



# Lake ecosystem on the Qinghai–Tibetan Plateau severely altered by climatic warming and human activity

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## ARTICLE INFO

Editor: Paul Hesse

### Keywords:

Top-down effect  
Carotenoid pigments  
Overharvesting  
Nutrients  
Paleolimnology

## ABSTRACT

Modelling, monitoring, and experimental data have shown that global climate change can impact aquatic phytoplankton communities directly, through the effects of warming on primary producers, as well as indirectly through cascading effects from higher trophic levels. Although both concepts are common in modern limnological studies, it remains unclear whether the ‘top-down’ effects from higher trophic levels on phytoplankton exert strong effects in natural systems over long (centennial) timescales. Here, we use multiproxy data including pigments, zooplankton remains, nutrient concentrations, and paleoclimate indicators from a sediment core in Dagze Co, Central Tibet (a two-trophic level lake) to reconstruct algal production, zooplankton community, nutrient and salinity changes. Our results show that top-down effects of higher trophic levels offset effects from warming and nutrient addition on algal growth. Warming enhanced glacial meltwater inflow to the lake, and intensive human activities increased nutrient inputs. Changes in lake salinity and N:P ratios coincided with zooplankton community shifts during the past 600 years, and *Daphnia tibetana* replaced the brine shrimp, *Artemia tibetana*, after the relocation of a town to upstream of the lake in the 1980s led to overharvesting of the brine shrimp. These shifts contributed strongly to changes in algal communities, with changes in zooplankton leading to strong top-down effects that decreased algal production through increasing grazing pressure despite increasing nutrient concentrations. Our results suggest that the typical external drivers (climate and nutrients) of lake ecosystems may be suppressed by internal shifts in plankton communities in lakes.

## 1. Introduction

The Earth is getting warmer (IPCC and Team, 2014) and human activities have significantly modified terrestrial landscapes in the Anthropocene (Steffen et al., 2007). Warming is already affecting the structure and function of aquatic ecosystems (Cohen et al., 2016;

Hampton et al., 2008; Jeppesen et al., 2010), and modern ecological studies have advanced our knowledge of the mechanisms by which warming has influenced ecosystems (Shimoda et al., 2011). Many studies have demonstrated strong impacts of climate change on lake ecosystems through direct effects, including rising lake temperatures, changes in water column stratification, and concomitant changes in

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<https://doi.org/10.1016/j.palaeo.2021.110509>

Received 16 January 2021; Received in revised form 29 April 2021; Accepted 25 May 2021

Available online 4 June 2021

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nutrient recycling that often result in decreased primary production (O'Reilly et al., 2003; Tierney et al., 2010). However, other studies have highlighted indirect mechanisms by which climate change may increase primary productivity. In an outdoor mesocosm experiment, algal blooms were enhanced by climatic warming in three-trophic-level systems, but showed the opposite response in two-trophic-level systems (Hansson et al., 2013). This indicates that the impacts of warming on aquatic ecosystems cannot be simply predicted from direct effects alone and that cascading effects from upper trophic levels can exert a strong influence on phytoplankton and aquatic ecosystem structure. Yet it is unclear whether such 'top-down' effects hold over long timescales. Paleoecological and paleolimnological studies can provide a long-term perspective on changes in environmental and ecosystem processes, and have documented both direct human impacts as well as the indirect impacts of humans on a variety of aquatic ecosystems and processes (Dearing et al., 2012; Smol, 2008). However, paleolimnological studies of human impacts have rarely investigated mechanisms involving top-down effects of grazers on phytoplankton in the context of global change.

The Qinghai-Tibetan Plateau (QTP) provides crucial ecosystem services, including water, pasture, timber, and recreational and tourism opportunities to billions of people in the surrounding regions which together account for approximately 40% of the world's population (Yao et al., 2012; Yu et al., 2012). There are over 1000 lakes larger than 1 km<sup>2</sup> on the QTP, constituting the largest group of alpine lakes (averaging 4500 m elevation) on Earth (Wang and Dou, 1998). The QTP has warmed by up to 0.3 °C per decade during the last century, three times faster than the global average (Qiu, 2008). This warming is associated with 82% of the QTP's glaciers retreating since 1950s (Yao et al., 2012; Yao et al., 2019). As a result of this increased meltwater, numerous lakes have expanded (Zhang et al., 2015) and lake levels have increased (Zhang et al., 2011). These thermal and hydrologic changes could have severe impacts on the structure and function of lake ecosystems (Lin et al., 2017). For instance, enhanced inputs of glacial meltwater can alter lake hydrology, salinity, enhanced stratification and nutrient regime, and thereby impede internal nutrient loading to limit algal blooms (Posch et al., 2012; Slemmons and Saros, 2012) and biodiversity (Milner et al., 2009). However, the mechanisms by which these stressors influence aquatic ecosystem response and their spatial extent across QTP lakes remain largely unknown.

The trophic structure of most Tibetan lakes is relatively simple, with *Daphnia tibetana* and/or *Artemia tibetana* forming the top trophic level in lakes without fish (Lin et al., 2017). *Daphnia* (Cladocera) are known to be of pivotal ecological importance in lakes and ponds because they are large filter-feeding zooplankton that consume copious amounts and varieties of algae (Carpenter and Kitchell, 1996). The brine shrimp *Artemia* (Anostraca) has a broad geographical distribution inhabiting both inland and coastal saline and hypersaline lakes (Abatzopoulos et al., 1998). Salinity is an important driver of the distribution of these zooplankton in QTP, as *Artemia tibetana* can survive salinities between 25 and 75 g/L, whereas *Daphnia tibetana* mainly survive between 5 and 28 g/L (Lin et al., 2017). Since the late 1970s, global commercial breeding of fish has led to increased human consumption of *Artemia* (Sorgeloos et al., 2001). China is one of biggest natural *Artemia* producers, accounting for 30% of *Artemia* cyst production (Jia et al., 2015), and the harvesting of *Artemia* from QTP lakes is a primary income source for many Tibetan people. For example, in one of the largest *Artemia*-producing lakes on the QTP, Qixiang Co, local people using hand-operated nets harvested 310 tons of *Artemia* cysts during autumn of 2010 (Jia et al., 2015). Such extreme levels of harvesting are likely to impact algal diversity and biomass (Leavitt and Brown, 1988), but it has been difficult to separate the effects of harvesting from other stressors as contemporary records are too short to discern centennial or longer ecosystem-level changes.

