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Late Holocene evolution of a dystrophic Tatra Lake: natural trophic changes revealed by multi-proxy data

Elwira Sienkiewicz[1*], Karolina Kaucha[1], Michał Gąsiorowski[1], Urszula Kowalewska[1], Michał Słowiński[2]

[1]Institute of Geological Sciences, Polish Academy of Sciences, Research Centre at Warsaw, St. Twarda 51/55, Warsaw, PL-00818, Poland

[2]Institute of Geography and Spatial Organization, Polish Academy of Sciences, Department of Past Landscape Dynamics, St. Twarda 51/55, 00-818 Warsaw, PL-00818, Poland

*Corresponding author.

E-mail addresses: esienkie@twarda.pan.pl **(E. Sienkiewicz),** k.kaucha@twarda.pan.pl (K. Kaucha), mgasior@twarda.pan.pl **(M. Gąsiorowski),** urszciolko@twarda.pan.pl **(U. Kowalewska), michal.slowinski@igipz.pan.pl (M. Słowiński).**

Abstract

Dystrophic lakes, characterized by dark-colored water, low transparency, and low pH, are relatively common in the mountainous and lowland regions of temperate and boreal zones. The occurrence of dystrophic conditions depends on hydrological, climatic, and biological factors, including surface and groundwater inflows and outflows, precipitation, air temperature, and vegetation within the lake's catchment. A change in any of these factors can lead to either an increase or a decrease in the degree of lake dystrophy. In this study, we present changes in the trophic status of a small forest lake located in the lower part of the Tatra Mountains (1,089 m a.s.l.; Western Carpathians, Poland). The lake is located within the Tatra National Park, and its natural dystrophic character is one of the features protected under the park's conservation objectives. We aimed to determine whether these dystrophic conditions are of natural origin and have persisted over a long period. To investigate this, we analysed a 1.4-m sediment core spanning the last 3,150 years using a range of geochemical and paleobiological methods, including elemental analysis, stable carbon and nitrogen isotope analyses, and analyses of diatom and Cladocera assemblages. Changes in the species composition of diatoms and Cladocera indicate that dystrophic conditions did not persist throughout the entire study period. The lake was dominated by species characteristic of meso-oligotrophic and oligotrophic water bodies, with only a brief period during which species indicative of dystrophic conditions appeared, coinciding with a low-water phase around

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2700–2350 cal. yr BP. Permanent dystrophic conditions became established no earlier than approximately 950 cal. yr BP, which is relatively late compared with many lowland lakes.

Keywords: trophic level, phyto- and zooplankton, dystrophic mountain lake, Holocene

1 Introduction

Dystrophic lakes, classified as humic or brown, are typically small water bodies found in mountain and boreal regions with relatively cold, humid climates (Kankaala et al., 2006; Górniak, 2017). They are characterized by a high amount of dissolved organic matter, including humic substances, together with decomposing organic matter, which cause low transparency and a brown coloration of the water. Many of them have transformed into peat bogs or have disappeared (Zawisza et al., 2019). Allochthonous organic matter from surrounding peat bogs and forests is hardly biodegradable and strongly affects water chemistry and optical properties. Dystrophication is the process of reducing the amount of nutrients available to organisms in a given ecosystem, in contrast to eutrophication. However, despite low nutrient availability, phytoplankton biomass may occasionally be relatively high, particularly where mixotrophic taxa, which can use both photosynthesis and other sources of organic carbon for growth and metabolic processes, are abundant. (Karpowicz et al., 2026). Their dual strategy allows them to adapt to fluctuating environmental conditions. Mixotrophic organisms are primarily represented by chrysophytes (Chrysophyceae), dinoflagellates (Dinophyceae), euglenoids (Euglenophyceae), and cryptophytes (Cryptophyceae), which combine photosynthetic and heterotrophic modes of nutrition. In addition, some diatoms can utilize bacterial resources present in organic-rich waters, allowing them to persist under conditions that generally limit primary productivity. For some algae, mixotrophy can be a source of essential nutrients and vitamins. The phenomenon of mixotrophy enables the survival and growth of algae at great depths in humic lakes with poor light conditions and under ice during winter (Jansson, 1998). However, in diatoms, only a limited number of species have been tested for mixotrophic metabolism, and further research is required to better understand how widely this process is conserved across the group (Villanova and Spetea, 2021).

Progressive dystrophy can be triggered by climate or/and changes in local geochemistry. Dystrophication involves a shift from autochthonous, labile organic matter to predominantly allochthonous, humic, and poorly bioavailable organic matter, thereby altering light

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conditions and nutrient availability rather than increasing primary productivity. Based on aerial photos and the latest orthophoto maps many humic lakes existed in the Tatra Mountains in the past (Kapusta et al., 2018; Bitušík et al., 2024). An example of a dystrophic Tatra's lake is Toporowy Staw Niżni (TSN). At present, among the permanent lakes located in the Polish part of the Tatra Mountains, there are only two other dystrophic lakes, namely Toporowy Staw Wyżni and Smreczyński Staw (Skierski, 1984; Gąsiorowski and Sienkiewicz, 2010a). Due to their unique character and sensitivity to environmental disturbances, they are formally protected by international law (EU Habitats Directive, Anonymous 2013). Currently, dystrophic lakes in Tatra Mountains are at various stages of terrestrialization (Bitušík et al., 2024). This process is accompanied by the expansion of sedge communities and the progressive infilling of the lake basin. In the case of the TSN study, the results showed that between 1955 and 2015 the lake became overgrown over 9.9% (i.e., 501.6 m^2) of its surface area (Kapusta et al., 2018; 2021).

In this study, we present the development of a humic lake located in the Polish part of the Tatra Mountains over the last 3000 years using paleobiological (diatoms and Cladocera remains) and geochemical (elemental and isotopic data) analyses. The primary focus of this study was to assess changes in the trophic status of TSN, to examine how phyto- and zooplankton changed over the last 3000 years, and to reconstruct the evolution of the lake not only in terms of trophic changes, but also in water pH. The lake is located within a strictly protected area, which provides an opportunity to observe natural transitions between trophic states in the absence of direct anthropogenic influence. We also have the opportunity to determine whether its present state results from natural lake development processes or whether the lake has exhibited dystrophic characteristics since its origin. Such conditions may occur when a lake forms within a peatland-dominated, organic-rich catchment and receives substantial inputs of dissolved organic matter and humic substances from the earliest stages of its development. Although the functioning and long-term evolution of lowland dystrophic lakes have been investigated, including lakes in northeastern Poland (Zawisza et al., 2016, 2019; Mirosław-Grabowska et al., 2020; Karpowicz et al., 2026), Scandinavia (Huttunen et al., 1978; Luoto et al., 2012), as well as Canada (Lacoul et al., 2011; Korosi and Smol, 2022), comparable studies from mountain environments remain exceptionally rare (Bitušík et al., 2024). Consequently, it is still unclear whether the mechanisms driving dystrophication and ecological succession in mountain lakes are similar to those described for lowland systems.

