



# Intense touristic activities exceed climate change to shape aquatic communities in a mountain lake

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## Abstract

Mountain lakes are especially vulnerable to climate change, but are also increasingly exposed to local anthropogenic development through winter and summer tourism. In this study, we aimed to tease apart the influence of tourism from that of climate in a mountain lake located within one of the largest French ski resorts, by combining paleolimnological and present ecological data. The reconstructed long-term ecological dynamics highlighted an increase in lake biological production from the end of the Little Ice Age up to the 1950s, suggesting a historical dominance of climate control. Afterward, a major drop in pelagic production occurred at the same time as the watershed erosion increased and peaked in the 1990s, concomitant with massive digging for the ski resort expansion. The benthic invertebrates collapsed in the 1980s, concomitantly with the onset of massive salmonid stocking and recent warming. Stable isotope analyses identified benthic invertebrates as the major salmonid diet resource and suggested a possible direct impact of salmonid stocking on benthic invertebrates. However, habitat use may differ among salmonid species as suggested by the way fish DNA was preserved in surficial sediment. The high abundances of macrozooplankton further confirmed the limited reliance of salmonids on pelagic resources. The variable thermal tolerance of benthic invertebrates suggested that the recent warming may mostly affect littoral habitats. Our results indicate that winter and summer tourism may differently affect the biodiversity of mountain lakes and could collectively interfere with the ecological impacts of recent warming, making local management of primary importance to preserve their ecological integrity.

**Keywords** Mountain lakes · Tourism · Ski resort · Climate warming · Fish introduction · Watershed erosion · Stable isotopes · eDNA

## Introduction

Mountain environments represent attractive areas for human populations, where both summer and winter tourism imply massive economic stakes (Scott 2006). The rise of mountain tourism generated tremendous development of ski resorts related to winter tourism from the second half of the twentieth century (George-Marcelpoil and François 2012). The implementation of ski resorts involved massive digging to create ski run networks, with the side effect of amplifying erosion of mineral matter and associated nutrients from bare soils (Ristić et al. 2009) (Wrońska-Wałach et al. 2019). These eroded particles can be washed into the aquatic ecosystems and typically decrease water transparency (i.e., increased turbidity, Zhang et al. 2007), thereby affecting primary production. Increased erosion can directly (through particle sedimentation) or indirectly (through changes in

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the light penetration) degrade benthic habitats due to clogging (Tullos et al. 2016) and dampened oxygen conditions (Schenk and Bragg 2021). As a consequence, dramatic ecological impacts on lakes could ensue from this radical reshaping of the mountain environment. However, case studies remain elusive, and the drastic decline in water transparency of the iconic Lake Tahoe where the Secchi depth dropped from more than 30 m in the late 1960s to ~20 m in the 2000s is a rare documented case of enhanced watershed erosion associated with ski resort expansion (Grismer and Eliss 2006; Swift et al. 2006; Sahoo et al. 2010).

The course for the winter “white gold” was more recently accompanied by the summer “green gold” quest, where nature-based tourism is increasingly sought after as summer “cold refuges” during heatwaves (Serquet and Rebetez 2011) and more recently by the COVID-19 pandemic (Seraphin and Dosquet 2020). Mountain lakes play a central role for summer tourism by supplying a wide variety of leisure activities (Jones et al. 2006), including recreational fishing. Since high mountain lakes are originally devoid of fish fauna (Ventura et al., 2017), game fish (i.e., salmonids, such as trout and charr) have been widely introduced within institutional fish stocking campaigns and illegal fish translocations. The latter are often associated with the collateral introduction of so-called forage fish, i.e., small fish—mainly minnows of the genus *Phoxinus*—used as live baits to fish or to forage the salmonids. Both salmonids and minnows have been shown to exert detrimental impacts on native invertebrates and amphibians (Knapp et al. 2001; Schilling et al. 2009; Tiberti et al. 2014; Osorio et al. 2022). Their impacts mostly rely on direct predation of conspicuous benthic invertebrates as well as large zooplankton (e.g., *Daphnia* sp.) but can also be subtler through imposed habitat shifts of native species (Milardi et al. 2016). The ecological consequences of salmonid introduction can further spread throughout lake food webs (i.e., top-down trophic cascade) by affecting zooplankton grazing control and nutrient cycling, possibly leading to enhanced algal production (Sarnelle and Knapp 2005; Schindler et al. 2001; Eby et al. 2006).

Winter and summer tourism would hence expose mountain lakes to major anthropogenic pressures. However, little is known regarding their interplay with climate change, to which mountain lakes are particularly exposed (Pepin et al. 2015; Råman Vinnå et al. 2021; Williamson et al. 2009) and diverse feedbacks can be envisaged due to the different natures of these forcings. For instance, the rise of temperature could amplify the number of mountain lakes exhibiting suitable thermal conditions for salmonid survivorship, thereby supporting the spread of salmonid introduction. Alternatively, warming typically fosters watershed productivity (Carlson et al. 2017; Volk et al. 2021), which can intensify nutrient runoff to aquatic ecosystems (Kaštovská et al. 2022), mimicking the effects of erosion. However, the

latter would involve high mobilization of mineral particles dampening water transparency, possibly resulting in divergent outcomes regarding primary production. Mountain lakes are therefore likely to experience drastic ecological changes because of these local and global anthropogenic pressures. Addressing their respective implications in driving their ecological trajectories is a prerequisite for their conservation.

In this study, we used paleolimnological investigations to reveal the long-term ecological trajectory (1850–2010) of a mountain lake (Lake Tignes) located within one of the largest French mountain resorts hosting both massive winter and summer tourism. Our overarching aim was to tease apart the impacts of local anthropogenic activities (i.e., winter and summer tourism) from the impacts of recent climate change on the ecological characteristics of this mountain lake. The paleolimnological investigations consisted of reconstructing the long-term dynamics of native communities (i.e., chironomids, zooplankton, primary production), herein considered as the response variables. Salmonid stocking practices related to summer tourism and watershed erosion due to digging related to winter tourism were regarded as the main potential local drivers for lake ecosystem changes, while climate change represents a global forcing. Historical salmonid stocking practices (involving lake trout (*Salvelinus namaycush*), brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), and arctic charr (*Salvelinus alpinus*)) were documented by combining a collection of historical data and ancient salmonid DNA preserved in the core sediment as an innovative proxy to reconstruct past salmonid abundances. Watershed erosion was reconstructed from mineral geochemistry analyses throughout the sediment core, dated by short-lived radionuclides.

We hypothesized that the lake productivity would increase from the 1850s as the climate warmed from the end of the Little Ice Age. However, by the ski resort initiation in the 1950s, digging would magnify watershed erosion leading to reduced water transparency, in turn dampening the whole food web production and possibly leading to deep oxygen alteration. Afterward, the initiation of massive salmonid stocking in the 1980s would maintain a major pressure on consumer communities, especially on benthic invertebrates. This expectation was specifically tested by screening the ecological characteristics of current benthic and pelagic invertebrate communities, but also using salmonid DNA preserved in surficial sediment combined with carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotopes to track habitats and resources used by the different salmonid species. Overall, we hypothesized that the ecological trajectory of this mountain lake would have drastically deviated from an expected trajectory under the unique climate constraint due to interferences generated by local tourism, suggesting that both winter and summer tourism may represent major

pressures for the preservation of mountain lake ecological integrity.

## Methods

### Study site and local history

Lake Tignes is a natural oligotrophic high-altitude lake (25 ha, max. depth = 42 m, total phosphorous concentration  $< 10 \mu\text{g L}^{-1}$ ) located in the French Alps at 2100 m above sea level (Fig. 1A). The lake is divided into two different sub-basins (Fig. 1B). The lake surface is frozen 6–7 months per year. The lake is dimictic and its surface temperature remains  $< 12\text{--}14 \text{ }^\circ\text{C}$  in summer, leading to a weak thermocline (i.e., monotonic decline in temperature down to 15 m), while the hypolimnetic temperature is generally stable at  $4\text{--}6 \text{ }^\circ\text{C}$  (Supplementary material: Appendix 1). Waters are well oxygenated at all depths, and hypoxia under the ice in winter was never observed. Maximum primary production generally occurs at depths of 5–10 m but remains limited (i.e., maximum oxygen saturation = 120–140%, Supplementary material: Appendix 1, Viboud et al. 2004), Supplementary material: Appendix 1), and the transparency is highly variable, ranging from a Secchi depth of  $\sim 1$  m during snow melt at the beginning of the ice-free period to a Secchi depth of more than 10 m at the end of summer. Its watershed is composed of two main geological formations with calc-schists in its southern part and Triassic formations with dedolomitized breccia (locally named “cagneule”) as well as evaporites such as gypsum in the central and northern parts. This geologic context favors especially high sulfate concentrations ( $100\text{--}600 \text{ mg L}^{-1}$ ), leading to high water conductivity ( $650 \mu\text{S cm}^{-1}$ , Supplementary material: Appendix 1) that can reach more than  $1000 \mu\text{S cm}^{-1}$  during snow-melt (Viboud et al. 2004). These water characteristics also provide significant buffer capacities, making Lake Tignes poorly susceptible to acidification induced by atmospheric depositions that could have drastic impacts on the ecological characteristics of mountain lakes lying on crystalline bedrock (Koinig et al. 1998; Sienkiewicz et al. 2006). The lake is fed by a main inlet, the Retort Creek, and closer to the lake by a secondary intermittent inlet, the Claret Brook. Both originate from miscellaneous resurgences from underground karstic circulation downstream to the Grande Motte Glacier. As a consequence, mineral particles present in the melt water of the glacier mostly deposit within the karst structures. Those two inlets consequently have especially clear water and the Retort Creek has rather stable discharge ( $\sim 400 \text{ L s}^{-1}$ ) and stable temperature ( $\sim 4 \text{ }^\circ\text{C}$ ) throughout the year although episodic floods reaching  $2000 \text{ L s}^{-1}$  have been noted over the last decades (Viboud et al. 2004).

