelfl, 2007). In addition, they exhibit characteristics that are unique to these lakes in relation to temperate northern hemisphere lakes. For example, they lack predators such as *Chaoborus* and *Leptodora* (Kamjunke et al., 2009, 2012). Moreover, in these lakes Calanoid copepods dominate the mesozooplankton followed by cyclopoid copepods and Cladocera (Campos, 1984; Soto and Zúñiga, 1991; Modenutti et al., 2010; De los Ríos-Escalante et al., In press). Also, the phytoplankton community is dominated by Diatoms (Campos, 1984).

In these lakes, the vertical distribution of zooplankton communities is particularly important, due to the influence of physical and chemical gradients formed in the water column (e.g. temperature, UV radiation) during the warm season (i.e. spring-summer). Biological factors such as the presence of predators can also influence the vertical distribution of organisms (Ringelberg, 2010). Together, these factors act at different spatial-temporal scales producing an heterogenous spatial distribution of zooplankton in the water column of these lakes (Geller, 1992; Woelfl and Geller, 2002; Kessler et al., 2008; Woelfl et al., 2010). Usually, the key mechanism involved in the vertical distribution of zooplankton communities is Diel Vertical Migration (DVM), a ubiquitous phenomenon exhibited by many zooplanktonic species in lakes of northern and southern hemispheres (Villafañ et al., 2001; Winder, 2001; Woelfl and Geller, 2002; Woelfl et al., 2010; Ringelberg, 2010; Leach et al., 2015). Thus, DVM has attracted great scientific interest in the last 30 years given its important implications for food web dynamics and biological productivity (Ringelberg, 2010).

There are three types of DWM that have characterised until this point. The "normal" DVM pattern is by far the most common observed movement in marine and freshwater ecosystems (Pearre, 2003). In such pattern species descend at dawn, whereas at dusk they rise to the upper layers. Typically, descending at dawn reduces the risk of predation, whereas ascending at dusk allows species to feed on zooplankton. In contrast, "twilight" and "reverse" DVM patterns are less common (Guerra et al., 2019).

The vertical distribution of microcrustacean zooplankton in Nord Patagonian lakes has already been studied seasonally (Campos et al. 1992a, b; Wõlfl,1996; Woelfl and Geller, 2002; Woelfl et al., 2010). However, the evaluation of their vertical distribution in terms of DVM (i.e. across the diel cycle) is still largely unknown. Only two studies have evaluated DVM across the diel cycle, but these were conducted in lakes of central Chile (Ramos-Jiliberto and Zúñiga, 2001; Ramos-Jiliberto et al. 2004). The first limnological studies in lakes in the north of Patagonia (Figure 1) described DVM but their goals did not point the principal regulator factors with enough details (Wõlfl, 1996; Woelfl and Geller, 2002; Woelfl et al., 2010). Recent studies have found a high dominance of cladoceran and low abundances of copepods in summer time in the first 40m of the water column of lake Caburgua (Woelfl et al., 2010),

