

1     **Historical human impact on productivity and biodiversity in a subalpine**  
2                                   **oligotrophic lake in Scandinavia**

3     Thomas C. Jensen<sup>1\*</sup>, Izabela Zawiska<sup>2</sup>, Mimmi Oksman<sup>3</sup>, Michał Słowiński<sup>4</sup>, Michał Woszczyk<sup>5</sup>,  
4     Tomi P. Luoto<sup>6</sup>, Wojciech Tylmann<sup>7</sup>, Liisa Nevalainen<sup>6</sup>, Milena Obremska<sup>8</sup>, Ann Kristin Schartau<sup>1</sup>,  
5     Bjørn Walseng<sup>1</sup>.

6     <sup>1</sup> Norwegian Institute for Nature Research, Oslo, Norway

7     <sup>2</sup> Polish Academy of Sciences, Department of Geoecology and Climatology, Warsaw, Poland

8     <sup>3</sup> Aarhus University, Department of Geoscience, Aarhus, Denmark

9     <sup>4</sup> Polish Academy of Sciences, Department of Environmental Resources and Geohazards, Toruń,  
10    Poland

11    <sup>5</sup> Adam Mickiewicz University, Department of Quaternary Geology and Palaeogeography, Poznań,  
12    Poland

13    <sup>6</sup> University of Helsinki, Faculty of Biological and Environmental Sciences, Ecosystems and  
14    Environment Research Programme, Lahti, Finland

15    <sup>7</sup> University of Gdańsk, Faculty of Oceanography and Geography, Gdańsk, Poland

16    <sup>8</sup> Polish Academy of Sciences, Institute of Geological Sciences, Research Centre in Warsaw, Poland

17    \* Corresponding author: Thomas C. Jensen, email [thomas.jensen@nina.no](mailto:thomas.jensen@nina.no), Norwegian Institute for  
18    Nature Research, Gaustadalléen 21, NO-0349 Oslo, Norway, telephone: +47 98826587

19    Running title: Human impact on an oligotrophic lake ecosystem

20    Keywords: Diatoms, Cladocera, Macrofossils, Land use, Climate, Scandinavia

21 **Abstract**

22 We conducted a paleolimnological study to examine how changes in human activity interacted with  
23 climate to influence productivity and biodiversity over the past millennium in oligotrophic Lake  
24 Atnsjøen, SE Norway. The study included analyses of sediment geochemistry, subfossil diatoms and  
25 cladocerans, and macrofossils. Results were compared with the historical record of human activities in  
26 the catchment, pollen analysis and paleoclimate inferences from the lake. During the first 750 years of  
27 the record (1000 CE –1750 CE), a time of relatively low human activity, lake productivity and  
28 biodiversity were strongly related to climate. During the Little Ice Age (1550-1800 CE), lake  
29 productivity and diatom diversity were constrained by cold climate. A century of climate warming  
30 (1780-1880 CE) initiated an increase in productivity. Accelerated human settlement after 1850 CE,  
31 however, had an even stronger impact on productivity, mediated by increased agriculture and/or  
32 forestry, which led to greater nutrient loading of the lake. Similarly, diatoms in the lake responded to  
33 the rise in temperature, but increasing human activity also had a moderate impact on the diatom  
34 community, which displayed weak signs of nutrient enrichment. From 1980-1990 CE onwards, lake  
35 productivity declined as a consequence of a recent decrease in human activity and changing land use.  
36 The human-induced increase in lake productivity starting ca. 1850 CE propagated through the food  
37 web and increased consumer productivity, as reflected by greater accumulation rates of cladocerans,  
38 trichopterans and turbellarians. The cladoceran community was likely under top-down control of fish,  
39 as indicated by changes in size structure and diversity. Our study showed that increasing human  
40 activity during the settlement period had a stronger impact on lake productivity than did climate.  
41 Furthermore, the slight human-mediated increase in nutrient loading had different impacts on  
42 productivity and biodiversity in the study lake. This study demonstrates that even relatively small  
43 changes in human activities in watersheds can have measurable impacts on nutrient-poor lakes.

44

45 **Introduction**

46

47 Anthropogenic forcing is increasingly impacting freshwater ecosystems (Dudgeon et al. 2006). At the  
48 watershed scale, this impact includes human activities like agriculture, forestry, urban development  
49 and fish stocking (Anderson et al. 1995; Alric et al. 2013; Brag e et al. 2013; Berthon et al. 2014).  
50 These activities affect productivity and biodiversity of freshwater communities (McQueen et al. 1986;  
51 Dodson et al. 2000; Dong et al. 2012a; Alric et al. 2013; Jensen et al. 2013) and often lead to poor  
52 water quality, ultimately threatening important ecosystem services provided by freshwater  
53 environments. Management of the freshwater environment to mitigate negative human impacts  
54 requires an understanding of how effects are related to the level of disturbance (i.e. low versus high  
55 disturbance) and how the whole ecosystem is affected.

56 Few comprehensive studies of anthropogenic forcing of lake ecosystems have focused on both  
57 productivity and biodiversity, the latter term used here in a broad “compositional” sense to refer to the  
58 variety of life, with organisms aggregated as species and communities (Callicott et al. 1999), and  
59 encompassing several trophic levels. The few studies with such a broad focus consider intermediate to  
60 high levels of disturbance (Jeppesen et al. 2000). The high number of oligotrophic and ultra-  
61 oligotrophic lakes found in remote regions with low human population densities, such as large parts of  
62 Scandinavia and North America (Hessen et al. 1995; Clark et al. 2010), are often perceived as near-  
63 pristine (undisturbed) freshwaters. There are, however, a number of studies that suggest even low  
64 levels of human activity have an impact on lake ecosystems (Perren et al. 2012; Wolfe et al. 2013;  
65 Neil and Gajewski 2017). The ecological response of an oligotrophic lake to increased human activity  
66 depends on the range and magnitude of activity change (Colby et al. 1972). Increased research on the  
67 consequences of low-level disturbance in these lakes will not only improve our understanding of  
68 human impacts on lake ecosystems, but will also have implications for the conceptual framework in  
69 management of these lakes, which are often viewed as reference sites from a monitoring perspective.

70 Climate change is increasingly threatening the biosphere (IPCC 2013). Climate influences  
71 aquatic ecosystems directly through changes in temperature, precipitation and wind exposure, but it  
72 may also interact with local anthropogenic stressors to affect lake ecosystems indirectly (Whitehead et  
73 al. 2009). Studies have shown that lake responses to climate change may depend on nutrient loading  
74 and vice versa. For example, climate warming may have stronger effects on temperate lakes that  
75 receive higher nutrient loads than on nutrient-poor lakes (Alric et al. 2013). Likewise, the response to  
76 increased nutrient loads may depend on temperature; e.g. lake responses to increasing nutrient loads at  
77 lower temperatures may be damped because of temperature constraints on biological processes and  
78 communities. Increasing human pressure on lake ecosystems, in combination with climate warming in  
79 recent centuries (Dong et al. 2012b; Cao et al. 2014), underpins the need to consider climate effects  
80 when striving to understand anthropogenic impacts on lake ecosystems.

81 The role of climate as a driver of natural biological communities has been investigated in  
82 studies that relate changes in biological communities in remote arctic and alpine lakes to instrumental  
83 climate records (Korhola et al. 2002). Paleolimnology has become an important tool in the assessment  
84 of human impacts (e.g. eutrophication) on lakes (Davidson and Jeppesen 2013). The combined effects  
85 of climate and human forcing of ecosystem structure and/or function were addressed in several  
86 paleolimnological studies in densely populated areas (Perga et al. 2010; Dong et al. 2012a; McGowan  
87 et al. 2012; Alric et al. 2013; Berthon et al. 2014; Cao et al. 2014). Few studies have addressed this  
88 issue in nutrient-poor lakes under low-intensity human impact.

89 This study was undertaken to assess how productivity and biodiversity in a nutrient-poor lake  
90 were affected by human activity in the catchment and by climate during the last millennium. We used  
91 paleolimnological methods and historical documentation to decipher the climate-human-lake  
92 ecosystem relationships. By focusing on both primary and secondary producers we were able to  
93 examine how different trophic levels responded to external stressors. We measured proxies for  
94 productivity (fluxes of trichopterans, turbellarians, cladocerans and organic carbon) and biodiversity

95 (species richness and community composition of diatoms and cladocerans) to test if the two responded  
96 differently to changing human activity and climate.

## 97 **Materials and methods**

98

99 Study site and catchment history

100

101 Oligotrophic Lake Atnsjøen (61°52'51 N, 10°09'55 E) is situated in southeast Norway, in the  
102 municipality of Stor-Elvdal. The lake is located at 701 m a.s.l. and has a surface area of 4.8 km<sup>2</sup>,  
103 maximum depth of 80 m, mean depth of 35.4 m and a water retention time of 6 months (Fig. 1). The  
104 catchment area is 457 km<sup>2</sup>, most of which (85 %) is above tree line (~1000 m a.s.l.). High-elevation  
105 flora consists of high- and low-alpine tundra, whereas pine (*Pinus sylvestris*) and birch (*Betula*  
106 *pubescens*) dominate below tree line. The catchment area consists mainly of feldspar quartzite, with  
107 locally large deposits of Quaternary and fluvial materials. The area around Lake Atnsjøen has a  
108 continental climate with average annual temperature and precipitation of 0.7 °C and 555 mm,  
109 respectively (Nordli and Grimenes 2004). Ice cover on the lake lasts from late November to late May.  
110 The Atna watershed, including Lake Atnsjøen, remains relatively unaffected by human activities  
111 because of its remote location and because a large part of the catchment lies within the Rondane  
112 National Park.