The beginning of the ski resort of Tignes started as early as the 1950s, but it remained under-equipped until the early 1970s, when extensive digging started to shape ski slopes and wetland drainage upstream to the lake to install ski lifts (Supplementary material: Appendix 2A). The implementation of the mountain resort continued over the following decades, with major events being the implementation of a golf course (1969, extended in 1991), the building of Grande-Motte’s funicular railway (1989–1991), and the further digging of ski slopes (1998–2000 and 2021). This mountain resort is currently one of the largest and most frequented ski infrastructures in the French Alps, with 64 ski slopes for a total length of 89 km,  $> 25,000$  accommodation places,  $> 2,000,000$  winter visitors, and  $> 350,000$  summer visitors (AnteaGroup 2019, Supplementary material: Appendix 2B).

Four salmonid species have been introduced into the lake since the nineteenth century, and we benefited from a precise chronicle of these introductions since the early 1980s, when they shifted from anecdotal (i.e., introduction of a few hundred juveniles) to recurrent and more massive stockings (Fig. 1C and D). We could not precisely date the very first introduction of brown trout (*Salmo trutta*, Linnaeus 1758) but it likely goes back to the nineteenth century when it was initially introduced as a complementary nutritional resource for shepherds, until annual stockings started in the early 1980s. The lake trout (*Salvelinus namaycush*, Walbaum 1792) was introduced twice, in 1955 and then in 1970, and then was annually introduced from 1985 to 2003. A few attempts at rainbow trout introductions (*Oncorhynchus mykiss*, Walbaum 1792) took place from the 1950s to the 1980s, followed by annual introductions from the mid-1980s. The arctic charr (*Salvelinus alpinus*, Linnaeus 1758) was only introduced on four occasions from 1991 to 1994 but seemed to have disappeared from the lake since the 2000s, as suggested by its absence from the fishermen’s catch (Hervé Genet personal communication). Complementary, minnows (*Phoxinus phoxinus*, Linnaeus, 1758) are also present in the lake, but the timing of their introduction is unknown and probably relates to punctual releases by fishermen when used as baits.

### Sampling

A 71-cm-long sediment core (TIG17-02) was collected at a depth of 35 m in August 2017 in the eastern sub-basin ( $45.464888 \text{ N}$ ,  $6.907478 \text{ E}$ , Fig. 1B) using an Uwitec gravity corer equipped with a hammer. The core was stored at  $4 \text{ }^\circ\text{C}$  until sampling.

For DNA-based analyses of salmonid spatial distributions, a total of 21 surficial sediments were collected using an Ekman grab at a depth of 1–2 m along the littoral shore (11 samples) and along five transects at depths of  $\sim 10$  m (5 samples) and  $\sim 20$  m (5 samples) (Fig. 1B). Once sediment

was retrieved from the lake bottom, ~10 g of surficial sediment was gently collected using a spatula rinsed with 90% alcohol between each sample to limit contamination and stored in 50 ml sterile Eppendorf tubes at 4 °C prior to being frozen at –20 °C for subsequent molecular analyses.

The current biodiversity of the lake was investigated by sampling benthic invertebrates and zooplankton. Benthic invertebrates were collected from the six representative lake habitats (i.e., sediment at depths of 2, 11, 13, and 15 m, formations of *Chara* sp., and gravel from the dominant inlet) using an Ekman grab (two samples per habitat). Zooplankton were sampled using a 100 µm mesh circular net, 15 cm in radius throughout the first 10 m of the water column and rinsed using a sieve of 100 µm mesh size to be concentrated into a 50 ml Eppendorf tube filled with 70% ethanol.

### Age-depth model and proxy for watershed erosion

In the laboratory, the cores were split lengthwise, photographed, and logged in detail, noting all physical sedimentary structures. A total of 25 samples of 1 cm thick were collected over the first 25 cm of the core to measure short-lived radionuclide activities at the Laboratoire Souterrain de Modane (Reyss et al. 1995) using SAGe well-type germanium detectors. Prior to analysis, samples were dried at 60 °C for ~48 h and were ground to a fine powder in an agate mortar and pressed into polyethylene containers. For all samples, dry bulk density (DBD) was estimated by sampling a known volume. The <sup>210</sup>Pb excess activity (half-life: 22.3 years) was calculated by subtracting the supported activity estimated through <sup>226</sup>Ra activity in each sample. Sediment core chronology was then carried out using the R package “serac” (Bruehl and Sabatier 2020), supporting the establishment of the <sup>210</sup>Pb excess age-depth model using the Constant Flux Constant Sedimentation (CFCS) model applied on mass depth and validated by artificial radionuclides (<sup>137</sup>Cs and <sup>241</sup>Am).

The sediment elemental composition was analyzed using X-ray fluorescence (XRF) with an Avaatech Core Scanner. The core surface was first covered with a 4-µm-thick Ultralene film, and was then scanned at a resolution of 1 mm at 10 kV/0.1 mA for 30 s to detect Al, Si, S, K, and Ca (Richter et al. 2006). Element relative abundances were expressed as centred log ratios (CLRs) to avoid matrix effects (Weltje et al. 2015). We select element K as K-CLR-transformed as a proxy of siliciclastic watershed erosion through glacial activity, in agreement with the geological context (Fouinat et al. 2017).

### Benthic invertebrate analyses

Sediment samples were sieved through a 500 µm mesh, and invertebrates were hand sorted from the sieve residues using

fine forceps and identified following Tachet et al. (2010) under a binocular magnifier (40–70 magnification), except for chironomids, whose identification was based on their head capsules (HC) following the same process as for sub-fossil HC (see below).

The temporal dynamics of chironomids were reconstructed over the first 25 cm of the sediment core split into 1-cm-thick sediment samples. These samples were treated following the classic procedure detailed in Walker (2002), which consisted of sediment sample exposure to successive baths of HCl (10%) and KOH (10%) to remove carbonates and residual organic matter. The sample residues were then sieved through a 200 µm mesh, and the remaining matter was inspected under a binocular magnifier (40–70 magnification) to retrieve HC using fine forceps. The HC were then mounted ventral side up on microscope slides using Aquatex and identified to the genus level under a microscope (100–1000 magnification) following Brooks et al. (2007).

HC counts were converted into HC fluxes quantifying their accumulation rates (HCAR, head capsules per 10 cm<sup>–2</sup> per year) based on the chronology established from the age-depth model. The HCARs for the different samples were then transformed into a dissimilarity matrix using the Bray–Curtis dissimilarity index, supporting the computation of constrained hierarchical clustering using the CONISS algorithm to identify major changes in the chironomid assemblages. Chironomid taxa with an HCAR representing less than 5% of the total HCAR were excluded from the computation of the Bray–Curtis dissimilarity index. All data analyses for the chironomid assemblages were performed using the R package “rioja” (Juggins 2020).

### Cladoceran analyses

A subsample of 1.5 ml from the 50 ml Eppendorf tube containing the concentrated zooplankton was used for counting and identification under a microscope (100–200 magnification) according to Frey (1986) and Szeroczyńska and Sarmaja-Korjonen (2007).

The temporal dynamics of cladocerans were reconstructed over the first 25 cm of the sediment core based on 1-cm-thick sediment. The sediment samples of ~1 g wet weight were heated in KOH (10%) for 1 h, filtered through a 31 µm mesh sieve, treated with HCl (10%), and sieved again. Safranin was added to the mixture to stain the remains, and subsamples of 0.1 ml were transferred to a slide for identification. The zooplankton remains (i.e., headshields, shells, post-abdomens, post-abdominal claws, mandibles, and others) were identified following the same procedure as the modern zooplankton. In each sample, an average of 130 cladoceran remains (min.–max. = 85–178, Kurek et al. 2010) were counted and identified. *Bosmina longirostris* (Müller 1785), *Eubosmina longispina*