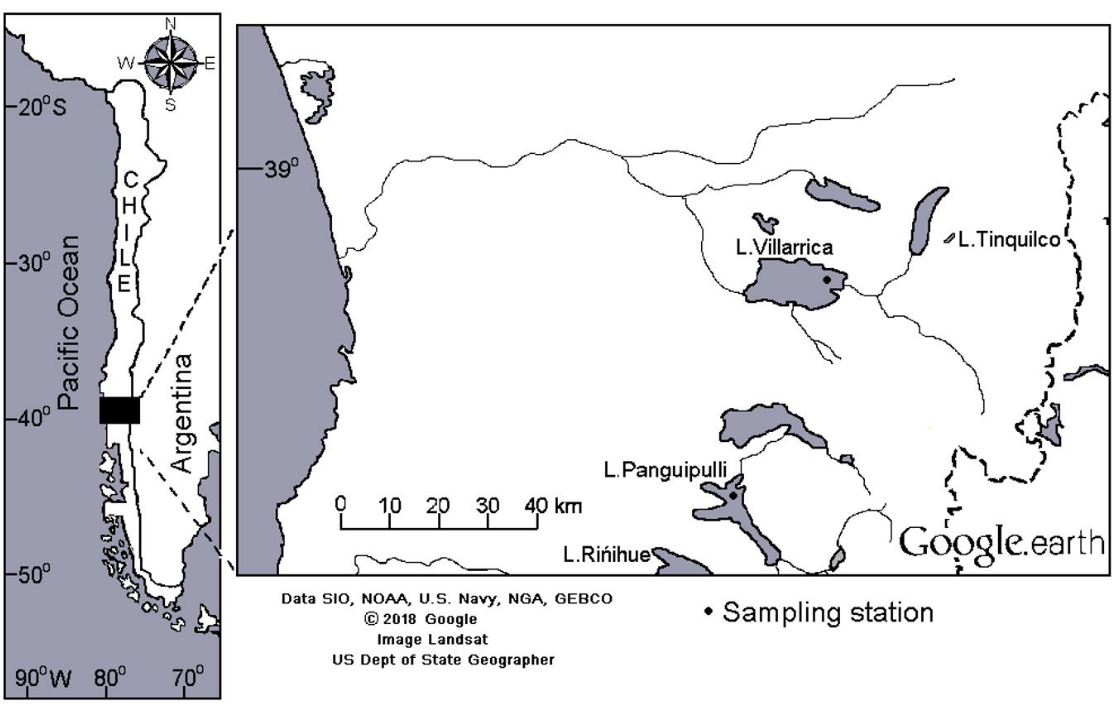

Figure 1. Location of sampling sites in lakes Panguipulli and Villarrica (•) in Southern Chile. Map was adapted on basis of Google earth image (Google Earth, 2020). The corresponding image was supplied by Data SIO, NOAA, U.S. Navy, NGA, GEBCO ©2018 Google, Image Landsat, US Dept. of State Geographer. The map was drawn using software PHOTOIMPACT version 4.2 under licence number RI630-903-61120 (Google, 2018).

and high zooplankton abundances in the first 5 m of the water column in Tinquilco lake both in early mornings and evenings (De los Ríos-Escalante et al., 2015). Some authors have suggested the combined role of natural ultraviolet radiation and chlorophyll concentration as key determinants of zooplankton community structure in Patagonian lakes (Marinone et al., 2006). In this scenario, the crustacean zooplankton community would increase its abundance and species composition in the upper layers during low solar radiation exposure (De los Ríos-Escalante et al., 2015).

Investigating DVM patterns of zooplankton is crucial for improving our understanding of biological productivity and of the fluxes of energy and matter in the pelagic environment (Ringelberg, 2010) of Nord Patagonian lakes. For instance, zooplankton can remove nitrogen and carbon from the surface layers and release them at depth (Schnetzer and Steinberg, 2002). But these fluxes depend on the type of migration, which in the latter case is considered the "normal" DVM pattern (Longhurst and Glen-Harrison, 1989). In turn, the type of migration can result from different set of ecological conditions for each particular lake (Ringelberg, 2010).

In this study we aim to analyse the DVM of crustacean zooplankton from two Patagonian oligo-mesotrophic lakes, Villarrica and Panguipulli (Campos, 1984; Woelfl, 2007), in summer of 2010 and 2011. To the best of our knowledge, this is the first description of this kind achieved for Chilean Nord Patagonian lakes.

2- Materials and Methods

Study sites: Villarrica (39°32'S; 72°09´W) and Panguipulli lakes (39° 39' 44"S; 72° 16' 50'W) (Figure 1) are two typical large (176 and 117 km^2), deep (maximum depths: 165 and 268 m) and oligotrophic Nord Patagonian lakes (Geller, 1992; Woelfl, 2007). They are warm monomictic with an epilimnion depth of about 10 to 15 m (Geller, 1992; DGA, 2019) and Secchi depth during summer between 7 and 15 m (Woelfl, 2007; DGA, 2019). Phytoplankton community during summer is dominated by diatoms in Lake Panguipulli and by cyanophytes in Lake Villarrica (DGA, 2019).

Zooplankton collection: Water samples from Villarrica lake were collected in January 2011 (21-22th January 2011) and in February for Panguipulli lake (02-03th February 2010. Vertical hauls were taken at different depth intervals (0-10 m; 10-20 m; 20-30 m; 30-40 m; and 40-50 m) using a Hydro-Bios plankton net (Kiel, Germany) with 80µm mesh size and 30 cm diameter equipped with a flowmeter. The sampling started at 12:00 PM and was repeated every six hours until 06:00 AM of the next day, before strong wind conditions at midday made zooplankton sampling unattainable. Zooplankton was preserved in absolute ethanol and counted using a Bogorov chamber to facilitate identification of species according to literature on taxonomical descriptions (Araya and Zúñiga, 1985; Reid, 1985).