2 Study site

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Toporowy Staw Niżni (TSN) is the lowest-lying lake (1089 m a.s.l.) in the Polish part of the Tatra Mountains (Fig. 1). It is located in the Sucha Woda Valley (49.2835806 N, 20.0305586 E), below the modern tree line, in the lower montane forest belt, which in the Tatra Mountains generally extends from ca. 650 to 1200–1250 m a.s.l. However, the closest surroundings of the Toporowe Lakes do not represent pristine lower-montane beech-fir forest. Instead, they are characterized by wetland and waterlogged habitats, including fens, peatlands and also spruce forest. Therefore, the general description of the lower montane belt should be treated only as a broad altitudinal and vegetation background, whereas the functioning of the Toporowe Lakes complex is more directly controlled by wetland, peatland and spruce-forest communities. TSN covers an area of 0.62 ha with a maximum depth of 5.7 m (Kopáček et al. 2006). The lake's basin was formed on a terminal moraine deposited (Fig.) during deglaciation after the last glacial maximum (Makos et al. 2018), but the lake itself is probably much younger and was formed after sealing of the lakes basin. In the Tatra Mountains, the vast majority of lakes are oligotrophic, whereas TSN is classified as a dystrophic (humic) water body. Currently, TSN it is a fishless forest lake surrounded by peat bogs, the shores of which are gradually disappearing due to the growing marsh plants. Floating mats cover more than one quarter part of lake surface. Rare plant species in the Carpathians occur around the lake, including Marsh Labrador (*Rhododendron tomentosum*), Issler's clubmoss (*Diphasiastrum issleri*), and closely related bur-reed (*Sparganium erectum*) (Mirek and Piękoś-Mirek, 2008).

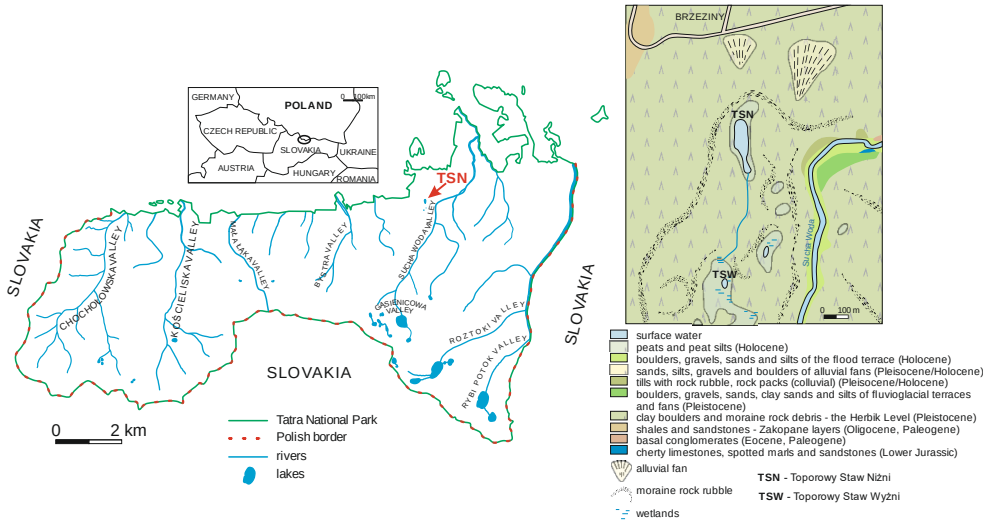

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Fig. 1. Location and geological setting of TSN lake. The geological data are based on the Detailed Geological Map of the Tatra Mountains at a scale of 1: 10 000, Zakopane – Toporowa Cyrhla sheet (Piotrowska, 2008).

3 Materials and methods

3.1 Sediment sampling and field work

Sediments from TSN were collected twice from the deepest site of the lake. The first core (50 cm in length) was taken in 2003 using a Kajak-type gravity corer. The second core (100 cm in length) was collected in 2018 using a Russian corer. Both cores were correlated based on radiocarbon dating and elemental and isotopic analysis. The sediments were transported to the Polish Academy of Sciences (Warsaw, Poland) in plastic tubes in cool conditions. Then, they were divided every 1 cm for individual analyses (dating, paleobiological, isotopic, geochemical and elemental).

3.2 Dating methods

Core chronology based on ^{210}Pb analysis (the upper 30 cm) and radiocarbon measurements. The radiocarbon analysis was performed in the Beta Analytic and in the Poznań Radiocarbon Laboratory with a 1.5 SDH-Pelletron Compact Carbon AMS instrument (National Electrostatics Corporation) from terrestrial macrofossils picked up from the sediment. Conventional radiocarbon dates were calibrated using OxCal ver. 4.4 software (Bronk Ramsey 2009) and the IntCal20 calibration curve (Reimer et al. 2020).

The ^{210}Pb activity was measured indirectly by determining the activity of its daughter radioisotope, polonium ^{210}Po (α = 5.31 MeV, T1/2 = 138 days), assuming isotopic equilibrium between them. Before chemical separation of polonium from the sample (0.1-0.5 g of dry sediment), known amounts of ^{208}Po and ^{209}Po (α = 5.11 MeV and 4.88 MeV, respectively) were added as an internal yield tracers. Polonium was separated from the sample using concentrated hydrochloric and nitric acids, and 30 wt% hydrogen peroxide was used to eliminate organic matter. Then, the polonium was deposited onto silver disks (Flynn, 1968). The activities of ^{210}Po, ^{209}Po, and ^{208}Po were measured using an alpha spectrometer (DUO by EG&G ORTEC) and were corrected for background measurements. Pb-210 ages were calculated using unsupported ^{210}Pb activities applying constant rate of supply (CRS) model (Appleby, 2001).

The age-depth model was calculated using MOD-AGE algorithm (Hercman and Pawlak, 2012). MOD-AGE uses the randomization method (a type of Monte Carlo simulation) for

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age-depth–model construction applying normal distribution of lead-210 dates and real distribution of radiocarbon dates. The age-depth function and its confidence bands were fitted with Locally Estimated Scatterplot Smoothing (LOESS) technique (Cleveland and Devlin, 1988).

3.3 Elemental and isotopic (C, N) analyses

Percent amount of carbon and nitrogen was determined using Vario MicroCUBE elemental analyzer. Samples (8-10 mg of dried and homogenized sediment) were wrapped in tin capsules and combusted at 1150° C. Released gases (CO_2, N_2, H_2O and SO_2) were separated in GC column and determined by thermal conductivity detector. Percent amount values are normalized by sulfanilic acid standard. The reference standard NCS DC 73016a was measured with each batch of samples. Measurement results are reported as wt%. Measurement precision (1σ) was 0.6 % and 0.18 % for C and N, respectively.

