



# Article Tracking Fish Introduction in a Mountain Lake over the Last 200 Years Using Chironomids, Diatoms, and Cladoceran Remains

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Abstract: We analysed a 24 cm long sediment sequence (past ~200 years) from an alpine lake (Tatra Mts., Slovakia) for chironomids, cladocerans, and diatoms to reconstruct the effects of a historically documented fish introduction. Our results indicate that fish introduction predated the age of the sequence, and thus, we did not cover the lake's fishless period. The individual proxies coincide in showing two main lake development stages. The first stage lasted until ~1950 CE and was interpreted as the stage when brown trout and alpine bullhead co-occurred. The extremely low concentration of cladocerans, the dominance of small-bodied chydorids, and the low share of daphnids, together with the low proportion/absence of large-bodied tanypod chironomids, suggest a strong effect of both species. The beginning of the next stage is probably related to the ban on fish manipulations and grazing in the catchment. A significant increase in the total abundance of cladocerans and of daphnids may indicate the extirpation of trout. The steep increase in thermally plastic chironomid taxa since the end of the 20th century indicates climate warming. Generally, while cladocerans primarily indicate fish manipulations, chironomids and diatoms mainly reflect other local and global environmental stressors.

**Keywords:** Chironomidae; Cladocera; Bacillariophyceae; alpine bullhead; brown trout; paleolimnology; Tatra Mountains; Western Carpathians

# 1. Introduction

Mountain areas are among the most sensitive environments worldwide. Although human pressure (grazing, agriculture, and forestry) in European mountains began several millennia ago [1], mountains have been increasingly affected by human activities since the industrial revolution [2]. Towards the end of the last century, anthropogenic pressure has become increasingly evident. The alpine zone above the local tree line has been recognized as a particularly fragile environment [3]. Recently, the remote and seemingly pristine alpine ecosystems have been affected by climate change, long-distance atmospherically transported pollution (acid deposition, persistent organic pollutants, and heavy metals), nutrients, dust, and the increasing exposure to exotic and invasive species [4–6].



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**Copyright:** © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). Although lakes represent only a small part of the high mountain landscape, they may support unique biodiversity and provide numerous ecosystem services [7]; hence, they have tremendous ecological and environmental value [8]. Moreover, we can consider them as important sentinels of global changes. Due to the extreme environmental conditions, they have a relatively simple community structure and react more rapidly and sensitively to environmental changes than lakes in the lowlands [9]. Even minor impacts can significantly affect the physical and chemical properties of lake water and induce qualitative and quantitative changes in their communities [10,11].

The high mountain lakes in the Tatra Mountains (Tatra Mts., Western Carpathians) are among the most intensively studied in the European lake district [12]. A number of studies have detected the very strong effects of acid atmospheric pollutants in the second half of the 20th century; these effects have led to major changes in the planktic and benthic communities [13–15], which were followed by a rapid reversal in the lake water chemistry to levels similar to those of the pre-acidification conditions in the early 1990s [16]. More recent studies based on instrumental and paleolimnological data have revealed the complexity of the biological recovery and water chemistry due to climate change [17–20].

Amongst several anthropogenic stressors that have been identified worldwide, biological invasions are now considered a major environmental problem of public concern [21]. Fish belong to the most introduced groups of aquatic animals [22], with a high number of invasive species in Europe [23]. The successful integration of fish species into a new environment is associated with a high probability of detrimental interactions with native species or even with changes in ecosystem functioning [21].

Fish stocking (usually with salmonids) into originally fishless high mountain lakes affects the fragile local biodiversity in many direct and indirect ways. As they are usually top predators, fish reduce the distribution and abundance of large zooplankton and produce indirect top-down and cascading effects that alter the structure and biomass of small zooplankton and phytoplankton species. Predation changes the structure of nektic and benthic macroinvertebrate fauna and causes the local extinction of some species [24–28]. Further negative impacts include the reduction in or elimination of amphibians [29] and the depletion of the aquatic biomass entering the terrestrial environment, which indirectly affects terrestrial vertebrate and invertebrate predators [30,31].

In addition to global stressors, regional and local disturbances may influence the biota of mountain lakes. The introduction of fish into previously fishless lakes in the European high mountains is a major anthropogenic factor leading to profound ecological changes [29]. Recently, fish have been introduced into high-altitude lakes in the Alps, Pyrenees, and Carpathians (e.g., Tatra and Retezat Mts.), mainly for the purpose of recreational fishing [32,33].

The lakes of the Tatra Mts. were (with two exceptions out of more than 220) originally fishless due to the presence of natural barriers (steep slopes, the high current velocity of the outlets, waterfalls, or the frequent complete isolation of lakes without outlets and inlets) that have prevented the natural colonization of fish species from streams situated lower down.