To compare algae and zooplankton community changes from pre-industrial time (~1400 CE) and evaluate the effects of climate, human activities, and plankton harvesting on long time scales, we measured

chlorophyll and carotenoid pigments, and zooplankton remains preserved in a lake sediment core from a closed meromictic lake, Dagze Co, and compared these changes with nutrient, paleoclimate, and historical records over the past 600 years. This lake, located in the central QTP, is a brackish lake today; annual evaporation exceeds rainfall causing high lake salinity. During the past 30 years, the town of Nyima was relocated to directly upstream of Dagze Co, significantly altering land use in the region (Fig. 1). During this time, the lake also experienced a large expansion due to increased glacial meltwater inflow. Our high-resolution reconstructions of zooplankton and algal communities in this lake provide insight into the influence of climate and human disturbance on plankton composition and community change.

## 2. Methods

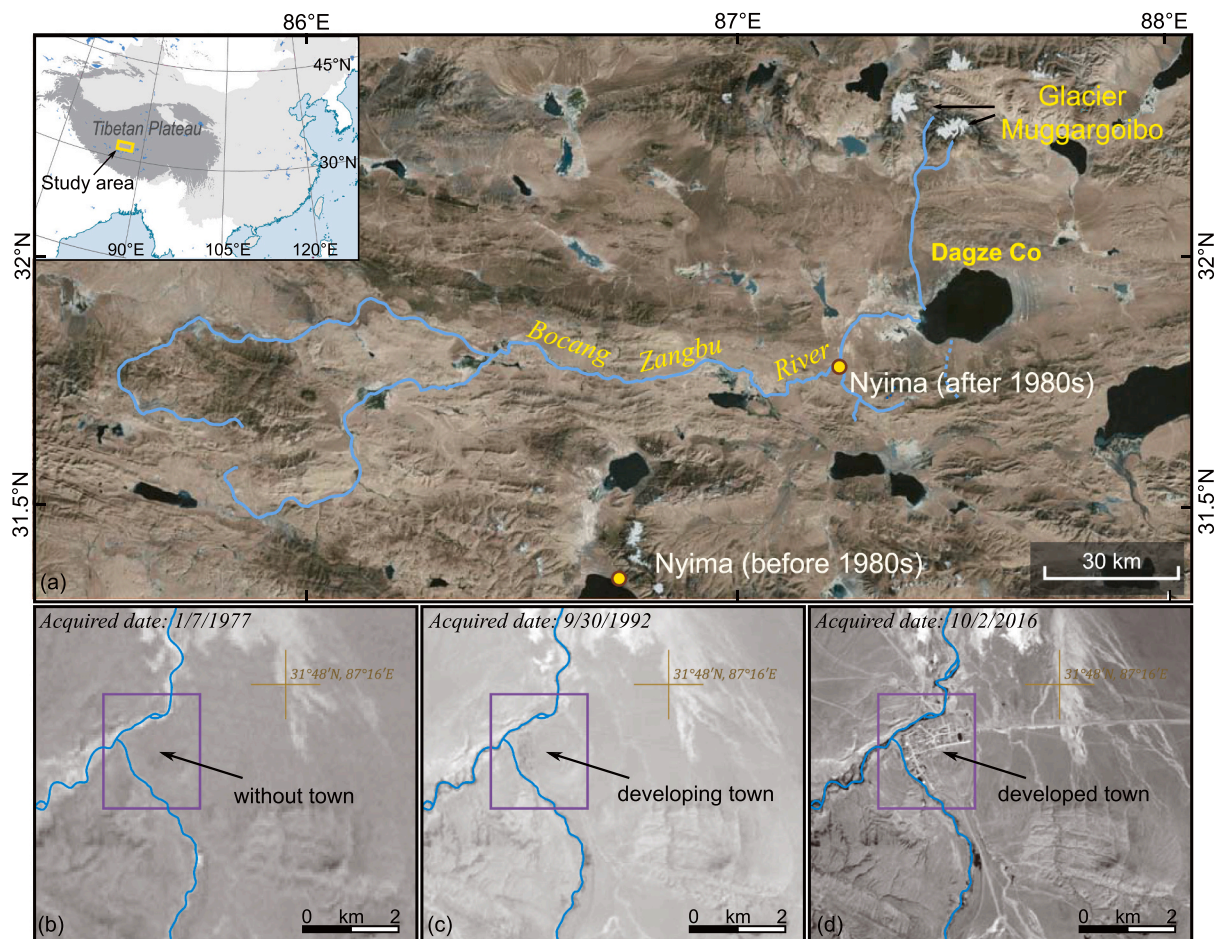
### 2.1. Dagze Co catchment system

Dagze Co (31°50' N, 87°32' E, 4472 m a.s.l., max depth 38 m) is a meromictic (chemically-stratified by salinity) (Wang et al., 2014), carbonate-rich, brackish lake located ~25 km east of the town of Nyima in the central QTP (Fig. 1a). The catchment of the lake is mostly covered by bare gravel with high-salinity soils. The lake is fed by glacial meltwater and precipitation (~300 mm/year) and there is no outflow, with water mainly lost to evaporation (Wang et al., 2014). The mean annual temperature is 0.55 °C and ice covers the lake from November to April (Wang et al., 2014). Surveys from 2012 to 2015 indicate a permanent thermocline was present at 16–23 m depth and the Secchi depth was ~6 m. The salinity of the lake water is ~14.69 g/L at the surface and increases to 21.41 g/L at the bottom. The total phosphorus (TP) concentration in summer (June and July) was ~112 µg/L (Lin et al., 2017) and the total nitrogen (TN) was 1320 µg/L (Chen et al., 2016), indicating a phosphorus-limited eutrophic system, and the concentration of chlorophyll *a* is ~1 µg/L (Lin et al., 2017). At present, Dagze Co has a short food chain with only two trophic levels and zooplankton dominated by *D. tibetana*, free from fish predation (Lin et al., 2017).