113 There are indications of early, low-level human activity in the area around Lake Atnsjøen  
114 during the last millennium (Mikkelsen 1980). Human development around Lake Atnsjøen during  
115 Medieval times and onwards is relatively well documented compared to what is known about many  
116 other remote areas in Norway, because the Atnsjøen region was repopulated relatively late after the  
117 Black Death (1348 - 1349 CE). Thus, it is possible to track settlement changes over time using  
118 historical records/sources (Fig. 2, Dahl 1960; Mikkelsen 1980). To verify the development of human

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Historical human impact on Productivity and biodiversity in a subalpine oligotrophic lake in Scandinavia. *Journal of Paleolimnology* 2019 ;Volum 42.(4)  
DOI [10.1007/s10933-019-00100-5](https://doi.org/10.1007/s10933-019-00100-5)

119 presence/activity in the area and to gain further insight into early human presence before and after the  
120 Black Death, historical records were supplemented with pollen analysis from Lake Atnsjøen, using  
121 human pollen indicators (HPI) and the ratio of arboreal pollen (AP, *arboreal pollen*: trees and shrubs)  
122 to nonarboreal pollen (NAP, *non-arboreal pollen*: herbs, excluding telmatic and aquatic plants),  
123 AP/NAP, as an indicator of landscape openness (Fig. 2, Zawiska et al. 2017).

124 Human activity around Lake Atnsjøen during the last millennium can be divided roughly into  
125 two periods: 1) 1000 CE –1750 CE, 2) 1750 CE – present (Table 1). The first permanent settlement in  
126 the catchment after the Black Death was established in 1756 CE (Table 1, Fig. 2, Dahl 1960). From  
127 that time onwards, human presence in the area increased until the first half of the 20th century, as  
128 estimated from settlements and summer farms in the catchment, and from the population density in  
129 Folldal, the neighboring community northwest of the Atna area (Fig. 2). Around 1950 CE, population  
130 in the area decreased (Fig. 2, Brænd 1989). A number of events during the 20th century, e.g. changing  
131 agricultural practices, adoption of chemical fertilizers, industrialization/mechanization of agriculture  
132 and forestry intensified anthropogenic pressures on the lake and likely helped maintain higher  
133 pressures even after the population/number of farms/settlements began to decrease around 1950 CE  
134 (Table 1). Pollen analysis supports the historical record on human activity. The HPI was generally  
135 lower before than after 1750 CE, the latter being the period of higher human activity. Second, many  
136 events in the historical record are verified/supported by the pollen analysis, e.g. the increase in the  
137 settlement and agricultural activity, and changes in agricultural practices between 1900 and 1950 CE  
138 (Table 1).

139 Population density in neighboring Folldal municipality varied between 0 and 1.86 inhabitants  
140 km<sup>-2</sup> (1950 - 1960 CE). Exact population densities in the Lake Atnsjøen catchment are not known, but  
141 assuming an average of six persons per household (H.E. Nettet pers. commun.), population densities  
142 in the catchment varied between 0 and 0.46 inhabitants km<sup>-2</sup> (1700 -1950 CE). These densities are low  
143 in Norwegian, European and North American contexts (Goldewijk 2005; Goldewijk et al. 2010;

144 Statistics Norway 2018) and highlight the low human pressure on the lake in a broad perspective, even  
145 during the period of highest population density in the catchment.

146

147 Sampling and dating

148

149 We collected a core in the southeastern end of the lake, relatively close to the outlet, at a water depth  
150 of 20 m (Fig. 1). Sediment in the western, deeper part of the lake consists of relatively coarse  
151 (gravelly) clastic material that originated from fluvial inputs to the water body. In addition, pelagic  
152 *Eubosmina* constitutes more than 96 % of the cladocaran remains in the sediment from that part of the  
153 basin (G. Halvorsen, pers. commun.). We chose a shallower sampling site in the eastern end of the  
154 lake to avoid the gravel layer and obtain a longer core that could also capture the littoral signal. A 34-  
155 cm-long sediment core was retrieved using a KC-Denmark Kajak-type gravity corer. The core was  
156 sectioned in the field into 1-cm layers, further separated into subsamples for different analyses, and  
157 stored at 5 °C.

158 Details of the core chronology were published in Zawiska et al. (2017). In short, the age-depth  
159 model for the core was based on <sup>210</sup>Pb dating of topmost sediments, AMS <sup>14</sup>C dating of terrestrial  
160 macrofossils in the lower part of the core, and pollen. Activity of total <sup>210</sup>Pb was determined indirectly  
161 using alpha spectrometry, described by Tylmann et al. (2016). Ages for topmost sediment layers were  
162 calculated with the CF:CS (Constant Flux:Constant Sedimentation) model. Only one radiocarbon date  
163 was obtained (32 cm, <sup>14</sup>C 1200 ± 30 BP) because of a lack of preserved terrestrial macrofossils in the  
164 sediments. Therefore, simple linear extrapolation, based on mean mass accumulation rate from the  
165 CF:CS model (0.013 g cm<sup>-2</sup> yr<sup>-1</sup>), was used to calculate sediment ages at different depths. Additional  
166 time control from pollen data came from a sharp decline in HPI related to the Black Death plague,  
167 which peaked in Norway about 1350 CE, killing 50% of the human population (Oeding 1990).

168 Comparison of extrapolated  $^{210}\text{Pb}$  dates, the AMS  $^{14}\text{C}$  date, and pollen data suggested that the  
169 radiocarbon date was too old by ca. 150 years. Hence, the combined  $^{210}\text{Pb}$  and pollen data were used  
170 for the final age-depth model (Electronic Supplementary Material [ESM] Fig. S1).

171

172 Diatom, Cladocera and macrofossil analysis

173

174 Diatom slides were prepared using sub-samples from 1-cm intervals along the length of the sediment  
175 core. Organic matter and carbonates were removed from samples with  $\text{H}_2\text{O}_2$  and HCl, respectively  
176 (Battarbee 1986), and superfluous mineral material was eliminated before preparing diatoms slides.  
177 The diatom suspension was dried on a cover slip and mounted with Naphrax® for microscopic  
178 analysis. At least 300 diatom valves on each slide were identified and counted according to Schrader  
179 and Gersonde (1978) and taxonomic determination was based on Krammer and Lange-Bertalot (1986,  
180 1988, 1991a, 1991b).

181 One- $\text{cm}^3$  sediment subsamples were prepared for Cladocera analysis following standard  
182 procedures (Frey 1986). A volume of 0.1 ml from each sample was used to prepare slides that were  
183 examined by microscopy. All skeletal elements (head shields, shells and post-abdomens) were used  
184 for identification of cladoceran taxa, following Szeroczyńska and Sarmaja-Korjonen (2007) and at  
185 least 100 individuals were counted per sample (Kurek et al. 2010). Cladoceran densities by volume  
186 were converted to density per g dry weight (DW), and species percentages were calculated. We  
187 calculated the fraction of large-bodied species according to Moss et al. (2003, *Daphnia longispina* and  
188 *Eurycercus lamellatus*) as a proxy for the size structure of the cladoceran community. We used  
189 cladoceran flux as a proxy for zooplankton/cladoceran productivity. Total cladoceran flux for the Lake  
190 Atnsjøen sediment core was presented by Zawiska et al. (2017). In the current study we present the  
191 fluxes of pelagic and littoral cladocerans separately to examine if productivity of the pelagic and



192 littoral zones responded differently to human impact. Cladoceran flux was calculated by multiplying  
193 pelagic or littoral cladoceran density by sediment dry density and dividing by the number of years  
194 represented by the sample.

195 Samples for macrofossil analysis were prepared according to Birks (2007). Identification of  
196 fossil remains was based on Katz et al. (1977), Birks (2007) and Velichkevich and Zastawniak (2008)  
197 and a reference collection (Institute of Geography, Polish Academy of Sciences). All macrofossil  
198 counts were standardized as numbers of fossils per 50 cm<sup>3</sup> and converted to density per g dry weight  
199 (DW). Here we present the results of trichopteran and turbellarian remains. Trichopteran and  
200 turbellarian flux were calculated by multiplying trichopteran or turbellarian density by sediment dry  
201 density and dividing by the number of years represented by the sample .

202

203 Geochemical analysis and climate reconstruction

204

205 For C and N analysis, sediment samples were first oven-dried at 50°C and powdered in a Pulverizette  
206 2 agate mill (Fritsch, Germany). Total concentrations of N and C, denoted as TN and TC,  
207 respectively, were determined using a VarioMax CNS analyzer (Elementar, Germany). To determine  
208 the content of total organic carbon (TOC), samples were first decarbonated with 1 M HCl. After the  
209 reaction was complete, the residue was air-dried and then oven-dried at 50°C and re-analyzed. The  
210 quality of measurements was controlled with certified reference materials provided by Elementar  
211 (Sulfadiazine, chalky soil (BN230229), sandy soil (BN225497) and peaty soil (BN230227)). Recovery  
212 was always greater than 95% for both elements. TN and TOC contents were expressed as wt. %. To  
213 assess lake paleoproductivity, the TOC flux (mg C cm<sup>-2</sup> yr<sup>-1</sup>) (Routh et al. 2009; Wang et al. 2013; Bao  
214 et al. 2015) was calculated by multiplying the TOC (mg g<sup>-1</sup>) by mass accumulation rate (MAR; 0.013  
215 g cm<sup>-2</sup> y<sup>-1</sup>). The molar TOC/TN ratio was calculated to infer the origin of sediment organic matter  
216 (Meyers and Teranes 2001).

217 We used the chironomid-inferred mean July temperature from the Lake Atnsjøen core to  
218 characterize summer climate conditions (Zawiska et al. 2017). The length of the ice-free season is an  
219 additional important climate driver of the ecology in ice-covered lakes. We used the bosminid  
220 (Bosminidae) sex ratio from Zawiska et al. (2017) as a proxy for the length of the growing season  
221 (Kultti et al. 2011).

222

223 Data analysis

224 A summary of the paleolimnological and historical variables included in the current study is given in  
225 ESM Table S1. In this study, species richness and community composition were used as biodiversity  
226 proxies to examine temporal changes in the diatom and cladoceran communities. Species richness is  
227 one component of biodiversity (Gaston and Spicer 2004) and is simply the number of species present  
228 in a sample (Gaston and Spicer 2004). Species composition (relative abundance) was chosen because  
229 it is more informative than “species-neutral” diversity indices. Assignment of samples to diatom and  
230 cladoceran zones was done using unweighted pair-group average (UPGMA) cluster analysis with a  
231 with Bray-Curtis distance as the measure of dissimilarity.