The published data on the native and introduced fish populations in the Tatra lakes are usually qualitative; some are decades old and largely scattered in grey literature [34], which makes compiling a coherent history of the stocking process difficult. The first mentions of the occurrence of brown trout (*Salmo trutta*) in the lakes, where its natural occurrence was impossible, date back to as early as the beginning and the second half of the 18th century [35]. While these activities were most likely to have been occasional and not thoroughly planned, an extensive program of fish stocking took place at the end of the 19th century when brown trout (and non-native brook trout, *Salvelinus fontinalis*, in Poland) was introduced into a great number of originally fishless Tatra lakes [36]. Another so-called "planned" stocking of the lakes began in the 1930s and continued during the first half of the 20th century. However, some introductions occurred later, even after the establishment of the Tatra National Park on the Slovak and Polish border, i.e., after 1950–1955 [34,37], when

such activities were officially forbidden. The main stages of fish introduction in the Tatra Mts. are roughly consistent with the situation in other European mountain ranges [33].

Overall, the lakes were stocked with three salmonid species: brown trout, brook trout, and rainbow trout (*Oncorhynchus mykiss*), as well as with alpine bullhead (*Cottus poecilopus*). An exception is Štrbské pleso lake located in the centre of tourism on the Slovak side of the Tatra Mts.; the lake was stocked with many other non-native fish species [38] as a result of both fish management and the collateral introductions of species used as live bait or released illegally.

The extent of the past stockings of the Tatra lakes remains unknown to this day. The introductions failed in many cases, but populations of brown trout and brook trout have remained in eight lakes (not including Štrbské pleso lake) to the present day [14]. In some lakes of the western part of the Tatra Mts., the population of alpine bullhead survived as a remnant of the common introduction with brown trout. Both species are native to the Tatra Mts. and coexist in sub-mountain and mountain brooks and rivers [39,40]. However, the intentional introduction of these two species with the aim of making alpine bullhead a natural prey for brown trout [34] is an exceptional and unprecedented case of fish introduction in European high mountain lakes [33]. Thus, we took this unique chance to study the lake ecosystem changes under the combined pressure of these two predatory fish species.

The overall aim of this paper is to provide a reconstruction of the development of a small alpine lake as a response to fish introduction using subfossil diatoms, cladocerans, and chironomids from sediments spanning the last ~200 years. Specifically, the study addresses the following questions: (1) What is the timing of the fish introduction to the lake? (2) Is it possible to distinguish periods with and without fish populations and to identify the influence of a single species and the intertwined ecological impact of both species? (3) Is there a synchronicity between the proxy records?

Surprisingly, little attention has been paid to the biology of fish and their ecological impact on the Tatra lakes. Recent research has focused on the somatic growth of the introduced brown trout and brook trout populations [41] and the effect of brook trout on planktic copepods [37,42]. However, only two studies used a paleolimnological approach to reconstruct the impact of fish introductions on the Tatra lakes [43,44].

Studies with a historical perspective are necessary to understand the impact of species introduction; in turn, these studies are the basis for the establishment of more appropriate management policies. Unfortunately, the historical (long-term) data are often missing, in which case a paleolimnological approach can be used [45].

## 2. Material and Methods

### 2.1. Study Lake

Vyšné Račkovo pleso (VRP, 49°11′59″ N, 19°48′06″ E) is a small (0.7 ha) subalpine lake of glacial origin with a maximum depth of 12.3 m. It is the uppermost lake (1697 m a.s.l.) in a chain of seven small lakes in the Račkova dolina valley in the Western Tatra Mts. (Figure 1). The lake has an inlet and an outlet, and its size slightly varies depending on climatic conditions. In the spring, increased water runoff due to snowmelt can cause the water level to rise and the lake can be connected with the two neighbouring lakes via its extensive outlet. The catchment is mostly made up of alpine meadows with dwarf pines and rocks. Due to the presence of metamorphic rocks in its catchment, VRP lake, such as the other lakes in the Western Tatra Mts., has a higher concentration of base cations, resulting in higher alkalinity. Thus, it did not undergo acidification in the past, in contrast with many other Tatra lakes located in the granitic central part [13]. For the basic physical properties and catchment of the lake, see Table 1.

### 2.2. Sediment Sampling

In October 2018, two short sediment cores (VRP-I 24 cm and VRP-2 21 cm long) were taken from the deepest part of the lake (12.3 m) using a Kajak gravity corer. The longer



core, VRP-I, was sectioned into 0.5 cm thick layers on site, and the sediment samples were stored in plastic zip bags at approximately 4 °C in a refrigerator for later analysis.

**Figure 1.** The location of the study lake, Vyšné Račkovo pleso (VRP), within Europe (**A**) and Slovakia (**B**); the photograph shows the study lake and part of itsded catchment (**C**). Data source: Database of Global Administrative Areas (GADM) and Digital Chart of the World (DCW). Photo: Opioła Jerzy, license: Creative Commons Attribution-Share Alike 3.0 Unported.