Watershed disturbances include both changes in meltwater inputs and land use. These disturbances accelerated at the turn of the 20th century with glacial responses to warming and meltwater input to lakes. The Muggargoibo Glacier is located ~35 km north of Dagze Co and its meltwaters flow into the lake during the warm season (Fig. 1a). The volume of meltwater input to the lake from glaciers since the Little Ice Age (LIA, 1400–1700 CE) was calculated using a Tibetan glacial volume formula by Liu et al. (2015). Glacial melt alone provided enough water to cause lake level to rise by 5.3 m in just seven years as years from 2003 to 2009 (Song et al., 2013). Indeed, the area of Dagze Co has increased by 71 km<sup>2</sup> since the 1970s based on Landsat TM/ETM data (Zhang et al., 2015; Landsat images). The largest land use change of the past 30 years in the catchment was the movement of the town Nyima onto the Bocang Zangbu River upstream of the lake (Fig. 1b, c and d). The development of the town contributed to local population expansion from 23,000 in 1994 to 30,000 in 2013 (data from <http://www.tpedatabase.cn>). The rapid rise in local population led to waste-water input, including sewage and gray water, into the river upstream of Dagze Co.

### 2.2. Lake sediment sampling, dating, and multiproxy analysis

The sediment core was retrieved from the deepest point of the lake (31°54' N, 87°33' E, depth 37 m) and upper 37 cm of sediment was used in this paper. Our age model, based upon <sup>210</sup>Pb dates and <sup>14</sup>C dates, exhibits a robust linear trend with depth and indicates that the core spans the last ~600 years (Li et al., 2015b). Age control for the core from Dagze Co was obtained using a combination of <sup>210</sup>Pb and <sup>137</sup>Cs dating in the uppermost sediment (1–11 cm) and AMS-<sup>14</sup>C dating in the sediment below 20 cm (Li et al., 2015b). The core's age-depth model was produced with the Bacon package using a Bayesian model (Blaauw and Christen, 2011) in R software (R Development Core Team, 2015).



**Fig. 1.** Overview map of the Tibetan Plateau (shaded in inset) with Dagze Co (a) Nyima town locations. The Landsat MSS (b), TM (c) and OLI (d) images indicate the development of the town during the past 30 years, with a spatial resolution of 60 m, 30 m and 15 m, respectively.

Accumulation rates at Dagze Co were low from 1600 CE to 1900 CE, but increased in deeper and the topmost samples (Fig. S2). As pigments are easily degraded during sampling, we removed the first 1 cm of sediment as it was in contact with the air and likely degraded. The rest of the core was immediately subsampled contiguously at intervals of 5 mm, and the samples were stored in a freezer prior to laboratory analysis.

About 0.2 g of freeze-dried sediments were extracted overnight at  $-4^{\circ}\text{C}$  in a mixture of acetone, methanol, and water (80:15:5) (Liang et al., 2016). The solution was centrifuged (2500 revolutions/min) and filtered with a  $0.22\ \mu\text{m}$  PTFE filter to remove sediment, dried under  $\text{N}_2$ , and re-dissolved in acetone and water (70:30) before injection into an Agilent 1200 high-performance liquid chromatography (HPLC) system equipped with a photo-diode array detector (DAD). We adopted the method by Wright et al. (1991) for HPLC analysis. The peak areas were identified with commercial standards (DHI Denmark) and quantified with an internal standard 8-apo-carotene (Sigma) at the maximum absorption wavelength (440 nm, 620 nm). The main identified pigments include fucoxanthin and diatoxanthin (siliceous algae), alloxanthin (cryptophytes), canthaxanthin and echinenone (cyanobacteria), chlorophyll *b*, lutein and phaeophytin *b* (chlorophytes), chlorophyll *a* and  $\beta$ -carotene (total algae), and phaeophorbide *a* (chlorophyll *a* degradation product). Pigment concentrations were expressed as nanomoles of pigment relative to the sediment organic content estimated by loss on ignition (LOI;  $550^{\circ}\text{C}$ , 4 h).

To obtain TP concentrations in the sediment, the powdered sample was digested using persulfate, neutralized with NaOH, and analyzed using a UV spectrophotometer (Murphy and Riley, 1962). The concentrations of TN were measured spectrophotometrically as nitrite after

potassium persulfate digestion (Solorzano and Sharp, 1980). Total organic carbon (TOC) contents were measured on sediment with a TOC analyzer (TOC-VCPH, Shimadzu, Japan). About 150 mg of dry sample was pretreated with phosphoric acid to remove inorganic carbonate.

Approximately 1 g of dried sediment was used to quantify the zooplankton concentrations. The samples were mixed with Milli-Q water and then filtered through a  $140\ \mu\text{m}$  plastic filter. The material retained on the filters was counted using an Olympus BX-4 microscope. Remains of *A. tibetiana* and *D. tibetana* were identified from carapaces and resting eggs respectively. Species identification was based on morphological criteria according to McCauley (1984). The grazing pressure was expressed as the quotient of the zooplankton abundances and algal production, the latter of which is characterized by algal PCA1 scores.

To evaluate the effects of degradation on pigment concentrations, we employed the Multi-G model. The first-order G-model has been widely used to simulate diagenetic degradation processes of sedimentary pigments (Chen et al., 2005; Sun et al., 1991). The model uses time and organic matter contents to simulate degradation rates. The first-order G-model may produce large error as it treats all organic matter the same, assuming a uniform degradation rate for less stable (e.g. pigments) and more stable fractions. The multi-G model separates organic matter into several parts, each with a unique degradation rate (Li et al., 2015a). We used a two component multi-G model to estimate the degradation of pigments (chlorins, include Chl *a*, phaeophytin *a* and phaeophorbide *a*) in Dagze Co (according to Stephens et al., 1997).

The Multi-G model is based on the following equation:



$$C_t = C_\infty + C_0 \times (1 - a) \times e^{(-k_1 \times t)} + C_0 \times a \times e^{(-k_2 \times t)} \quad (1)$$

where  $C_0$  (2.9 nmol/g OC) is the content of organic matter in surface sediment,  $C_\infty$  (177.7 nmol/g OC) is the asymptotic organic matter content at the infinite depth, and  $C_t$  (nmol/g OC) is the organic content at certain time  $t$  (years),  $k_1$  and  $k_2$  are degradation rate of different organic matter and we set  $2E-3$  and  $0.3$  respectively (Li et al., 2015a),  $a$  is the percentage of refractory portion in organic matter (the value is  $0.7$ ),  $t$  can be calculated as the quotient of layer depth  $d$  (cm) divided by sedimentation rate  $s$  (0.06 cm/yr).