**Table 1** Characteristics of the primers designed in this study

Species	Primer name	Sequence 5'→3'	Target	Amplicon size	Process of qPCR cycles	Number of qPCR cycles	Efficiency
<i>Salvelinus namaycush</i>	Salvnam 1	CGTGATAATAACCAACTAGGTTGTC	D-loop	72 pb	Initial denaturation 5 min 95 °C/denaturation time 15 s at 95 °C/ annealing–elongation time 30 s at 64 °C	40	91.5 ± 7.9 (R <sup>2</sup> > 0.98)
	Salvnam 2	GCCCGTGTAGTTGGAGTTTATTA					
	Salvnam quat 1	AACCTACTACAGGGCTTATCCTGTCT	NADH 2	66 pb	Initial denaturation 5 min at 95 °C, denaturation time 15 s at 95 °C annealing–elongation time 11 s at 62 °C	40	97.1 ± 7.9 (R <sup>2</sup> > 0.96)
	Salvnam quat 2	CTTGAATTTAAGTGCAGAAAGGTGCC					
<i>Onconhynchus mykiss</i>	Mykiss 1	GCTAGCCAACATAATTTGGTCC	12S	80 pb	Initial denaturation 5 min at 95 °C denaturation time 15 s at 95 °C annealing–elongation time 11 s at 54 °C	40	87.15 ± 4.89 (R <sup>2</sup> > 0.99)
	Mykiss 2	GGA AAAATGGTTTGTGACTTAATTC					
	Mykiss ter 1	CCTTTTGCATC-ATGATTTAGCCAGCACAC	16S	75 pb	initial denaturation 5 min at 95 °C denaturation time 15 s at 95 °C annealing–elongation time 10 s at 72 °C	40	95.85 ± 4.11 (R <sup>2</sup> > 0.98)
	Mykiss ter 2	AGCTCGTCTAGTTTCGGGGCCCTA					
<i>Salmo trutta fario</i>	Fario 1	GCTGAATAAGCAAAACACTACAAGCATT	NADH 6	106 pb	initial denaturation 5 min at 95 °C denaturation time 15 s at 95 °C annealing–elongation time 11 s at 60°	40	92.72 ± 12.5 (R <sup>2</sup> > 0.98)
	Fario 2	CAGGTGTGGTTTGTGGAGTTC					
	Fario ter 1	GCTFACTCCGGGACAGCCTG	16S	101 pb	Initial denaturation 5 min at 95 °C, touchdown from 72 °C to 67 °C, denaturation time 15 s at 95 °C, annealing–elongation time 12 s at 66 °C	40	91.52 ± 13.01 (R <sup>2</sup> > 0.98)
	Fario ter 2	AACCAGCTATAACTAGGCTCGATAGG					

(Leydig 1860), and *Chydorids* were determined to the species level. With regard to the complexity of the taxa and the possible hybridation processes (Alric et al. 2016), *Daphnia* spp. (O.F. Müller 1776) were identified to the genus level. Species of the genus *Alona* sp. were pooled together for visualization due to their relative rarity. Cladoceran accumulation rates (CAR, individual cm<sup>-2</sup> year<sup>-1</sup>) representing the fluxes of cladoceran deposition in the sediment were then computed based on the chronology established from the age-depth model. Analyses similar to those for the chironomid remains were conducted to perform constrained hierarchical clustering and identify major changes in the cladoceran assemblages.

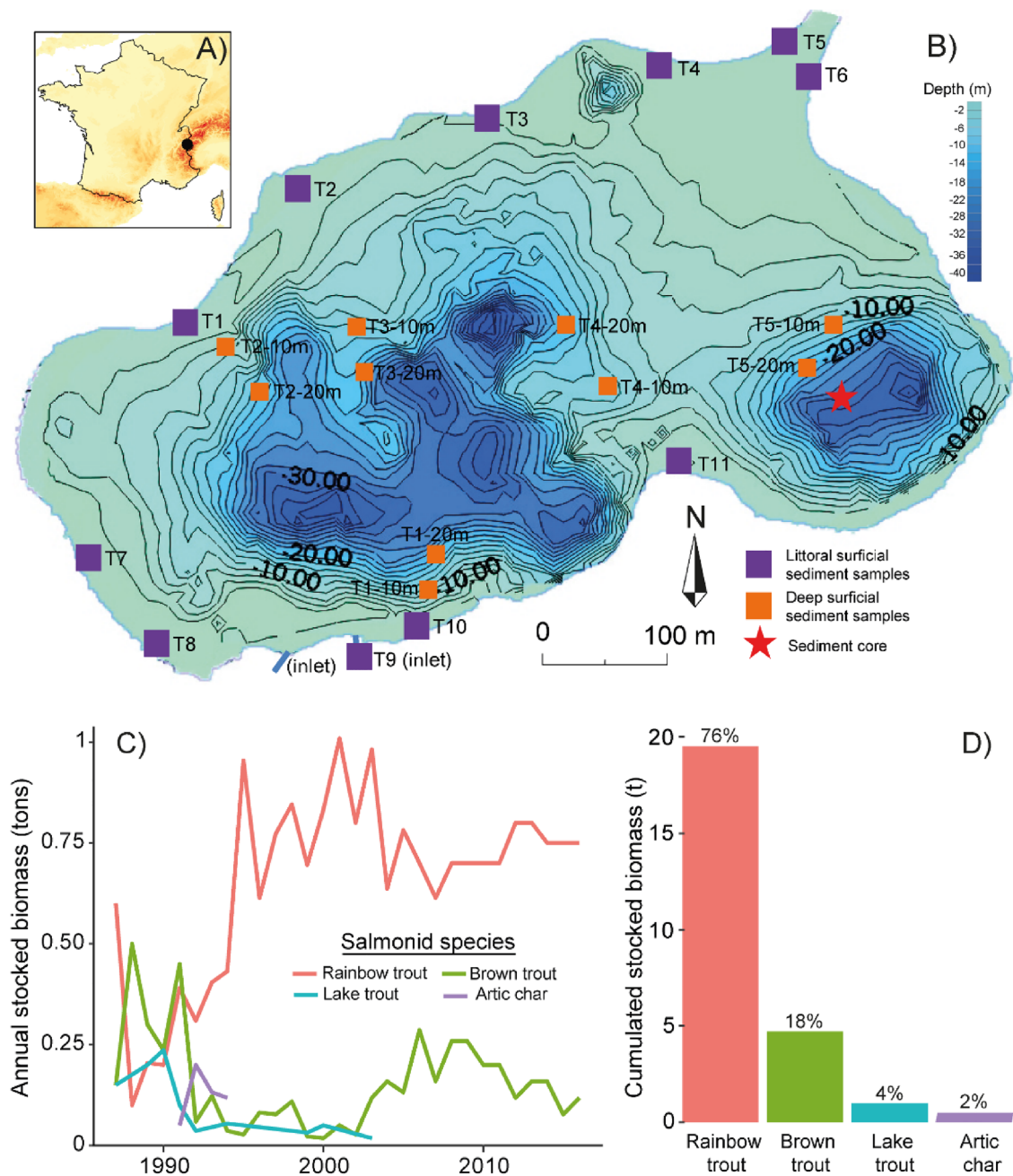
### Complementary paleolimnological proxies

Two complementary paleolimnological proxies were obtained from the sediment core to detail the lake history. Chlorophyll-A concentration was inferred based on (Wolfe et al. 2006) from reflectance measurements performed every 5 mm with a wavelength range spanning from 400 to 700 nm and expressed as Z scores (Jeziorski et al. 2021). The organic matter (OM) content (%) of the sediment was estimated though loss on ignition at 550 °C (LOI550) for each 1-cm-thick sample following Heiri et al. (2001) over the first 25 cm of the sediment core.

The mean annual temperatures from 1850 to 2014 were retrieved from the CMIP6 experiments (Eyring et al. 2016) that used the five models forced with climate projections, bias adjusted (Lange 2019) and statistically downscaled (ISIMIP3BASD method, Cucchi et al. 2020; Lange 2019). This proxy enabled us to address long-term climate variability over the time period studied, highlighting the recent warming in the Alps since the mid-1980s (Durand et al. 2009; Einhorn et al. 2015).

### Molecular analyses

Fish specimens of the three salmonid species (*S. namaycush*, *O. mykiss*, *S. trutta*) in Lake Tignes were collected from recreational fishermen, and their cellular DNA was extracted from muscle using a DNeasy Blood & Tissue Kit (Qiagen) following the manufacturer's recommendations. Cellular DNA was then quantified in duplicate with the Quantifluor dsDNA System (Promega), and two specific primer couples were designed in the mitochondrial genome of the three salmonids using Primer BLAST facilities at NCBI (Table 1). The specificity of each primer couple was checked by conducting qPCR on environmental DNA originating from ecosystems that shelter a known set of salmonid species. The amplicon obtained from these qPCR were bidirectionally



**Fig. 1** Location of Lake Tignes (black circle) in the French Alps (A). Bathymetry of Lake Tignes with the location of the different samples for the fish DNA search comprising littoral (purple squares) and deep (orange squares) surficial sediment. The sediment core (red star) was

collected in the deepest zone of one of the Eastern sub-basins of the lake (B). Summary of the stocking history in the lake for the four salmonid species highlighting temporal trends (C) and cumulated stocked biomasses (D). (color figure online)

sequenced at Plateform NGS DTAMP at Lyon, France, and gave specific sequences of the target species.

qPCR reactions were performed in 20  $\mu$ l using SsoAdvanced Universal Inhibitor-Tolerant Sybr-green Supermix (Bio-rad), with 0.3  $\mu$ M of each primer (0.15  $\mu$ M for Fario ter 1 and 2) and 5  $\mu$ l of DNA to be analyzed. Amplification was performed with an AriaMx Real-Time PCR system

(Agilent). qPCR cycles were followed by a melting curve obtained by ramping the temperature from 55 to 95  $^{\circ}$ C (1  $^{\circ}$ C 30  $s^{-1}$ , Table 1). Each qPCR plate contained a standard range with 100, 10, 1 and 0.1 pg of DNA of the considered species and negative controls.