Data analysis: we used the Weighted Mean Depth (WMD) index proposed by Frost and Bollens, (1992) and Durbin et al., (2010). This index allows to estimate the tendency of vertical distribution for a certain species in the water column. The formula of this index is the following:

$$WMD = S(N_i * d_i) / SN_i$$

Where:

N_i = individual abundance of determined population at a specific depth

d_i = depth. We used the centre of the sampled depth intervals.

3- Results

The results revealed the presence of seven species in studied lakes: three cladocerans: *Daphnia pulex* De Geer, 1877 (Panguipulli), *Ceriodaphnia dubia* Richard, 1894 (Caburgua and Panguipulli) and *Neobosmina chilensis* Daday, 1902 (Villarrica), and four copepods *Tumeodiaptomus diabolicus* Brehm 1935 (Panguipulli), *Boeckella gracilipes* Daday, 1901 (Panguipulli),, *Mesocyclops araucanus* Löffler, 1962 and *Tropocyclops prasinus* (Fischer, 1860) (Tables 1 and 2). Among them, *T. prasinus* was only present in lake Villarrica, whereas *M. araucanus* inhabited only lake Panguipulli.

Lake Panguipulli (Table 1**,** Figure 2**):** Both cladoceran species (*D. pulex*, *C. dubia*) displayed a small DVM and were mostly concentrated in the epilimnion between 10 m and 20 m at daytime (*D. pulex*: WMD = 20.5m, *D. dubia*: WMD = 15.9m) and between 0-20 m (*D. pulex:* WMD = 15.4 m*; C. dubia:* WMD =16.2m) during night (Figure 2). For the case of *C. dubia*, about 81% of the population were concentrated in the 10-20 m depth range at midday. Only a small percentage of the population (< 25%) of both cladocerans were found within or

Table 1. Weighted Mean Depth (WMD) index of crustacean species in lake Panguipulli during summer 2010.

	Sampling time			
	6 am	**12 pm**	**18 pm**	**12 am**
Daphnia pulex	11.3	20.5	12.8	15.4
Ceriodaphnia dubia	16.6	15.9	9.3	16.2
Mesocyclops araucanus	17.5	26.3	17.2	16.0
Tumeodiaptomus diabolicus	11.7	18.2	9.4	10.7
Boeckella gracilipes	30.0	37.4	31.1	19.6
Copepodites (mainly calanoid)	18.4	33.9	21.2	15.4

Table 2. Weighted Mean Depth (WMD) index of crustacean species in lake Villarrica during summer 2011.

	Sampling time			
	6 am	**12 pm**	**18 pm**	**12 am**
Ceriodaphnia dubia	18.1	25.8	20.5	8.3
Neobosmina chilensis	29.1	24.5	26.3	24.4
Tropocyclops prasinus	29.7	30.5	29.7	17.7
Calanoid copepodites	33.9	36.0	36.8	35.7