232 The differential influences of climate and settlement/nutrients on organism communities or  
233 productivity were based predominantly on correlation analyses and comparison of the graphs of  
234 individual variables. Temporal changes in community composition of diatoms and cladocerans,  
235 however, were analysed by principal component analysis (PCA) using Hellinger-transformed relative  
236 occurrences of diatoms and cladocerans as input data in the PCA-analysis. Chironomid-inferred July  
237 temperature and TOC flux were added passively as environmental variables. For the diatom  
238 community, percent pelagic species was added passively to examine if changes in the community  
239 contrasted the pelagic and benthic species. Likewise, the percentage of large-bodied cladocerans  
240 (Moss et al. 2003) was added passively in the PCA of the cladoceran community to infer changes in  
241 the community size structure and composition. Relationships between environmental variables and  
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DOI [10.1007/s10933-019-00100-5](https://doi.org/10.1007/s10933-019-00100-5)

242 response variables were assessed by Pearson's correlation coefficient. Non-normally distributed  
243 variables were transformed ( $\log_{10}(X + 1)$ ). Statistical analyses were conducted in SPSS Statistics 24  
244 (IBM 2017), PAST (Hammer et al. 2001) and CANOCO 5.0 (ter Braak and Šmilauer 2012).

245 **Results**

246

247 Diatom community composition and species richness

248

249 We recorded 126 diatom taxa in the studied sediment core. The most common species, *Tabellaria*  
250 *flocculosa*, constituted on average 54 % of the diatom community and occurred in high abundances  
251 throughout the period studied (Fig. 3). *Tetracyclus glans* was also rather common, constituting on  
252 average 8.5 % of the community. The rest of the species occurred at average relative abundances of <  
253 3 %. Cluster analysis identified three distinct diatom zones (Figs. 3 and 4): Diatom zone 1, from 1000  
254 CE to 1580 CE (samples 34-16), Diatom zone 2 from 1580 CE to 1710 CE (samples 15-13) and  
255 Diatom zone 3 from 1710 CE to present (samples 12-1).

256 PCA1<sub>diat</sub> and PCA2<sub>diat</sub> had eigenvalues of 0.23 and 0.16 and accounted for 23.4 % and 15.9 %  
257 of the variation in the diatom community, respectively. Development of diatom community  
258 composition during the past millennium followed a clear trajectory of the PCA<sub>diat</sub> scores of the first  
259 two PCA axes, shifting between different communities that correspond to the three diatom zones  
260 (Figs. 3 and 4). The community of zone 1 had low scores of both PCA1<sub>diat</sub> and PCA2<sub>diat</sub> and was  
261 characterized to some extent by species like *T. glans*, *Gomphonema acuminatum*, *Fragilaria*  
262 *brevistriata*, *Achnanthes minutissima* and *Fragilaria virescens*. The community of zone 2 had higher  
263 PCA1<sub>diat</sub> scores and lower PCA2<sub>diat</sub> scores compared to zone 1, mainly as a consequence of lower  
264 occurrences of *A. minutissima*, *F. virescens* and *E. minor*, and higher occurrences of *C. radiosa* and *C.*  
265 *bodanica*. The most characteristic species of zone 2 were *Aulacoseira lirata*, *C. radiosa*, *T.*  
266 *quadriseptata* and *Synedra parasitica*. The zone 3 assemblage again displayed lower PCA1<sub>diat</sub> scores  
267 and higher PCA2<sub>diat</sub> scores. The community changed during zone 3, but overall the most characteristic  
268 species were *N. scutiformis*, *N. ampliatum*, *N. clementis* and *F. rhomboides* v. *amphipleuroides*,

269 *Navicula pupula* and *Eunotia pectinalis*. From 1710 CE to 1850 CE the community was relatively  
270 stable and still characterized by *C. radiosa*, but *C. bodanica* was also typical in the initial part of zone  
271 3. From 1850 CE, the community changed gradually towards even lower PCA1<sub>diat</sub> scores and higher  
272 PCA2<sub>diat</sub> scores. Thus, from 1950 CE until present, the community clusters around PCA1<sub>diat</sub> scores of 0  
273 +/- and PCA2<sub>diat</sub> scores of 0.75-0.84. The most recent shift in the community within zone 3 was a  
274 consequence of decreasing occurrences of *C. radiosa*, *C. bodanica*, *T. glans* and *T. quadrisepata* and  
275 increasing frequencies of species such as *N. pupula*, *E. pectinalis*, *F. rhomboides* v. *amphipleuroides*,  
276 *Neidium ampliatum*, and *N. scutiformis* further up core.

277         Supplementary variables, including pelagic diatoms, TOC flux and temperature, account for  
278 57.3 % of the variation of the fitted response data along PCA1<sub>diat</sub> (pseudo-canonical correlation 0.88)  
279 and for 29.9 % along PCA2<sub>diat</sub> (pseudo-canonical correlation 0.78). PCA1<sub>diat</sub> was contrasting benthic  
280 and pelagic species, as indicated by the strong correlation between pelagic diatoms and PCA1<sub>diat</sub> (Figs.  
281 3 and 4,  $r = 0.87$ ,  $p < 0.01$ ). The most common pelagic species were *C. radiosa* and *C. bodanica*, with  
282 *A. lirata* occasionally a subdominant species, for example from 1600 to 1680 CE (data not shown).  
283 Over the whole time period studied, PCA2<sub>diat</sub> was significantly correlated with TOC flux (Fig. 4,  $r =$   
284  $0.75$ ,  $p < 0.01$ ) and with temperature (Fig. 4,  $r = 0.55$ ,  $p < 0.01$ ).

285         Diatom species richness fluctuated throughout the time period studied (Fig. 3). Minimum  
286 species richness was recorded around 1600 CE, associated with the maximum PCA1<sub>diat</sub> scores and  
287 minimum in PCA2<sub>diat</sub> scores. There was a positive, although weak trend in species richness from this  
288 time until the most recent period when species richness peaked (Fig. 3 lower panel).

289

290 Cladoceran community composition and species richness

291

292 We recorded 23 cladoceran taxa in the sediment of Lake Atnsjøen. The most common was  
293 *Eubosmina*, constituting between 71.8 and 91.3 % of the community (Fig. 3). Except for *Acroporus*  
294 *harpa* in the 12th century, no other taxon constituted > 10 %. Most of the species recorded are  
295 considered littoral species. PCA1<sub>clad</sub> and PCA2<sub>clad</sub> had eigenvalues of 0.20 and 0.14 and accounted for  
296 19.9 % and 14.3 % of the variation in the cladoceran community, respectively. The cluster analysis of  
297 the cladoceran community showed no strong zonation in the sediment core (Fig. 3 lower panel and  
298 Fig. 4 lower panels). The size structure of the community fluctuated during the study period, as  
299 indicated by the variation in the fraction of large-bodied species (*D. longispina* and *E. lamellatus*), but  
300 showed no specific trend (Fig. 3). Supplementary variables large-bodied cladocerans, TOC flux and  
301 temperature account for 57.3 % of the variation of the fitted response data along PCA1<sub>clad</sub> (pseudo-  
302 canonical correlation 0.77) and for 15.2 % along PCA2<sub>clad</sub> (pseudo-canonical correlation 0.47). The  
303 fraction of large-bodied species was significantly negatively correlated to PCA1<sub>clad</sub> ( $r = -0.69$ ,  $p <$   
304  $0.01$ ). Cladoceran species richness fluctuated throughout the studied time period, with no specific  
305 trend (Fig. 3). Species richness, however, was significantly positively correlated with the fraction of  
306 large-bodied species ( $r = 0.68$ ,  $p < 0.01$ ). Overall, relatively high occurrence of large-bodied species  
307 was associated with low PCA1<sub>clad</sub> scores and high species richness, whereas relatively low occurrence  
308 of large-bodied species was associated with high PCA1<sub>clad</sub> scores and low species richness.

309

310 Lake productivity – flux of consumers and TOC

311

312 Accumulation rates (fluxes) of turbellarians and cladocerans (both pelagic and littoral) were low until  
313 the 14th century (Fig. 5). Throughout the core, pelagic cladoceran flux was 3 to 12 times higher than  
314 littoral flux, because of the dominance of pelagic *Eubosmina*. The two, however, show similar trends,  
315 and are hereafter referred to collectively as cladoceran flux. Trichopterans were not recorded during  
316 the initial period.

**Jensen, Thomas Correll; Zawiska, Izabela; Oksman, Mimmi; Słowiński, Michał; Woszczyk, Michał; Luoto, Tomi P.; Tylmann, Wojciech; Nevalainen, Liisa; Obremska, Milena; Schartau, Ann Kristin; Walseng, Bjørn.**

Historical human impact on Productivity and biodiversity in a subalpine oligotrophic lake in Scandinavia. *Journal of Paleolimnology* 2019 ;Volum 42.(4)

DOI [10.1007/s10933-019-00100-5](https://doi.org/10.1007/s10933-019-00100-5)

317           Around 1400 CE there was a minor peak in turbellarian and cladoceran fluxes. For  
318 cladocerans this was followed by another peak of corresponding size around 1550 CE. Except for  
319 these peaks, fluxes of cladocerans and trichopterans were low until 1850 – 1880 CE. Turbellarian flux  
320 increased slightly between about 1750 CE and 1850 CE. From 1850 CE and 1880 CE, fluxes of  
321 trichopterans and cladocerans, respectively, increased to the highest levels during the whole study  
322 period. Turbellarian flux also showed a pronounced increase to a maximum around 1980 CE. This  
323 increase was somewhat delayed relative to the rise in cladoceran and trichopteran fluxes. After 1960  
324 CE there was a decrease in flux for trichopterans and somewhat later, about 1980 CE, a similar  
325 decrease for cladocerans and turbellarians.