A total of 17 samples of  $\sim$ 2 g of wet sediment were collected from the center of the sediment core throughout the

first 25 cm. We excluded the border of the sediment core to prevent possible DNA contamination. These 17 sediment core samples, as well as the 21 surficial sediment samples, were analyzed by extracting DNA using the NucleoSpin soil kit (Macherey Nagel) using SL1 lysis buffer and SX solution according to the manufacturer's protocol, among three replicates of 0.5 g of wet sediment considering an elution volume of 100  $\mu$ l. Extracted DNA was quantified in duplicate with the Quantifluor dsDNA System (Promega) prior to performing each qPCR twice, leading to six salmonid DNA quantifications per surficial sediment sample per primer pair, and therefore 12 quantifications per sample considering the use of two primer couples per species. Such replication and the use of multiple primer couples per species is expected to provide more robust results to track the occupancy and temporal dynamics of salmonids (Olajos et al. 2017). Additionally, the amount of salmonid DNA retrieved from sediment samples was highly variable among replicates, with a few samples containing high amounts of salmonid DNA, and the sum of salmonid DNA for the 12 replicates per sample was positively correlated with the proportion of positive replicates (Supplementary material: Appendix 3A). The proportions of positive replicates were expected to be a robust proxy for species occurrence and abundance, in line with the many processes involved in species DNA deposition in the sediment (Barnes et al. 2014; Turner et al. 2015) and we therefore used this former variable to track salmonid spatial occupancy and temporal trends in the sediment core. Additionally, as we were interested in reconstructing the overall stocked salmonid signal from the sediment core, we computed the proportions of positive replicates for all three salmonid species rather than focusing on the species-specific temporal patterns (Supplementary material: Appendix 3B).

All DNA investigations were carried out in a room dedicated to rare DNA treatment where specific constraints were observed (distance from other molecular biology laboratory, disposable cloths and material, hoods with UV decontamination).

### Stable isotope analyses

A total of 37 salmonids from the three salmonid species were retrieved from recreational fishermen in the summers of 2017 and 2018, from which a caudal fin clip of  $\sim 1$  cm<sup>2</sup> was collected on each individual as a surrogate for muscle tissue (Hanisch et al. 2010). Concomitantly, zooplankton and benthic invertebrates from 2, 10, and 15 m were collected using the same procedure as described in the "Sampling" section. Biological samples were oven-dried at 40 °C for 48 h, and  $\sim 1$  mg was conditioned in tin cups

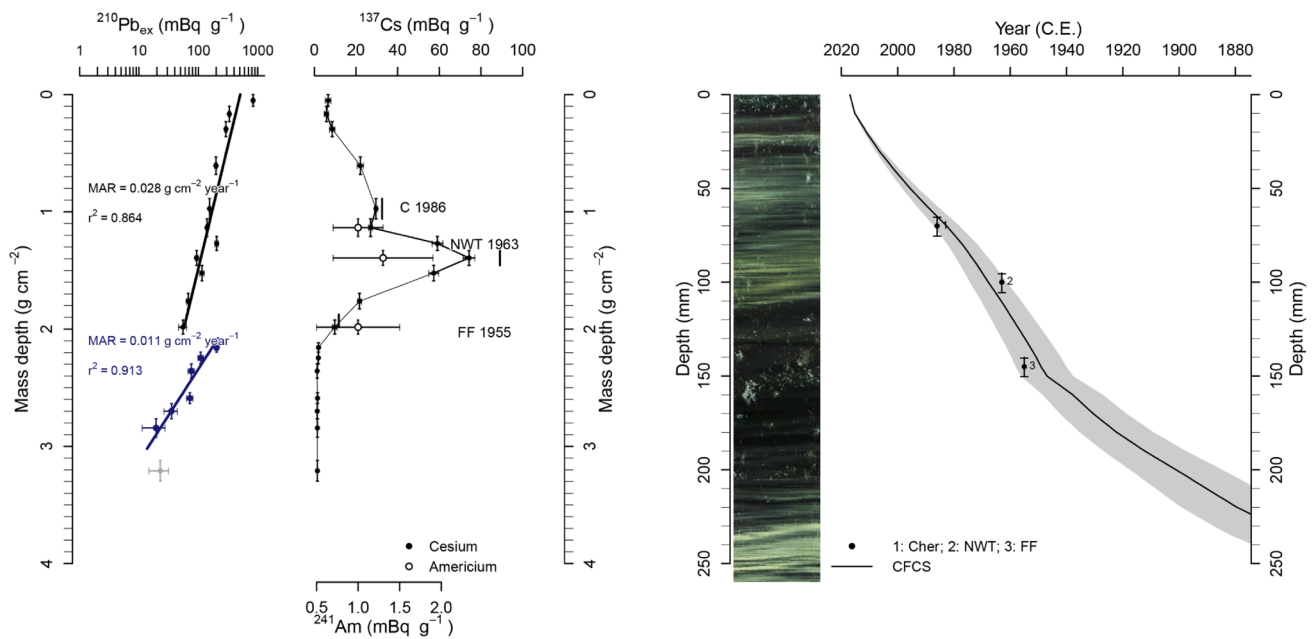
prior to stable isotope analyses conducted at the research center INRAE Grand-Est Nancy SILVATECH (Structural and functional analysis of tree and wood Facility) using an elemental analyzer (vario ISOTOPE cube, Elementar, Langensfeld, Germany) coupled, via a gas box interface, to a continuous-flow isotope ratio mass spectrometer (Isoprime100, IRMS, Elementar UK, Cheadle, UK). The carbon and nitrogen isotope ratios are expressed as delta values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , ‰) relative to the isotope ratios of the Vienna Pee Dee Belemnite (VPDB) standard and to air N<sub>2</sub>, respectively. The uncertainty of measurements was 0.3‰ and 0.5‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively. The relative contributions of the three putative resources (i.e., aquatic and terrestrial invertebrate and zooplankton) for each individual salmonid were retrieved as the mode values of the posterior distributions of the resource contributions inferred from Bayesian mixing models (Parnell et al. 2013) using the R package "simmr" (Parnell 2021) with default settings (1.10<sup>4</sup> iterations, four Markov chains, and a burn-in period of 10<sup>3</sup>). The trophic fractionations were assumed to be  $0.8 \pm 1\text{‰}$  and  $3.4 \pm 1\text{‰}$  for carbon and nitrogen isotopes, respectively (Minagawa and Wada 1984; Vander Zanden and Rasmussen 1999).

## Results

### Chronology

Core TIG17-02 presented different sedimentary facies. The upper 11.5 cm was mainly composed of dark-gray silt to clay with diffuse  $\sim 5$  mm laminations. From 11.5 to 23 cm, the sediment consisted of dark silt to clay. From 23 to 71 cm, the sediment was mainly light-gray silt to clay with some  $\sim 1$  cm light-brown silty lamination and some more dark organic layers in the deepest part of the core (Fig. 2).

The logarithmic plot of <sup>210</sup>Pb<sub>ex</sub> activities showed a general decrease, with two distinct linear trends (black and dark blue in Fig. 2). According to the mass depth CFCS model (Brueel and Sabatier 2020) applied to each segment of the profile, the <sup>210</sup>Pb<sub>ex</sub> activities indicated an increase in the mass accumulation rate from  $0.011 \pm 0.002$  (R<sup>2</sup> = 0.86) to  $0.028 \pm 0.004$  g cm<sup>-2</sup> year<sup>-1</sup> (R<sup>2</sup> = 0.91) with changes in 1947 (uncertainty range: 1938–1956). The full <sup>137</sup>Cs inventory was estimated to be 587.6 Bq m<sup>-2</sup> ( $\pm 11.8$  Bq m<sup>-2</sup>). The <sup>137</sup>Cs activity profile showed a clear peak between 9 and 10 cm with a maximum activity of 74 mBq g<sup>-1</sup>; this peak was associated with a small peak of <sup>241</sup>Am activity and was widely attributed in the literature to the maximum nuclear weapon tests in 1963 (Appleby et al. 1991). A small <sup>137</sup>Cs peak is also observable between 6 and 7 cm and could correspond to nuclear fallout from the 1986 Chernobyl accident. The first <sup>137</sup>Cs activities were recorded between 14



**Fig. 2** Synoptic of the age-depth modelling of the TIG17-02 core with  $^{210}\text{Pb}_{\text{ex}}$ ,  $^{137}\text{Cs}$  (black dots), and  $^{241}\text{Am}$  (white dots) activities versus mass depth, core photography, and the  $^{210}\text{Pb}_{\text{ex}}$ -CFCS age model versus depth including artificial markers.

and 15 cm and probably corresponded to the first nuclear fallout in 1955 (Bruel and Sabatier 2020). All these  $^{137}\text{Cs}$  markers were in good agreement with the mass depth CFCS age model (Fig. 2) and allowed validation of the  $^{210}\text{Pb}_{\text{ex}}$  derived age model for the upper 22 cm corresponding to the last 140 years, which was then extrapolated to the last 180 years (25 cm)

### Forcing dynamics

The three forcings considered to drive the ecological trajectory of Lake Tignes exhibited contrasting dynamics over the last 180 years (Fig. 3). The K-CLR index, tracking watershed erosion, progressively decreased from the 1850s to the mid-1940s. The K-CLR trend abruptly reversed from mid-1950 with a first local maximum in K-CLR values in the 1960s and peak values in the 1990s, corresponding to the very early development of the ski resort (Fig. 3A). Greater values for the erosion proxy coincide with the different phases of the development of the ski resort, i.e., slope digging and funicular railway (Fig. 3A). Since then, it fluctuated around slightly lower values, although a drop was apparent in the topmost sediment core samples.