Stable isotopic composition of carbon and nitrogen was determined using elemental analyzer Thermo Flash EA 1112HT coupled to a Thermo Delta V Advantage isotope ratio mass spectrometer in Continuous Flow system. Samples wrapped in tin capsules were combusted at 1020°C. Released gases (CO_2 and N_2) split in a GC column went to MS source through a capillary. Isotope ratios were reported as delta (δ) and expressed relative to V-PDB for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$. Delta values were normalized by calibration curve based on international standards USGS 40, USGS 41, IAEA 600. Measurement precision (1σ) was 0.12‰ and 0.27‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

3.4 Diatom analysis

Slides for diatom analysis were prepared following the standard procedure (Battarbee 1986). Sediment samples of $1cm^3$ were heated with 30% hydrogen peroxide (H_2O_2) to oxidize the organic matter, washed three times with distilled water and diluted to 15-80 ml. Finally, the suspension obtained was transported to coverslips, and after evaporation mounted with Naphrax® (R.I. = 1.75). Diatom valves were examined under an Olympus BX40 and Nikon Eclipse E600 light microscope with a ×100 oil immersion objective. Diatoms were counted until 400 diatom valves were enumerated. For samples with low concentration of diatoms, at least 200 valves were counted. Taxa were identified to the species level based on Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b), Lange-Bertalot and Metzeltin (1996), Krammer (2000) and Lange-Bertalot et al. (2017). The diatom assemblage zones (DAZ) were defined based on a clustering analysis powered by riojaPlot 1.03 using the broken-stick model

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(Juggings, 2023). Names of diatom species were updated according to the AlgaeBase (Guiry and Guiry, 2022). An estimation of the trophic state of the lake was performed by calculating the frequency of diatom-based trophic state categories. The ecological preferences of the diatoms were based on Lowe (1974), van Dam et al. (1994), Kwandrans and Eloranta (2005) and Lange-Bertalot et al. (2017).

3.4.1 Diatom-inferred pH reconstruction (DI-pH)

The reconstruction of the diatom-inferred pH (DI-pH) was performed using the POL_SLOV training set, which include contemporary samples of sediments taken from 33 lakes located in the Tatra Mts. (Western Carpathians) from the Polish side (11 lakes) and Slovakian side (22 lakes) (Sienkiewicz et al., 2021). The analysis was carried out in the C2 software version 1.8 (Juggins, 2001). Identified species have been harmonized against the POL_SLOV database. Some taxa have been grouped together, e.g., *Eunotia incisa* and *Eunotia boreoalpina* have been merged into the *Eunotia incisa* group. The best values of the pH were obtained using the weighted averaging model with inverse deshrinking (WA_Inv). The cross-validated root mean square error for the training set (RMSE) was 0.16 pH unit and the coefficient of correlation (R2) reached value 0.94.

3.5 Cladocera analysis

The Cladocera species composition was determined according to standard methodology for soft freshwater sediments (Korhola and Rautio, 2001). The 1 cm^3 of wet sediment samples were heated and stirred in 8% KOH on a hot plate for approximately 30 minutes and sieved through a 33-µm mesh screen. The sieved material was stored in 10 mL of distilled water. Temporary slides, each prepared from a 0.1 mL of a sample, were used for identification and to count the cladoceran remains. The slides were prepared for examination under a light microscope at magnifications of 100–400x until a minimum of 200 remains were encountered and identified following Szeroczyńska and Sarmaja-Korjonen (2007). *Chydorus sphaericus* was considered *C. sphaericus* sensu lato (s.l.) (Frey, 1986). Cladocera percentage abundances were calculated from the sum of individuals. The most abundant body part was chosen for each taxon to represent the number of individuals. The relative abundance diagram was drawn with POLPAL software. The diagram zonation was performer with riojaPlot 1.03 package in R software (Juggings, 2023) with broken-stick model as evaluation of the zone number. Changes in Cladocera assemblage were tracked with variation in principal component analysis (PCA). PCA was run on log-transformed relative abundance of species data.

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4 Results

4.1 Chronology

Seven samples of terrestrial macrofossils, mostly leaf of *Picea*, was dated with radiocarbon method (Table 1). The obtained dates were in stratigraphic order and all were included into the age-depth model.

Table 1. Radiocarbon dating

Sample name	Lab. number	Dated material	Depth in profile (cm)	^{14}C date BP	Calibrated date (95.4% probability) cal BP	Modelled μ (BP)	Modelled range (BP)
TSN 34	Poz-20066	Leaf *Picea*	33-34	85 ± 30	262 (26.1%) 220 143 (69.3%) 26	241	260-218
TSN1_6	Beta-649247	Leaf *Picea*	45-46	760 ± 30	728 (95.4%) 665	686	726-661
TSN1 46	Poz-155236	Leaf *Picea*	85-86	1510 ± 30	1511 (2.4%) 1494 1473 (3.6%) 1454 1417 (89.5%) 1310	1415	1518-1346
TSN2 10	Poz-155838	Leaf *Picea*	99-100	1950 ± 30	1986 (4.1%) 1962 1947 (87.4%) 1818 1811 (2.7%) 1791 1761 (1.4%) 1750	1785	1860-1735
TSN2 21	Poz-155228	Leaf *Picea*	110-111	1920 ± 30	1925 (95.4%) 1740	1937	1993-1866
TSN2 42	Poz-155381	*Carex*	131-132	2760 ± 30	2939 (95.4%) 2775	2842	2929-2775
TSN2 50	Poz-106991	*Carex*	139-140	3010 ± 30	3355 (15.1%) 3288 3265 (75.9%) 3106 3096 (4.5%) 3076	3076	3255-3007

The total specific activity of ^{210}Pb varied between 858 ± 23 Bq kg^{-1} at 3 cm and 11±1 Bq kg^{-1} at 50 cm and decreased with depth in the sediment column. The supported ^{210}Pb activity was calculated from the activity of the lowest measured samples and was 16±7 Bq kg^{-1}.

The age depth model was based on radiocarbon and ^{210}Pb dates. It used real probability distributions of ^{14}C dates and ^{210}Pb dates were assumed to be normal distribution of ages. The youngest radiocarbon date (TSN 34; 2σ age range 262 (26.1%) 220 cal. BP, 143 (69.3%) 26 cal. BP) was in good agreement with dates extrapolated for this depth (34 cm) from CRS model based only on ^{210}Pb activities (2σ age range 245-175 BP). The age–depth model (Fig. 2) indicates that sediment accumulation of studied core occurred during the last 3,150 years. The mean sedimentation rate was 0.04 cm yr^{-1} and changed from ~0.02 cm yr^{-1} in lower and middle portion of the core to over 0.25 cm yr^{-1} during the last 100 years.