### 2.3. Chronology

The age of each layer was calculated with the <sup>210</sup>Pb method using the constant rate of supply (CRS) model. The method uses the law of radioactive decay and changes in the concentration of the so-called unsupported lead <sup>210</sup>Pb<sub>unsup</sub>, which is washed out of the atmosphere and incorporated into lake sediments. Its amount decreases over time. The radioactivity of <sup>210</sup>Pb<sub>unsup</sub> was calculated from the total <sup>210</sup>Pb (<sup>210</sup>Pb<sub>total</sub>) and the supported <sup>210</sup>Pb (<sup>210</sup>Pb<sub>sup</sub>) radioactivity. The concentrations of the radionuclides were calculated using gamma spectrometry. The measurements of <sup>210</sup>Pb via line 46.5 keV give the radioactivity of <sup>210</sup>Pb<sub>total</sub>. The concentration of <sup>210</sup>Pb<sub>sup</sub> was determined via the measurement of <sup>226</sup>Ra. The supported lead is formed in situ in a sediment through the decay of <sup>222</sup>Rn, whose source is <sup>226</sup>Ra, which is contained in the sediment. To calculate the <sup>226</sup>Ra radioactivity, five energy lines were used, specifically 1764.5 keV, 1120.3 keV, 609.3 keV (<sup>214</sup>Bi), 351.9 keV, and 295.2 keV (<sup>214</sup>Pb). By subtracting the value of <sup>210</sup>Pb<sub>sup</sub> from (<sup>210</sup>Pb<sub>total</sub>), the values of <sup>210</sup>Pb<sub>unsup</sub> and the age were calculated [47,48].

All the gamma measurements were conducted on the Broad Energy Germanium Detector using Canberra Packard (BE 3830) with 34% relative efficiency. The results were validated using reference material from the International Atomic Energy Agency (IAEA). Before analysis, the containers were stored for at least four weeks to allow <sup>226</sup>Ra and its short-lived decay products to reach secular equilibrium. Finally, each sample was measured for at least 72 h. Additionally, the chosen sediment samples, especially the upper layer with the smallest weight (below 1.5 g), were measured on an alpha spectrometer with a PIPS detector (34% efficiency), according to the procedure described previously [49].

Variable/Site Name	Unit	Value
Coordinates		49°11′59″ N
		19°48′06″ E
Altitude	m	1697
Max. depth	m	12.3
Area	ha	0.74
Littoral habitat description (R:S:O)	%	75:15:10
Catchment characteristics		
Maximum altitude	m	2137
Catchment area	ha	56
Rock	%	20
Moraine	%	20
Meadow, dwarf pines	%	60
Forest	%	0
Water chemistry		
рН		7.49
Alkalinity	$\mu eq L^{-1}$	219.15
Conductivity	$\mu S \operatorname{cm} L^{-1}$	29.11
ANC	$\mu$ mol L $^{-1}$	254
TON	$\mu$ mol L <sup>-1</sup>	7.7
TP	$\mu$ mol L <sup>-1</sup>	0.094
TOC	$\mu$ mol L $^{-1}$	100
Cl <sup>-</sup>	$\mu$ mol L <sup>-1</sup>	4.9
$SO_4^{2-}$	$\mu$ mol L <sup>-1</sup>	32
$NO_3^{-}$	$\mu$ mol L <sup>-1</sup>	13
$NH_4^+$	$\mu$ mol L <sup>-1</sup>	0.7
Na <sup>+*</sup>	$\mu$ mol L <sup>-1</sup>	21
K <sup>+</sup>	$\mu$ mol L <sup>-1</sup>	2.5
Ca <sup>2+</sup>	$\mu$ mol L <sup>-1</sup>	81
$Mg^{2+}$	$\mu$ mol L <sup>-1</sup>	69

**Table 1.** Hydromorphological and physicochemical characteristics of the study lake, Vyšné Račkovo pleso, and its catchment [16,46]. Abbreviations: R—rocks, S—sand, O—organic matter. Conductivity was measured at 20 °C.

The <sup>210</sup>Pb method is mainly used to date within a period of 100–150 years in the past. At most, it can be used to determine an age of 200 years. The estimated age of the sediment core was confirmed using the <sup>137</sup>Cs method. The <sup>137</sup>Cs radionuclide is a fission product. It is determined using gamma spectrometry via 661.6 keV. In sediment cores, two maxima of <sup>137</sup>Cs radioactivity should be visible. A large amount of this radionuclide was introduced into the atmosphere during nuclear tests (1945–1963) and the Chernobyl accident of 1986 [47,50].

### 2.4. Chironomid Analysis

To remove coarse organic and inorganic particles, we used sieves with mesh sizes of 90  $\mu$ m and 200  $\mu$ m. Head capsules were manually picked from the fractions on both sieves at 40× magnification. At least 50 head capsules were collected from each layer. Chironomid head capsules were mounted ventral side up in Berlese mounting medium on microscopic slides. Taxonomic identification was performed under a compound microscope at up to 400× magnification in accordance with the standard identification guides [51,52]. Water flow preferences, larval body size, and the feeding groups of individual taxa were assigned to chironomid taxa [53,54].

# 2.5. Cladocera Analysis

Subfossil Cladocera analyses were carried out according to the standard methodology [55]. Fresh sediment samples (ca. 2 cm<sup>3</sup>) were treated with 10% HCl to remove carbonate and then heated in a 10% KOH solution. Later, the residue was put into a magnetic stirrer for 20 min to eliminate the humic matter. Finally, the samples were sieved through a 38  $\mu$ m sieve and transferred into test tubes, which were then filled with up to 5 cc of distilled water. Each sample was stained with safranin. Depending on the amount of remains, three to five slides (0.1 cm<sup>3</sup> liquid suspension) were examined for each sample. The taxonomic identification followed the standard literature [56].

