

Paleoecological evidence for a multi-trophic regime shift in a perialpine lake (Lake Joux, Switzerland)

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ABSTRACT

Freshwater ecosystems are under new and increasing threats from anthropogenic change. Ability to detect and predict consequences of environmental perturbations on ecosystem function and water quality is limited by the lack of empirical data over relevant time scales. Paleoecological records present a unique opportunity to broaden understanding of ecological transitions over decadal to millennial timescales. This study tested the occurrence of regime shifts to track changes throughout the lake food web beyond the typical instrumental era, using both “traditional” paleoecological proxies (e.g., cladoceran zooplankton, zoobenthos, and pigments) and more recently developed molecular genetic methods based on sedimentary DNA. We used sediment cores from the perialpine Lake Joux (Swiss Jura), where the history of human settlement and land-use practices in the catchment has been well documented since the Medieval period. Paleoecological evidence revealed an abrupt and unprecedented biological reorganization in the second half of the 20th century, following several centuries of relatively stable communities despite growing human pressure. Time-varying autoregression computed using dynamic linear modelling identified this transition, triggered by the onset of rapid cultural eutrophication in the 1950s, as a true regime shift. Since this time, despite decades of re-oligotrophication, biotic communities of Lake Joux have not returned to pre-disturbance composition, most likely due to other confounding factors, including climate warming, that may prevent the lake from returning to an earlier equilibrium state. Paleoecological reconstruction further suggested that cladocerans responded earlier to disturbance, which is highly relevant for lake monitoring and management strategies.

1. Introduction

Lake ecosystems are changing at an increasing rate as a consequence of global climate change, as well as regional and local environmental and anthropogenic disturbances (Jenny et al., 2020). Threats to lake

ecosystems arise from the accumulation of local and global human stressors, but also from their potentially non-linear and sudden responses to the stressors after years of relative stability. Such transitions are referenced as regime shifts, and can occur without easily detectable early-warning signals (Scheffer et al., 2001). Regime shifts typically

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occur at multiple trophic levels, after exposure to discrete or continuous stressors (Bestelmeyer et al., 2011; Randsalu-Wendrup et al., 2016). That happens abruptly and has prolonged consequences on ecosystem structure and function (McGowan et al., 2005) that would delay the efficiency of management actions (Andersen et al., 2009; Randsalu-Wendrup et al., 2016; Scheffer et al., 2001). Detecting the occurrence and quantifying the strength of such major shifts in lakes is fundamental to identify causes of catastrophic changes and to help develop management strategies for the protection and the conservation of freshwaters.

Regime shifts raise important management issues, yet there are few documented records of true regime shifts, especially for deep lakes. Our ability to detect regime shifts and to determine their underlying causes is currently limited by the lack of long-term high-resolution data (Smol, 2010; Taranu et al., 2018). Lacustrine sediments provide unique archives of climatic, environmental and ecological changes that constitute an alternative option for the retrieval of information from the past (Gregory-Eaves and Beisner, 2011). Paleolimnological records archive evidence for major events such as regime shifts through community changes. Therefore, paleolimnological approaches have potential to shed light on the dynamics of environmental and biological change over decadal to millennial time scales.

Subfossil-based paleolimnological proxies that are readily preserved in the sediment over thousands of years include diatoms, cladocerans and chironomids (Leavitt and Hodgson, 2001; Watts and Maxwell, 1977). Used widely to track various facets of lake histories, such as primary production (Deshpande et al., 2014; Leavitt and Hodgson, 2001; Makri et al., 2019), these proxies can support assessment of long-term responses of biological communities to key environmental drivers. These drivers include changes in nutrient regime (eutrophication and re-oligotrophication) (Hall et al., 1999) or pH (Battarbee, 1991), climate change (e.g., Walker et al., 1991; Perga et al., 2015; Bruel et al., 2018) and human impacts (Battarbee and Bennion, 2011; Dubois et al., 2017).

More recently developed molecular-based proxies have further opened sedimentary archives to ecologists by enabling the investigation of all organisms across the tree of life. Such proxies include those that do not leave identifiable morphological remains or fossils, such as microbes and microeukaryotes (Capo et al., 2021; Domaizon et al., 2017; Taberlet et al., 2012; Thomsen and Willerslev, 2015). Sedimentary DNA (*sedDNA*) approaches applied to lakes have led to successful ecological reconstructions of primary producers at deeper taxonomic resolutions compared to photosynthetic pigments. They have made possible the estimation of their genetic diversity (Capo et al., 2016; Coolen et al., 2006; Domaizon et al., 2013; Monchamp et al., 2018, 2019a). Further, studies combining both *sedDNA* and other paleolimnological proxies have proven useful to validate temporal trends in lake biodiversity (Coolen et al., 2006; Stoof-Leichsenring et al., 2012; Tse et al., 2018; Wirth et al., 2013).

Both paleoecological and neolimnological studies on the changing dynamics of systems usually cover a limited range of diversity or trophic levels (for example, pigments (Makri et al., 2019); cladocerans (Bruel et al., 2018)). Processes leading to an ecosystem-wide shift, on the other hand, result from intricate relationships at multiple trophic levels. The coupling of molecular genetics and more classical paleolimnological approaches can help evaluate the evolutionary response of aquatic organisms to changing environments and to uncover trophic interactions (Ellegaard et al., 2020). So far, multi-trophic assessments of biodiversity dynamics at a lake scale have not been available.

Lake Joux, a mountain lake located in the Swiss Jura, is particularly well suited to paleoecological work. The history of human activities in the catchment, back to the early settlement of humans (~300 CE), is well known. Regular monitoring of the lake since the 1980s provides decades of valuable information on biological communities and water quality. Similar to other perialpine lakes (Tolotti et al., 2018), Lake Joux has undergone eutrophication over the second half of the 20th century

(max. 35 µg total phosphorus (TP)/L), with consequences on the zoobenthos and phytoplankton composition documented by contemporary monitoring.

To improve ability to detect and to quantify the consequences of regime shifts over the entire ecosystem, this study addressed the following questions. First, how did ecological communities change in Lake Joux during the last millennium. Second, to what extent do identified change point(s) qualify as critical transitions or regime shifts? What is the character of the changes? For example, were the changes restricted to some biological compartments or did it spread/ripple across all trophic levels? In brief, we aimed at qualifying and quantifying biological change attributable to local human activities, specifically land use and pollution in the watershed.

2. Study area

Lac de Joux (Lake Joux) is located in the Swiss Jura at 1004 m above sea level (m a.s.l.). It is the largest of four lakes that lie in the Joux Valley, which is flanked by 1300–1600 m a.s.l. mountains (Fig. 1a). Table 1 lists the lake's main morphological and limnological features.

2.1. Local human impact

Major environmental and anthropogenic forces (summarized in Fig. 1b) have influenced the physical and chemical structure of Lake Joux, and in turn, the lake ecology over the last millennium (Fiaux et al., 2006; Lavrieux et al., 2017). The history of human presence in this catchment goes back to 6850 cal yr BP, continuous since the roman period, including the establishment of a monastery (5–6th century) and later an abbey (12–16th century; see Lavrieux et al., 2017 and references therein). The Valley became only extensively settled in the late Middle Ages, however, followed by intensive industrial development starting in the late 17th century (Lavrieux et al., 2017). Although human presence in the catchment dates back to the Neolithic, anthropogenic impact on the environment remained relatively low until the 14th century, when soils were drained and forest cleared (Lavrieux et al., 2017). The sedimentary record of Lake Joux only started recording anthropogenic perturbations and of a warmer climate around 1280 CE (Lavrieux et al., 2017). Intensive land clearing started around that time and reached a maximum around 1500 CE. The period between the 18th and the mid-20th century was marked by overall warmer climatic conditions and in 1777, the failure of a newly built dike, which caused a sudden decline in the water level of ~3.6 m within 24 h, an event that is imprinted in the sediments (Lavrieux et al., 2017; Nicole, 1840). Concomitantly, development of the watch-making industry in the region increased inputs of heavy metal (Iron (Fe), Zinc (Zn), Lead (Pb)) into the lake (Lavrieux et al., 2017).