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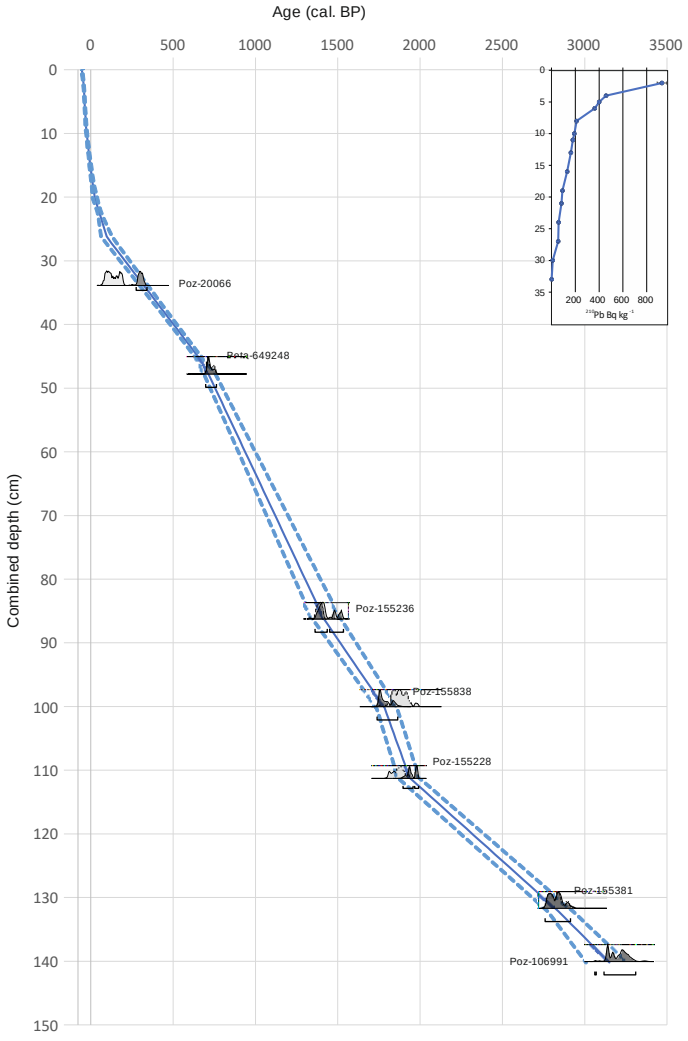

Fig. 2. Age-depth model (solid line) with its 2σ confidence bands (dashed lines) for TSN collected in 2018. Insert figure: ^{210}Pb total specific activity (Bq kg^{-1}) of the core collected in 2003.

4.2 Stable isotopic data ($\delta^{13}C$ and $\delta^{15}N$) and elemental analyses (TOC, TON, C/N)

The amount of total organic carbon (%TOC) fluctuated between 31 and 52 %, whereas the total nitrogen (%TN), was relatively stable thought the core and ranged from 1.5 to 3 %. The C/N ratio was between 14 and 24, with decreasing trends toward sediment surface (the lowest values in the youngest sediments).

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The values of $\delta^{13}C$ ranged between -31.41 and -27.22 ‰, , whereas $\delta^{15}N$ varied from -1.27 to +1.88 ‰, (Fig. 3). The highest decrease in carbon stable isotope was observed at depth of 129 cm. The highest value of $\delta^{15}N$ was in the lower portion of lake sediments and it was at depths of 131-133 cm.

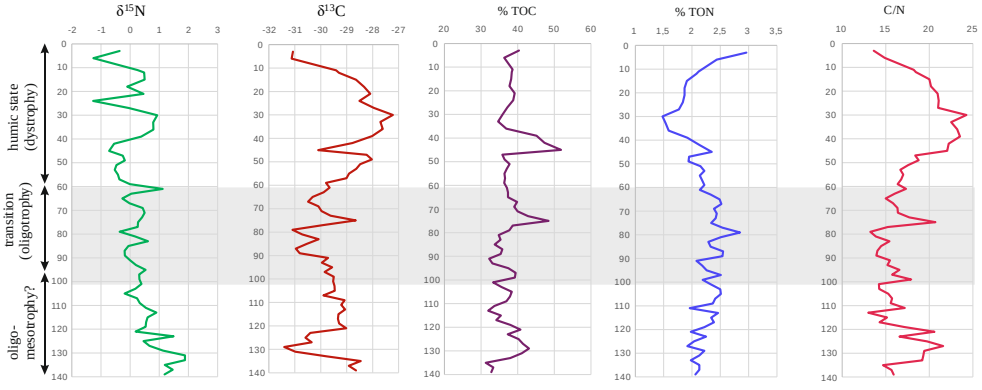

Fig. 3. Elemental and isotopic data for TSN including $\delta^{15}N$, $\delta^{13}C$, % TOC, % TON and C/N ratio.

4.3 Diatom stratigraphy

A total of 126 diatom species belonging to 36 genera were identified. In the sediments of the TSN lake, four diatom zones were distinguished. The most abundant taxa were *Pinnularia microstauron* (Ehr.) Cleve, *Staurosira construens* var. *venter* (Ehr.) P.B.Hamilton, *Encyonema hebridicum* Grunow ex Cleve and *Tabellaria flocculosa* (Roth) Kützing in the upper part of the core (Fig. 4A). According to trophic preferences, the lower part of the core is dominated by oligo- to eutrophic diatom taxa, whereas the middle part is characterized by the occurrence of oligotrophic diatoms. An increase in dystrophic taxa is observed in the upper part of the core. In general, relatively large changes occurred in the diatom assemblage. The values of axis 1 (PCA analysis) varied between -1.28 and 1.73.

DAZ 1 (140-100.5 cm, 3150-1791 cal. BP)

This zone is characterized by a low frequency and species diversity. The assemblage was dominated by *Staurosira construens* var. *venter*, which accounts around 80%. *Gomphonema brebissonii* Kützing was detected, which rapidly increased to 18% at the lower part of the zone and was never recorded in the core afterwards. The frequency of *Encyonema hebridicum* gradually increased (up to almost 30%) in the upper part of the zone. A large portion of damaged diatoms were found. In the middle part of the zone diatom valves were extremely crumbled, which resulted in the impossibility of counting the minimum number of diatoms for

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quantitative analysis. Towards the end of the zone, the number of diatoms decreased to 200 counts and only in one sample managed to count up to 400 valves (133 cm).

DAZ 2 (100.5-60.5 cm, 1791-950 cal. BP)

In this zone species such *Encyonema hebridicum* and *Pinnularia microstauron* were mainly present. Compared with the previous zone, *Staurosira construens* var. *venter* decreased in frequency, especially in the upper part of the zone. Oligotrophic diatoms, together with taxa with a wide ecological tolerance (ranging from oligo- to eutrophic conditions), remained dominant; however, their abundance significantly decreased in the upper part of the zone. A peak of dystrophic diatoms was observed in the lower and upper part of the zone.

DAZ 3 (60.5-42.5 cm, 950 -515 cal. BP)

In this zone significant decline of *P. microstauron* and *E. hebridicum* were observed. The frequency of a few diatom taxa, such as *Navicula heimansioides* Lange-Bertalot, *Nitzschia perminuta* Grunow, and *Rossitidium anastasiae* (Kaczmarska) Potapova, was largely limited to this part of the core. In this zone many small forms of diatoms were detected, such as *A. minutissimum* (Kütz.) Czarnecki, *Sellaphora seminulum* (Grun.) D.G.Mann, *Navicula minima* Grunow, *Mayamaea atomus* (Kütz.) Lange-Bertalot. The frequency of *S. venter* increased compared with that in the upper part of the previous zone.

DAZ 4 (42.5-0 cm, 515 cal. BP-present)

In this zone, diatoms typical of dystrophic (humic) waters increased in frequency compared to those present earlier in the lake. A small amount of *S. construens* var. *venter* gradually increased, but not exceeding 20%. The zone is dominated by *Tabellaria flocculosa* reaching the highest frequency throughout the core. The diatom diversity in this zone was the greatest in the entire core (close to 50 species in the sample). The frequency of *E. hebridicum* decreased compared with the previous zone. A higher abundance of diatoms such as *Tabellaria flocculosa*, *Achnanthidium minutissimum*, and *Eunotia* spp., often occurring in humic lakes, was noted.