326           TOC flux showed substantial variation during the last millennium (Fig. 5). Initially it  
327 decreased slightly until 1210 CE, followed by a slight increase until 1390. From that time onward the  
328 TOC flux displayed a decreasing trend until it reached the lowest recorded value in 1550 CE. Around  
329 1620 CE there was a peak in the TOC flux, followed by a low value in 1680 CE. Then the TOC flux  
330 increased slightly until 1850 CE, followed by an accelerated increase until the greatest maximum was  
331 reached during the period 1980 – 2000 CE, corresponding to a 5.5-fold increase in TOC flux. This  
332 noteworthy rise in TOC flux coincided with the steep increase in cladoceran and trichopteran flux, but  
333 it came somewhat before the rise in turbellarian flux. From 1990 CE onwards TOC flux decreased  
334 again, concurrent with the recent decreases in fluxes of trichopterans, turbellarians and cladocerans.

335           For the whole millennium, temperature was significantly correlated with fluxes of  
336 trichopterans, turbellarians, pelagic and littoral cladocerans and TOC (trichopteran flux:  $r = 0.49$ ,  $p <$   
337  $0.01$ ; turbellarian flux:  $r = 0.54$ ,  $p < 0.01$ ; pelagic cladoceran flux:  $r = 0.60$ ,  $p < 0.01$ ; littoral  
338 cladoceran flux:  $r = 0.67$ ,  $p < 0.01$ ; TOC flux:  $r = 0.51$ ,  $p < 0.01$ ). Furthermore, fluxes of trichopterans,  
339 turbellarians, and pelagic and littoral cladocerans were significantly correlated with TOC flux  
340 (trichopteran flux:  $r = 0.68$ ,  $p < 0.01$ ; turbellarian flux:  $r = 0.64$ ,  $p < 0.01$ ; pelagic cladoceran flux:  $r =$   
341  $0.67$ ,  $p < 0.01$ ; littoral cladoceran flux:  $r = 0.62$ ,  $p < 0.01$ ).

342           The molar TOC/TN ratio of the sediment did not show a trend, but varied between 3 and 12  
343 (mostly <10, Fig. 5) except for one value < 2 (27 cm, ~ 1220 CE) and one > 18 (14 cm, ~ 1620 CE).  
344 On the basis of a relatively high intercept of the TOC vs TN plot, it appears that there is some  
345 contribution from inorganic N in the sediments (ESM Fig. S3).

346



347 **Discussion**

348

349 Ecological changes 1000-1750 CE

350 The climate reconstruction showed large variation from 1000 to 1750 CE, as indicated by alternation  
351 between colder and warmer phases (Zawiska et al. 2017). During this long period, human activity was  
352 relatively low and climate was a strong driver of the Lake Atnsjøen ecosystem properties. The most  
353 conspicuous ecological change during this period was related to biodiversity, i.e. changes in the  
354 diatom community starting with the transition from the pre-1580 CE community towards the 1580-  
355 1710 CE community (Figs. 3 and 4). This change coincided with a considerable drop and subsequent  
356 increase in diatom species richness. The change spanned the transition from a warmer to a colder  
357 climate during the LIA. The community change involved a shift towards pelagic species dominance;  
358 in particular, *C. radioasa* increased, but *C. bodanica* and *A. lirata* also became more common. During  
359 this phase, climate changed from having relative warm and short summers (relatively high July  
360 temperatures and high bosminid sex ratios), towards longer and colder summers (lower July  
361 temperature and lower bosminid sex ratios). The increase in pelagic species at this time could have  
362 been caused by stronger mixing of the water column during the long, cold summers, caused by ocean-  
363 dominated climate that favored relatively large pelagic species (Dressler et al. 2011). *Aulacoseira*,  
364 especially, has been associated with increased periods of turbulence (Rühland et al. 2015). In general,  
365 smaller cyclotelloid species like *D. stelligera* and *C. commensis* seem to increase during periods of  
366 stronger water column stratification (Rühland et al. 2015). The *Cyclotella* species that occur in Lake  
367 Atnsjøen, *C. bodanica* and *C. radiososa*, are both relatively large species. Rühland et al (2015) also  
368 suggest that larger cyclotelloid species may increase during periods of more turbulence in the water  
369 column. The shift between benthic and pelagic species could also be related to development of the  
370 littoral zone. Whereas low occurrences of quillwort (*Isöetes lacustris*) are associated with both high  
371 and low frequencies of pelagic species in Lake Atnsjøen, higher frequencies of this macrophyte were

372 only accompanied by lower frequencies of pelagic diatoms (data not shown). Length of the growing  
373 season may have a strong impact on macrophyte communities (Lacoul and Freedman 2006). Varying  
374 growing season length could have impacted the abundance of *I. lacustris* through effects on light and  
375 temperature and/or the availability of nutrients (via stratification). Higher occurrences of *I. lacustris*,  
376 reflecting development of the littoral zone, would favor benthic diatom species and vice versa. The  
377 transition from the 1580-1710 CE diatom community to the 1710-1850 CE community is discussed  
378 further below.

379         Climate shifts also influenced lake productivity until 1750 CE, as indicated by changes in  
380 fluxes of consumers and TOC (Manca et al. 2007). The first cold period, 1050-1150 CE, was  
381 associated with a slight decrease in fluxes of TOC and turbellarians. A very low TOC/TN ratio  
382 occurred during the warm period from 1150–1270 CE, but it was not accompanied by increased TOC  
383 flux. Presence of inorganic N in the sediment could explain the low TOC/TN ratio. Inorganic nitrogen  
384 in the sediment could have several sources. Nitrogen released from decomposition of organic matter  
385 within the sediments has little impact on the TOC/TN ratio, so the low ratio could be a consequence of  
386 inorganic nitrogen from catchment soils, e.g. as ammonia adsorbed to clay particles (Schubert and  
387 Calvert 2001), or from volcanic eruptions (Robinson 1994). We cannot, however, identify the nitrogen  
388 sources using our data.

389         The warmer period from 1370 CE to 1420 CE was associated with increasing fluxes of TOC,  
390 cladocerans and turbellarians. A short, very cold period in the 15th century affected lake productivity  
391 negatively, as indicated by decreasing fluxes of TOC, cladocerans and turbellarians. The subsequent  
392 short, moderately warm period from 1490 to 1550 CE led to minor increases in TOC and cladoceran  
393 fluxes. A longer cold phase from 1550 to 1800 CE, the LIA, ended the period of lower human activity  
394 and overlapped with the period of human settlement that began after 1750 CE (Table 1). This long  
395 cold period had a strong impact on lake productivity, as was observed at other lakes in Scandinavia  
396 (Luoto et al. 2008). In Lake Atnsjøen, it manifested as decreased fluxes of TOC and consumers. The

397 peak in TOC/TN ratio around 1620 CE suggests that soil-derived organic matter from the catchment  
398 may have contributed to the coincident local peak in TOC flux (Meyers 1994). In addition to low  
399 summer temperatures, climate impacts during the LIA also seemed to be mediated by a shorter open-  
400 water season, as indicated by the increasing bosminid sex ratio.

401

402 Ecological changes – 1750 CE to present

403

404 The most striking ecological change during the last 250 years of increasing human activity was related  
405 to changes in lake productivity. The initial part of this period overlapped with the LIA, as noted above,  
406 associated with dramatic climate changes. Initially, the length of growing season increased (decreasing  
407 bosminid sex ratio) and the time window from 1750 CE to 1880 CE was associated with an  
408 unprecedented increase in temperature (4.4 °C). During the first part of the settlement period there  
409 were no major changes in fluxes of TOC and consumers. From 1850 to 1900 CE productivity began to  
410 increase, as indicated by increasing fluxes of TOC, trichopterans, turbellarians and cladocerans.  
411 Hence, the pronounced temperature increases caused only a moderate increase in fluxes. Low  
412 temperatures may have damped potential productivity effects of the initial human settlement in this  
413 time window.

414 The fluxes of TOC, trichopterans, turbellarians and cladocerans, all showed a remarkable  
415 increase after 1880 CE, peaking in the period 1950 – 1980 CE, although the exact timing differed  
416 slightly among proxies. This was after the period of accelerated climate warming. From 1880 CE to  
417 present, July temperature showed only a minor increase and low variation. Hence, climate was of  
418 minor importance for this increase in lake productivity. The increase in productivity paralleled the  
419 increase in human settlements, suggesting that greater human activity contributed to the rise in lake  
420 productivity. Additionally, several changes in land use in the catchment occurred in this period. This

421 involved changes in agriculture and industrialization (Table 1 and references cited therein). Forestry  
422 was mechanized ca. 1950 CE and in subsequent decades. Thus, there was land-use intensification in  
423 the catchment, which stimulated lake productivity even after the number of settlements and the  
424 population size decreased from 1950 CE. Although the area around Lake Atnsjøen was not used for  
425 crop cultivation because of harsh climate and nutrient-poor soils (Brænd 1989), extensive agricultural  
426 practices, including grazing and hay production (Table 1), may have contributed to increased erosion  
427 and nutrient flux from the catchment (Massa et al. 2012). Likewise, deforestation during the settlement  
428 period (Table 1) likely also contributed to increased erosion and washout of nutrients (Koinig et al.  
429 2003). Intensification of land use, beginning about 1920 CE, would have amplified this process. For  
430 example, cultivation of infields/pastures and initiation and increasing use of chemical fertilizers  
431 between the world wars, in addition to the mechanization of forestry, likely also contributed to greater  
432 input of nutrients to the catchment, thereby stimulating lake productivity (Bragée et al. 2013; Millet et  
433 al. 2014). Even though increasing human activity in the catchment of Lake Atnsjøen stimulated lake  
434 productivity, it did not manifest in decreased TOC/TN ratios. On the contrary, the TOC/TN ratio  
435 increased somewhat from 1880 CE onwards. Likewise, a study by Millet et al. (2014) at Lake Igaliku  
436 in southern Greenland showed that extensive Norse farming (grazing of cattle, sheep and goats) from  
437 1000- to 1400 CE, as well as Norse-analog farming from 1900 to 1980 CE, elicited increased TOC  
438 flux and higher TOC/TN ratio in the sediments. It was only with the shift from Norse-analog farming  
439 to modern practices after 1980 that the sediment TOC/TN ratio decreased, showing a strong human  
440 impact on the lake ecosystem. Apparently, anthropogenic pressures in the Lake Atnsjøen catchment,  
441 even during the periods of highest human activity, were too low to elicit a decrease in sediment  
442 TOC/TN ratio.