More recently, construction of a subaquatic tunnel between Lake Joux and Lake Brenet in the middle of the 20th century restricted water flow and led to the development of standing water areas along the northeastern shoreline. These changes in lake dynamics might have promoted eutrophic conditions. Lake Joux shares a common perturbation history with other perialpine lakes—that is, rapid eutrophication in the 1950s followed by a re-oligotrophication phase beginning around the 1980s. In the early 1950s, total phosphorus (TP) concentration in Lake Joux waters averaged around 10 µg/L (Bosset, 1961). Increasing human presence in the catchment and possibly changes in lake dynamics stemming from the tunnel construction increased TP concentrations rapidly, with concentrations reaching 35 µg/L in 1979. This increase was followed by a re-oligotrophication phase starting in 1988–89 after phosphate-containing detergents were banned and sewage treatment and management of manure were improved. Data from lake monitoring documented the re-oligotrophication process (from 35 µg TP/L in 1979 to 12 µg TP/L in 2015) (Lods-Crozet et al., 2006) and recorded ages for the sediment cores analysed in this study, covering both the eutrophication and re-oligotrophication phases (Figs. S1 and S2).

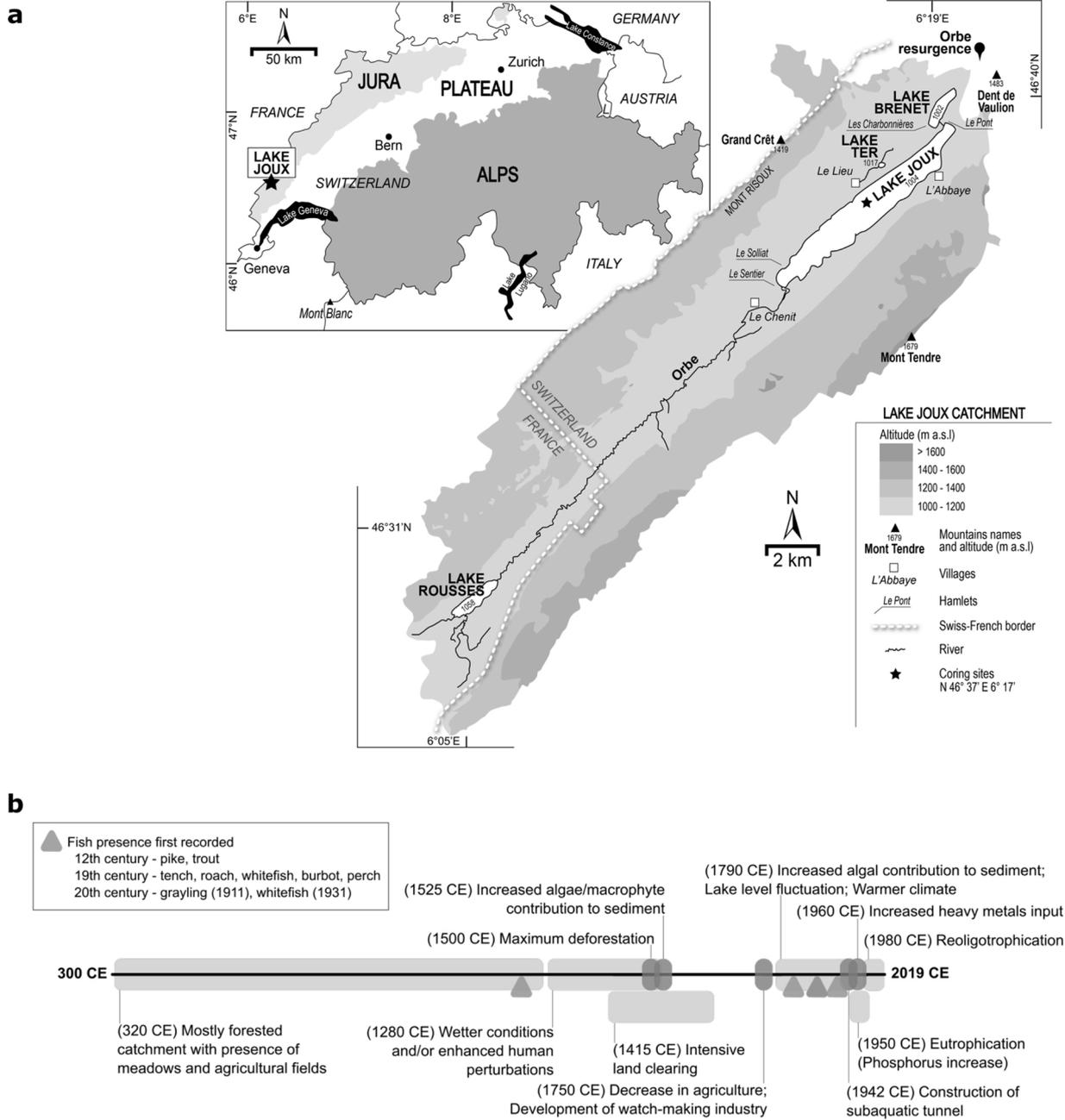


Fig. 1. a) Map of Lake Joux catchment showing the location of the lake and the coring sites (modified from Lavrieux et al., 2017). The inset identifies the geographical location of the lake in the perialpine area. All sediment cores were collected within 20 m of the original coring site location. b) Timeline showing major climatic and human-driven events in Lake Joux and its catchment documented since the early presence of humans in the region (historical information derived from Lavrieux et al., 2017 and references therein).

Table 1
Morphological and limnological characteristics of Lake Joux.

Lake elevation (m a.s.l.)	1001.5–1005.0
Lake area (km ²)	8.7
Lake volume (10 ⁶ m ³)	132
Maximum depth (m)	33
Average depth (m)	21
Water retention time (yrs.)	0.83
Catchment area (km ²)	211

(Data from Fiaux et al., 2006; Lods-Crozet et al., 2006).

2.2. Fish stocking

Over the last eight centuries, Lake Joux's fish community underwent large changes, likely profoundly affecting the ecosystem as a whole. Historical records indicate that fish were introduced into Lake Joux during medieval times (Fiaux et al., 2006). Records of the Abbey of Lac de Joux mentioned the presence of both trout (*Salmo trutta*) and pike (*Esox lucius*) in the 12th century (Nicole, 1840). These species were noted for their use as tax payment, and it is unclear if other, less valued species were also present at that time. By the late 19th century, five additional species were recorded (Fatio, 1890, 1882): tench (*Tinca tinca*), roach (*Rutilus rutilus*), whitefish (*Coregonus* sp.), burbot (*Lota lota*), and perch (*Perca fluviatilis*). Of these, the year of introduction

(1982) is only known for whitefish, according to Fatio (1890). In the 20th century, further introductions and additional stocking took place, e.g., of grayling (*Thymallus thymallus*) in 1911 and whitefish in 1931 (Fiaux et al., 2006), increasing the number of historically recorded fish species in Lake Joux to 14 (Périer and Vonlanthen, 2015).

2.3. Climate

Climate has varied substantially in the Lake Joux region over the past millennium. The Little Ice Age (LIA) period (ca. 1300–1750 CE) followed a prolonged warm period known as the Medieval Climate Anomaly and is characterized in European mid-latitudes by a colder and wetter climate (Magny et al., 2008). Substantial warming of surface waters has been observed over the 20th century in mid-latitude temperate lakes as a consequence of climate change (Woolway et al., 2019, 2017).

3. Methods

To pursue the research questions posed, we used an integrated approach combining paleolimnological and *sedDNA* proxies to reconstruct the multi-trophic dynamics (i.e., decomposers; bacteria, primary producers; photosynthetic plankton, primary consumers; cladocerans and chironomids, and secondary consumers; fish) over a period of ~1000 years in Lake Joux. We then used a change-point analysis to identify major shifts in communities and tested for the occurrence of regime shifts using a modelling approach.