The proportions of positive samples for salmonid DNA presence in the sediment core were generally limited (0–30%) and tended to be greater at the top of the core. However, changes in salmonid DNA presence along the core were nonmonotonic with maximum proportions of positive samples in the 1980s and 2010s. The increased DNA

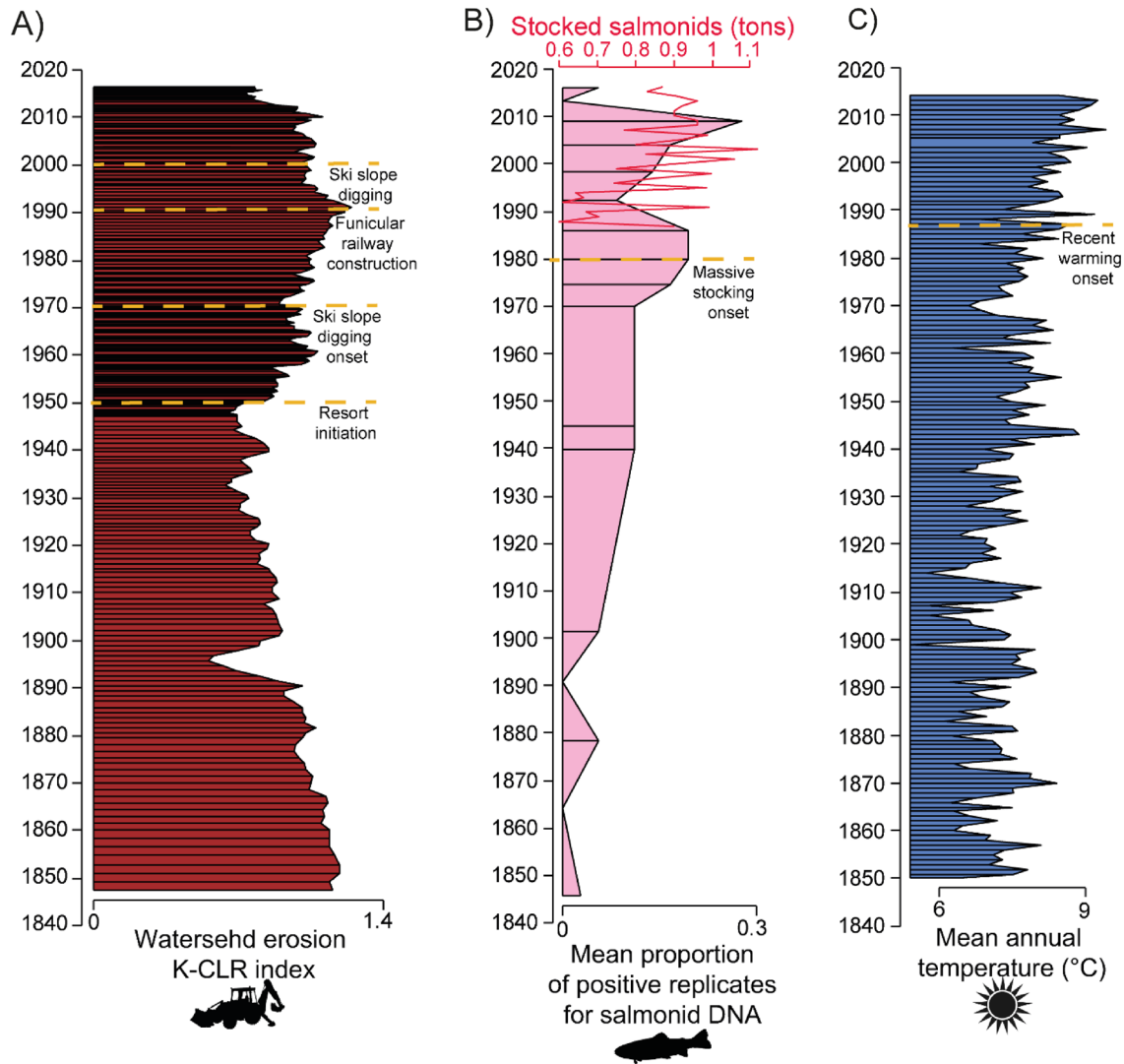
presence from the late 1970s to early 1980s corresponds to the start of massive salmonid stocking. The documented salmonid practices underlined an intensification of salmonid stocking since the mid-1980s (Kendall's Tau = 0.26,  $p = 0.05$ ) associated with considerable interannual variability in the stocking extent until the 2010s. Although the extent of stocking is not directly related to population, it can be expected that the overall salmonid abundances dropped since the 1980s with the transition from episodic stocking to annual massive stocking. The nonmonotonic salmonid DNA pattern along the sediment core and its correspondence with the contemporary documentation of stocking practices seem to support this suggestion. The DNA signal may hence indeed be related to historical changes in salmonid abundances rather than differential states of DNA preservation with sediment age and depth (Fig. 3B).

The long-term dynamic of mean annual temperature from the CMIP6 experiments indicated nonnegligible interannual variations throughout the studied period, with a first increase in temperature from the 1910s to the 1940s followed by a more pronounced warming since the late 1970s (Fig. 3C).

### Paleoecological reconstructions

We reconstructed a set of biological proxies to assess the ecological trajectory of Lake Tignes over the last 180 years (Fig. 4). The sediment organic matter (OM, from LOI550) varied poorly over the time period and was, on average,  $4.3 \pm 1.2\%$  (Fig. 4A). In contrast, the reconstructed Chl-*a*





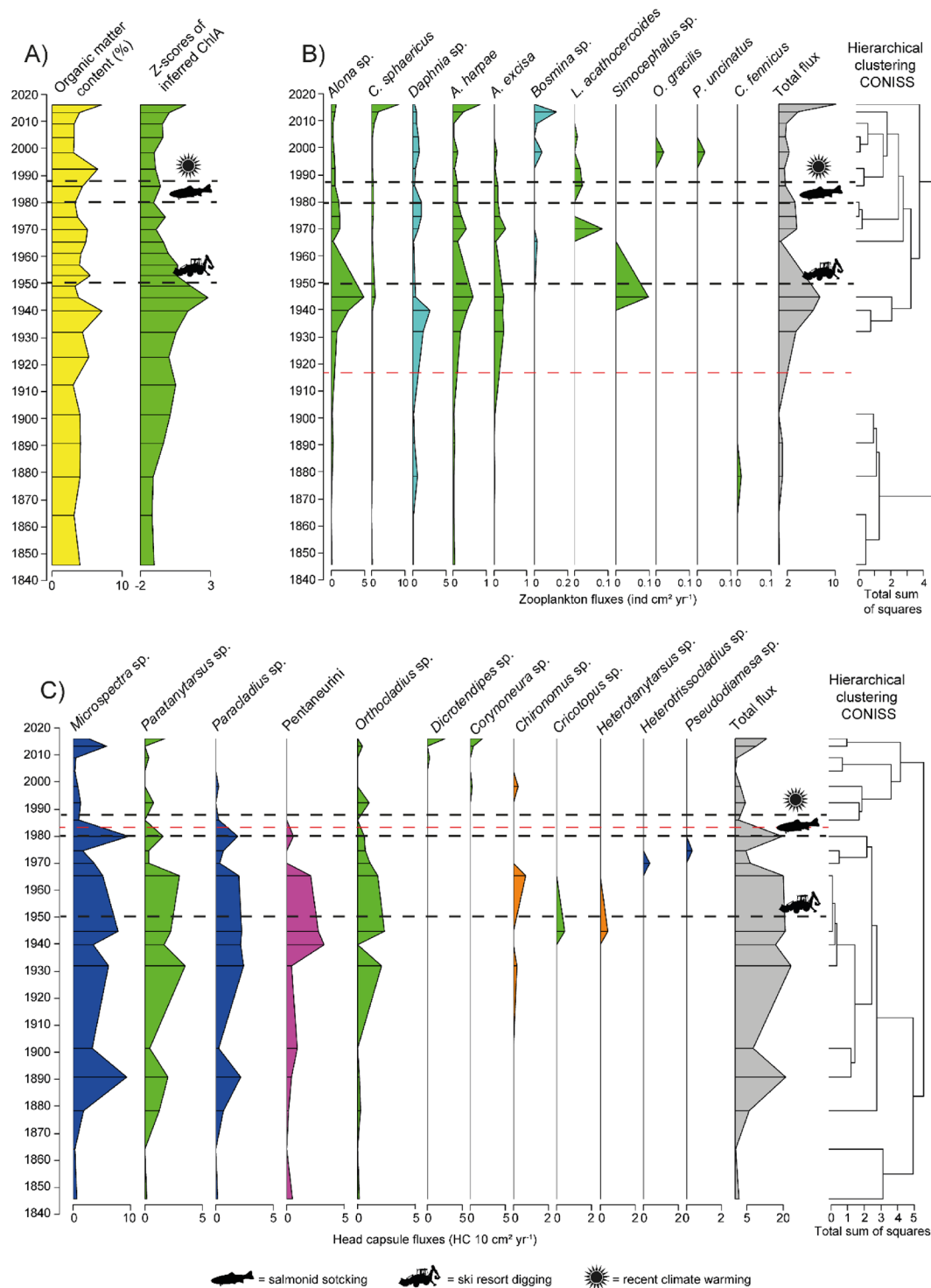
**Fig. 3** Proxies used to track anthropogenic constraints on Lake Tignes: watershed erosion (centered log ratios of potassium (K-CLR)) for winter tourism (A), salmonid DNA signal in the sediment core with the annual salmonid stocking (in red) for summer tourism (B),

and the mean annual temperature from the CMIP6 experiments (C). Horizontal dashed-yellow lines indicate major events for each proxy with the onsets of ski resort digging, massive salmonid stocking and recent warming. (color figure online)

experienced a clear increasing trend from the beginning of the record before peaking in the mid-1940s. The reconstructed Chl-*a* thereafter decreased to reach low and stable values in the 1970s. The reconstructed Chl-*a* values were higher for the most surficial sediment, but we cannot exclude the possibility that this signal arises from incomplete taphonomic processes for the most recent sediment (Fig. 4A).