443         Low molar TOC/TN ratio of the sediment (< 10) indicates that the carbon pool in the sediment  
444 was mostly autochthonous in origin (Meyers 1994). Lake Atnsjøen is relatively large and deep, with a  
445 very poorly developed littoral zone because of steep slopes close to the lake shore. The lake has a  
446 sparse macrophyte community, consisting mainly of *I. lacustris* (Halvorsen 2004; Zawiska et al.

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Historical human impact on Productivity and biodiversity in a subalpine oligotrophic lake in Scandinavia. *Journal of Paleolimnology* 2019 ;Volum 42.(4)  
DOI [10.1007/s10933-019-00100-5](https://doi.org/10.1007/s10933-019-00100-5)

447 2017). The contribution of littoral primary producers to total primary production in large and deep  
448 lakes is relatively small (Doi 2009). Hence, phytoplankton production likely dominated primary  
449 production in Lake Atnsjøen, and is confirmed by the low TOC/TN values.

450         Decreasing fluxes of TOC, trichopterans, turbellarians and cladocerans, during the most recent  
451 decades, indicate decreasing lake productivity, which is supported by lake monitoring data. In 1980  
452 CE average concentrations of phytoplankton biomass, total phosphorus and total nitrogen were 240  
453  $\text{mm}^3/\text{m}^3$ ,  $7.4 \mu\text{g l}^{-1}$  and  $396 \mu\text{g l}^{-1}$  respectively (Holtan et al. 1982). For the period 2003 - 2011 CE  
454 these variables had decreased to  $132 \text{mm}^3/\text{m}^3$ ,  $4.2 \mu\text{g l}^{-1}$  (2005 – 2011 CE) and  $135 \mu\text{g l}^{-1}$  (2005 –  
455 2009, CE Jensen unpublished data), respectively, indicating decreased lake productivity. Nevertheless,  
456 the lake was oligotrophic even during the most productive period. Decreased lake productivity after  
457 1980 CE corresponds with information about human settlement/activity and land use in the area. From  
458 1950 CE, the number of permanent settlements with agricultural activity (livestock and/or land used  
459 for fodder production) in the catchment decreased by 25 %, and in the neighboring Folldal  
460 municipality the population decreased by 27 % from 1950 CE to present (Table 1, Dahl [1960]; A.  
461 Alander pers. commun.; H.E. Nettet pers. commun.). Apparently, this overall reduction in human  
462 pressure resulted in decreased lake productivity, likely a consequence of reduced erosion and input of  
463 nutrients to the lake from the catchment. Overall, both climate and human presence/activity affected  
464 productivity in Lake Atnsjøen during the settlement period, but productivity was more closely related  
465 to human presence and changes in land use than to climate, especially during the last 130 years.

466         The transition from the 1580 - 1710 CE diatom community to the 1710 - 1850 CE community  
467 coincided with the end of the LIA and the beginning of accelerated climate warming, with strong  
468 impact on the length of the growing season. The 1710 - 1850 CE community also overlapped with the  
469 initial settlement period. Low TOC fluxes at that time, however, indicated that human impact from  
470 1800 – 1850 CE was still very low. Hence, climate was probably still a major driver of the diatom  
471 community, explaining the decreasing frequencies of pelagic *A. lirata* and pelagic/benthic *T.*

472 *quadriSeptata* (Rühland et al. 2015). The change in the diatom community from 1850 CE to the post-  
473 1950 community was also associated with a decrease in pelagic species, initially *C. radiosa*, and later,  
474 *C. bodanica*. The almost complete disappearance of pelagic species after 1960 CE is probably partly  
475 climate-induced, caused by warm, relatively long summers with stronger stratification of the water  
476 column. As the increase in lake productivity in Lake Atnsjøen after 1850 CE was relatively moderate,  
477 within the ultraoligotrophic to oligotrophic range, one would not expect a major shift in diatom species  
478 composition. In accordance with this, most of the diatom species recorded are oligotrophic or  
479 oligotrophic/mesotrophic indicators (Philibert and Prairie 2002; Miettinen 2003; Bigler et al. 2007;  
480 Chen et al. 2008; Ptacnik et al. 2008; Hobæk et al. 2012). Some of the species, however, that appeared  
481 in higher frequencies after 1850 CE are mesotrophic (*N. pupula*, *N. ampliatum*) or even eutrophic  
482 indicators (*N. clemensis*). It thus appears that increasing human settlement and activity after 1850 CE,  
483 in addition to climate, had a moderate impact on the diatom community, which is indicative of a  
484 slightly higher trophic status than before 1850 CE.

485

486 Effects of human impacts on productivity and biodiversity

487

488 Bottom-up control of aquatic food webs is typically strongest at the base of the food web and  
489 decreases at higher trophic levels (McQueen et al. 1986). Our results from Lake Atnsjøen agree with  
490 this claim. The magnitude of the bottom-up signal, however, seemed to differ for biodiversity and lake  
491 productivity. Regarding biodiversity, the increase in human activity was associated with a moderate  
492 change in diatom community composition, i.e. relative abundances, but not species richness. This  
493 bottom-up influence on biodiversity, however, did not propagate up the food web to the consumers, as  
494 no noticeable effect on cladoceran community composition and species richness was detected. In  
495 contrast, the bottom-up signal mediated by human impact, resulting in increased TOC flux, cascaded

496 up the food web, resulting in greater fluxes of different groups of consumers (trichopterans,  
497 turbellarians and cladocerans).

498         There are several possible reasons for different responses to increasing human activity around  
499 Lake Atnsjøen with respect to biodiversity and lake productivity. Factors other than human impact  
500 may have been more important in regulating biodiversity in Lake Atnsjøen. For example, silicon is an  
501 important nutrient for diatoms and has been shown to be an important driver of diatom communities  
502 (Willén 1991). The long-term decrease of *T. glans* in Lake Atnsjøen from 1500 CE onwards, might be  
503 related to silica availability, as this species has relatively high Si requirements (Michel et al. 2006).  
504 Regarding consumers, the cladoceran community in Lake Atnsjøen could be under stronger top-down,  
505 relative to bottom-up control. We observed a change in the size ratio of the cladoceran community  
506 with the change in community composition and species richness. Fish predation often has an  
507 overriding impact on this zooplankton community trait, with large-bodied species favored at relative  
508 low levels of fish predation, and smaller species favored under conditions of higher fish predation  
509 (Brooks and Dodson 1965). The most common fish species in Lake Atnsjøen are Arctic char  
510 (*Salvelinus alpinus*) and brown trout (*Salmo trutta*), which dominate the pelagic and littoral zones,  
511 respectively. Although both species utilize crustacean zooplankton (largely cladocerans) as food, char  
512 is the most important zooplankton predator in Lake Atnsjøen and shows a strong preference for larger  
513 species like *Daphnia* (Saksgård and Hesthagen 2004, O.T. Sandlund et al. unpublished data). We  
514 suggest that changing fish predation was a main driver of cladoceran diversity (community  
515 composition and species richness) in Lake Atnsjøen over the last millennium. Furthermore, we cannot  
516 exclude the possibility that zooplankton exert a top-down control on the diatom assemblages in Lake  
517 Atnsjøen through grazing, although losses of diatoms to zooplankton grazing are likely more  
518 important at higher trophic state (Sommer et al. 1986). Finally, the different responses to increasing  
519 human activity, with respect to biodiversity and productivity in Lake Atnsjøen, could relate to the  
520 range of changes in trophic state/nutrient concentrations that Lake Atnsjøen has endured. The lake  
521 constitutes a low-resource environment with low concentrations of nutrients and low phytoplankton

522 biomass. Even during the most productive period in the lake, from 1960 to 1990 CE, the lake was still  
523 oligotrophic (Holtan et al. 1982). The cladoceran community in the Lake Atnsjøen sediment resembles  
524 that typically encountered in nutrient-poor Norwegian lakes, characterized by oligotrophic indicators.  
525 For example, the dominant cladoceran taxon throughout the millennium, *Eubosmina*, is a common  
526 species that often dominates the zooplankton in ultraoligotrophic to oligotrophic lakes. In more  
527 productive lakes it is replaced by *B. longirostris* (Jensen et al. 2013). Thus, from the limited change in  
528 productivity experienced in Lake Atnsjøen, one would not expect a major species replacement (Jensen  
529 et al. 2013), in agreement with the low species turnover in Lake Atnsjøen (short primary DCA-axes  
530 cladocerans, 0.99). For comparison, a slight increase in resource availability in the low-resource range  
531 for cladocerans causes a major increase in cladoceran growth/production (Urabe 1991; Lampert and  
532 Trubetskova 1996). In ultraoligotrophic and oligotrophic lakes, a minor increase in nutrient input and  
533 primary productivity may therefore lead to significant bottom-up cascades on productivity of  
534 consumers because consumers are somewhat relieved from strong resource limitation.

535         There are few comprehensive single lake studies of increasing human impact/nutrient loading  
536 in oligotrophic lakes that include aspects of both biodiversity and productivity and consider multiple  
537 trophic levels. Oligotrophic, perialpine Lake Annecy, was studied intensively and showed a period  
538 human-induced eutrophication ca. 1950-1980, followed by oligotrophication (Perga et al. 2010; Alric  
539 et al. 2013; Berthon et al. 2014). In contrast to Lake Atnsjøen, both the productivity signal and the  
540 biodiversity signal in Lake Annecy propagated to the trophic level of the consumers, in response to  
541 increasing nutrient loading. Differences in human pressure and different ranges of change in trophic  
542 state likely explain the different ecological responses of the two lakes. Lake Atnsjøen, exposed to low  
543 human pressures, underwent change in the ultraoligotrophic to oligotrophic range. Lake Annecy,  
544 exposed to much greater human pressure (Crook et al. 2004), experienced a change in the  
545 oligotrophic-mesotrophic range (Perga et al. 2010; Berthon et al. 2014). Hence, the trophic state in  
546 Lake Annecy was skewed toward optima for mesotrophic and eutrophic indicators during the more



547 productive period. For example, the eutrophic indicator *B. longirostris* appeared in the lake after  
548 eutrophication (Perga et al. 2010).