To identify changes in algal community structure, we applied breakpoint analysis in the R software “segmented” package to the pigment and zooplankton data, and used analysis of variance to test the significance of breakpoints (Muggeo, 2008; R Development Core Team, 2015; Stevenson et al., 2016). Differences between environmental variables in the pre- and post-settlement were assessed using nonparametric Mann-Whitney  $U$  test in SPSS (v16, IBM Corp, Portsmouth, UK), as we have small sample sizes after settlement that do not exhibit a normal distribution. Principal components analysis (PCA) was conducted on pigment concentrations to determine dominant trends over time. The pigment data was  $\log(x + 1)$  transformed prior to PCA. The PCA1 of pigments strongly correlated with  $\beta$ -carotene and chlorophyll  $a$  (Pearson coefficients are  $0.85$  and  $0.70$  respectively) and therefore could reflect algal community changes and primary production during the past 600 yrs. Variance partitioning analysis (VPA) was carried out using adjusted  $R^2$  values in partial RDA to determine the relative importance of each reconstructed variable in explaining past changes of the algal community, including climate variables (expressed as C; containing temperature (Christiansen and Ljungqvist, 2012) and precipitation records (Grießinger et al., 2011)), nutrient (expressed as N; containing TP and TN from this study), zooplankton grazing pressure (expressed as Z; calculated by the zooplankton population/algal PCA1) and salinity changes (expressed as S;  $\%C_{37:4}$  record from (Li et al., 2015b)). Separate VPA was conducted for the periods “1950–2002”, “1400–1950” and “1400–2002”. Both PCA and VPA was performed using R software “vegan” package (Oksanen, 2011). We integrate these data with previously published records to investigate the controls on phytoplankton changes through time.

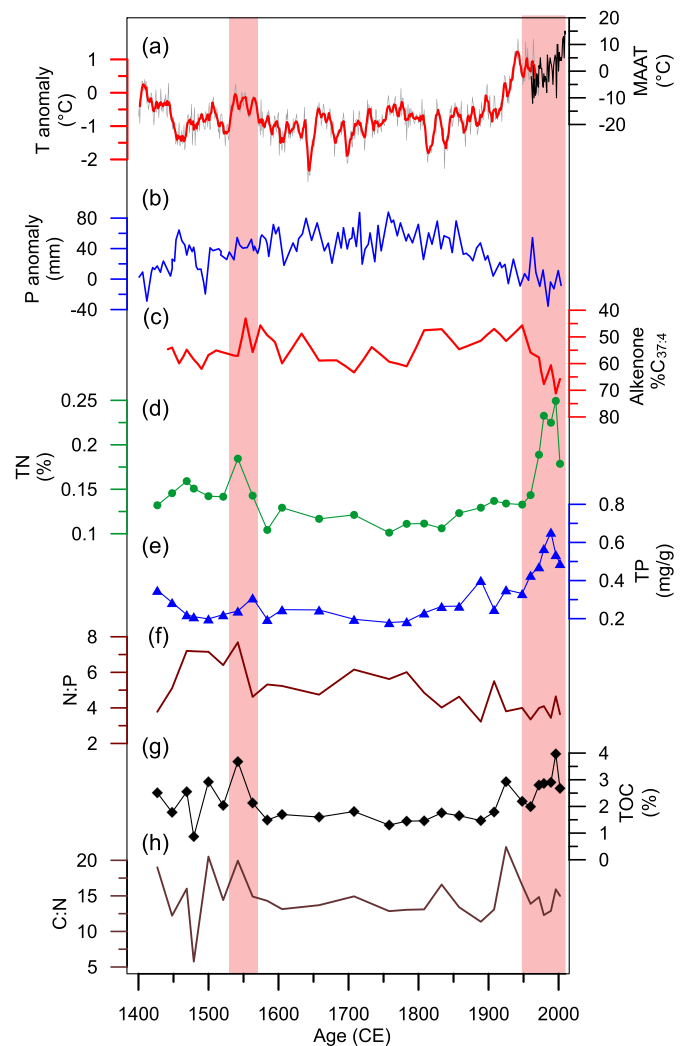
### 3. Results

#### 3.1. Environmental and nutrient change

Proxy reconstructions and observational data indicate that mean annual temperatures were generally low during the LIA until the 20th century (Fig. 2a), followed by warming after 1950 CE (Christiansen and Ljungqvist, 2012). The warming in the last century contributed to a 16% decrease in the area of Muggargoibo Glacier, releasing a volume of meltwater of  $0.05 \text{ km}^3$  toward Dagze Co (Table S1; Fig. S1). Precipitation in this region, revealed by the tree-ring oxygen isotope record (Grießinger et al., 2011) is thought to have increased before 1850 CE and decreased during past  $\sim 150$  years (Fig. 2b).

Dagze Co is a closed lake in an arid region where annual evaporation exceeds rainfall, causing high lake salinity. To investigate past changes in salinity of the lake, we use the alkenone  $\%C_{37:4}$  index ( $C_{37:4}$  as a percentage of all the  $C_{37}$  alkenones) which calibration studies have shown is negatively correlated with lake salinity (Song et al., 2016). Previously published data showed that  $\%C_{37:4}$  values in Dagze Co varied from  $\sim 45\%$  to  $\sim 70\%$  (Li et al., 2015b), and the  $\%C_{37:4}$  values in the sediment indicate that the salinity of Dagze Co was stable from  $\sim 1450$  to 1950 CE but decreased since 1950 CE in response to these changes in meltwater inputs (Fig. 2c).

The concentrations of total nitrogen (TN) and total phosphorus (TP) were generally low and stable before 1900 CE and then increased, with a gradual rise beginning at  $\sim 1900$  CE and a sharper rise starting at  $\sim 1960$  CE (Fig. 2d). TN exhibits more variability than TP prior to the 1900 CE,



**Fig. 2.** Environmental changes over the past 600 years in Dagze Co. Mean annual air temperature (MAAT) from an extra-tropical Northern Hemisphere temperature stack based on compilations of 91 proxies (Christiansen and Ljungqvist, 2012) (a); precipitation anomaly from tree-ring  $\delta^{18}\text{O}$  record at Reting, Tibet (Grießinger et al., 2011) (b); alkenone  $\%C_{37:4}$  record at Dagze Co (Li et al., 2015b) (c); nutrients from TN (d), TP (e) and the N:P ratio (f); TOC (g) and C:N ratio (h).

with higher concentrations between  $\sim 1450$  and  $1550$  CE. TP preserved in the sediment varied from  $0.18$  to  $0.65 \text{ mg/g}$ , with the highest values in 1989 CE, and TN varied from  $1.01$  to  $2.49 \text{ mg/g}$  (Fig. 2e) with the highest values in recent decades. Some of the increase in nutrient concentrations may be due to nitrogen deposition, particularly emission from agriculture in Asia (Li et al., 2020), but meltwater can also carry nutrients, especially P, into the lake (Fig. 2a, d and e). The N:P ratio was about  $7$  between  $\sim 1470$  and  $1550$  CE, then declined until reaching the lowest values in the 20th century (Fig. 2f).