#### 2.6. Diatom Analysis

In total, 48 samples were used for the diatom analyses. The diatoms (Bacillariophyceae) were mounted in Naphrax resin after the standard cleaning procedure, which used 30%  $H_2O_2$  as the oxidizing reagent for the elimination of the organic material, followed by a 10% HCl treatment to remove the carbonates [57]. A minimum of 400 valves was counted in a sample across randomly selected transects using a 1000× oil immersion objective and a Nikon Eclipse Ni-U microscope. The diatom identification was mainly based on [58–64]. The nomenclature was checked and updated according to AlgaeBase [65]. Only diatoms with total abundances >5% were included in the stratigraphic diagram.

### 2.7. Data Analysis

Biological data were compiled and graphed using C2 software version 1.7.7 [66]. Stratigraphically constrained sum-of-squares cluster analysis (CONISS) was applied in Tilia version 1.7.16 [67] to objectively divide the downcore changes in the assemblage composition and abundance into zones. To show the changes on a community level, all the biological proxies were analysed using DCA (detrended correspondence analysis) in Canoco for Windows version 5.01 [68], using untransformed relative abundance data. The results were shown as the DCA first axis scores plotted against age.

### 3. Results

#### 3.1. Chronology

The 24 cm long sediment core was estimated to have been deposited in the last 195 years (Figure 2). The sedimentation rate varied over time. The top 10 cm layers (1952–the present) were settled within 3 years on average. The fastest sedimentation was observed from 15 to 10.5 cm (1938–1950). From 21 to 15.5 cm (1895–1936) a slower sedimentation rate was observed, and the oldest sequence (1823–1889) had the slowest sedimentation rate. The results of the <sup>137</sup>Cs radionuclide method confirmed the accuracy of the lead dating. Indeed, elevated levels of <sup>137</sup>Cs concentrations were identified around the 1980s and 1960s, corresponding to the Chernobyl accident and nuclear weapon tests. However, due to the organic nature of the sediments, this radionuclide migrates down the profile, and there is no possibility to determine the visible maximum of the <sup>137</sup>Cs radioactivity. This is also the reason why it is measurable in the lower layers [48,69]. The presence of caesium between 9.5 and 8.5 cm can be attributed to the global fallout after the nuclear weapon testing. According to the <sup>210</sup>Pb method, at a depth of 6 cm, the sediment was dated to 1986; in addition, the radioactivity of the <sup>137</sup>Cs at this depth reached one of the highest values. However, because of its migration, the expected peak was blurred.

#### 3.2. Chironomid Assemblages

A total of 3474 chironomid head capsules, representing 30 taxa of five subfamilies, were identified. The subfamily Orthocladiinae, followed by the tribe Tanytarsini (Chironominae), dominated the entire sequence, with the most common taxa being *Paratanytarsus austriacus*-type, *Heterotrissocladius marcidus*-type, *Eukiefferiella fittkaui*-type, *Tanytarsus lugens*-type, and *Diamesa* spp. Rheophilic and rheobiontic taxa, such as *Diamesa* spp. and *Eukiefferiella fittkaui*-type, constituted a substantial proportion of the assemblages, ranging from 5 to more than 25% in the individual samples (Figure 3). Regarding the feeding strategy, grazers/scrapers and collectors dominated the whole sediment sequence and did not show considerable changes over time. The proportion of predators, on the other hand, showed marked



dynamics ranging from 0 to 10% (Figure 4). Two Chironomidae assemblage zones (CHAZ I, II) and two sub-zones (CHAZ IA and IB) were identified based on community composition.

**Figure 2.** Age-depth model of the sediment sequence from VRP lake showing changes in <sup>210</sup>Pbuns and <sup>137</sup>Cs concentrations in the sediment core samples.



**Figure 3.** Relative abundances of the most common chironomid taxa (>5%), values of the taxonomic richness, and head capsule counts in the VRP sediment sequence. Colours denote: **a** taxa with relative abundance >10%, **b** taxa with relative abundance 5–10%, **b** thermophilic taxa, **b** number of taxa and number of head capsules.



**Figure 4.** Subfamilies and ecological groups of the chironomid fauna based on feeding habits and relationship to flow. Colours denote: subfamilies, food strategy, republic taxa.

# CHAZ IA (24.0-12.0 cm, ~1823-1946 CE)

The most abundant taxa for the zone CHAZ I were *Tanytarsus lugens*-type (29% on average), *Paratanytarsus austriacus*-type (21%), and *Heterotrissocladius marcidus*-type (18%). The tribe Tanytarsini slightly predominated over Orthocladiinae, while the proportion of Tanypodinae was negligible. In general, this zone had both the lowest taxonomic richness and the lowest proportion of rheophilic taxa compared to the other parts of the sequence.

In the sub-zone, *Heterotrissocladius marcidus*-type became dominant, while the proportion of *Tanytarsus lugens*-type slightly decreased. This trend is mirrored in the decline in Tanytarsini and in the increase in Orthocladiinae. Tanypodinae are almost entirely missing until the end of the sub-zone. The proportion of Diamesinae remained relatively high in the sub-zone and reached its maximum (~20%) at a depth of around 13 cm. The number of taxa and the proportion of rheophilic taxa varied significantly, especially between 15 and 12 cm.