549

## 550 **Conclusions**

551

552 Our study of Lake Atnsjøen showed that even low levels of human activity can have profound effects  
553 on oligotrophic subalpine lake ecosystems. Climate was the primary driver of lake ecology in the first  
554 750 years of the study period, whereas human presence and changes in land use were more important  
555 drivers of ecosystem change in the last two centuries, especially during the most recent 130 years. Our  
556 study emphasizes the need to study human and climate impacts on aquatic ecosystems in concert. The  
557 results also demonstrate that increasing trophic status in the ultraoligotrophic to oligotrophic range  
558 may have different effects on productivity and biodiversity, which has implications for monitoring and  
559 management of freshwaters. Many biological indices used for assessment of water quality are based  
560 on changes in the diversity of biological communities in response to a given stressor, for example  
561 eutrophication. Because increasing nutrient loading of lakes at the very low end of the trophic state  
562 spectrum may have stronger effects on production than on biodiversity, the indices based on biological  
563 diversity may not capture this early evidence of eutrophication. This study highlights the importance  
564 of emphasizing aspects of productivity in biological indices that are used to assess water quality, thus  
565 providing an early warning signal for the eutrophication process.

566

## 567 **Acknowledgements**

568

569 This research was funded by the EEA and Norway Grants (Grant no. FSS/2013/IIC/W/0022) and the  
570 Norwegian Institute for Nature Research. We thank H.E. Nettet, A. Alander and B. Brænd for help  
571 and information about the local history of the study area. We thank Kristin Thorsrud Teien for  
572 linguistic corrections. The manuscript also benefited from valuable suggestions and comments of two  
573 anonymous reviewers.

574

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804

805 **Tables**

806 **Table 1** Human activity and land use in the Lake Atnsjøen catchment and vicinity during the last  
 807 millennium. Text in italics is information from pollen analysis (Zawiska et al. 2017)

Period	Human activity/land-use from historical records and pollen analysis
1756 – present, <i>higher human activity</i>	<ul style="list-style-type: none"> <li>• 1950s-1980s: Industrialization/mechanization of agriculture and forestry in the Atna area. Construction of forest roads opened new areas for forestry.</li> <li>• 1950s-present: Decreasing population, number of farms/settlements in the catchment, as well as the number of livestock.</li> <li>• 1920s/1930s onwards: Initiation in use of chemical fertilizers in the Atna area (more cultivated areas and higher production of hay/fodder for the livestock).</li> <li>• 1920s/1930s: State subsidies to manure and cultivate pastures/infields for production of hay/fodder.</li> <li>• 1900-1950: Decreasing number of saeters, cessation of vertical transhumance and production of hay (NO: “slåttebruk”) around 1950 – <i>decreasing HPI and increasing AP/NAP reflect reforestation of the landscape likely due to decreased use of the area for grazing and hay/fodder production.</i></li> <li>• 1756-1950: Increasing population in the catchment – <i>reflected in increasing HPI.</i></li> <li>• 1756: First permanent settlements established in the catchment.</li> <li>• ~1750-1950: Extensive agricultural practices mainly based on animal husbandry including vertical transhumance combined with production of hay. Vertical transhumance consisted in moving the livestock to a mountain farm (saeter) in summer in order to preserve meadows in valleys for producing hay. During autumn, grazing in the mountains became limited and the livestock were moved back to the home farm. “Slåttebruk” is the harvesting of grass/hay from uncultivated areas (e.g. mires, meadows etc.) and use of this resource as food for the livestock - <i>increasing HPI and decreasing AP/NAP reflect increasing agricultural activity and related deforestations. Pollen from cereals recorded only occasionally in the sediments which confirms the animal-based agricultural practice with few attempts to grow crops due to a harsh climate and a nutrient poor soil.</i></li> </ul>

Period	Human activity/land-use from historical records and pollen analysis
<p>Eleventh century – 1756, <i>low human activity</i></p>	<ul style="list-style-type: none"> <li>• 1748(-1993): Mining activity (copper, sulfur, zinc, iron, gold and silver) in the neighboring Folldal community (“Folldal verk”), 30 km from Lake Atnsjøen. No direct influence on the lake because mining area was not located in the catchment of Lake Atnsjøen. Forests in the area, however, were utilized as a source of wood for mining in Folldal and elsewhere in the region. Timber was also used for tar production in the Atna area. Collectively, these activities likely led to deforestation of the area – <i>low levels of AP/NAP from mid-18th to mid-20<sup>th</sup> century reflect landscape opening.</i></li> <li>• 1700-1750: Several saeters established in the catchment.</li> <li>• ~1700: Two attempts to establish permanent settlement upstream of Lake Atnsjøen.</li> <li>• 1690s: Several permanent settlements established downstream of Lake Atnsjøen.</li> <li>• 1550-1800: Little Ice Age – <i>decreasing HPI indicate strong climate constraints on human activity.</i></li> <li>• 1400-1600: Increase in human activity in the area from evidence for hunting - <i>increasing HPI and decreasing AP/NAP indicate landscape opening in the middle/late 16th century as a result of vertical transhumance /production of hay.</i></li> <li>• 1350-1756: No permanent settlements in the Lake Atnsjøen catchment - <i>very low HPI and high AP/NAP indicate low human presence immediately after the Black Death.</i></li> <li>• 1348/1349 and the following decades: Population in Norway reduced by ~50% by the Black Death.</li> <li>• 1050-1348/1349: Expansion of human activity in the area, likely with permanent settlements - <i>increasing HPI and decreasing AP/NAP indicate increasing human activity (landscape opening) in the beginning of the 13th century.</i></li> <li>• ~800-1050: Archeological findings from the outlet of Lake Atnsjøen suggest permanent settlements in the area in Viking age, related to animal husbandry and reindeer hunting - <i>low HPI and high AP/NAP indicate relatively low human activity until the middle/late 11th century.</i></li> </ul>

808 Information based on Dahl (1960), Mikkelsen (1980), Brænd (1989, 2007, 2009), Oeding (Oeding 1990),  
809 Bækkelund and Kalvatn (1998), Zawiska et al (2017), A. Alander (pers. commun.), H.E. Nasset (pers. commun.)  
810

811 **Figure captions**

812

813 **Fig. 1** Left panel: Map of Scandinavia with the location of Lake Atnsjøen (white circle). Right panel:  
814 Map of Lake Atnsjøen with sampling site (white circle). Also indicated are inlet and outlet rivers  
815 (black arrows), and depth contours (grey shading)

816 **Fig. 2** Historical records of population in Folldal, the neighboring community to the area around Lake  
817 Atnsjøen), permanent settlements and “saeters” in the catchment of Lake Atnsjøen, human pollen  
818 indicators (sum of *Rumex acetosa/acetosella* type, *Plantago lanceolata*, *Plantago media/major* type,  
819 *Anthemis* type, *Artemisia*, Chenopodiaceae, *Urtica*, *Cannabis sativa* type, *Secale cereale* and Cerealia  
820 undiff.) and ratio of arboreal pollen (AP) to non-arboreal pollen (NAP) in the Lake Atnsjøen sediment  
821 core. Data on Folldal population are from A. Alander (pers. commun.) and relate to the area of the  
822 current Folldal municipality. Data on permanent settlements and “seaters” come from Dahl (1960) and  
823 H.E. Nasset (pers. commun.). Pollen data are from Zawiska et al. (2017). Periods of low (1000 – 1750  
824 CE) and high (1750 CE - present) human activity are separated by a dashed line. Periods of cooling  
825 according to Zawiska et al. (2017) are highlighted by grey shading

826

827 **Fig. 3** Stratigraphic diagrams from the Lake Atnsjøen sediment core. Upper panel: Relative  
828 abundances of the 21 most common diatoms in the sediment. *Cyclotella bodanica*, *C. radiosa* and  
829 *Aulacoseira lirata* (not shown in figure) comprise the pelagic species. The rest are  
830 benthic/meroplanktonic. Middle panel: Relative abundances of cladocerans in the sediment. *Daphnia*  
831 *longispina* and *Eubosmina* comprise the pelagic taxa and the rest are littoral taxa. Lower panel:  
832 Diatom PCA1 and PCA2 scores, diatom species richness (SR), percentage of pelagic diatoms,  
833 cladoceran PCA1 and PCA2 scores, cladoceran species richness (SR), percentage of pelagic  
834 cladocerans and percentage of large-bodied cladocerans. Periods of low (1000 – 1750 CE) and high

835 (1750 CE - present) human activity are separated by dashed line. Periods of cooling according to  
836 Zawiska et al. (2017) are highlighted by grey shading. In the diatom diagram, zones are indicated by  
837 Diat 1, Diat 2 and Diat 3, and are separated by grey lines