The TOC concentrations ranged between  $0.87\%$  to  $3.97\%$ , and with an average of  $2.15\%$  (Fig. 2g). The C:N ratio was gently stable with an average value of  $14.65$  during the past 600 years (Fig. 2h). Higher C:N ratio occurred at about  $1500$  CE and  $1900$  CE, which could indicate an increase in terrestrial organic matter inputs (Meyers and Teranes, 2001).

#### 3.2. Plankton community changes

Microfossil remains of the two dominant species of zooplankton (*A. tibetiana* eggs and *D. tibetana* shells) were identified in lake sediment cores at Dagze Co. However, in recent water column sampling, only

*D. tibetana* was observed in the lake. The egg abundance of *A. tibetana* fluctuated markedly over the past 600 years, with peaks evident between 1500 and 1600 CE and 1900–1980 CE. *A. tibetana* abruptly disappeared in 1980 CE. *D. tibetana* was rare before 1850 CE but became abundant after 1850 CE, and had a maximum in 1990 CE, about the same time that *A. tibetana* populations crashed (Fig. 3).

Pigments can be degraded by oxidation, photolysis, and grazing. Pigment degradation under anoxia is extremely slow, and because Dagze Co is an anoxic, meromictic lake we expect the effects of oxidative degradation in the sediment to be minimal. Results from the multi-G model of pigment degradation indicate that pigment relative abundances were not strongly altered by degradation (Fig. S3). PCA axis 1 explained 49.6% variance of algal community (Fig. S4) and exhibited positive loading from all pigments. Total algal production, as indicated by  $\beta$ -carotene and pigment PCA1, oscillated through time with the lowest values around ~1500 CE and after ~1950 CE (Fig. 3). Analysis of individual pigments showed algal communities experienced significant changes in the relative abundances of cryptophytes, chlorophytes, siliceous algae, and cyanobacteria at the start of the 20th century (average breakpoint is  $\sim 1920 \pm 43$  yrs.; Table S2). The alloxanthin indicated cryptophytes dominated from 1400 to 1900 CE, whereas diatoxanthin (siliceous algae) and echinenone (cyanobacteria) dominated around 1950 CE. After 1980 CE, the alloxanthin (cryptophytes) reestablished dominance of all pigments (Fig. 3).

The VPA showed that nutrients (N), climate (C), salinity (S) and zooplankton grazing pressure (Z) together explained 78.3% of the historical changes in the algal community since the 1950s, 31.8% between ~1400–1950 and 32.5% for the entire period (Fig. 4 and Table S3). Comparison of unique and interactive categories revealed that nutrients and zooplankton grazing effects explained the most variance of any single variable ( $N = 4.3\%$ ,  $Z = 17.2\%$ ,  $C = 0.3\%$ ,  $S = 0$  during 1400–1950 CE;  $N = 7.4\%$ ,  $Z = 2.7\%$ ,  $C = 1.8\%$  and  $S = 1.4\%$  during 1950–2002 CE). More of the explained variation arose from zooplankton grazing rather than from other changes between ~1400–1950 CE. However, interactions among nutrients and salinity explained 33.1% of the variance after 1950 CE.

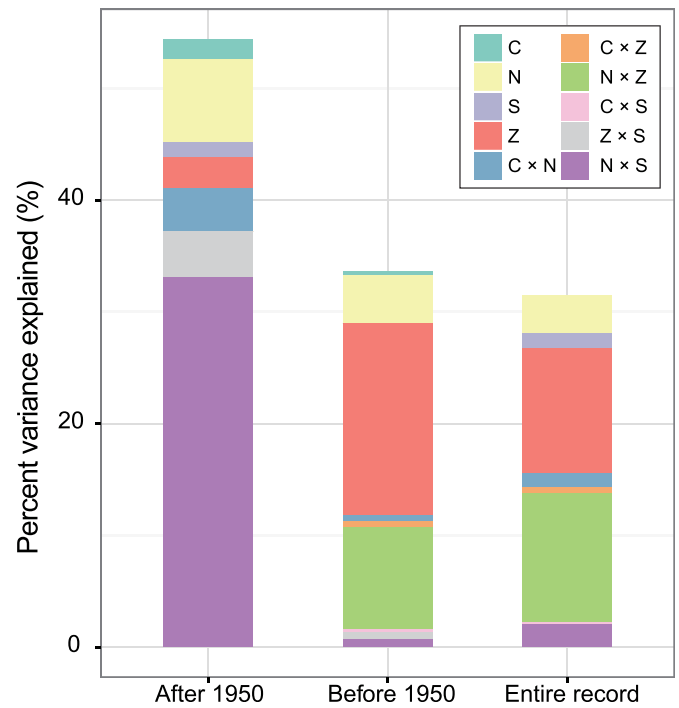


Fig. 4. Effect of climate (C), nutrients (N), salinity (S) and zooplankton grazing pressure (Z) on fossil assemblages of pigments through variance partitioning analyses (VPA). VPA results for 1950–2002, 1400–1950 and 1400–2002 CE.