# CHAZ IB (12.0-4.5 cm, ~1946-1996 CE)

While the dominating taxa remained the same, a considerable increase in taxonomic richness and head capsule counts marked the beginning of this sub-zone. The dominating subfamilies remained the same, but tanypod predators became stable, although not an abundant part of the assemblage. The proportion of taxa with large-sized larvae increased in this sub-zone.

### CHAZ II (4.5–0.0 cm, ~1996–2018 CE)

The decline in the proportion of *Tanytarsus lugens*-type and the decreasing trend of *Heterotrissocladius marcidus*-type, combined with the appearance of new thermophilic taxa (e.g., *Macropelopia* sp., *Tanytarsus mendax*-type), were characteristic for the last zone. Tanytarsini increased rapidly at the expense of Orthocladiinae, and Tanypodinae reached their maximum relative abundance in this zone. The proportion of large-bodied taxa also increased significantly. From the beginning of the zone, the proportion of grazers/scrapers showed an increasing trend, while that of the collectors decreased.

### 3.3. Cladocera Assemblages

In total, six Cladocera taxa belonging to two families were identified: Daphniidae and Chydoridae. The littoral taxa of the family Chydoridae dominated the species composition through the entire core. Based on assemblage composition and relative abundance, the cluster analysis distinguished two main Cladocera assemblage zones (CAZ I and CAZ II) and two sub-zones (CAZ IIA and CAZ IIB) (Figure 5).



**Figure 5.** Stratigraphy diagram of the absolute (ind./1 g of dry sediment) and relative (%) abundances of all Cladocera species recorded in the VRP sediment core. Colours represent: ■ pelagial taxa, ■ littoral taxa.

#### CAZ I (24.0-21.5 cm, ~1823-1889 CE)

The Cladocera assemblages were dominated by *Chydorus sphaericus*, with an average abundance of 56%, followed by another cold-tolerant species, *Alona affinis* (32% on average). The average share of pelagic taxa represented by the *Daphnia longispina* group constituted less than 7%. *Camptocercus rectirostris* and *Pleuroxus trigonellus* were also sporadically present. In general, the Cladocera concentration of the zone was extremely low, with a maximum of 551 individuals per g of dry sediment (d.s.) at a depth of 22 cm.

# CAZ IIA (21.5-10.5 cm, ~1889-1950 CE)

In this sub-zone, the ratio of *Chydorus sphaericus* gradually decreased (Figure 5), while that of *Alona affinis* increased (38% and 51% on average, respectively). At a depth of 15 cm, *Alona affinis* took over and became the dominating species of the sequence. *Camptocercus rectirostris* and *Pleuroxus trigonellus* were sporadically noted in the zone. The total Cladocera sum was still low, corresponding to an average of 641 ind/g d.s.

### CAZ IIB (10.5–0.0 cm, ~1950–2018 CE)

The most significant feature of the sub-zone was the dramatic increase in the total number of cladocerans to ca. 8800 ind/g d.s at a depth of 8 cm, while the average Cladocera abundance equalled 2433 ind/g d.s. From 4.5 cm to the top, *Alona affinis* constituted more than 75% (from 695 to 4657 ind/g d.s) of the total Cladocera abundance. During this period, the absolute abundance of the *Daphnia longispina* group increased, but its proportion within the assemblage did not change significantly since the abundance of *Alona affinis* (and to a lesser extent *Chydorus sphaericus*) also increased considerably. *Camptocercus rectirostris* and *Pleuroxus trigonellus* were sporadically observed, although both in higher numbers than previously. *Alona quadrangularis* was found in the sediment record (0–0.5 cm) for the first time.

# 3.4. Diatom Assemblages

A total of 110 diatom taxa were found in the sediment sequence. The relative abundance of 15 species was higher than 5% in at least one sample. Disregarding *Orthoseira roeseana* (a centric species, from which only two valves were recorded), the diatom composition consisted exclusively of pennate species, which were present through the sedimentation core. The most common and abundant diatoms in the assemblages were small fragilarioid forms, namely *Staurosira pseudoconstruens*, *S. venter*, *Staurosirella pinnata*, and *Pseudostaurosira parasitoides*. Two significant diatom assemblage zones were identified, with two sub-zones in each (Figure 6).



**Figure 6.** Diatom stratigraphy of the dominant taxa (>5%) in the VRP sediment core. Colours represent: **I** taxa with increasing relative abundance towards the sediment surface, **I** taxa with decreasing relative abundance towards the sediment surface, **I** other species.

# DAZ IA (24.0-22.0 cm, ~1823-1885 CE)

The Achnanthidium minutissimum complex (14%), together with small fragilarioid taxa, such as Staurosirella pinnata (up to 15%), Staurosira venter (up to 9%), and Staurosira pseudoconstrues (8%), dominated in this sub-zone. Species such as Tryblionella angustata, Sellaphora mutatoides, Psammothidium subatomoides, Encyonema minutum, Karayevia suchlandtii, Psammothidium lacus-vulcani, and Skabitschewskia oestrupii were present in very low amounts and together accounted for 0.8% of the total abundance.