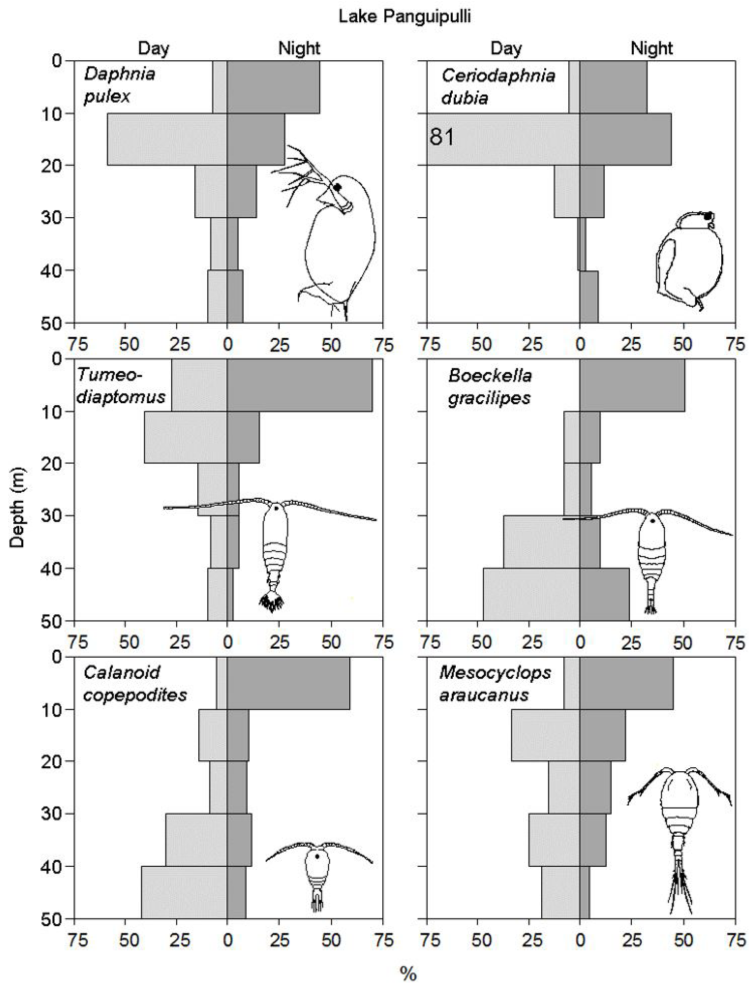

Figure 2. Vertical distribution of microcrustacean species during day and night in Lake Panguipulli.

below the thermocline (20 - 50 m) during daytime and night.

In relation to copepods, only calanoid copepodites (C1-C5 instars) and *B. gracilipes* (adults) displayed a large DVM, whereas adults of *T. diaptomus* and *M. araucanus* were found during daytime and night in the upper 20 m of depth. During daytime about 70% of the copepodites were concentrated below 30 m of the water column (WMD: 37.4 m), whereas at night about 65% of the population were found in the upper10 m of the water column (WMD: 15.4 m) (Figure 2). Individuals of *M. araucanus* (adults) displayed a fairly uniform distribution throughout the water column (WMD: 26.3 m) showing moderate DVM at night (WMD =16.0 m).

Lake Villarrica (Table 1**,** Figure 3**):** Regarding the other two small cladoceran species, *D. dubia* and *N. chilensis*, presented in lake Villarrica, only *C. dubia* revealed a notable DVM comparable to the results obtained in lake Panguipulli. During daytime, it presented a fairly homogenous distribution from surface to 50 m depth (WMD = 25.8 m), but during night about 80% of the population was concentrated in the upper 10 m water layer (WMD = 8.3 m) (Figure 3). In contrast, the second small cladoceran

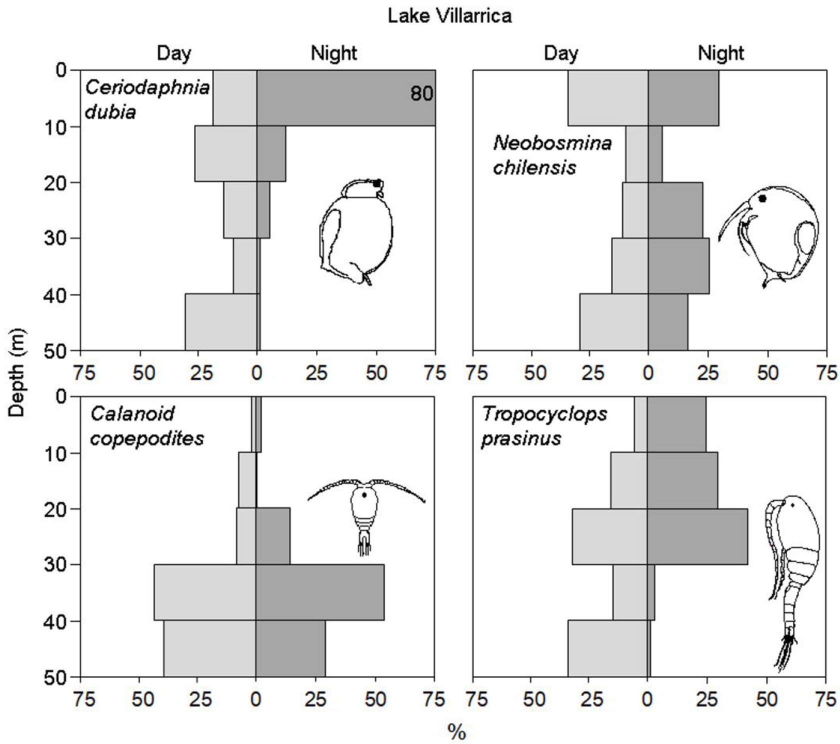

Figure 3. Vertical distribution of microcrustacean species during day and night in Lake Villarrcia.

N. chilensis was distributed in the whole water column (0-50 m) during daytime and night (WMD: 24.4 - 29.1 m) (Figure 3).