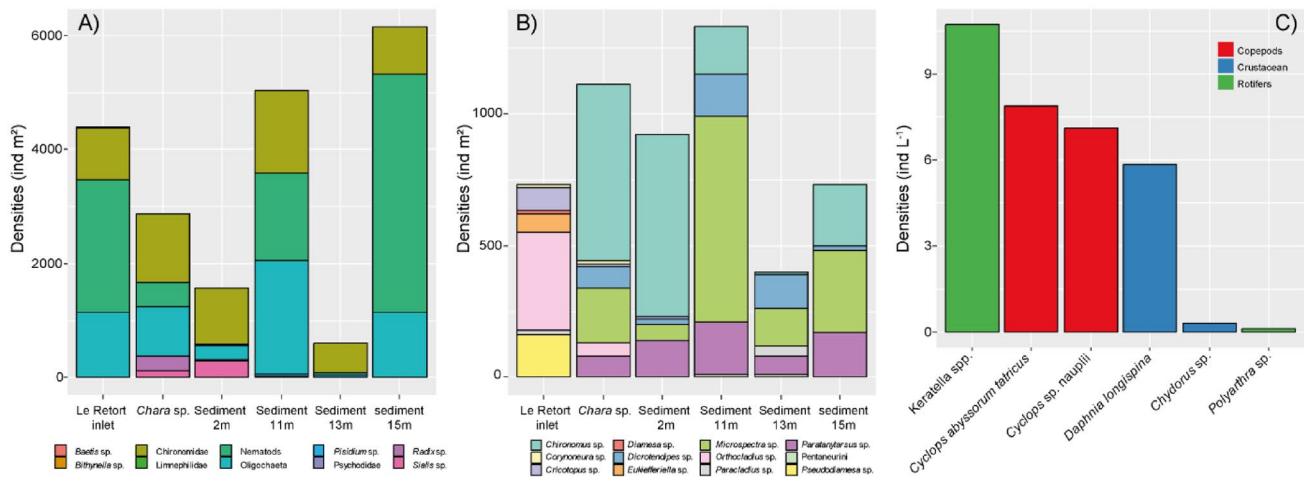
A total of 11 genera of zooplanktonic cladocerans were identified in the sediment core, among which 9 genera were associated with the littoral habitat and 3 genera were associated with the pelagic habitat. *Alona* spp. was the dominant taxon, representing 32% of the total fluxes, followed by *Chydorus sphaericus* (29%), *Daphnia* sp. (27%), and *Acropaerus harpae* (7%). Other genera comprised less than 5% of

the total fluxes (Fig. 4B). There was barely any zooplankton remaining below 18 cm, i.e., the 1930s with a total flux < 2 ind cm<sup>2</sup> year<sup>-1</sup>. Thereafter, the total flux of zooplankton matched that of reconstructed Chl-*a*, with maximum values reached between the 1960s and 1970s and low stable values from the 1970s. The constrained hierarchical clustering did not identify significant temporal changes in the zooplankton community. Stratigraphic changes in cladoceran remains along the core were quantitative rather than qualitative, highlighting that zooplankton secondary production rather than community composition was affected by environmental modifications over time in Lake Tignes. As for cladocerans, the stratigraphic changes in chironomid remains were mostly quantitative (total flux) rather than qualitative (community



**Fig. 4** Temporal dynamics of the different biological components of Lake Tignes: organic carbon content and inferred chlorophyll-A shown as Z scores (A), stratigraphies of cladoceran (B) and chironomid (C) assemblages. Horizontal dashed lines highlight the onsets of local (onsets of ski resort digging and massive salmonid stocking for winter and summer tourism, respectively) and global (warming) pressures. In these two cladoceran and chironomid stratigraphies, hori-

zontal dashed-red lines suggest the most remarkable changes in the assemblage changes despite insignificance according to the broken stick model. Note the variable ranges for the x axes. In the cladoceran assemblages, littoral taxa are represented in green, and pelagic taxa are represented in light blue. In the chironomid assemblages, oxyphilous cold-adapted taxa are represented in dark blue, warm-adapted in orange, littoral taxa in green, and predator in purple.



**Fig. 5** Synopsis of the modern biodiversity assessment with macroinvertebrate densities in the different habitats of the lake (A), with a specific focus on chironomid genera (B) to characterize littoral and deep benthic habitats and on zooplankton (C) to characterize the pelagic habitat.

composition). A total of 12 chironomid genera were identified within the sediment core. The constrained hierarchical clustering again could not identify significant successions in assemblage compositions over time. *Microspectra* sp. was the dominant genus representing ~50% of the total HC fluxes over the studied period, followed by *Paratanytarsus* sp. (15%), *Paracletus* sp. (12%), Pentaneurini (8%), and *Orthocladus* sp. (8%) (Fig. 4C). The other genera represented less than 5% of the total HC fluxes. There were more contrasted changes in total fluxes to the sediments, whose timing was different from that of cladocerans. Specifically, HC fluxes started to increase as soon as the 1850s, up to the 1930s. HC fluxes were high and stable between the 1930s and 1980s, when HC fluxes collapsed. Some taxa could no longer be detected in the core from the 1990s–2000s (i.e., *Paracletus* sp. and Pentaneurini).

### Modern biodiversity

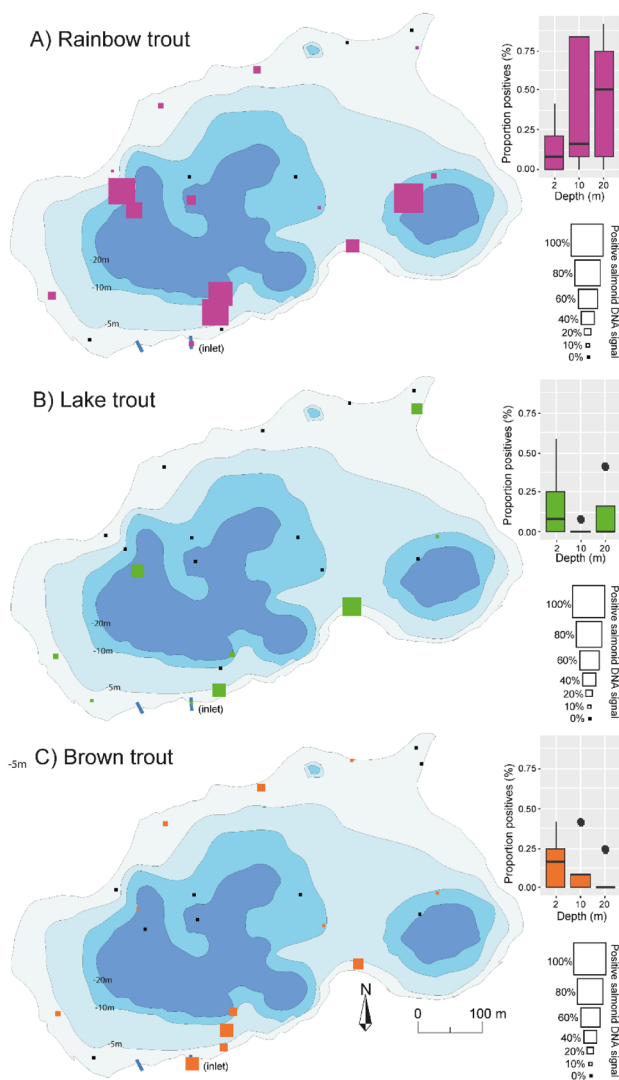
The densities of benthic invertebrates varied widely among lake habitats, and oligochaeta and nematodes were dominant in most habitats (Fig. 5A). Chironomidae was the most diverse invertebrate family in the lake, with 12 different genera with an overall density of  $980 \pm 320$  ind m<sup>-2</sup> (Fig. 5B). Genera typical from cold flowing water were identified in the Retort inlet (*Pseudodiamesa* sp., *Eukiefferiella* sp., *Orthocladus* sp.). In contrast, the lake community was dominated by three genera with different ecological requirements, with the warm-adapted *Chironomus* sp. mostly present in the littoral shore, and the cold-adapted *Microspectra* sp. mostly present in sediment below 10 m depth, while *Paratanytarsus* sp. that can tolerate a wide temperature range had similar densities in the different habitats. The gastropod Lymnaeidae and the predator Sialidae were also present in the lake

littoral shore (*Chara* sp. and sediment at 2 m depth) down to 15 m depth.

The rotifer genera *Keratella* sp. and *Polyarthra* sp. ( $< 1$  ind L<sup>-1</sup>) were the most and least abundant zooplankton, respectively (Fig. 5C). *Cyclops abyssorum taticus* was the only copepod identified, and it exhibited high densities (i.e.,  $> 7$  ind L<sup>-1</sup>), similar to that of *Cyclops nauplii* as well as the large *Daphnia longispina* that reached a density of  $\sim 6$  ind L<sup>-1</sup>, while *Chydorus* sp. was below 1 ind L<sup>-1</sup>. The overall zooplankton community had a density of 32 ind L<sup>-1</sup>, with 14 ind L<sup>-1</sup> adult copepods and cladocerans.