### DAZ IB (22.0–10.0 cm, ~1885–1952 CE)

As with the previous sub-zone, the assemblage was dominated by the *Achnanthidium minutissimum* complex (representing 11 to 16% of the total abundance). Small taxa such as *Staurosirella pinnata* (12%), *Staurosira venter* (9%), *Staurosira pseudoconstruens* (8%), and *Pseudostaurosira parasitoides* (8%) were also important components of the diatom assemblage. At the end of this zone, the proportion of the benthic monoraphid species *Karayevia suchlandtii* started to increase gradually (from 2 to 13%). *Encyonema ventricosum, Psammothidium lacus-vulcani,* and *Amphora pediculus* were also recorded (together comprising up to approximately 6% of the total abundance). *Tryblionella angustata, Encyonema minutum, Fragilaria pararumpens, Skabitschewskia oestrupii, Psammothidium subatomoides,* and *Sellaphora mutatoides* occurred as minor components of the diatom flora (with a less than 5% share in the samples).

# DAZ IIA (10.0-6.0 cm, ~1952-1986 CE)

This zone represents the period of the greatest change in the diatom assemblage and is delineated by the marked increase in the proportion of benthic monoraphiod species such as *Karayevia suchlandii* (max. relative abundance 19%) and *Skabitschewskia oestrupii* (11%). At the same time, the proportion of *Staurosirella pinnata* and *Staurosira parasitoides* started to decline gradually. The *Achnanthidium minutissimum* complex and *Staurosira pseudoconstruens* remained a stable part of the assemblage.

# DAZ IIB (6.0-0.0 cm, ~1986-2018 CE)

In this sub-zone, *Karayevia suchladtii* and *Skabitschewskia oestrupii* became the dominant species (with up to 19% each), together with the *Achnanthidium minutissimum* complex (16%), which slightly declined at the end of the sequence to 9%. In the uppermost 5 cm of the sediment, the share of *Staurosira pseudoconstruens* increased significantly. In contrast, the relative abundances of *Pseudostaurosira parasitoides* and *Staurosirella pinnata* were considerably lower compared to the bottom part of the sediment sequence.

### 4. Discussion

The timings of the pronounced changes documented in the biological proxies coincide throughout the sedimentary record, showing two main lake-development stages over the last 200 years (Figure 7), with the main borderline at 10.0–12.0 cm, corresponding with ~1950 CE.



**Figure 7.** Comparison of the full community response of cladocerans, diatoms, and chironomids, expressed as DCA 1st axis scores.

Even though the first well-documented, large-scale historical fish stocking in the Slovak Tatra Mts. took place at the end of the 19th century [36], the assemblage composition

of chironomids and cladocerans does not indicate significant change at that time, suggesting that fish could have been released into VRP lake earlier. The first mention of the common introduction of brown trout and alpine bullhead into the lakes in the valley adjacent to Račkova dolina valley comes from the end of the 18th century [35]. It is likely that VRP lake, together with the other lakes in the Western Tatra Mts., was subject to fish introduction at the same time; hence, the analysed sedimentary record (starting with 1823 CE) does not capture the period with fishless conditions. Thus, we assume that the composition of the chironomid and cladoceran assemblages in the older part of the sediment sequence already reflects the combined predatory pressure of brown trout and alpine bullhead. Overall, the two mentioned species have similar diets with respect to benthic prey, both being visual predators [70,71], which select the larger and heavier prey items. However, the brown trout is more opportunistic and feeds on zooplankton, drifting invertebrates, chironomid pupae in the water column, and insects that have fallen onto the water surface [72,73].

The significant effects of fish on the structure and dynamics of zooplankton communities are well known [74–77] and include, among others, the decrease in density and body size of individuals [75,78] and, consequently, the increase in the proportion of small-sized species [79]. The extremely low concentration of cladocerans, the dominance of smallbodied chydorids, and the low share of the *Daphnia longispina* group suggest a strong effect of brown trout. *Chydorus sphaericus* and *Alona affinis* are the most common and abundant littoral cladocerans in the Tatra Mts. Both species enter the pelagic zone regularly [80,81], where they can be exposed to the predation pressure of brown trout. The few studies on the trout diet in the Tatra Mts. showed that the species mainly utilised zooplankton, especially *Cyclops abyssorum*, and emerging chironomid pupae were the second most important food item [41]. The alpine bullhead is a poor swimmer; therefore, its ability to catch zooplankton in the water column is limited [82]. However, it can prey on small zooplankton species living on or among sediment particles [83].

The *Daphnia longispina* group has evidently survived fish predation in VRP lake, albeit in low abundance. There is evidence of the co-existence of large-bodied species such as *Daphnia "pulicaria"*, with the fish in both the lakes with a native brown trout population and those stocked with brook trout and brown trout, respectively [14]. One explanation could be that *Daphnia* can occupy a refuge in the deeper parts of lakes with low light intensity [84] and may therefore be unavailable for the brown trout, which requires a certain amount of light for optimal foraging and thus hunts near the surface [70]. Another possible explanation is that the population of brook trout was never abundant enough to eliminate its prey; in addition, the dormant eggs of *Daphnia* could survive the passage through the fish digestive system [85], allowing the population to regenerate. This peculiar survival mechanism was first described in the Tatra Mts. for *Cyclops abyssorum* [37].