With respect to copepods, almost the entire population of calanoid copepods (*Boeckella gracilipes*) was always below the thermocline between 30 and 50 m and no DVM was found (WMD: 35.7 - 36.8 m) (Figure 3). The very small cyclopoid copepod *T. prasinus* exhibited a moderate DVM, but only within the hypolimnion/thermocline layer at night (30-10 m). During daytime, more than 70% of the population (mostly males) were concentrated between 40 m and 50 m (WMD: 30.5 m), and revealed DVM of about 13 m during night into water layers between 10 m an 30 m (WMD: 17.7 m) (Figure 3).

4. Discussion

The presence of small bodies crustaceans would be probably to top down fish predation, because under zooplanktivorous fish predation, small bodies zooplankton are abundant in zooplankton community, such as was observed in Europe (Alpine lakes, Tartarotti et al., 2017; Sweden, Zheng, 2018) North America (Leech and Williamson, 2000; Leech et al., 2005a, b; Leach et al., 2015), Patagonian lakes of Argentina (Reissig et al., 2004, 2006; Hylander et al., 2012) and Chile (Woelfl and Geller, 2002; Woelfl, 2007; De los Ríos-Escalante, 2015). This situation would explain also, the presence of copepods under thermocline, such as was observed for Argentinean Patagonian lakes (Reissig et al., 2004, 2006).

These presents results (Tables 1 and 2, Figure 2 and 3) agree with the first descriptions of vertical patterns for zooplankton of Nord Patagonian Lakes in monthly samples, without included daily variations (Campos et al., 1992a, b), nevertheless, both studies described monthly vertical distribution of total zooplankton. Similar description was done for mixotrophic ciliates for lakes Pirihueico (Woelfl and Geller, 2002), and Caburgua (Woelfl et al., 2010) in northern Chilean Patagonia. In this scenario, the importance of the present study is the first comparative description of DVM for Chilean Patagonian lakes, and second that the present study involves crustacean zooplankton species in two north Patagonian lakes without mixotrophic ciliates (Woelfl, 2007) but different phytoplankton communities.

However, these samples were collected at mid-day or early afternoon Similar results have been reported for Argentinean Patagonian lakes (Balseiro et al., 2001, Reissig et al., 2006), North America (Leech and Williamson, 2000; Leech et al., 2005a, b; Leach et al., 2015), Europe (Alpine lakes, Tartarotti et al., 2017; Sweden, Zheng, 2018) in which descriptions of crustacean zooplankton DVM only included data collected at mid-day and night. These investigations were similar to our investigation where zooplankton was abundant in upper layers at night and showing low abundances during daytime (Wölfl, 1996). Similar results have been reported for Europe (Alpes mountains, and Swedish lakes) North American and

Argentinean Patagonian lakes. The potential cause would be the exposure to natural ultraviolet radiation (Leech and Williamson, 2000; Villafañ et al., 2001; Leech et al., 2005a, b; De los Ríos-Escalante et al., 2015; Leach et al., 2015; Tartarotti et al., 2017; Zheng, 2018).

Our results agree with observations for northern hemisphere lakes, where marked vertical migrations are common during day and night hours. These are regulated mainly by natural ultraviolet radiation (Leech and Williamson, 2000; Villafañ et al., 2001; Leech et al., 2005a, b; De los Ríos-Escalante et al., 2015; Tartarotti et al. 2017; Zheng, 2018), fish predation exposure (Williamson et al., 2011; Hylander et al., 2012), or food resources availability (Overholt et al., 2015). Water column transparence and UV have been recently found to influence this distribution (Häder et al., 2015; Fischer et al., 2015; Leach et al., 2015; Urmy et al., 2016; Tartarotti et al., 2017). If we consider that North American lakes and Argentinean Patagonian lakes are both exposed to natural ultraviolet radiation, and that the former have a wide water column transparence gradient (Morris et al., 1995), the current results would agree with the potential role of natural ultraviolet radiation as a regulating factor of vertical migration of zooplankton species.

The obtained results (Tables 1 and 2, Figures 2 and 3) would denote the existence of marked daily vertical migration on zooplankton in Patagonian lakes, nevertheless it would be necessary confirm what would be the key role as regulator of ultraviolet radiation (Hylander et al., 2012) and preys (phytoplankton, protozoa) availability (Woelfl and Geller, 2002; Woelfl, 2007) on daily vertical migration in Patagonian lakes.

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