838

839 **Fig. 4** PCA of the diatom and cladoceran communities in the sediment of Lake Atnsjøen. Upper left  
840 panel: PCA ordination plot of the diatom community in the sediment layers from 1 to 34 cm depth.  
841 Upper right panel: PCA ordination plot of diatom species (showing the 25 best fitting species on both  
842 axes) with the three major diatom zones delineated. Chironomid-inferred July temperature  
843 (Temperature), flux of organic carbon (TOC flux) and percentage of pelagic diatoms (pelagic diatoms)  
844 are added as supplementary variables and do not affect the PCA analysis. Diatom species in plot are  
845 abbreviated as follows: *Achnantes minutissima* (Aminut), *Aulacoseira lirata* (Alirata), *Cyclotella*  
846 *bodanica* (Cbodan), *C. radiosa* (Cradio), *Cymbella minuta* (Cminuta), *Denticula tenuis* (Dtenuis),  
847 *Eunotia argus* (Earcus), *E. minor* (Eminor), *E. muscicola v. tridentula* (Emusciv), *E. pectinalis* (Epect),  
848 *E. praerupta* (Epraer), *Fragilaria brevistriata* (Fbrevs), *F. virescens* (Fvires), *Frustulia rhomboides v.*  
849 *amphipleuroides* (Frombv), *Gomphonema acuminatum* (Gacumn), *Navicula clementis* (Nclem), *N.*  
850 *pupula* (Npupula), *N. scutiformis* (Nscutf), *Neidium ampliatum* (Nampli), *N. productum* (Nprodc),  
851 *Synedra parasitica* (Sparas), *Tabellaria quadriseptata* (Tquadr), *T. ventricosa* (Tventr), *Tetracyclus*  
852 *glans* (Tglans). Lower left panel: PCA ordination plot of the cladoceran community in the sediment  
853 layers from 1 to 34 cm depth. Lower right panel: PCA ordination plot of cladoceran species with the  
854 three cladoceran zones delineated (samples 23 and 29 were not grouped with any of the other  
855 samples). Temperature, TOC flux and large cladocerans are added as supplementary variables and do  
856 not affect the PCA analysis. Cladoceran species in plot abbreviated as: *Acroperus harpae* (Aharp),  
857 *Alona affinis* (Aaff), *A. costata* (Acost), *A. guttata* (Agutt), *A. intermedia* (Ainter), *A. quadrangularis*  
858 (Aquadr), *A. rectangula* (Arect), *Alonella excisa* (Aexci), *A. nana* (Anan), *Alonopsis elongata*  
859 (Aelong), *Camptocercus lilljeborgi* (Clill), *C. rectirostris* (Crect), *Chydorus sphaericus* (Csphae),



860 *Daphnia longispina* (Dlong), *Eubosmina* (Eubosm), *Eurycercus lamellatus* (Elam), *Graptolebris*  
861 *testudinaria* (Gtest), *Kurzia latissima* (Klati), *Leydigia leydigi* (Lley), *Paralona pigra* (Ppigr),  
862 *Pleuroxus laevis* (Plaev), *P. truncates* (Ptrunc), *Rhynchotalona falcata* (Rfalc)

863

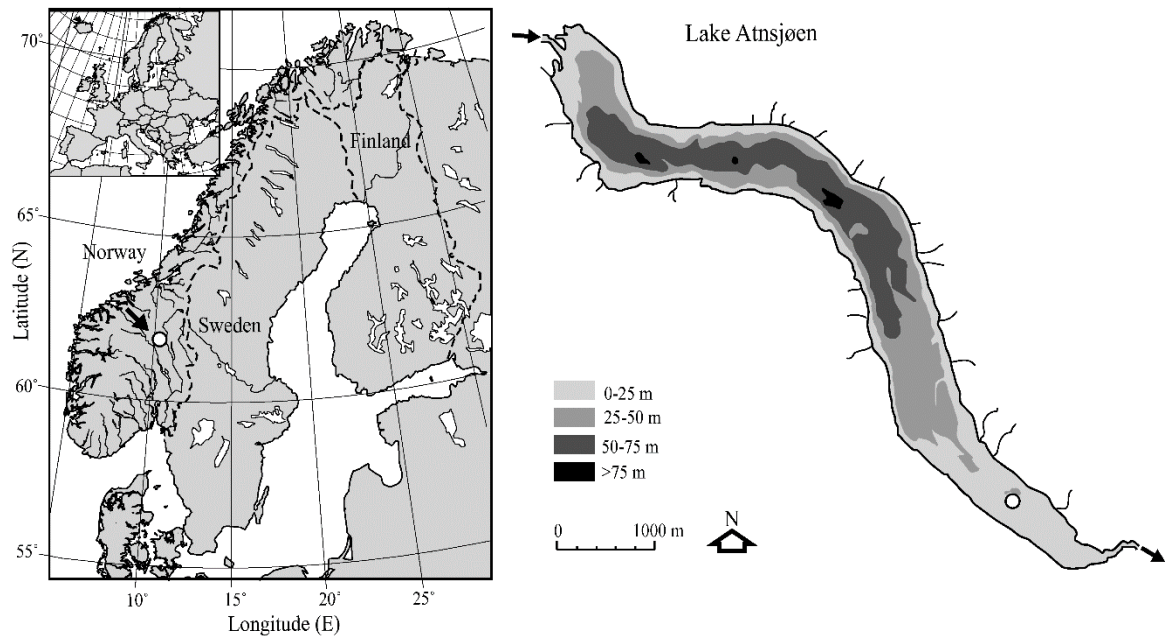
864 **Fig. 5** Stratigraphic diagram from Lake Atnsjøen sediment core showing trichopteran flux, turbellarian  
865 flux, pelagic cladoceran flux, littoral cladoceran flux, TOC flux (Zawiska et al 2017), ratio of arboreal  
866 pollen (AP) to non-arboreal pollen (NAP), human pollen indicators (HPI, Zawiska et al. 2017),  
867 chironomid-inferred July air temperature (Zawiska et al. 2017) and bosminid sex ratio (Zawiska et al.  
868 2017), and TOC/TN ratio (molar). Periods of low (1000 – 1750 CE) and high (1750 CE - present)  
869 human activity are indicated in the diagram. Also, periods of cooling, according to Zawiska et al.  
870 (2017), are highlighted