The majority of studies on the diet of salmonids and sculpins living in sympatry have been conducted in flowing waters [86], and only a few works deal with lakes [83]. In streams, both species consume a number of invertebrate taxa, the most important being the larvae of aquatic insects (above all, Chironomidae, Trichoptera, Ephemeroptera, Plecoptera, and Simuliidae) and crustaceans (*Gammarus*) [72,86,87]. Even though both species are strongly size-selective predators, preferring the largest prey available [88], chironomid larvae can constitute a substantial part of the diet for their small (juvenile) specimens [73].

The composition of the subfossil chironomid assemblage of VRP lake corresponds to the modern chironomid fauna of the alpine Tatra lakes situated below 2000 m a.s.l. [89], while a relatively high proportion of rheophilic taxa (*Diamesa* spp. and *Eukiefferiella fittkaui*-type) is most likely related to a strong inflow [90]. The subfossil chironomid assemblages in the VRP sediment sequence do not show any compositional changes associated with the presence of fish, with the exception of an apparently low proportion or absence of the Tanypodinae subfamily. Tanypodinae larvae are large and free-living and as such are more sensitive to fish predation than the larvae of tube-building or burrowing species [91,92]. We assume that the decline in the proportion of large Tanypodinae was caused by the alpine

bullhead, which, unlike the brown trout, selectively chooses larger and heavier food items, also among chironomid larvae [72].

Chironomids are an important, but certainly not the only, insect group of the littoral macroinvertebrate fauna of alpine lakes. The large larvae of Ephemeroptera, Plecoptera, and Trichoptera, which are abundant in the oxygen-rich, stony littoral of the Tatra lakes [15], are attractive prey for fish, and they respond to fish predation promptly. Even though historical data on the mentioned groups are scarce, studies from 1981 to 1985 and 2000 [15,93] show a destructive effect on benthic macroinvertebrates in all the Tatra lakes populated with alpine bullhead. The littoral communities of those lakes consist only of oligochaetes and chironomids, in contrast to the comparatively fishless Tatra lakes with littoral communities rich in Trichoptera, Plecoptera, and Ephemeroptera. Thus, chironomid remains preserved in the sediment sequence provide only partial information on the overall fish impact on the benthic fauna.

The establishment of the Tatra National Park in 1948 led gradually to the limitation of human activities in the Tatra Mts., particularly those of livestock grazing, logging, and mineral raw material exploitation, and at the same time, the protection of species and ecosystems became stricter [36]. By the 1950s, all the above activities ceased, and we assume that the same thing happened with fish stocking, which is confirmed by the changes in the cladoceran assemblages (and partially in chironomids) that indicate lower fish predation pressure at that time. A sudden and significant increase in the total number of cladocerans and the absolute abundance of the *Daphnia longispina* group indicate the extirpation of trout. Although adapted to harsh conditions of the mountain streams, the population of brown trout suffered from extreme lake conditions (low temperature, long ice-cover periods, low ionic concentrations, and low productivity) at the edge of its ecological limits. The rare studies on the native and introduced trout population in the Tatra lakes [41,94] reported slow growth and starvation as a result of a lack of food in an unproductive environment and intraspecific competition.

Moreover, interspecific competition has to be taken into account. Alpine bullhead and brown trout have similar requirements for space and food, and living in sympatry, they can be potential competitors [73]. Previous studies have shown variable outcomes of the competitive interactions between sculpins and salmonids [73,86]. The extinction of brown trout in all the Tatra lakes where it was stocked together with alpine bullhead (not only in VRP lake) indicates that brown trout could suffer from competition with alpine bullhead as a superior competitor. It can be assumed that after brown trout went extinct, alpine bullhead expanded its diet with other benthic organisms and therefore reduced the predation pressure on large Tanypodinae larvae, whose proportion increased.

We assume that both fish populations were maintained in the lake by repeated stockings. In this context, the occurrence of two cladoceran species is worth noticing. *Camptocercus rectirostris* and *Pleuroxus trigonellus* mainly occupy water bodies situated up to 500 m a.s.l. [95] and are not common in the Tatra lakes [81]. We assume that these two species were released unintentionally into VRP lake together with the introduced fish. In an alpine lake such as VRP, they existed under suboptimal conditions, and after some time, their populations declined and even disappeared, as we have seen in the sediment record.

We are aware that, in addition to fish introduction, the lake was under the influence of the complex interactions of different environmental stressors operating on regional or global levels. While changes in the assemblage composition of cladocerans and partly in that of chironomids could be ascribed to fish manipulations in VRP lake, that of diatoms, owing to their complex and mainly indirect response to fish, may reflect other environmental stressors.

The diatom assemblages of VRP lake were composed mainly of small benthic forms during the whole studied period, which can be connected to the requirement of planktic species for stratification of the water column to maintain their position in the photic zone [96]. VRP lake has a strong inlet influence that induces water currents and, in turn, weakens stratification. The significant effect of the inlet in the past was confirmed by the high proportion of rheobiontic/rheophilic chironomid taxa.