3.1. Sediment coring, subsampling, and dating

We collected four sediment cores at the deepest point of Lake Joux (Lat. N 46° 37', Long. E 6° 17') in 2016 and 2017 using a gravity corer. We measured magnetic susceptibility on all cores at intervals of 0.5 cm using a GEOTEK multi-sensor core logger (Geotek Limited, Daventry, UK). The JOU16-02 core was extruded at 1 cm intervals, and the sediment layers were divided into two subsamples. We used one subsample collected from the inner part of the core for analysis of chlorophyll and carotenoid pigments. The other subsample provided identification and counts of cladoceran and chironomid remains. Cores JOU17-01, JOU17-02 and JOU17-03 were opened longitudinally in the laboratory prior to sediment subsampling. JOU17-01 and JOU17-02 used for identification and counts of fish scales and bones, and JOU17-03 for bacterial DNA analyses. Sediment subsamples for DNA analyses were collected at intervals of 1 cm from one half of the core using sterile disposable instruments in a room where no DNA work had been done before. We further cleaned surfaces and instruments with hypochlorite solution. Subsamples were collected in sterile Eppendorf tubes and transported to the DNA clean laboratory facility where we conducted DNA extractions. The four core profiles (JOU16-02, JOU17-01, JOU17-02 and JOU17-03) were correlated using magnetic susceptibility (Loizeau et al., 1997; Thompson et al., 1975) with a reference core (JOU13-02) previously collected at the same location and dated with radiocarbon (^{14}C) and ^{210}Pb (Lavrieux et al., 2017) (Fig. S1).

3.2. Bacterial and cyanobacterial DNA analysis

The *sedDNA* extractions were performed in batches of 7 samples with the addition of one negative extraction blank to each batch using the PowerSoil DNA isolation kit (Mo Bio Laboratories Inc., Carlsbad, California, USA) following strict ancient DNA laboratory procedures (Monchamp et al., 2018, 2016). We performed two independent DNA extractions per layer using 0.5 g–1 g wet sediments each. We obtained between 2.8 and ~60 ng DNA/ μL from each layer cut. Primer pairs Univ519-F and Univ802-R (Claesson et al., 2009; Wang and Qian, 2009) were used to amplify a 284 bp-long fragment within the V4 region of the 16S rRNA gene. The primers were supplemented with unique tags of 8

nucleotides and with an additional 2–4 random bases to increase heterogeneity in amplicon length (Monchamp et al., 2016). Polymerase chain reaction (PCR) was done in triplicate using 12 ng of template DNA per 40 μL reaction, and both extraction and PCR blanks were added to each plate. The products of PCR triplicates (including the blanks) were pooled and purified using the Illustra GFX PCR DNA and Gel Band Purification Kit (GE Healthcare, Little Chalfont, United Kingdom). The final product was eluted in Tris-EDTA buffer (10 mM) and quantified using a Qubit 2.0 fluorometer (Thermo Fisher Scientific) using the high sensitivity reagent kit. Finally, we pooled the 48 tagged libraries in equimolar concentrations and added three negative PCR controls were added in a final pool at a concentration of 30 ng/ μL , which was sent to the Fasteris AG sequencing facilities (Geneva, Switzerland) for indexing and paired-end sequencing (2×250 bp) on an Illumina MiSeq platform.

3.3. Bioinformatics and sequence data processing

We performed quality control and processing of the sequence data following a modified protocol developed at the Genetic Diversity Centre (ETH Zürich) (see Monchamp et al., 2016). Primers and adapters were trimmed and sequences were clustered in operational taxonomic units (OTUs) with a 97 % similarity threshold using the UPARSE workflow (Edgar, 2013). Taxonomic assignment of OTUs was based on the SILVA database (v128) (Quast et al., 2013). Finally, OTU reference sequences were aligned using PyNAST (Caporaso et al., 2010) and a phylogenetic tree was estimated using FastTree (Price et al., 2010). Sequences assigned to phyla other than Bacteria, as well as poorly known bacterial phyla were removed from the dataset. Rarefaction of the number of sequences in each sample (146,851 reads per sample) avoided biases related to uneven sequencing depth across samples. After filtering, 425 OTUs remained, consisting of bacteria and cyanobacteria.

3.4. Chlorophyll and carotenoid pigments

We extracted sedimentary pigments to determine the presence of algae and photosynthetic bacteria (Leavitt and Hodgson, 2001) using a mixture of acetone: methanol: water (80:15:5) at -4 °C, filtered with a PTFE 0.2 μm filter and dried down under nitrogen gas. After dissolution in a 70:25:5 solution of acetone, ion-pairing reagent (0.75 g of tetra butyl ammonium acetate and 7.7 g of ammonium acetate in 100 ml water) and methanol were injected into an Agilent 1200 series high performance liquid chromatography (HPLC) unit. The mobile phase comprised Solvent A (80:20 methanol: 0.5 M ammonium acetate), solvent B (9:1 acetonitrile: water) and solvent C (ethyl acetate) with a Thermo Scientific ODS Hypersil column (205 \times 4.6 mm; 5 μm particle size). The separation conditions were initially 100 % solvent A ramping to 100 % solvent B over 4 min, and then to 75 % solvent C for 34 min., held for 1 min followed by a return to initial conditions. Total runtime was 43 min. (a modification of Chen et al. (2001)). Eluted pigments passed through a photo-diode array detector and UV-visible spectral characteristics were scanned between 350–750 nm. Quantification based on scanning peak areas at 435 nm was calibrated to a set of commercial standards (DHI Denmark). Pigment concentrations are reported as molecular weights per dry weight of sediment.

Chlorophyll-a, β -carotene, and pheophytin-a are overall indicators of phytoplankton biomass and myxoxanthophyll, oscillaxanthin, cantaxanthin, echinenone, and aphanizophyll are indicators of cyanobacterial biomass. We used diatoxanthin to estimate siliceous algae (diatoms and chrysophytes), alloxanthin for cryptophytes, and lutein, chlorophyll-b and pheophytin-b for chlorophytes. UV-absorbing compounds derived the UVR index, a proxy for water clarity, using the following equation: $(\text{UVR pigment}/\text{alloxanthin} + \text{diatoxanthin} + \text{zeaxanthin} + \text{lutein})^*100$ (Leavitt et al., 1997). Higher UVR values signified increased UV exposure, a consequence of increased water clarity. Separation conditions sometimes co-elute lutein and zeaxanthin. In Lake Joux sediments, these compounds showed clear separation, enabling quantification.

3.5. Subfossil cladocerans and chironomids

We analyzed cladoceran remains according to Frey (1986). Briefly, 2 h-baths of hydrochloric acid (HCl 10 %) and potassium hydroxide (KOH 10 %) enabled sediment samples to extirpate carbonates and to deflocculate organic matter. At each step, we sieved the remaining sediment materials using a net of 31 µm mesh. In each sample, >400 cladoceran remains (head shields, shells, post-abdomens, post-abdominal claws, mandibles, and others) were counted and identified. The determination keys of Szeroczyńska and Sarmaja-Korjonen (2007) and an Olympus BX41 microscope at 100–200 × magnification enabled identification of the cladoceran remains. We determined *Bosmina* (*B. longirostris*, *E. longispina*, *E. coregoni*) and Chydorids to the species level, and *Daphnia* to the genus level.

We sieved the remaining deflocculated sediment materials using a 150 µm mesh. Chironomid head capsules were gently collected under a stereomicroscope and mounted for microscopic observations using Aquatex® mounting agent. Brooks et al. (2007) provided guidance for identifying head capsule remains.

3.6. Fish remains

We subsampled JOU17-01 and JOU17-02 sediment cores at 2.5 cm intervals. Subsamples were washed through a 250 µm sieve and sieve fractions were screened for fish remains (i.e., scales and bones) using a stereomicroscope. In total, we screened 4453 cm³ of sediments. Scales were classified as either percid (i.e., perch (*Perca fluviatilis*), as no other percid species has been recorded in Lake Joux) or non-percid scales.