4.3.1 The diatom-inferred pH (DI-pH) values of the water in TSN indicate acidic conditions over the last 3000 years, ranging between pH 5.4 and 6.6 (Fig. 4A).

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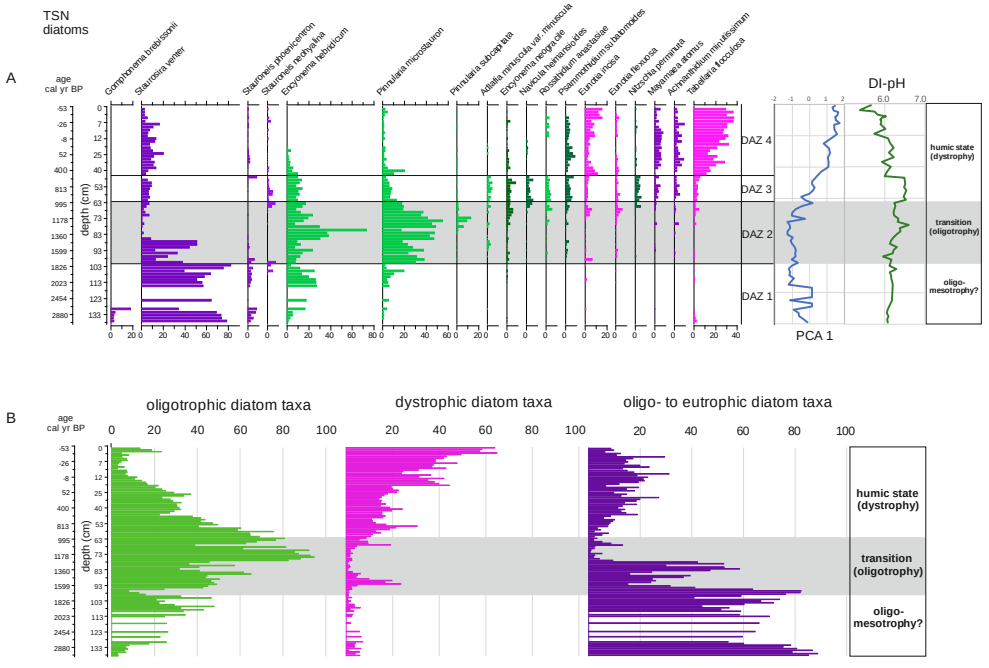

Fig. 4. Relative occurrence (%) of dominant diatoms (minimum 5 % of relative abundance in at least one sample), first axis PCA and diatom-inferred pH (DI-pH) (A); relative abundance of the main trophic groups of diatoms in the lake sediments (B).

4.4 Cladocera stratigraphy

The remains of 16 taxa of Cladocera: two of family Daphniidae, one of Iliocryptidae, one of Macrothricidae and 12 of Chydoridae, were found in the sediment of studied core. Three cladoceran zones (CLZ) were distinguished basing on species composition changes, CONISS and PCA results (Fig. 5). The first and second PC axes explained 31 and 20 % of variation in Cladocera assemblage, respectively.

CLZ 1 (140-120 cm, 3150-2325 cal. BP)

Remains of 4 cladoceran taxa: *Chydorus sphaericus* sensu lato, *Alonella excisa*, *Alona guttata* and small number of *Alona quadrangularis* were found in this zone. Additionally a few remains of *Daphnia longispina* group and *Ceriodaphnia* spp. were also presented at the beginning of the record. The *Chydorus sphaericus* s.l. was a dominant taxon with exception of depths 130-120 cm (2755-2325 cal. BP) where remains of *Alonella excisa* predominated.

CLZ 2 (120-82.5 cm, 2325-1342 cal. BP)

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The beginning of this zone was marked with occurrence of *Daphnia longispina* group and increase in *Alona quadrangularis*. Dominant taxon was *Chydorus sphaericus* sensu lato with relative abundance over 50 %. *Alonella excisa* was less abundant than in CLZ 1.

CLZ 3 (82.5-0 cm, 1342 cal. BP-present)

Daphnia longispina group attended its maximum abundance (over 30%) in this zone. *Chydorus sphaericus* sensu lato decreased, but still was an important part of Cladocera assemblage. The most distinguishing feature of this zone was appearance of *Camptocercus rectirostris* and *Pleuroxus* spp.

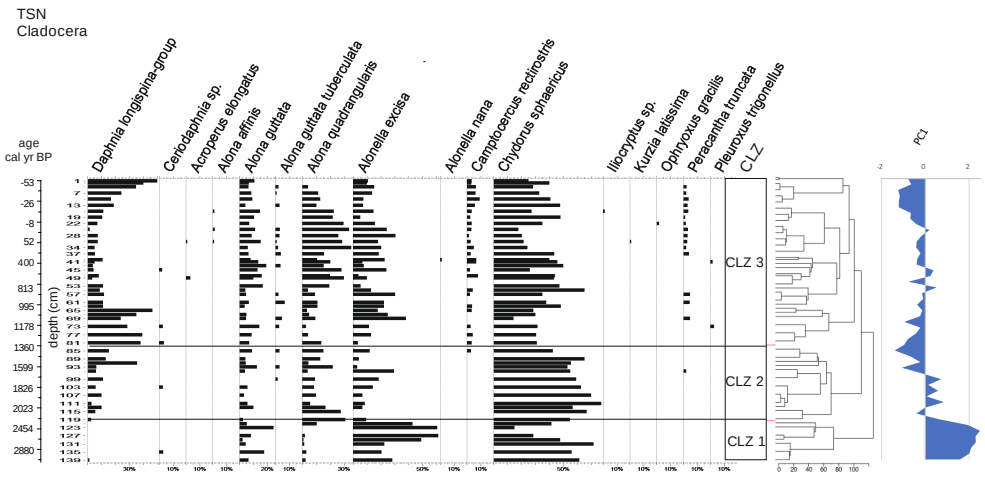

Fig. 5. Relative occurrence (%) of Cladocera species remains in the lake sediments and first axis PCA. Cladocera zones (CAZ) were distinguished on the basis of ConsLink analysis.

4.5 Principal Component Analysis (PCA)

Principal Component Analysis (PCA) was applied to the diatom and Cladocera data to find the most prominent changes in the phyto- and zooplankton assemblages (Fig. 6). In general, diatom and Cladocera taxa associated with changes in trophic level are aligned along the axis 1. A PCA analysis shows that both phyto- and zooplankton taxa with a wide ecological tolerance occur on the left-hand side of the diagram, mainly in its upper part. A shift toward increasingly oligotrophic conditions, indicative of a transitional stage preceding dystrophy, is evident in the lower-left quadrant of the diagram. The longest vectors, representing *Pinnularia microstauron, Encyonema hybridicum*, and *Tabellaria flocculosa*, are the most influential in the analysis (ter Braak, 1988). Among the cladoceran remains, *Daphnia longispina* group is the most significant species. Subsequent shifts toward dystrophic conditions are demonstrated

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on the right-hand side of the diagram. The dystrophic diatom taxa occurred only in the lower-right guardant, while in the upper-right quadrant cladoceran species tolerant of acidification such as *Alonella excisa, Alona guttata* and *Alona affinis*.