The most remarkable change in the assemblage structure appeared in the 1950s, simultaneously with the subfossil cladocerans and chironomids, when *Skabitschewskia oestrupii* and *Karayevia suchlandtii* became dominant at the expense of the fragilarioid species, mainly *Staurosira* spp., *Staurosirella* sp., *Pseudostaurosira parasitoides*, and *Fragilaria pararumpens*, which declined. Small fragilarioids are considered r-strategists, with the ability to tolerate and proliferate in cold environmental conditions and to resist changes in the littoral habitats [97]. We assume that their predominance could also be related to low light requirements and thus their ability to compete well in lakes with low light penetration, such as those associated with ice cover and minerogenic turbidity [96–98]. For example, *P. parasitoides* in lake Rappensee apparently increased in abundance under conditions of enriched nutrient supply and turbidity [98].

The supply of allogenic material with nutrient loads leading to a decrease in water transparency could be related to former livestock grazing that enhanced soil erosion in the lake basin and caused the erosion of its banks. The valley of VRP lake was intensively used as pastureland since the Middle Ages [99], and its alpine zone still bears visible traces of grazing (removed dwarf pine and the presence of nitrophilous plants, see (Table 1)). The definitive cessation of grazing in the second half of the 1950s could have resulted in an improvement in the light conditions in the lake. This assumption is supported by an increase in the proportion of *Karayevia suchlandtii* after ~1950. The species requires a sunlit lake floor [100], and it was restricted during the period of lower water transparency [101]. The better light penetration could also lead to higher benthic production, resulting in the higher proportion of benthic cladocerans. However, we acknowledge that the same effect could have been caused by additional climate-related factors, e.g., a shorter ice-cover period.

The sudden steep increase in the small lightly silicified species Skabitschewskia oestrupii in the 1950s, which is associated with a lower nutrient content [102], indicates oligomesotrophic conditions. In general, the taxonomic composition of this younger sediment section with the domination of low-profile life forms [103] compared to the bottom section points to the decreasing nutrient level of the lake. Lower nutrient input and decreased turbidity may be related to the decline in fish population and the termination of grazing in the catchment. However, this relationship may not be straightforward. Diatom trends observed in the sedimentary record from the remote mountain lakes of the Northern Hemisphere [9,104–107] seem to reflect general changes in the thermal stratification of lakes as well as atmospheric deposition (mainly reactive nitrogen) [105]. However, admittedly, these changes can be clearly followed in planktic or planktic/benthic ratio alterations rather than the species compositions in benthic diatom assemblages. Skabitschewskia oestrupii is a good example in that some algal changes began ca. 1900 but shifts in most of the sedimentary proxies accelerated ca. 1950, corresponding to many human-caused changes in the Earth's system. A very similar abundance pattern of Skabitschewskia oestrupii to that of VRP lake was observed in Svalbard, where it shows higher percentages from ~1950 onwards and profoundly increases from ~1995 onwards [102]. Climate-driven ecological change has occurred in recent years, regardless of the exact locality or the remoteness of the records or the depth of the lakes.

Indeed, temperature is one of the key variables directly controlling the life histories of aquatic organisms, such as chironomids, and indirectly affecting the abiotic properties of water bodies [108]. Lakes have responded rapidly to the abrupt climate warming in the late 1980s [109], triggered by anthropogenic and natural forces [110]. Warming was especially relevant in the alpine regions where the temperature rose to an unprecedented level [111]. In the Tatra Mts., a particularly steep rise in air temperature, which was evident from 1980 onwards, had a dominating effect on the chironomid communities of the alpine lakes [20]. In the VRP sediment record, the onset of this warming is indicated by the decline in the proportion of cold-stenothermal taxa, such as *Tanytarus lugens*-type and

*Heterotrissocladius marcidus* in the 1980s and later by the appearance of the thermally less restricted *Macropelopia* sp. and *Tanytarsus mendax*-type. In the Tatra training-set, *Tanytarus lugens*-type and *Heterotrissocladius marcidus* belong to the cold end of the gradient while *Tanytarsus mendax*-type and *Macropelopia* sp. have higher temperature optima of 0.5–0.8 °C, respectively (own unpublished data). The appearance of *Macropelopia* at the beginning of the 21st century in alpine lakes, where it had not been recorded in the past (unpublished data), can be considered an upward shift of the distribution ranges induced by climate warming, which has been frequently reported in the terrestrial environment [112] and less often in aquatic ecosystems [20].

As mentioned earlier, the influence of temperature on the chironomid assemblage structure may be indirect, through climate-induced changes in the physical and chemical properties of lakes. Over the last decades, the proportion of Orthocladiinae has decreased (this has been especially visible with regard to *Heterotrissocladius marcidus*), while that of Tanytarsini has increased. According to [113], the driving force behind chironomid community changes in the Holarctic lakes is the interplay between mineral sediment accumulation and the availability of organic food resources rather than direct temperature change. The decline in *Hetrerotrissocladius marcidus* (and orthoclads in general) may have been the result of the change of mineral habitats into soft sediments. While soft sediments with a high amount of organic matter suit Chironominae, hard substrates are favoured by orthoclads, e.g., *H. marcidus* [114]. As the amount of organic matter in substrates increases, the larvae of *Heterotrissocladius* can no longer compete and are replaced by species that require soft bottom sediments and readily accessible food resources [113].

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