3.7. Community composition

The R v.3.3.2 (R Core Team, 2013) provided the software for data analysis. The *phyloseq* package in Bioconductor (McMurdie and Holmes, 2013) imported, filtered, rarefied, and analyzed the DNA sequence data. The *changepoint* package (Killick et al., 2016) (<https://github.com/rkillick/changepoint.git>) enabled identification of significant shifts in community composition over time. Hierarchical constrained clustering was performed using the *rioja* package with the Constrained Incremental Sums of Squares (CONISS) algorithm (Grimm, 1987) to delimit and visualize biostratigraphic zones in the sediment profiles. Pigment concentrations, as well as chironomid and cladoceran relative abundance values were square root-transformed before clustering. We also applied a Hellinger transformation before the principal component analysis (PCA) (Legendre and Gallagher, 2001), which were used to visualize the temporal trajectories of each assemblage. To test whether temporal dynamics of the communities relate to the change in lake trophic status, we extracted PC1 scores for use as proxy for pigment, cladoceran and chironomid composition. We plotted the trajectory of each proxy against a time series for total phosphorus (TP) comprising data from direct measurements in water for the period ~1961–2015, as well as simulated values for sediment layers prior to 1961. For the simulation, a mean TP concentration of 10 ± 3 µg/L was used based on the premise that the lake was oligotrophic until the mid-20th century. Because TP measured in recent sediments did not reflect the known re-oligotrophication of the lake since the 1980s, we did not use the sedimentary TP data in any of the analyses. In addition to the community plots, the concentrations of individual pigments, the percentage of chironomids and the abundance of cladocerans were plotted against the TP time-series to examine temporal dynamics at a more refined taxonomic scale and potentially determine “key taxa” that might constitute early indicators of disturbance.

3.8. Regime shifts and critical transitions

To test for the presence and the time of regime shifts and evidence of critical transitions throughout Lake Joux sediment cores, we applied

time-varying autoregression using Online Dynamic Linear Models (DLMs) (Carpenter and Kinne, 2003; Pole et al., 1994; Taranu et al., 2018) to the sedimentary pigment record. Briefly, DLMs are statistical methods that allow parameters to slowly change with addition of new data points (Carpenter et al., 2014). “Online” implies that the models are automated and instantaneous such that the statistic of interest (e.g., autoregression coefficient) is updated recursively at each step of the time series (or in this case, each sediment core interval) (Ives and Dakos, 2012). This method allows the user to detect any sharp change in the statistic, and thus an early detection of an impending critical transition, or in the case of paleoecological data series, to retrace back in time when the system would experience a critical transition. Given that lower sample size, resolution and density were previously shown to degrade critical transition signals (Thomas, 2016), we chose pigments as proxy because we had a better temporal resolution throughout the sediment core, with 68 sediment layers analyzed compared to 26 layers for cladocerans and chironomids. To detect critical transitions, we examined the rate with which the system returned to its equilibrium state. When working with observed time series, approximating the recovery rate (or dominant eigenvalue of the variance-covariance matrix of a given dynamical model) by fitting an AR(1) model is common. An AR(1) coefficient near zero implies that the state variable returns rapidly towards the mean, but as the AR(1) coefficient approaches 1, this tendency to return towards the mean disappears and we have evidence of a critical transition. To determine which algal pigment provided the best and earliest indicator of a change in state, we ran univariate models to find the dominant eigenvalues, summed them, and then calculated their ratio (Carpenter et al., 2011). The pigment with the highest ratio represented the best indicator.

4. Results

As detailed below, the data analysis revealed significant changes in communities at multiple levels across the food web. These changes reflect the ecosystem’s response to human and climate changes, including the physical and chemical properties of the lake. The shift from oligotrophic to eutrophic status, (Bosset, 1961) and the following re-oligotrophication of the lake (Lods-Crozet et al., 2006) reported in the literature, is partly reflected in the concentrations of total phosphorus measured in sediments (Fig. S2) and in the primary producer community dynamics conveyed by photosynthetic pigments (Figs. 2 and S3).

4.1. Temporal dynamics across trophic levels

4.1.1. Photosynthetic plankton

The analysis detected sedimentary pigments in each of the sixty-nine layers investigated corresponding to ~1000 to 2015 CE. We excluded the layer between 50 and 51 cm downcore because of a sudden peak in pigment concentration. This peak is possibly due to the presence of terrestrial plant or macrofossil material and is therefore very likely an outlier.

Pigment analysis revealed compositional changes down core. In the oldest sediments, pigment concentrations were generally low, and remained stable over several centuries (Fig. 2). The pheophytin a/chlorophyll a preservation index (not shown) shows an expected increase in preservation of materials in the upper 6 cm of the core (i.e., since ~1980). Increases in lutein, chlorophyll-b and pheophytin-b pigments between the years ~1000 and 1200 CE, were indicative of enhanced growth of chlorophytes (green algae) during this time frame. The next major change occurred centuries later, in the 1800s, when the okenone-like pigments characteristic of purple-sulphur bacteria (phylum Proteobacteria) were no longer detected after having been found sporadically in older sediments (Fig. 2). This result suggests that purple-sulphur bacteria disappeared or became too rare for detection via pigment analysis in the sedimentary archive after the 1800s. Finally, in the 1900s, the concentration of some chlorophyte- and cyanobacteria-

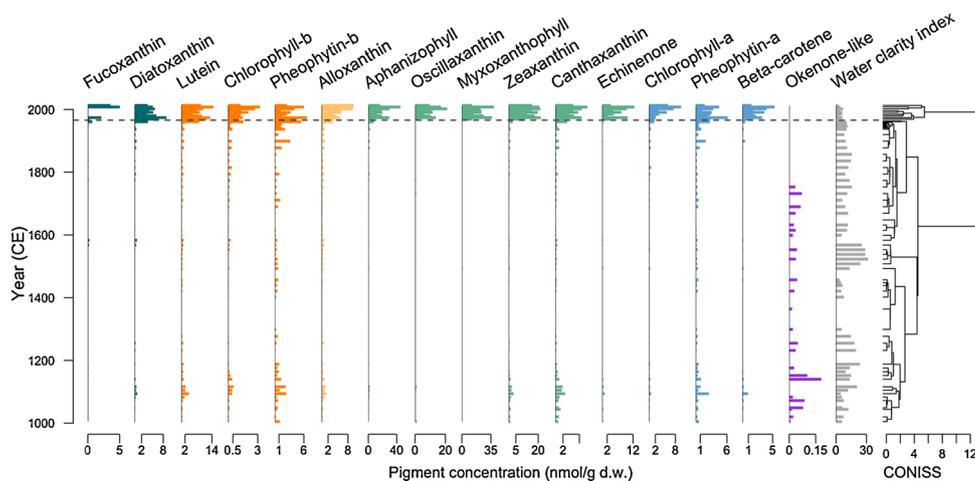


Fig. 2. Stratigraphy of Lake Joux showing the concentration of the main sedimentary pigments in sixty-eight sediment layers. Colors represent the main group of phytoplankton or bacteria associated with specific pigments (dark green; siliceous algae, orange; chlorophytes, yellow; cryptophytes, green; cyanobacteria, blue; all algae, purple; purple sulfur bacteria). The last column (grey) shows the water clarity index. The dendrogram at the far right informs about similarity in pigment composition across sediment layers. Two distinct clusters (delimited in the plot by the horizontal dashed line; transition ca. 1963 – 1969) are determined by CONISS.

associated pigments increased slightly in the decades preceding the onset of eutrophication in the mid-1950s. Around 1959 (± 3 years), total pigment concentration suddenly increased by 4-fold and remained high thereafter (Figs. 2 and S4). The change-point analysis identified a significant transition in photosynthetic pigments a few years later, between ~1963 and 1969, when total pigment concentration increased from around 9.6 to 74.2 nmol/g sediment dry weight. This change-point was also identified by CONISS (Fig. 2). During the same period, cyanobacteria-specific pigments became prominent and some of them (e.g., myxoxanthophyll) appeared for the first time.