The distribution of phyto- and zooplankton along axis 2 may primarily reflect changes in habitat structure and water depth. In particular, *Alonella excisa* often occurs in shallow, overgrown (macrophyte-rich) reservoirs, whereas *D. longispina* is associated with deeper lakes, likely due to its vertical migration within the water column.

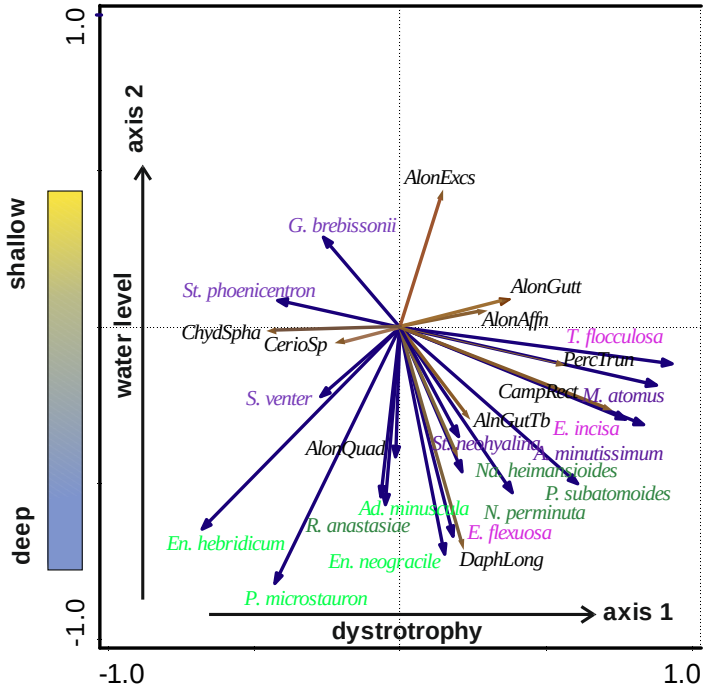

Fig. 6. Principal component analysis (PCA). The relationship between diatom and Cladocera remains in TSN. Codes for diatom genera names: *G. = Gomphonema, St. = Stauroneis, S. = Staurosira, R. = Rossitidium, E. = Eunotia, N. = Nitzschia, P. = Pinnularia, A. = Achnanthidium, M. = Mayamaea, T. = Tabellaria*. Codes for Cladocera species names: *ChydSpha – Chydorus sphaericus, CerioSp – Ceriodaphnia sp, AlonQuad – Alona quadrangularis, DaphLong – Daphnia longispina-group, AlnGutTb – Alona guttata tubercatulata, CampRect – Camptocercus rectirostris, PercTrun – Peracantha truncata, AlonAffn – Alona affinis, AlonGutt – Alona gutata, AlonExcs – Alonella excisa*

5 Discussion

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At present, Toporowy Staw Niżni is classified as dystrophic (humic) forest lake. It contains a high concentration of dissolved organic matter, primarily humic substances, which give the water a dark brown color and contribute to its low pH (Kopáček et al. 2006a). Among Polish and Slovak Tatra lakes including to the Tatra Mountain database (Sienkiewicz et al., 2021), TSN had the highest value of dissolved organic carbon (DOC) equaling 661 µmol L^{-1}. This is the median value of available readings from the lake 1994-2014 (Stuchlík et al., 2006; Kopáček et al., 2015, 2006 a, b). DOC concentrations including remaining oligotrophic and dystrophic water bodies in the training set were between 10.5 and 458 µmol L^{-1} (Sienkiewicz at al., 2021). The process of dystrophication may develop at some stage of lake evolution and depends on the amount of humic substances delivered to the lake from the surrounding peatlands, including raised bogs and transitional mires near Toporowy Staw Niżni, especially along its southern and northern shores. In TSN, dystrophication should therefore be interpreted not only as a change in trophic status, but also as a catchment-driven hydrological and biogeochemical process. The immediate surroundings of the lake are dominated by wetland habitats, transitional mires, peat bogs and coniferous forest, which may supply the basin with allochthonous dissolved organic matter, including humic and fulvic acids. These compounds reduce water transparency, bind nutrients, contribute to water acidification and favor the development of humic-water biological communities. Water-level fluctuations and changes in groundwater or surface-water supply could have intensified the contact between lake water and organic-rich peat substrates, thereby enhancing the leaching of humic substances into the basin.

From the definition, dystrophic lakes are considered as poor in (bio)available nutrients and, in the consequence, low productivity (Luoto et al., 2012). However, Toporowy Staw Niżni is an exception among dystrophic water bodies, as it is characterized by abundant organic life—both fauna and flora (Szafer, 1962, Sienkiewicz et al., 2021). The factors explaining this phenomenon include an advanced stage of ecological succession—i.e., the lake is gradually overgrown—which leads to the formation of specific, rich transitional ecosystem that supports biodiversity. Close to TSN occurred raised and transitional peat bogs. Low altitude and relatively shallow depth favor overgrowth and intensive biological production in the littoral zone. Although TSN meets the physicochemical criteria of dystrophic water bodies (dark-colored water, high humic substance content, low pH), it is situated in unique ecological conditions that locally promote elevated biodiversity. The present-day expansion of floating mats is particularly important in this context. Floating mats do not only represent the final stage of lake terrestrialization, but may also reinforce dystrophic conditions by trapping

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organic matter, limiting water exchange, increasing the contact between lake water and peat-forming vegetation, and promoting the accumulation of poorly decomposable organic material. If peat-forming mosses such as Sphagnum are present or become dominant, they may further stabilize acidic and humic conditions. However, without direct macrofossil or pollen evidence from the TSN core, the role of Sphagnum should be treated as a plausible feedback mechanism rather than as a directly demonstrated cause of acidification.

The compilation of diatom-based classes allows for estimating the trophic history development of TSN. Based on the multi-proxy record, the evolution of this lake can be divided into three main stages: an early oligo-mesotrophic stage, a transitional oligotrophic stage, and a dystrophic stage.

5.1 Paleoecological reconstruction of the lake development

Oligo- mesotrophy? (from ~3150 to ~1791 cal. yr BP)

In this development phase, diatom assemblage was dominated by *Staurosira construens* var. *venter* having very broad trophic tolerance and ranges nearly over the whole trophic spectrum (Lange-Bertalot et al., 2017). Due to this reason, *S. construens* var. *venter* is considered a diatom capable of living in waters ranging from oligotrophic to eutrophic conditions (Van Dam et al., 1994). The wide adaptability of *S. construens* var. *venter* excludes it as a potential indicator of trophic status. Domination of small form of *Staurosira* is characteristic for boreal forest lakes, shallow, nutrient-poor cold environments with short growing season (Rühland et al., 2003). There are diatom taxa occurring very often in oligotrophic and mesotrophic water bodies, but not typical for dystrophic waters (Morales, 2001). According to Van Dam et al. (1994), the presence of diatoms such as *Encyonema hebridicum* and *Stauroneis neohyalina* Lange-Bertalot & Krammer (oligo-mesotrophic taxa), as well as the *Pinularia microstaurom* (mesotrophic), suggests an oligo-mesotrophic character of the lake. Approximately 80% of the diatoms in this section of the core exhibit a broad trophic spectrum—including *S. construens* var. *venter*, which may indicate meso-eutrophic conditions (Cantonati et al., 2021)—the lake is tentatively classified as oligo-mesotrophic. Although this classification remains uncertain, it is based on the predominance of oligotrophic taxa over species preferring more nutrient-rich conditions, i.e. eutrophic taxa, which were present but in lower abundances. However, the dominance of *S. construens* var. *venter* may reflect not only trophic state, but also low water level, habitat instability and the expansion of shallow littoral conditions. Another ecological qualification indicates that those particular species i.e., *E. hebridicum* and *P. microstauron* live in oligotrophic water bodies while *S. neohyalina* can appear in oligo- to eutrophic waters