## 4. Discussion

### 4.1. Algal community changes during past 600 years

Pigments in Dagze Co sediment show that both algal biomass and community structure fluctuated during the past 600 years, with declines in most groups in the 20th century (Fig. 3). In many lakes from the

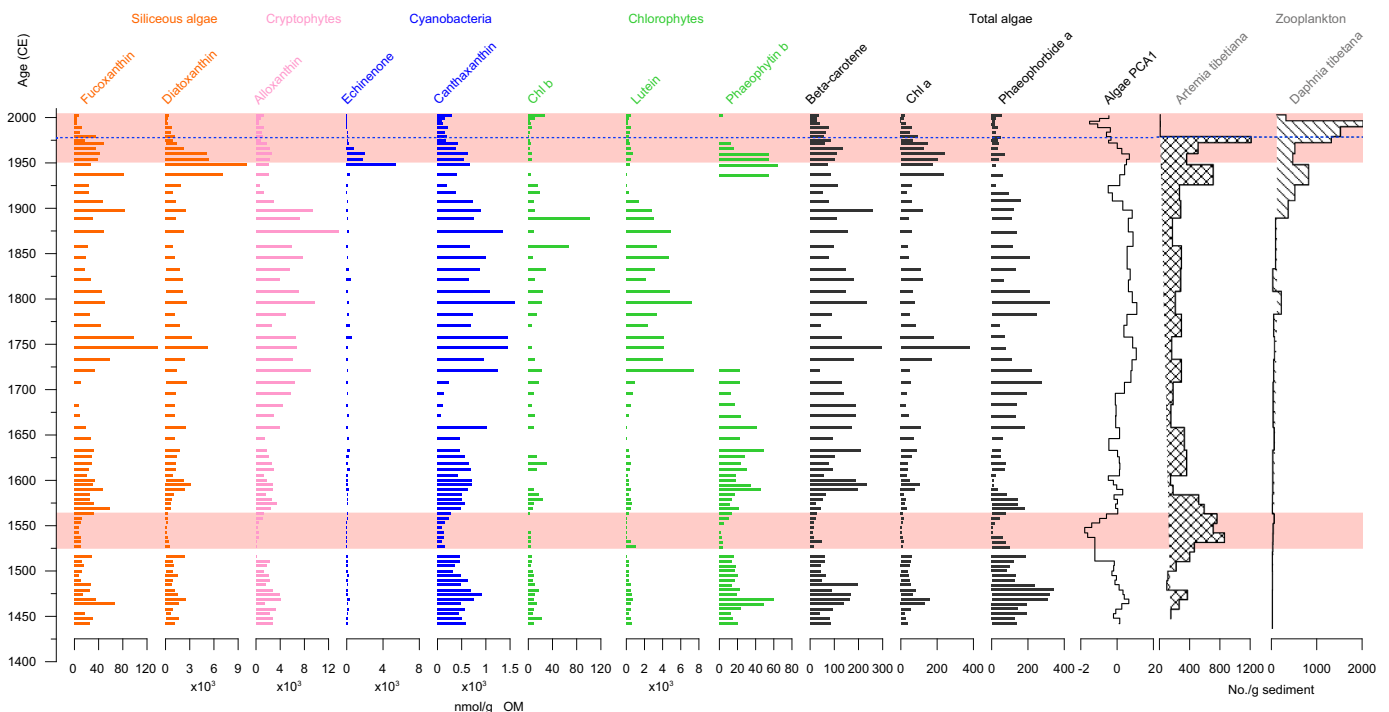


Fig. 3. Time series of chlorophyll and carotenoid pigments, pigment PCA 1 and population of zooplankton extracted from sediment cores at Dagze Co.

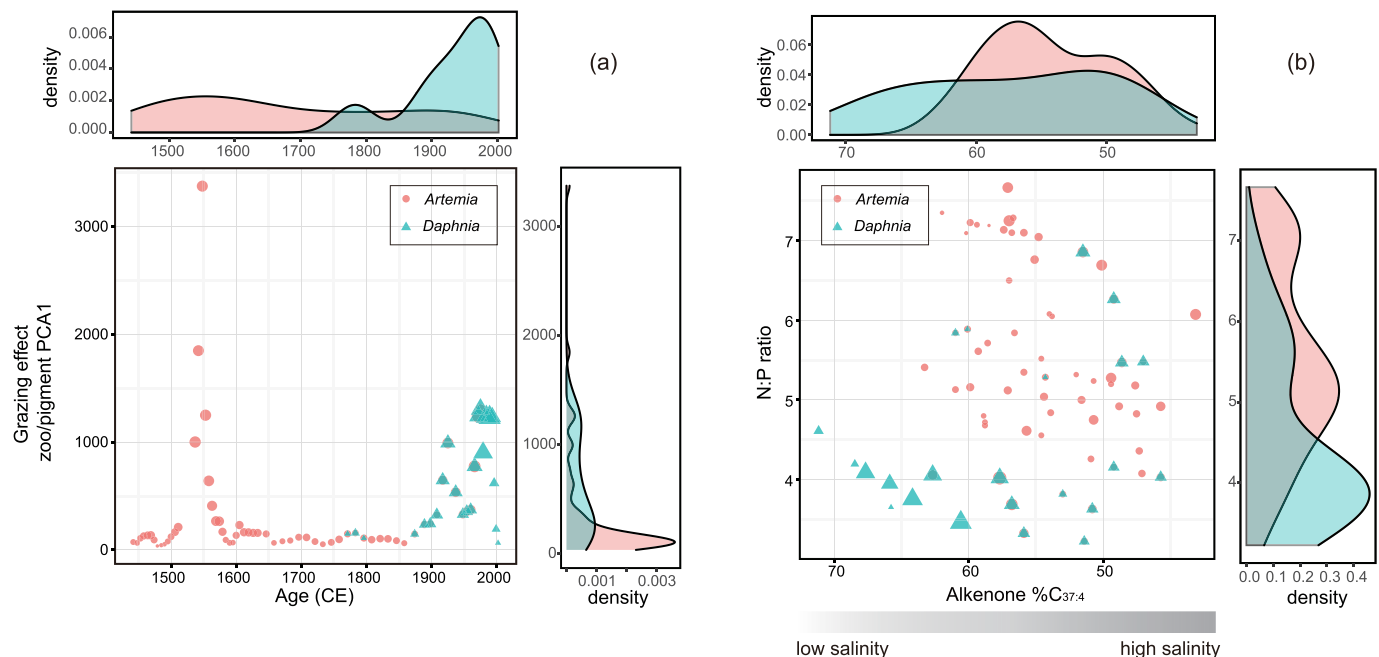
Northern Hemisphere, cyanobacteria, and often total phytoplankton abundance, have increased significantly over the past two centuries in response to anthropogenic nutrient addition (Bunting et al., 2016; Taranu et al., 2015), but at Dagze Co, there is evidence of a very different trend with declines in cyanobacteria as well as other phytoplankton groups. Although some records in the Tibet indicate an increase in algal production since the 1800s (Hu et al., 2014; Lami et al., 2010), we observe declines in the algal production at Dagze Co despite increasing nutrients. The reason for this decoupling may be derived from bacteria, as bacteria growing on terrestrial organic carbon can block the diffusion of these nutrients and outcompete phytoplankton for nutrients, thereby suppressing phytoplankton growth (Ask et al., 2012). This differing biological response to nutrients is also seen in a Japanese meromictic lake (Mikami et al., 2002).