4.1.2. Bacteria

DNA analysis showed variations in the composition and relative abundance of the main bacterial phyla throughout the sediment core (Fig. 3a). The main change was observable in the early 1900s, when the relative proportions of Verrucomicrobia and Proteobacteria increase. At the same time, the relative abundance of reads assigned to Planctomycetes began to decline. Overall, Firmicutes accounted for a relatively low proportion of the reads, but they become rarer in the uppermost sediment layers. The proportion of Bacteroidetes and Actinobacteria

sequenced reads increased in the 1900s, but both phyla represented generally a low proportion of bacteria. A slight decrease in relative abundance of Acidobacteria was detectable between 1200 and 1700 CE, before a slight increase towards the end of the 1800s. Finally, we discovered 43 cyanobacterial operational taxonomic units (OTUs) in the 47 samples collected for DNA analysis. Although cyanobacteria generally accounted for a small proportion of all bacterial phyla, a rapid increase in cyanobacteria abundance was detectable around the middle of the 20th century (Fig. 3b). Thereafter, cyanobacteria sequences remained abundant in all subsequent sediment layers, with the maximum number of reads recorded in the sample corresponding approximately to 2002–2006 (between 3 and 4 cm-depth in the JOU17-03 sediment core). Cyanobacterial OTUs were also supportive of an observed increase in cyanobacterial pigments in the 1950s (Fig. S4b).

4.1.3. Chironomids (benthic community)

A total of 11 chironomid taxa or groups were detectable in the JOU16-02 sediment core, and three main clusters emerged based on the dendrogram (Fig. 4). In the period between ~1000 and 1650 CE, *Tanytarsus* spp., *Microspectra* sp., *Sergentia* sp. and Tanyptodinae were

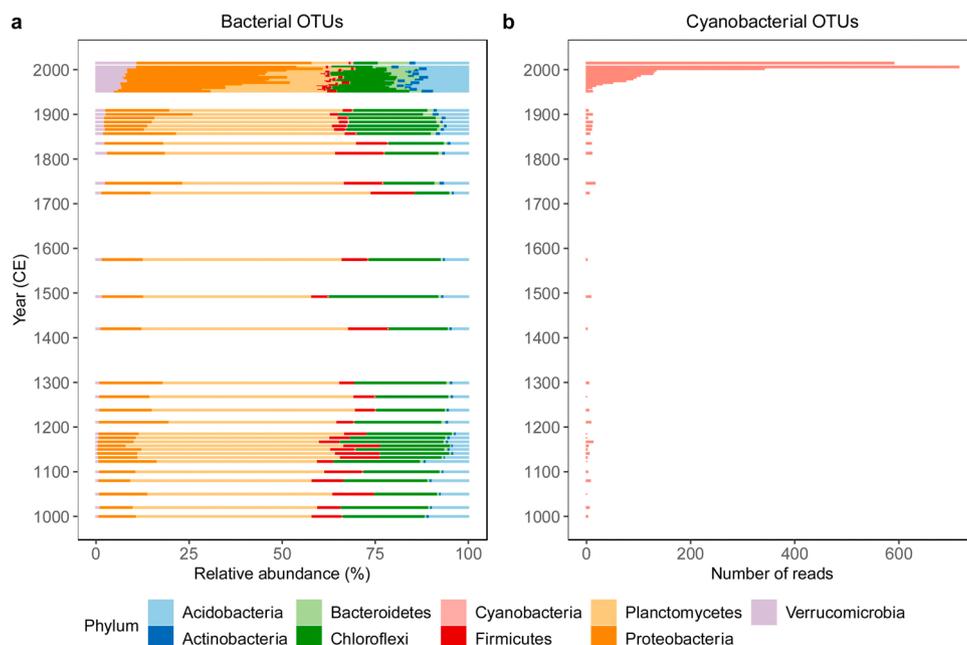


Fig. 3. Downcore profiles showing a) the relative percentage of sequences assigned to the main bacterial phyla, and b) the abundance of cyanobacterial sequences recovered from the JOU17-03 sediments core (both plots are based on rarefied read counts to account for sequencing depth).

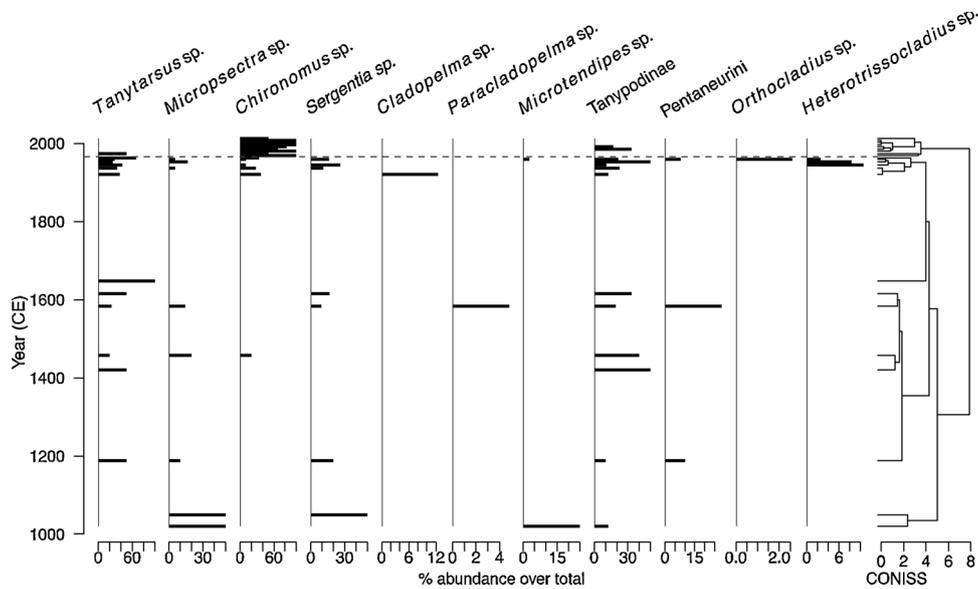


Fig. 4. Stratigraphy of chironomids in the JOU16-02 sediment core expressed as percentage over total abundance. The horizontal dashed line identifies the significant transition (1953 – 1959) in community composition identified by CONISS.

dominant. At the end of the 1600s, the proportion of *Paracladopelma* sp. and Pantaneurini increased in addition to *Tanytarsus* spp. and *Microspectra* sp. This was not a significant transition, however, based on the change-point analysis. A single significant transition in the chironomid assemblage was detectable between ~1953 to 1959 (10–12 cm down-core). This recent transition marked the shift from a community dominated by *Tanytarsus* spp. and *Microspectra* sp. towards an assemblage dominated by *Chironomus* sp.