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(Lange-Bertalot et. al, 2017). During this period, the PCA results (axis 1) for diatoms showed negative values, with the exception of a few samples where the number of diatom valves was not sufficient to perform a qualitative analysis (Fig. 6). Source of organic matter was mixture of phytoplankton and terrestrial plants (C/N>13 and $\delta^{13}C$ between -31.41 and –28.46). In the lower part of core the increase of %TOC, decrease in $\delta^{13}C$ and increase of C/N ratio suggest enrichment in allochthonous organic matter (Meyers and Teranes, 2001). Low carbon isotopic signal means that organic matter is dominated by peat, leaves, humus and low internal production in lake. The low primary production was likely a result of limited availability of nutrients, particularly nitrogen and phosphorus (Fig. 3). At the same depths, the number of diatom valves was too low to allow for reliable qualitative analysis. The increase of $\delta^{15}N$ with minimal decrease in %TON may indicate denitrification of allochthonous organic matter. The diatom-inferred pH ranged from 5.9 to 6.6 during this period. However, a DI-pH value of 5.9 was recorded in only one sample, while in the remaining samples the values were above 6. During this stage the lake experienced dramatic decrease in water level between ~2750 and 2350 cal. BP. It was expressed in Cladocera species composition by domination of *Alonella excisa*, a species often associated with overgrowing of lakes and peat bogs (Gąsiorowski and Kupryjanowicz, 2009; Nevalainen, 2011; Gąsiorowski, 2013), and disappearance of *Daphnia* and *Ceriodaphnia*. The diatom remains are very scarce in the sediment of this period. It can be a result both low frequency of diatoms or post-depositional dissolution of diatom silica, the process which occurred in peats (Bennett et al., 1991). The process of lake level decrease at that time was described also in other lakes of the Tatra (Gąsiorowski et al., 2023) and had at least regional character.

This shallow-water episode may have been important for the later development of dystrophy in TSN. Lowered or strongly fluctuating water levels could have promoted the expansion of marginal wetland vegetation and increased the contact between lake water and organic-rich sediments or peat-forming substrates. Such conditions may have strengthened peatland–lake coupling and made the basin more sensitive to later inputs of humic substances. Therefore, the early water-level decline can be interpreted as a preconditioning stage for subsequent dystrophication rather than only as a short-term hydrological event.

5.2 Transition period (oligotrophy) (from ~1791 to ~950 cal. yr BP)

Patterns of change toward dystrophy appear to be similar in lakes located in both mountainous and lowland regions. Typically, these lakes evolve from oligotrophic or oligo-mesotrophic conditions to dystrophic states, with the transitional phase lasting for either relatively short or

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prolonged periods (Zawisza et al., 2019; Mirosław-Grabowska et al., 2020; Bitušík et al., 2024). It depends on climate change, the accumulation of organic matter, the development of surrounding peat bogs, and the input of humic acids into lakes (Górniak, 2017). The transition to the first more significant trophic change in lake TSN began around 1790 cal. yr BP and ended around 950 cal. BP. During this period a prominent change in diatom community was observed. At the beginning of this period, abrupt decrease in *S. construens* var. *venter* was recorded. Dominating diatoms were *E. hebridicum, P. microtauron* and *P. subcapitata*. There are typical taxa characteristic for oligotrophic conditions; *E. hebridicum* and *P. subcapitata* reached the highest frequency in the core. Axis 1 (Fig. 4A), based on diatoms, indicates changes toward positive values and fluctuated between -1.0 and 0.1. During this period, a significant increase in oligotrophic taxa (up to 95%) and oligo-mesotrophic taxa (up to 32%) was observed, while the remaining taxa representing other trophic types showed a decline (Fig. 4). They reached the highest frequency in the core, while the frequency of remain diatoms dropped significantly to compare with a previous zone. The C/N ratio was between 13 and 21, suggesting a variable input of allochthonous material to the lake (Fig. 3). These values indicate that the organic matter consists of a mixture of both aquatic and terrestrial plant material. Both the isotopic data ($\delta^{13}C$) and %TOC indicate a slight increasing trend during this period. $\delta^{15}N$ ranged from -0.36 to 0.6‰. Values of $\delta^{15}N$ close to 0‰ are generally considered indicative of nitrogen derived from natural sources, particularly atmospheric N_2 fixed biologically (Robinson, 2001). Excluding the uppermost samples, %TN reached its highest values in the core. During the transition period, DI-pH fluctuated within a range of 0.6 pH units (6.0–6.6), indicating a slight decrease in water pH at the beginning of this period and a slight increase towards the end. Between 1500 and 1300 cal. BP, the Late Antique Little Ice Age (LALIA) occurred. This period was characterized by rapid cooling, including cooler summers, crop failures, and glacier expansion related to a solar minimum (Büntgen et al., 2016) and is widely attributed to a series of large volcanic eruptions in 536, 540 and 547 AD (Sigl et al., 2015). In the case of TSN, the increase in the abundance of dystrophic diatoms during this interval (lower part of DAZ 2, Fig. 4B) may indicate an enhanced input of humic substances into the lake, most likely as a result of intensified leaching of organic matter from the peatlands surrounding the basin. Change into a humic lake were not simultaneous with those in another Tatra lake (Nižné Rakytovské pleso) located in the Slovak part of the mountains (Bitušík et al., 2024), suggesting that rather local than regional factors driven this process. This process in TSN was also asynchronous with timing of the transition in lakes of

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other regions (Luoto et al., 2012; Zawisza et al., 2019). The PCA sample scores show a change from negative values towards positive values in the upper part of DAZ 2 (Fig. 4A).