### Spatial variability of salmonid eDNA

The molecular analyses performed on surficial sediments revealed highly variable salmonid DNA signals throughout the lake as well as species-specific depth variability, although the results were not significant (Kruskal–Wallis tests,  $p > 0.3$ ) (Fig. 6). Rainbow trout had the highest rates of positive replicates, which could reach more than 75% at specific locations, and the mean proportions of positive replicates tended to increase with depth despite considerable variations among samples (Fig. 6A). Lake trout had much lower rates of positive replicates with medians  $> 0\%$  only obtained at 2 m, but that could reach up to 58% of positive replicates at one specific location (Fig. 6B). Additionally, no clear depth pattern was apparent for this salmonid species. Brown trout had low rates of positive replicates, with maximal proportions not exceeding 41.6% at 2 m and 10 m, yet a decreasing pattern for the rate of positive replicates with depth was clearly identifiable (Fig. 6C).



**Fig. 6** Spatial distribution of the salmonid DNA signal within surficial littoral and deep sediment for rainbow trout (A), lake trout (B), and brown trout (C) expressed as the proportions of positive replicates. The extent of the positive salmonid DNA signal is characterized by an increasing area, as shown by blank boxes. Box plots summarize the spatial distribution of the salmonid DNA signal among depths, with medians represented by horizontal black lines, boxes comprising the 25th and 75th percentiles, whiskers accounting for 1.5 times the interquartile ranges (IQRs) and points indicating proportions higher than  $1.5 \times \text{IQR}$ .

### Salmonid resources used

A total of 37 individual salmonids and 27 samples characterizing their possible resources were used to address salmonid resource reliance in Lake Tignes (Fig. 7A). The possible salmonid prey exhibited clear distinct isotope signals mostly related to variable  $^{13}\text{C}$  depletion and salmonid isotope compositions had a restricted  $\delta^{13}\text{C}$  range ( $-26.02\text{‰}$  to  $-21.42\text{‰}$ ) corresponding to the range of littoral invertebrates. In contrast, salmonid isotopic

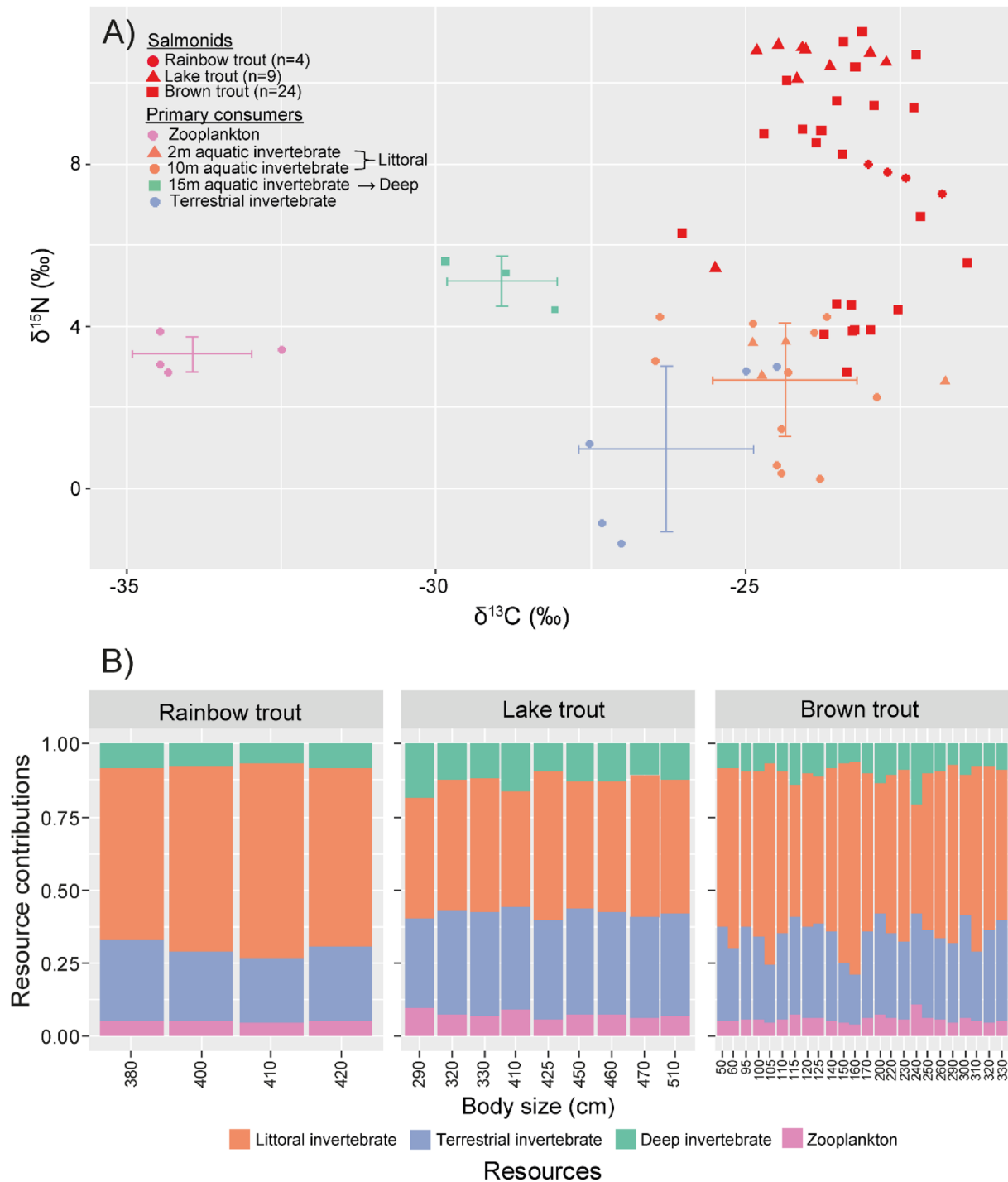
compositions were clearly  $^{15}\text{N}$ -enriched compared with the invertebrates and zooplankton baselines, even if several individuals had  $\delta^{15}\text{N}$  values similar to those of littoral invertebrates. The Bayesian mixed models suggested limited interindividual diet variations except for brown trout (Fig. 7B). Littoral and terrestrial invertebrates represented the dominant resources used by the different salmonid species, while deep invertebrates and zooplankton had minor contributions. Consequently, littoral invertebrates were the major aquatic resource fueling salmonids, with mean inferred proportions of  $62 \pm 3\%$  for rainbow trout,  $56 \pm 8\%$  for brown trout and  $45 \pm 4\%$  for lake trout.

### Discussion

In this study, we aimed at identifying whether the different facets of local tourism development (winter and summer tourism) could affect the ecological characteristics of mountain lakes and possibly alter their responses to climate forcing. This objective was supported by combining a diversified set of analyses that could capture specific features of ecological characteristics and their putative forcing over different time scales since the end of the Little Ice Age (Le Roy et al., 2015). We showed that the primary and secondary productivities of Lake Tignes have undergone drastic changes over the course of the last two centuries, whose timing and characteristics suggested that local tourism may be a prominent driver of the lake ecological state since the mid-twentieth century, which led to a limited identifiable ecological impact of recent climate warming. Consequently, although climate constraints are expected to be exacerbated at high altitudes, the consideration of local tourism development may be a key driver to be considered and possibly regulated to preserve mountain lake ecological integrity.

### Early climate-driven lake productivity

While the oldest core samples indicated low productivity by the end of the Little Ice Age, we observed a general increase in lake primary and secondary littoral and pelagic productions, from 1850 to 1940. Paleolimnological climate reconstruction in the Alps indicated that especially harsh climate conditions prevailed prior to the 1850s (Millet et al. 2009). The Little Ice Age was dated to end in the 1860s in the studied region, characterized by the initiation of glacier retreats (Le Roy et al. 2015) that seemed in good agreement with our erosion interpretation of the K-CLR proxy showing a decreasing trend between 1850 and the early twentieth century. Consequently, although climate reconstruction from the CMIP6 scenario did not show an apparent temperature increase until the 1940s, improved climate conditions since the end of the Little Ice Age would have



**Fig. 7**  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  biplot showing how salmonids and their putative resources organized according to their isotope compositions (A). Error bars represent mean  $\pm 1$  SD for each resource. Outputs of the

Bayesian mixing models summarizing resource contributions to the assimilated diets for the three salmonid species (B). Note that individuals are organized with increasing size.

been much more favorable to the watershed vegetation (Volk et al. 2021) that could favor nutrient leaching to the lake (Kaštovská et al. 2022). Complementarily, more favorable climate conditions may also support human colonization that is generally characterized by pastoralism, which may

also participate in fostering lake productivity via nutrient leaching (Etienne et al. 2013; Bajard et al. 2017). Unfortunately, we did not have any information regarding this early possible human colonization in this massif, but at the regional scale in such a high elevation catchment, the main

vegetation changes and erosional phases related to pastoralism were during the Roman (Giguet-Covex et al. 2014; Sabatier et al. 2017) or the Middle Age (Bajard et al. 2017; Bajard et al. 2020) periods. In any case, vegetation development alone or combined with early human development are fostered by climate improvement during the end of the Little Ice Age. Consequently, the observed increase of primary and secondary biological productions seemed to support our primary hypothesis of a climate-driven amplification of lake production during the early time of the period studied. Similar observations of increasing biological production by the end of the LIA have been made in other alpine lakes (Nevalainen and Luoto 2012). However, we did not observe any community turnover as did Nevalainen and Luoto (2012) in Lake Oberer Landschitzsee (Austrian Alps) by the end of the LIA. Rather, the maintained dominance of the cold stenotherm and oxyphilous chironomids (i.e., *Micropsectra* sp. and *Paracladius* sp., Brooks et al. 2007; Quilan and Smol 2010) suggested that the lake remained well oxygenated and oligotrophic throughout this time period. Additionally, the increasing abundance of littoral macrophyte-associated zooplankton typical of postglacial phases (i.e., *Alona* sp., *A. harpae*, and *A. excisa*; Hofmann 2000; Lotter et al. 1997; Nevalainen and Luoto 2012) also likely indicated an increase in water transparency. The noticeable decrease in watershed erosion was likely associated with both the decrease of glacial activity at the end of the LIA and the development of watershed vegetation due to climate improvement over this time period, and may have been the major driver of the enhancement of the water transparency triggering the observed ecological changes. Indeed, increasing water transparency amplifies the overall volume of the euphotic zone and consequently the overall pelagic primary production (Finger et al. 2013) but also favors littoral productivity, supporting littoral benthic production (Vadeboncoeur et al. 2008).