4.1.4. Cladocerans (littoral and pelagic communities)

Twenty-eight Cladocera species were identifiable in the sediments of Lake Joux. For simplicity, we discuss the dynamics of the eight main

taxa identified. The overall temporal trends in the cladoceran assemblage resembled the trajectories observed in chironomids. A single significant shift in cladocerans was revealed by the change-point analysis at the same time as chironomids (i.e., between 1953 and 1959; Fig. 5). Earlier changes in species composition were visible, however throughout the core. Between ca. 1016 and 1118 CE (61–68 cm depth), the pelagic *Eubosmina longispina* and two littoral species, *Sida crystallina* and *Rhynchotalona falcata* (Chydorids) were abundant. Between ca. 1187 and 1950 CE, *Daphnia longispina* replaced *E. longispina* in the pelagic compartment. Later, during the height of eutrophication between 1958 and 1980, the littoral species *Bosmina longirostris* was present in higher abundance and *Eubosmina coregoni* appeared for the first

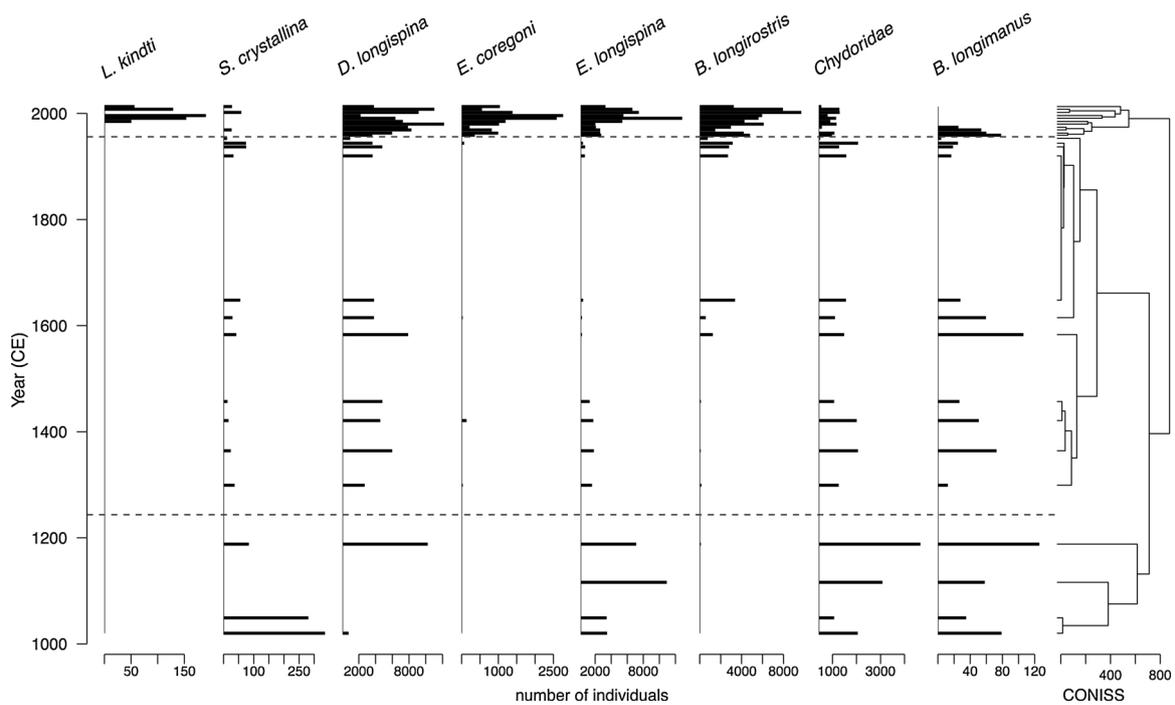


Fig. 5. Stratigraphic plot of the main cladocerans observed in the JOU16-02 sediment core. Abundance was expressed as number of individuals per gram of organic matter. The uppermost dashed line marks the only statistically significant transition in cladoceran assemblages as identified by the change-point analysis and CONISS (transition 1953–1959). The earlier transition (~1188 to 1299 CE; not significant) is shown for reference.

time. The high abundance of *E. coregoni* correlated inversely with the abundance of *Eurycercus* spp. (not shown). *Eurycercus* spp. are littoral species capable of migrating within sediments due to vulnerability and pressure associated with fish predation (Beklioglu and Jeppesen, 1999). We also observed a slight decrease in *Daphnia* size, from $\sim 170 \mu\text{m}$ to $\sim 140 \mu\text{m}$ (non-significant; not shown) which is stable from 10 cm-depth (early 1960s) to the core surface. Finally, in the most recent time period (~ 1980 to 2015), *Bythotrephes longimanus*, a large predatory pelagic species that was found throughout the sediment core was replaced by *Leptodora kindtii*, which played a similar ecological role (predatory and pelagic), but that does better in warmer (Palmer et al., 2001) and more hypoxic (Sorensen and Branstrator, 2017) waters.

4.1.5. Fish

Fish remains were generally low in abundance, although an increasing trend was observable towards the upper portion of the sediment core (except for the top-most interval between 7.5 and 2.5 cm-depth (~ 1987 to 2008)). The large majority of the remains were percid scales ($n = 73$; Table S1). Only two non-percid scales and three bones were found but could not be identified further.

4.2. Regime shift

Because dominant modifications to the lake biota were only detectable from the mid 20th century, changes in total phosphorus (TP) appear as the dominant structuring force over the study period. To verify this, we extracted the scores of the main PCA axis (which explained between 28 and 41 % of the variance in community composition) and plotted them against a time-series of TP concentrations. The results suggested a relationship between TP and the composition and abundance of pigments, cladocerans, and chironomids that varies through time (Fig. 6). When the temporal trajectory of individual proxies (i.e., each taxon or individual pigment concentration) was plotted against TP (Figs. S3, S5 and S6), similar general trends were observed in the majority of cladocerans, chironomids, and pigments, supporting the relationship between TP and species turnover in the PCA.

Applying time-varying autoregression using Online Dynamic Linear Models (DLMs) to the time-series of echinenone pigment concentration provided the best indicator for the presence and the timing of regime shifts and critical transitions in Lake Joux over the last ca. 1000 years. The sharp increase in the intercept (Fig. 7) identified a recent regime shift during 1963–1969 CE. This observation was further supported by the abrupt changes notable in the pigment composition (Fig. 2) and the turnover of cladocerans and chironomids (Figs. 4 and 5). The pronounced increase in eigenvalue (eigenvalue > 1 ; Fig. 7, bottom panel) provides evidence of critical transition.

5. Discussion

5.1. Dynamics of the transition and regime shift

The paleolimnological data from this study provided distinctive biostratigraphic signatures that suggests resilience of the lake over several hundreds of years followed by an ecosystem-level response to environmental forcing (González Sagrario et al., 2020). These changes are consistent with a possible transition from the Holocene to a proposed Anthropocene, with a stratigraphic signal around the mid-20th century of the Common Era. This transition marks an intensification of human impacts causing unprecedented changes to the Earth system (Syvitski et al., 2020; Zalasiewicz et al., 2020). Earlier disturbances can certainly have an impact, but they are usually more limited and potentially reversible. Mid-20th century eutrophication surpassed all other disturbances observed in the catchment of large lakes in the perialpine area (Tolotti et al., 2018). Loss of resilience caused by long-term perturbation, however, may increase vulnerability to further stressors such as eutrophication (Bruel et al., 2021; Scheffer et al., 2001). Multiple

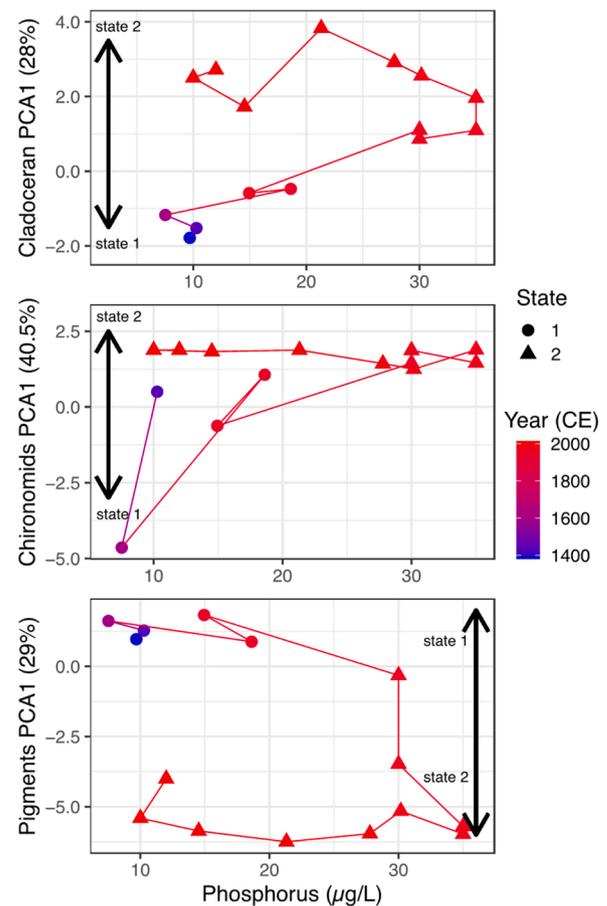


Fig. 6. Temporal trajectories of PCA scores for Cladocerans, Chironomids, and pigments (axis 1) plotted against a gradient of total phosphorus concentrations. Arrows indicate the direction of the transition from ecological state 1 (baseline, pre-eutrophication; circles) to state 2 (eutrophication and re-oligotrophication phases; triangles).

perturbations of Lake Joux since the settlement of the first humans in the catchment (Fig. 1b) may have contributed to increase the lake vulnerability to eutrophication leading to a regime shift.