871

872 **Figures**

873

874 Fig. 1

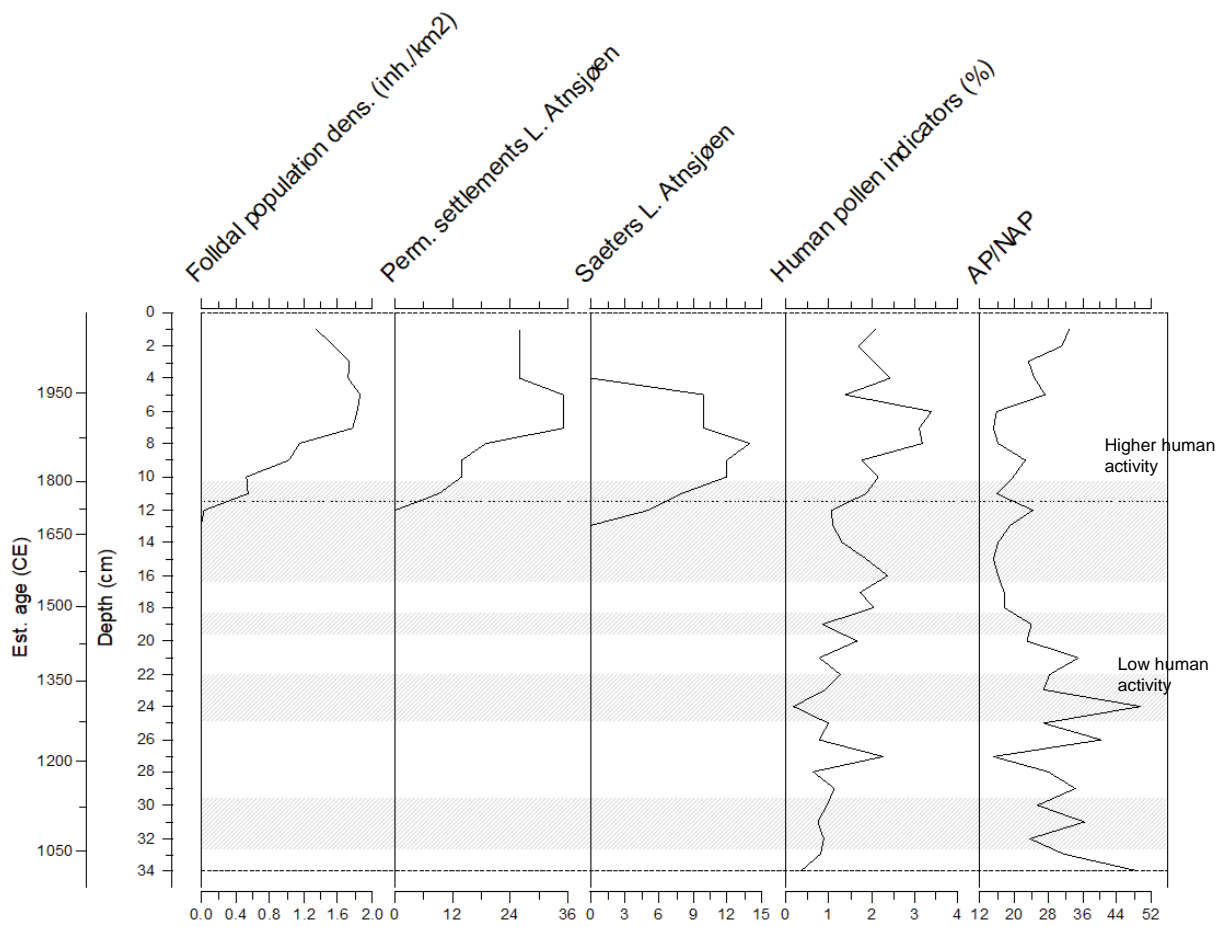


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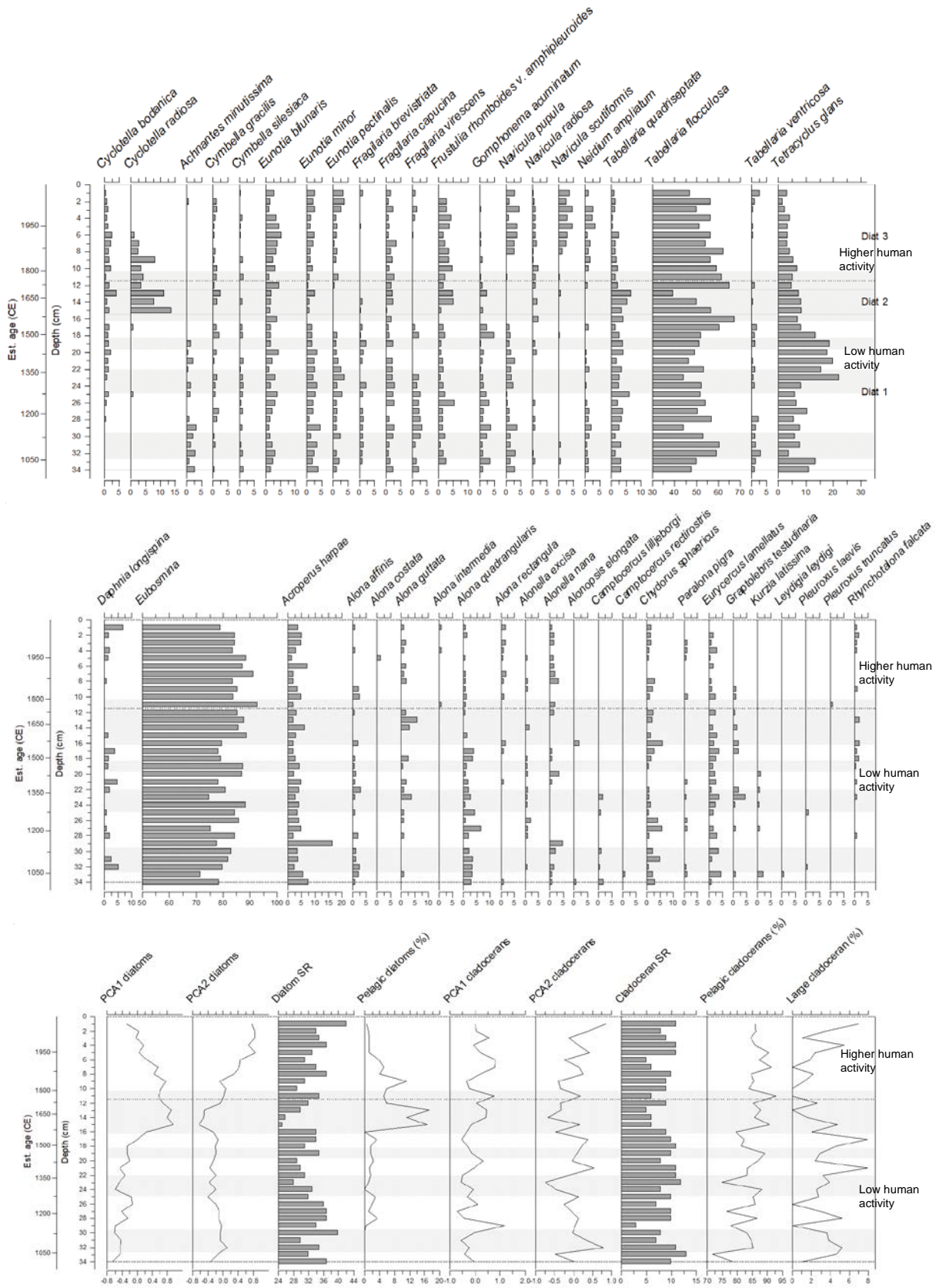
878 Fig. 2



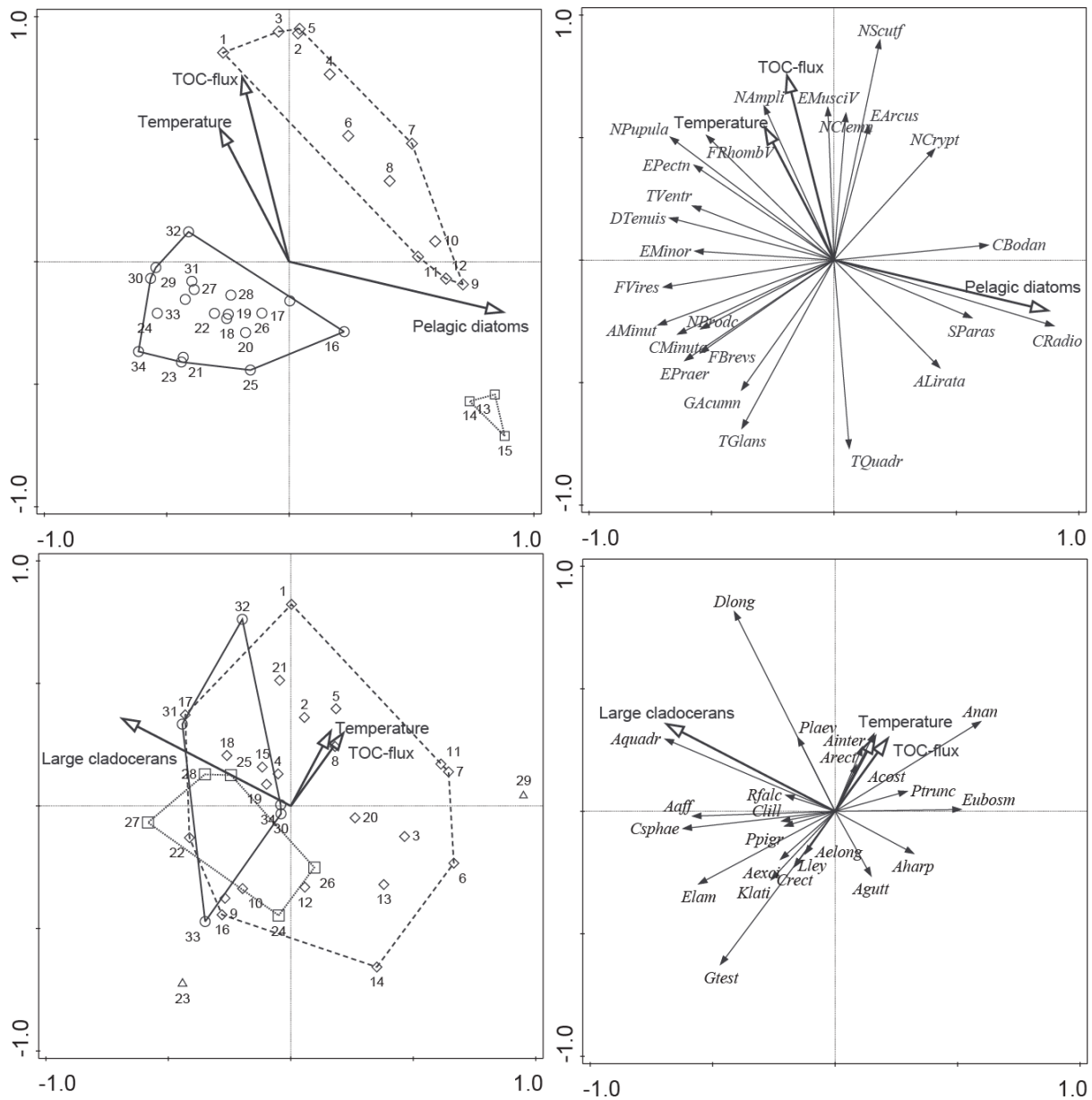
879

880

881 Fig. 3



883 Fig. 4

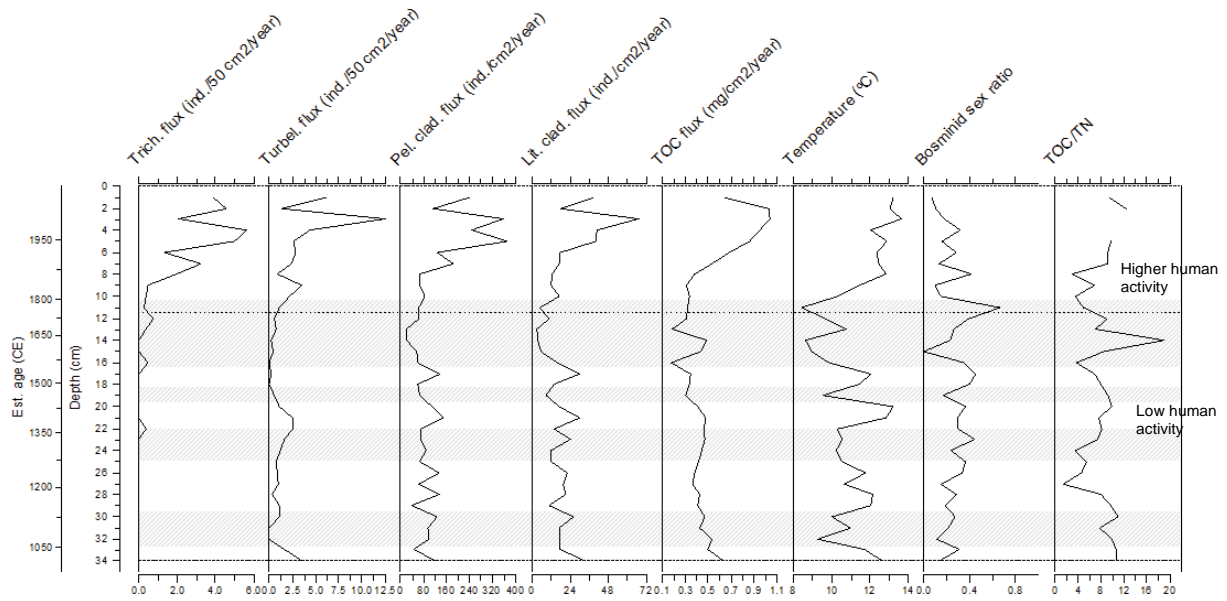


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885

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887 Fig. 5



Jensen, Thomas Correll; Zawiska, Izabela; Oksman, Mimmi; Słowiński, Michał; Woszczyk, Michał; Luoto, Tomi P.; Tylmann, Wojciech; Nevalainen, Liisa; Obremska, Milena; Schartau, Ann Kristin; Walseng, Bjørn. Historical human impact on Productivity and biodiversity in a subalpine oligotrophic lake in Scandinavia. *Journal of Paleolimnology* 2019 ;Volum 42.(4)  
DOI [10.1007/s10933-019-00100-5](https://doi.org/10.1007/s10933-019-00100-5)