Declines in algal production despite climate warming could have several causes. Higher sedimentation rates were observed after 1950 CE (Fig. S2), suggesting that increasing meltwater may have delivered more sediment to the lake. The meltwater flow into Dagze Co increased due to climatic warming, which could have a dual effect on lake ecosystem production. On one hand, the increased meltwater could be partly responsible for more nutrient inputs from the influent river (Slemmons et al., 2013). Our VPA does suggest algal community composition changes are partially explained by changes in nutrients since 1950 CE (Fig. 4). Nutrient inputs rose since 1950 CE; however, in the present-day, measured nutrient concentrations of Dagze Co are not high compared with other lakes (Kenney et al., 2002). Alternatively, and more likely in Dagze Co, the increasing meltwater flux could suppress primary production by limiting light, since glacial meltwater often has high turbidity (Barouillet et al., 2019; Carpenter et al., 1998). Poor light conditions would greatly affect benthic habitat where most total primary production would take place in unproductive lakes such as Dagze Co (Ask et al., 2009; Vadeboncoeur et al., 2001). This may further explain the shift in algal community composition from cryptophytes to siliceous algae and cyanobacteria around 1950 CE, as the reductions in the depth of the photic zone may reduce cryptophyte populations. Cryptophytes are

motile algae, which can sometimes thrive at the chemocline or thermocline if there is enough light penetration (Ojala et al., 1996), and where an increase in turbidity could be very influential. Taken together, we suggest that low water clarity may have influenced the decline in algal production during 1950–2002 CE.

Relationships between algal community, climate, nutrients, and limnological processes show a different pattern in the interval from ~1400–1950 CE relative to the post~1950 CE interval. In the older sediments, decreased algal biomass coincided with low nutrient conditions, particularly from 1400 to 1700 CE and ~1900 CE. Although these changes in nutrients may have influenced algal communities, the VPA results suggest that zooplankton grazing pressure explained most of the variability in the algal community (Fig. 4). It has been shown that in a two-trophic-level system such as Dagze Co, the top-down effects of zooplankton grazing may outweigh the influence of climate and nutrient variability on photoautotrophs (Graham and Vinebrooke, 2009; Hansson et al., 2013). Cladocerans are known to exert very strong controls on food web dynamics (Sommer and Sommer, 2006); Hampton et al. (2008) found that cladocerans depressed nutrient cycling and had negative relationships with chrysophytes, cryptophytes, and chlorophytes. In addition, a sustained period of high salinity and high nitrogen content could potentially enhance the growth of the brine shrimp, *A. tibetiana*, which consequently could cause elevated grazing and declining populations of phytoplankton (Fig. 5a). Our VPA modeling results suggest the increased grazing associated with increased biomass of *A. tibetiana* and *D. tibetana* caused reduced algal production despite growth conditions (nutrients, temperature) that might be expected to favor phytoplankton growth.

Previous microcosm and experimental studies have revealed that warming effects on grazing can offset warming-enhanced algal growth in two-trophic ecosystems (Hansson et al., 2013; He et al., 2015). Investigation of modern lakes shows that warming strengthens grazing in Tibetan lakes, due to both indirect effects as well as direct, enhanced metabolic processes (Lin et al., 2017). If the latter mechanism dominates, we would expect that the decline of algal biomass would be coeval



**Fig. 5.** *Artemia tibetiana* and *Daphnia tibetana* grazing effect on total algal production (pigment PCA1), indicating *Artemia tibetiana* control algal production before 20th century and *Daphnia tibetana* control algal production after 20th century (a); Zooplankton abundance relative to N:P ratio and salinity (%C<sub>37:4</sub>), demonstrating that *Artemia tibetiana* had high abundance at high salinity with high N:P ratio and *Daphnia tibetana* had high abundance at low salinity with low N:P ratio (b). The size illustrates the abundance of *Artemia tibetiana* (red) and *Daphnia tibetana* (green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with rising temperatures throughout our study interval. We found there are two warm periods of low algal production that coincide with abundant zooplankton, about ~1550 CE and ~1950 CE (Fig. 5a). These two intervals coincide with slightly elevated temperatures and fluctuating nutrients (Fig. 2). However, both periods were characterized by low algal production, associated with an elevated population of zooplankton. Given the low primary production at this time, it is likely that warming-enhanced grazing led to decreased abundance of algae (Lotze and Worm, 2002). In addition, the pigments from cryptophyte, cyanobacteria and chlorophyte increased from 1700 to 1900 CE, an interval with low temperature and decreased population of zooplankton. Thus, as hypothesized, both natural warming and anthropogenic warming triggered enhanced zooplankton grazing that affected phytoplankton dynamics. Some studies have suggested that climatic warming is associated with increasing algal biomass, via mechanisms such as assisting recruitment and growth of algae (Lotze and Worm, 2002) and improving the rate of algal enzymatic reactions important to algal blooms (Duan et al., 2009). In contrast, our records stress the role of warming on grazing in the sediment pigment record. These results are consistent with previous studies which used modelling approaches to assess lake pigment flux in lakes (Cuddington and Leavitt, 1999) and factorial laboratory experiments (Lotze and Worm, 2002).