Despite decades of re-oligotrophication leading to a return to pre-eutrophication total phosphorus concentrations (11–13 $\mu\text{g/L}$; Lods-Crozat et al. (2006)), Lake Joux has not returned to its pre-disturbance ecological state. As such, across the same concentrations of total phosphorus, biological assemblages in Lake Joux exist in two states: pre-eutrophication and re-oligotrophication states (Figs. 6 and 7). Although this study was not designed to test whether the permanence of the observed modifications to Lake Joux's communities, no clear indications was apparent whether the lake might return to its previous configuration in the near future. However, the trajectory of chironomids estimated, based on PCA, suggests that the recent zoo-benthos configuration was more similar to some of the pre-eutrophication assemblages compared to the communities at the height of eutrophication. Confounding effects of additional environmental disturbances, including climate change, might explain the delay in water quality recovery despite reduced nutrient loadings in Lake Joux since the 1980s (Bruel et al., 2018; Perga et al., 2015). Enhanced warming of surface waters has been observed in perialpine lakes and elsewhere (Livingstone, 2003; Woolway et al., 2019, 2017). Warming has direct and indirect effects on lake processes (e.g., stratification length and strength, hypoxia, phosphorus release from sediment, calcium carbonate precipitation) and in turn, these alterations to the physical and chemical structure of lakes have consequences on the lake ecology (phenology or species life history traits).

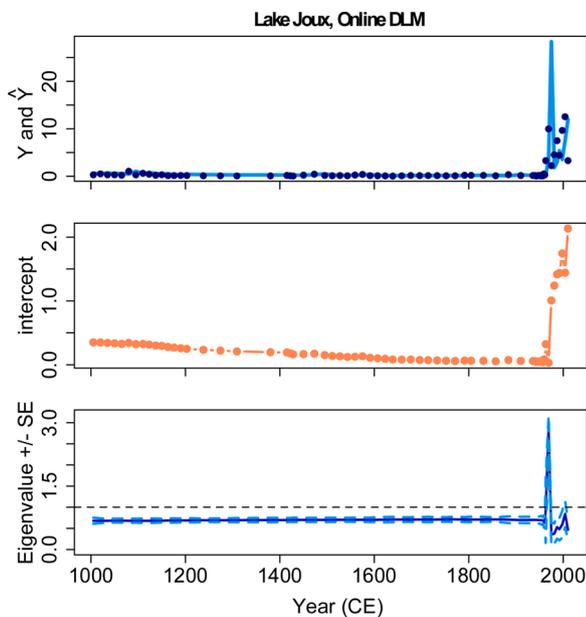


Fig. 7. Main results of the online dynamic linear model (DLM) for Lake Joux echinenone pigment ($n = 68$). In the top plot, the time series is shown in dark blue dots and the goodness of fit is the clear blue line. The middle plot shows the intercept in orange dots, and the bottom plot shows the eigenvalues (blue line) and standard deviation dotted light blue line.

5.2. Biodiversity change

Alterations to Lake Joux physical and chemical characteristics due to eutrophication are visible through biotic changes at multiple trophic levels. Sedimentary pigments and bacterial *sedDNA* analyses revealed an increase in primary productivity during the eutrophication period (~1950 to 1980), leading to a phase of reduced water clarity. The decline in the UV-Index (Fig. 2) with the onset of eutrophication may be a response to higher phytoplankton biomass, which creates shade for organisms that live deeper in the water column, such as photosynthetic bacteria (Lami et al., 1991; McGowan, 2017). This change in the lake's ecology also contributed greatly to modify the composition of primary producers. A major change observed in phytoplankton assemblage was the establishment of the invasive cyanobacterium *Planktothrix rubescens*, as conveyed by monitoring data and supported by the analysis of pigments. *P. rubescens* often forms metalimnetic (deep) blooms, which firstly may be undetected by some monitoring programmes. Metalimnetic phytoplankton are generally more readily incorporated into the sediment record intact, however, as they have smaller distances to travel when sinking and are less exposed to photodegradation (Cuddington and Leavitt, 1999). The presence of *P. rubescens* in Lake Joux was first reported in 1972 (Bosset, 1981) and since 1979, local environmental agencies have regularly reported high biomasses of this filamentous cyanobacterium. *Planktothrix* (both *P. agardhii* and *P. rubescens*) remained the dominant phytoplankton in the lake over the following decades despite the ongoing reduction of pollution by phosphorus (Lods-crozet et al., 2006 and references therein). *P. rubescens* is a potentially toxic cyanobacterium that has recently widened its geographical distribution in the perialpine area (Ernst et al., 2009; Jacquet et al., 2005; Monchamp et al., 2018), posing a threat to water quality in several lakes. It thrives in deep and stratified lakes with moderate light and moderate nutrient availability (Dokulil and Teubner, 2000). *P. rubescens* is also more suited than other phytoplankton to the warmer conditions and the current meso- to oligo- trophic state characterizing Lake Joux (Lods-Crozet et al., 2006), as well as, other lakes in the region (Monchamp et al., 2019b, 2018; Posch et al., 2012).

DNA metabarcoding can provide estimates of the proportion of

bacterial taxa within communities, which enables detection of species turnover and investigation of community responses to environmental gradients (e.g., Bálint et al., 2018; Stoeck et al., 2018). The time of the drastic increase in the proportion of cyanobacteria agrees with the sedimentary pigments signal and is further validated by lake monitoring data (Lods-Crozet et al., 2006). This study did not detect other drastic turnover in the rest of the bacterial assemblage over the period of high disturbance, but rather gradual changes in the proportion of the main phyla (e.g., Planctomycetes and Proteobacteria; Fig. 3). The increase in relative abundance of Verrucomicrobia, Proteobacteria and Bacteroidetes indicates a community better adapted to eutrophic conditions (Huang et al., 2017). The concomitant decrease in the proportion of Chloroflexi, many of which generally thrive in the oxygenated hypolimnion of deep lakes (Okazaki et al., 2018), agrees with the more hypoxic conditions that prevail in the bottom waters of Lake Joux.

Modifications in the zoobenthos assemblage (Fig. 4) also reflect warmer and more eutrophic conditions reported in Lake Joux over the second half of the 20th century. Around 1953–1959, the community shifted from a taxa adapted to cold and well-oxygenated waters towards an assemblage dominated by *Chironomus* sp., which is tolerant of warmer waters and possibly hypoxic conditions. Our findings corroborate previous reports of the presence of oligochaete worms and chironomid larvae at the lake bottom after the onset of eutrophication (Lang and Raymond, 1996, 1993).

In the cladoceran assemblage (Fig. 5), the replacement of *Eubosmina longispina* by *Daphnia longispina* in the pelagic compartment around 1250 CE may indicate a period of slight eutrophication, as *D. longispina* has higher stoichiometric requirements (Elser et al., 2001). More recently, the replacement in the pelagic compartment of *Bythotrephes longimanus* by the heat-tolerant *Leptodora kindtii* towards the end of the 1970s – early 1980s concurred with enhanced warming of surface waters.