5.3 Dystrophy (from ~950 to 0 cal. yr BP)

After a period of typical oligotrophic conditions, changes in the trophic status of TSN were observed. A shift toward dystrophic conditions is reflected in the increasing frequency of diatom taxa tolerant of dystrophic environments, while a decreasing trend was observed in oligotrophic diatom taxa and in diatoms with broad ecological tolerance. (Fig. 4B). In Cladocera, the best indicator of changes in trophic state was *Camptocercus rectirostris*, a species previously reported from dystrophic lake (Zawisza et al., 2019). The increase in dystrophic diatoms and the appearance of cladoceran taxa associated with macrophyte-rich, acidic or humic habitats indicate that the lake was not only becoming poorer in bioavailable nutrients, but also increasingly structured by humic-water conditions and littoral habitat expansion. This is consistent with progressive terrestrialization and the development of floating mats along the lake margins. Although dystrophic lakes are usually very poor in biogenic substances and rich in humic and fulvic acids, organisms preferring other trophic levels may also occur, especially in the littoral zone (Drzymulska and Zieliński, 2013). This is connected with the mosaic nature of habitats, such as areas with more light, littoral zones with higher pH, or better oxygen and nutrient availability. In addition, the decomposition of organic matter by bacteria releases nitrogen and phosphorus in forms available to algae. The spatial structure of dystrophic lakes is often highly heterogeneous, and the littoral zone may differ chemically than the pelagic zone as a result of groundwater inflow, contact with mineral substrates, and intensive photosynthetic activity of macrophytes (Kostrzewska-Szlakowska and Jasser, 2011; Drzymulska and Zieliński, 2013). Therefore, the coexistence of dystrophic taxa with species of broader ecological tolerance should not be interpreted as contradictory, but rather as evidence of a spatially heterogeneous lake–peatland system. In the sediments of TSN collected in 2003 (Gąsiorowski and Sienkiewicz, 2010b), the proportion of dystrophic taxa exceeded 60%, especially in the upper part of the core. This confirms that the process of dystrophication is still ongoing. The $\delta^{13}C$ values indicate an increasing contribution of terrestrial organic matter and, at values around −31‰, even its dominance, mainly in the form of peat, leaves, and humus, accompanied by low autochthonous productivity. That value was recorded in the uppermost sample, suggesting further terrestrialization. Despite an overall increasing trend in the carbon isotopic curve across the core, the upper section (from 20 cm to the top), corresponding to the early 20th century onward, is characterized by more negative

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values. The $\delta^{15}N$ values in the lake sediments range from −1.27 to +1.12‰, indicating dominance of natural nitrogen sources. These values are typically associated with atmospheric nitrogen inputs and biological N_2 fixation, reflecting low-intensity nitrogen cycling in oligotrophic to dystrophic mountain lakes with minimal anthropogenic influence (Finlay and Kendall, 2007; Nanus et al., 2018). The C/N ratio initially shows an increasing trend, suggesting enrichment in allochthonous organic matter. However, in the upper part of the core, the values decrease, although they still indicate a mixture of organic matter derived from phytoplankton and terrestrial plants. A period between 635 and 345 cal. BP is characterized by the highest %TOC values in the entire core. This may indicate a significant increase in allochthonous organic matter, as confirmed also by the highest C/N ratios. This interval may correspond to intensified peatland influence and enhanced delivery or accumulation of humic organic matter in the lake. Such a signal is consistent with the development of a more advanced lake–peatland system, in which floating mats and marginal peat-forming vegetation increasingly controlled the amount and character of organic matter entering the basin. In the youngest sediments, nitrogen content increased, reaching the highest values in the entire core. Reconstruction of water pH varied between 5.4 and 6.5. At the beginning of dystrophication the DI-pH was above 6. Since 18 cal. BP water pH was below 6 with two examples that DI-pH equals 6.0. In the earlier analysis of the sediments from TSN the values of the reconstruction pH were little lower in the last 1000 years (Gąsiorowski and Sienkiewicz, 2010b), This was most likely due to the use of the AL:PE calibration dataset, which includes 118 mountain lakes in Europe, for the pH reconstruction. In the present study, DI-pH was reconstructed using the POL_SLOV training set, developed exclusively from Polish and Slovak lakes in the Tatra Mountains (Sienkiewicz et al., 2021). This approach provides more reliable results because the database was constructed from lakes located within a relatively small area, under similar bedrock conditions, and in close geographic proximity to one another. The development of floating mats may have further accelerated and stabilized the dystrophic state of TSN. Floating mats reduce the area of open water, trap organic matter and create semi-terrestrial habitats along the lake margin. If dominated or co-dominated by peat-forming mosses such as Sphagnum, they may promote the accumulation of acidic, poorly decomposable peat and enhance the production or retention of humic substances. However, the acidifying effect of Sphagnum should not be overstated as a single causal factor. In TSN, Sphagnum and other peat-forming vegetation are best interpreted as components of a broader feedback system involving hydrology, organic-matter accumulation, humic-substance export and reduced lake-water exchange with mineral-rich sources. This feedback mechanism

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provides a plausible explanation for why dystrophy became persistent during the last millennium. Once peatlands and floating mats expanded around the basin, the lake would have received more organic-rich, acidic waters. The resulting lower pH and lower light availability would have favoured acidophilous and humic-water diatoms, reduced the importance of clear-water oligotrophic taxa and promoted further accumulation of organic sediments. In this way, dystrophication in TSN may have become self-reinforcing.

6 Implications for the natural development of TSN

Overall, the development of TSN can be interpreted as a natural transition from a shallow oligo-mesotrophic lake, through an oligotrophic phase, toward a dystrophic lake–peatland system. This trajectory was probably controlled by the interaction between water-level fluctuations, progressive terrestrialization, peatland expansion, floating-mat development and increasing delivery of humic substances from the catchment. The comparison with Lake Suchar IV is particularly useful in this context, because Zawisza et al. (2019) showed that dystrophication may represent an alternative pathway of lake development, driven by lake–peatland succession and humic-matter input rather than by classical eutrophication. In TSN, a similar mechanism is suggested by the increase in allochthonous organic matter, the decline in DI-pH, the rise of dystrophic diatoms and the development of littoral Cladocera communities associated with shallow, vegetated and humic habitats.

7 Conclusions

The combined diatom, Cladocera, and geochemical records indicate that TSN did not follow a classical eutrophication trajectory. Instead, the lake evolved from an early oligo-mesotrophic stage, through a more clearly oligotrophic phase, toward persistent dystrophic conditions during the last millennium. This transition was likely driven by progressive catchment terrestrialization, the increasing influence of surrounding peatlands, enhanced delivery of humic organic matter, and hydrological isolation of the basin. The Cladocera record additionally suggests major changes in water level and littoral habitat structure, particularly during the shallow-water episode between ca. 2750 and 2350 cal. BP.

Long-term climatic changes and catchment-lake interactions were therefore the most important factors controlling changes in the trophic state of TSN. At present, most lakes in the Tatra Mountains are classified as oligotrophic water bodies, whereas TSN represents a rare example of a mountain dystrophic lake. The present dystrophic state of TSN appears to be the result of long-term natural lake development rather than direct anthropogenic impact. The

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record demonstrates that dystrophication in mountain lakes may be highly local, asynchronous between basins and strongly dependent on catchment vegetation, water-level changes and hydrological thresholds. Therefore, TSN provides an important case study for understanding how small mountain lakes may transform into humic lake–peatland systems during the late Holocene.

Code and data availability. The data supporting the findings of this study are available from the corresponding author upon reasonable request.

Autor contributions. ES: conceptualization, methodology, formal analysis, writing-original draft, supervision; KK; methodology, formal analysis, writing-original draft, editing; MG: conceptualization, methodology, data curation, formal analysis, writing-original draft; UK: methodology, formal analysis, writing-original draft, art work; MS: writing-original draft.

Competing interests. The contact author has declared that none of the authors has any competing interests.

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