### Watershed erosion as a pelagic forcing

Since the late 1950s, watershed erosion increased and was concomitant with a decrease in both primary and secondary pelagic productions. This opposite pattern lasted up to the most recent times when the watershed erosion remained high with minimal pelagic production. Such concomitancy suggested that watershed erosion was indeed a major driver of pelagic production through its control of water transparency, as previously suggested. Over a decadal timescale, glacier retreat may have been a possible candidate for the magnification of watershed erosion, as it strongly constrains the release of fine mineral particles from the bedrock (Herman et al. 2021). However, the Grande Motte Glacier upstream to Lake Tignes has not directly fed the lake over the last decades, nor over the last centuries (Gardent 2014, Supplementary

material: Appendix 4). In fact, the melt water infiltrates in karst structures beneath the glacier acting as a natural filter for mineral particles. The lake inlets are consequently fed by miscellaneous clear water resurgences that may not have significantly contributed to changes in the erosion signal recorded in the sediment core. Alternatively, changes in the precipitation regime can affect particle erosion, but it remained fairly unchanged over the time period studied (Supplementary material: Appendix 5). As a consequence, the major changes in watershed erosion recorded in the sediment core seemed mostly related to major phases of the ski resort expansion. Specifically, the main massive digging events upstream of the lake related to ski resort expansion corresponded to rebounds of our watershed erosion proxy in the 1970s (Supplementary material: Appendix 1), 1990s, and over the last decade with the most recent ski slope creations. The expansion of the ski resort may hence exert an indirect negative impact on the pelagic compartment of the lake, as initially hypothesized, by affecting watershed erosion. However, chironomids were poorly affected by the increase in watershed erosion and the maintenance of oxyphilous chironomids, such as *Micropsectra* sp., suggested that watershed erosion did not trigger significant alteration in the benthic oxygen conditions. Therefore, watershed erosion related to winter tourism development may not have impacted the whole ecosystem as primarily expected, but rather preferentially affected the pelagic compartment of Lake Tignes.

### Salmonid stocking as a benthic forcing

The presence of salmonids in the lake likely goes back to the nineteenth century, but salmonid populations may remain especially scarce as suggested by the very few positive salmonid DNA samples down in the sediment core. This low-density population seemed to exert a very limited, if any, impact on invertebrates whose abundances in the sediment core tended to increase overtime from the 1850 to the 1980s. The dramatic decrease in chironomid abundance occurred in the 1980s, at the time of both massive salmonid stocking, and recent warming emerged as new possible drivers. The most impacted chironomid taxa were large non-tube dwellers (Pentaneurini and *Paracladius* sp.) that are particularly vulnerable to salmonid predation, providing a first insight into the possible implication of salmonid stocking on the dynamics of chironomid communities. This result is supported by the current chironomid densities, with tube-dwelling chironomids having much higher densities (i.e.,  $> 500 \text{ ind m}^{-2}$ ) than non-tube-dwelling chironomids (Pentaneurini and *Paracladius* sp.,  $< 50 \text{ ind m}^{-2}$ ). Additionally, although differences in the spatial occupancy of salmonid species were highlighted using their DNA signal preserved in surficial sediment, the Bayesian mixed models suggested

that salmonids had highly similar diets mostly based on littoral invertebrates. These inferences indicated that littoral invertebrates, mostly dominated by chironomids, would be mainly exposed to salmonid predation in the lake and are consistent with empirical diet analyses conducted in mountain lakes, identifying chironomids as a primary resource for stocked salmonids (Cavalli 1997; Tiberti et al. 2016; Mouillet et al. 2018). As a consequence, the chironomid collapse was likely related to the massive salmonid stocking from the 1980s, which was related to summer tourism development. It is worth noting that the presence of minnows in the littoral of the lake that likely relates to the intensification of fishing practices since the 1980s could have also contributed to alter the abundances littoral invertebrates (Osorio et al. 2022).

Salmonid's limited reliance on zooplankton may be supported by the actual composition of the zooplankton community that exhibited high abundances of a cyclops species (*C. abyssorum taticus*) and *Daphnia* sp., although only a single zooplankton sample could be analyzed. In stocked lakes, both species have been shown to be either extirpated or maintained at minimal abundances in the case of active salmonid predation (Parker et al. 2001; Sarnelle and Knapp 2005). Gliwicz and Rowan (1984) suggested that *C. abyssorum taticus* was able to maintain high densities in fish-stocked lakes by using deep habitat refugia and *Daphnia* sp. is also capable of important diel migration of dozens of meters, which is amplified in the presence of predator fish (Weiss et al. 2012). These behavioral features may partly explain the poor reliance of salmonids on zooplankton, especially considering the relatively important depth of Lake Tignes ( $Z_{\max} = 42$  m). However, due to their relatively small sizes, zooplankton could be mostly consumed by small salmonids (i.e., young of the year) that we could not efficiently sample. Additionally, zooplankton has been shown to be an important resource for salmonids in other lakes (e.g., Eloranta et al. 2013; Tiberti et al. 2016), and it could contribute in greater proportions to salmonid diets out of the summer period when other resources may be especially scarce such as during winter periods.

### Seeking warning signs of warming

The chironomid community was characterized by the co-occurrence of genera covering a wide range of temperatures and trophic affinities at the different studied depths, indicating contrasting environmental conditions within the lake. The dominance of *Chironomus* sp. in the littoral zone suggested warm and nutrient-rich conditions, while *Micropsectra* sp. was dominant in deep waters characterized by cooler and well-oxygenated environments (Armitage et al. 1994; Brooks et al. 2007; Moller Pillot 2009). These results are further supported by the chironomid assemblages obtained

from the surficial sediment samples where *Micropsectra* sp. was identified along with *Dicrotendipes* sp. and *Corynoneura* sp., generally associated with macrophytes in littoral habitats favored by warm environments (Brooks et al. 2007; Moller Pillot 2009). The occurrence of these warm-adapted taxa in this high-altitude lake (> 2000 m) suggested possible warming in the littoral habitat during the summer season, potentially related to recent atmospheric warming. The consequence of climate change in Lake Tignes may be habitat specific and especially expressed in shallow waters, although it seemed relatively minor compared with the salmonid impacts on the overall benthic invertebrate community and to the ski resort development on the pelagic community.

### Concluding remarks

Mountain lakes belong to the rare class of ecosystems whose number is predicted to increase over the last decades due to warming-induced glacier retreats (Cathala et al. 2021; Mölg et al. 2021). Such features open up rare opportunities for the implementation of adaptive management that necessitate precise knowledge regarding their vulnerability to anthropogenic forcings. We showed that both winter and summer tourism, representing two complementary facets of mountain anthropization, had significant effects on the lake ecological trajectory but also differently affected the pelagic and benthic compartments. Complementarily, the direct ecological consequences of climate warming could mostly be identified within the littoral zone and may be habitat specific. The cumulative effects of mountain tourism development therefore seemed to interfere with the constraint of the recent climate warming at the whole ecosystem scale, in line with the recent warning from Schmeller et al. (2022). Our study hence suggests that conservation plans implemented to preserve the biodiversity in mountain lakes may primarily focus on the regulation of local recreational activities, because ski resort development for winter activities and fishing for summer practice may modulate, if not override, the effect of climate change. In this sense, banning fish introductions from pristine and newly formed lakes and conducting fish eradication campaigns in stocked lakes, but also avoiding of ski-related digging and infrastructure development could be key features for the preservation of the ecological integrity of mountain lakes.

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**Author contributions** VF, PS, and ME conceptualized the research. VF and PS performed the field investigations. VF and CV analyzed the isotope data. RB analyzed the cladoceran subfossils. VF analyzed the chironomid subfossils. PS established the age-depth model and the K-CLR erosion proxy. NCGG and NT performed the molecular analyses and VF analyzed the molecular data. VF lead the writing with critical contribution of all coauthors.

**Data availability** All data and R codes are available from the corresponding authors upon reasonable request.

## Declarations

**Conflict of interest** The authors have no conflicts of interest to declare that are relevant to the content of this article.

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