Given the generally low abundance of fish scales and bones in the sediment, and the coarse taxonomic resolution achieved (Table S1), these data were, however, not sufficient to infer the dates of introduction of species, or changes in their abundance over time. Records of fish catches showed that whitefish was most abundant between 1959 and 1998, while perch comprised a maximum of 15 % of catches during this period (Naceur and Büttiker, 1999). We report a drastic decrease in perch populations between 1971 and 1984 as well as decrease in average productivity of whitefish since 1987 in Lake Joux. This overall decline in whitefish productivity has been hypothetically linked to the regular development of high biomass of the cyanobacterium *Planktothrix rubescens* (previously *Oscillatoria rubescens*) since the end of the 1970s (Naceur and Büttiker, 1999). To our knowledge, however, validation of this hypothesis has not yet occurred. Other factors affecting whitefish productivity, and that have been observed in other lakes of the region, include intraspecific competition and the timing and duration of the lake thermal stratification (Eckmann et al., 1988). The reduction in *Daphnia* size (not shown), often used as a proxy for high fish predation pressure, as well as the sudden increase in abundance of the small *Eubosmina coregoni* during the eutrophication phase also concur with increased fish predation. *E. coregoni* is also tolerant to the presence of filamentous cyanobacteria, which gives this taxa a competitive advantage (Mayer et al., 1997). Interestingly, the main change-point in cladoceran and chironomid assemblages were detected slightly earlier (~1953–1959) than the transition in phytoplankton (1963–1969). Although a first change was detectable in pigment composition between 1959 and 1961, the community shift towards the second ecological state (post-eutrophication) were apparently more gradual and slightly delayed compared to zooplankton and micro-zoobenthos. Because the time series of pigments, cladocerans, and chironomids were all derived from the same sediment core (JOU16-02), we can rule out discrepancies in timing due to age model correlation. Our observation is consistent with other studies in perialpine lakes, where cladocerans systematically showed an early response to increased total phosphorus before diatoms signaled

any change (Alric et al., 2013; Bruel et al., 2018). Cladocerans are highly responsive to climate, nutrient availability as well as fish predation pressure. In the case of Lake Joux, cladocerans have been simultaneously exposed to both top-down (fish predation) and bottom-up (nutrients) processes in addition to warming, and the accumulation of external stressors may have led to a stronger and potentially early response. Similarly, chironomids are extremely sensitive to environmental factors, including oxygen concentration and temperature (Walker, 2001), making them good indicators of pollution and climate change.

5.3. Methodological aspects

A strength of this study lies in the combination of multiple paleolimnological and *sedDNA*-based proxies that allows investigation of temporal dynamics of the ecosystem as a whole, and cross-validation of multiple markers. Congruent patterns through time and across proxies increase the robustness of paleo-reconstructions. Previous studies have described methodological concerns related to *sedDNA* metabarcoding (Pedersen et al., 2015; Ruppert et al., 2019). A main concern in *sedDNA* studies is the degradation and the loss of DNA molecules over time. Although DNA has been shown to preserve over several millennia in sediments (Pedersen et al., 2015), some limitations due to taphonomic processes after burial have been identified (Gilbert et al., 2005). Deep cold lakes with anoxic bottoms, prevalent in perialpine lakes, provide excellent conditions for DNA preservation (Boere et al., 2011; Coolen et al., 2004). To reduce potential biases related to DNA degradation, we targeted a short gene fragment and used technical replicates. In addition, we visually inspected the sequence data for patterns that might point towards temporal *sedDNA* degradation. For example, a sudden disappearance of specific taxa or a loss of the molecular signal in older sediment layers could indicate DNA damage or degradation. Sedimentary pigments are also prone to degradation over time, which can bias the ecological signal. The pheophytin a/chlorophyll a ratio in Lake Joux sediments indicated a recent increase in the preservation since ~1980 CE, however, which is at least two decades after the general increase in pigment concentration is measured in both the sedimentary pigments and DNA. Finally, our multi-proxy survey allowed cross-validation of the sequencing and the sedimentary pigment data in corresponding sediment layers.

Despite the success of using fish remains from marine and freshwater sediments to infer changes in ecosystem state or community composition (e.g., Davidson et al., 2003; Dieleman et al., 2019; O'Connell and Tunnicliffe, 2001), many confounding factors are still poorly understood. For example, species with more strongly mineralized, and therefore better preserving, bones and scales might be relatively over-represented in the subfossil record (Kalvoda et al., 2009). Additionally, perch, roach and dace (*Leuciscus leuciscus*) were reported in higher densities in the littoral zone of Lake Joux, in contrast to whitefish, which was found to be most abundant in the pelagic zone (Périat and Vonlanthen, 2015). This might partially explain the general scarcity of fish remains in Lake Joux pelagic sediments despite a recent comprehensive census (Périat and Vonlanthen, 2015) illustrating the predominant presence of perch and reporting both roach and dace as common in Lake Joux. Future studies that reconstruct fish diversity through time using lake sediments could improve the approach by screening larger volumes of sediment, ideally also including core sites representing more littoral communities. Extending the *sedDNA* approach to fishes could also increase detection sensitivity and chronological resolution, especially for poorly preserving species.

6. Conclusions

The analyses presented above provide answers to the three research questions asked in this paper. First, our unique multi-level paleo-reconstruction dataset compiles important biological change over the

last 1000 years in Lake Joux and reveals enhanced human impact on the ecosystem over the second half of the 20th century, mainly linked to cultural eutrophication. Consequently, there was a rapid turnover in community composition in phytoplankton, Cladocera, and chironomid assemblages, with taxa adapted to eutrophic waters becoming dominant over original species configuration. Second, the PCA suggests that the major change in nutrient regime led to the regime shift (~1963 to 1969) and apparent bi-stability between two states, as also conveyed by the dynamic lineal model. Lastly, the results further suggest that the reconfiguration in Lake Joux is not restricted to some biological compartments, but rather spreads across trophic levels, at least partially. The lack of a complete fish dataset does not allow conclusions on the extent of the regime shift at the top of the food chain (i.e., in fish communities), but the concomitant changes reported at all other trophic levels investigated provide evidence for reorganization of the lake's ecology at multiple levels (both in primary producers and primary consumers).

Although earlier disturbances might have increased vulnerability of the lake to eutrophication, the rapid increase in phosphorus concentrations triggered the regime shift at a moderate concentration (~20 to 35 µg/L) of total phosphorus. The fact that the lake has not returned to its pre-eutrophication state in over >70 years of re-oligotrophication leads to the conclusion that the lake has shifted to an alternative stable state and its biological configuration is not easily reversible. In the case of Lake Joux, this might mean recurring cyanobacterial blooms in the future. More generally, the shift to an alternative stable state typically has major consequences on water quality and ecosystem services that humans derive from lakes. This study adds to the body of evidence suggesting that a key aspect to effective management strategies is maintaining resilience of ecosystems in their desired state. To achieve this, a need exists to improve understanding of the underlying mechanisms of critical transitions that may reveal early-warning signals through paleoecological records. Ecosystem-wide paleoecological approaches, demonstrated in this study, provide a wealth of biological and genetic information that can significantly improve ability to quantify the rate and amplitude of change in ecosystems under anthropogenic forcing.

Data availability

The sequence data produced in this study have been deposited in the European Nucleotide Archive (ENA) with the study accession number PRJEB36317.

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CRedit authorship contribution statement

Marie-Ève Monchamp: Conceptualization, Data curation, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization, Project administration, Funding acquisition. **Rosalie Bruel:** Formal analysis, Investigation, Visualization, Writing - review & editing. **Victor Frossard:** Investigation, Writing - review & editing, Resources. **Suzanne McGowan:** Investigation, Writing - review & editing, Resources. **Marlène Lavrieux:** Visualization, Writing - review & editing. **Moritz Muschick:** Investigation, Writing - review & editing. **Marie-Élodie Perga:** Writing - review & editing, Resources. **Nathalie Dubois:** Conceptualization, Methodology, Supervision, Project administration, Resources, Writing - review & editing, Funding acquisition.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ancene.2021.100301>.

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