Phaeophorbide *a* has previously been used to estimate the effect of grazing using lake sediments (Carpenter et al., 1986). However, phaeophorbide *a* in Dagze Co sediment was anticorrelated with both *A. tibetiana* and *D. tibetana* over the study period (Fig. 3). This may indicate that there could be zooplankton in Dagze Co other than *A. tibetiana* and *D. tibetana* that produce phaeophorbide *a* (Pandolfi et al., 2000; Sathish et al., 2020). Moreover, there are doubts over the use of phaeopigments as relevant indicators of herbivory. For example, several studies suggest that the phytoplankton chlorophyll-breakdown pathway varies among different zooplankton species due to grazer-specific feeding habits (Ford and Honeywill, 2002; Pandolfi et al., 2000). In addition, grazing and senescence have different chlorophyll-breakdown pathways, such as chlorophyll-chlorophyllide-pheophorbide (CCP) and chlorophyll-pheophytin-pheophorbide (CPP) (Leavitt, 1993; Sathish et al., 2020). Sampling from freshwater, estuarine, and marine ecosystems has demonstrated that the distribution of chlorophyll degradation products (pheophorbide and pheophytin) exhibits distinct spatial and seasonal variation, suggesting that algal senescence or sinking of ungrazed phytoplankton contribute to production of chlorophyll derivatives, which cannot be ruled out (Sathish et al., 2020). Given this, we assume that phaeophorbide *a* in Dagze Co indicates not only *A. tibetiana* and *D. tibetana* gut pigment, but also other zooplankton grazing or the sinking of ungrazed algae.

#### 4.2. Impacts of salinity and N:P ratio changes on zooplankton community

The significant increases in zooplankton after the 1900s in Dagze Co suggest a large change in factors regulating abundances of *A. tibetiana* and *D. tibetana*. Salinity is the critical environmental variable controlling zooplankton community composition in brackish and inland saline lakes from Tibet (Lin et al., 2017). Although the lake zooplankton community fluctuated between 1400 and 1900 CE, our records show that generally *A. tibetiana* was abundant and *D. tibetana* was rare prior to the 20th century (Fig. 3). Prior to the 20th century, the lake was characterized by relatively high salinity, reflected by low alkenone %C<sub>37:4</sub>. The high salinity promoted the more salt-tolerant *A. tibetiana* (Fig. 5b). Glacier meltwater in the 20th century linked to climatic warming likely lowered the salinity, promoting increased populations of *D. tibetana*.

Other factors may also influence the zooplankton populations, including top-down (predation) and bottom-up (algal production) controls. Fish are absent at Dagze Co in the present day, so a top-down relationship is unlikely to control zooplankton community changes in the past. Many studies have suggested that declining algal production would decrease the production of higher trophic levels (Andersson et al.,

2003; Cohen et al., 2016; Wurtsbaugh and Gliwicz, 2001). Both *D. tibetana* and *A. tibetiana* are large-bodied, filter-feeding zooplankton, and they compete for food resources. Continued increases in zooplankton biomass may consume other potential food sources, besides algae. Based on C:N ratio data (Fig. 2h), high biomass of zooplankton clearly coincided with an increase in terrestrial organic matter inputs. However, a variety of field and experimental data also indicate that food quality, notably the phosphorus (P) and nitrogen (N) content consumed, plays an important role in zooplankton performance (Laspoumaderes et al., 2013; Sterner and Elser, 2002). *Artemia* prefer high nitrogen foods, whereas *Daphnia* typically feed on organisms with a higher P and lower N content (Hall et al., 2004). The decline of the N:P ratio coincided with a decrease in *Artemia* and an increase in *Daphnia*, in keeping with these organisms' requirements (Fig. 5b). The species changes of *D. tibetana* and *A. tibetiana* were not strongly influenced by algal production in Dagze Co food web, but salinity and supply N:P ratio changes are likely the main controls on zooplankton communities.

#### 4.3. Effects of local settlement on the Dagze Co ecosystem

*A. tibetiana* disappeared suddenly in ~1980 CE (Fig. 3), and *D. tibetana* reached maximum levels ~10 years later. This transition coincides with the movement of the town of Nyima to its present location upstream of Dagze Co. Local land-use disturbance is often associated with shifts in aquatic ecosystems, and we suggest that the movement of Nyima may have resulted in overexploitation of *A. tibetiana* causing these population declines. Harvesting *A. tibetiana* is a key source of income for local people, and the gross domestic product (GDP) of the fishery industry in Tibet has increased markedly since the 1970s (data from <http://www.tpdatabase.cn>). The lower salinity and increased meltwater also contributed to the collapse of *Artemia* in the 1980s, allowing for the rapid expansion of *D. tibetana*.

The complete replacement of *A. tibetiana* by *D. tibetana* coincides with marked decreases of algal production. Though both *A. tibetiana* and *D. tibetana* are filter-feeding zooplankton, the appearance of these zooplankton in lakes could easily influence algal community structure (Jia et al., 2015; Leavitt and Brown, 1988), and may have resulted in cryptophytes replacing siliceous algae, which are susceptible to grazing. Monitoring data suggests that regional climatic warming and enhanced stratification would impede internal nutrient loading to limit algal blooms (Posch et al., 2012). Finally, the persistently elevated nutrient content from human activities and climate change may alter the lake ecosystem, such as occurred elsewhere in China (Hu et al., 2014; Liu et al., 2017; Wang et al., 2019), Europe (Moorhouse et al., 2018; Wiik et al., 2015), and Canada (Bunting et al., 2016), though whether this should promote cryptophytes at the expense of other taxa is less clear.

## 5. Conclusions

We present records of plankton dynamics at an alpine meromictic lake during the past 600 years. Warming leading to strong top-down effect was likely the primary factor controlling algal production. Lake salinity and N:P ratio coincided with zooplankton community shifts during the past 600 years. Local anthropogenic activity, overharvesting of the brine shrimp *A. tibetiana*, promoted the replacement of *A. tibetiana* by *D. tibetana* after 1980s. From a management perspective, under modern climatic warming and intensified human activities, proper aquatic harvesting may help maintain aquatic ecosystem function and species richness. Finally, by comparing typical external drivers with internal shifts in plankton communities, we show that top-down effect could not be ignored when interpreted lake primary producers.

#### Declaration of Competing Interest

The author declare that they have no known competing financial interests or personal relationships that could have appeared to influence



the work reported in this paper.

## Acknowledgements

We would like to thank Dr. Dong Li for providing pigment degradation model and valuable discussion. We also thank Dr. Qian Zhang for mapping the boundaries of both modern (December 2002) and LIA glaciers based on Shuttle Radar Topography Mission data to estimate meltwater inputs to the lake. This study was supported by the Natural Science Foundation of China (Grant No 42007409); Chinese Academy of Sciences Key Project (XDA20090000); the Open Research Fund of Key Laboratory of Tibetan Environment Changes and Land Surface Processes.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2021.110509>.

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