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Large and deep perialpine lakes: a paleolimnological perspective for the advance of ecosystem science.

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Abstract

The present paper aims at reviewing general knowledges of large European perialpine lakes as provided by sediment studies, and at outlining the contribution, from several lines of evidence, of modern paleolimnology in both interpreting past lake ecological evolution and forecasting lake responses to future human impacts. A literature survey mainly based on papers published in international journals indexed on ISI-Wos and Scopus from 1975 to April 2017 has been conducted on the 20 perialpine lakes with $z_{\max} \geq 100$ m and lake area ≥ 10 km², and on four shallower perialpine lakes representing hotspots of extensive neo- and paleo-limnological research. By pinpointing temporal and spatial differences in paleolimnological studies conducted in the Alpine countries, the review identifies knowledge gaps in the perialpine area, and shows how sediment-based reconstructions represent a powerful tool, in mutual support with limnological surveys, to help predicting future scenarios through the “past-forward” principle, which consists in

32 reconstructing past lake responses to conditions comparable to those to come. The most recent methodological
33 developments of sediment studies show the potential to cope with the increasing ecosystem variability induced by
34 climate change, and to produce innovative and crucial information for tuning future management and sustainable use of
35 Alpine waters.

36

37 **Key words:** perialpine lakes, lake sediments, human impact, eutrophication, paleoclimate, global change.

38

Introduction

According to the classification by Timms (1992), large and deep perialpine lakes (LDPL) are distinguished from the other two major categories of alpine lakes (i.e. high alpine and alpine) based on their piedmont position and their tectonic-glacial origin, which is related to the past dynamics of large Alpine glaciers occupying ancient and deep canyon-valleys (Bini et al., 1978).

LDPL represent a key water resource for the densely populated Alpine region. For example, the five largest Italian subalpine lakes represent ~80% of the total Italian freshwater resources (Salmaso & Mosello, 2010), while L. Geneva and L. Constance provide drinking water for >800,000, respectively ~ 5 million people (CIPEL, Commission internationale pour la protection des eaux du Léman, www.cipel.org, Petri, 2006). LDPL are extensively used also for irrigation and industry, and represent key regional resources for tourism, while waters within the LDPL catchments are intensively used for hydropower production since the 1930s (Salmaso & Mosello, 2010; Wüest et al., 2007). Concern about the sustainability of these ecosystem services among stakeholders and end-users stimulated the launching of long term monitoring programmes of some key LDPL already in the 1950/60s. Intensification of the research activity at local and regional level took place at some sites in the late 1990s (e.g. within the European Long Term Ecological Research network, LTER, <http://www.lter-europe.net>), with the objective of assessing future vulnerability of perialpine lakes and outlining common developing trends within the modern context of multiple and transboundary human impacts. The results of these studies pinpointed that nutrient enrichment related to resident and tourist population still represents a major human threat for several LDPL. Perialpine lakes are still exposed to point-source pollution (e.g. from productive activities), but airborne NO_x (Rogora et al., 2006), persistent organic pollutants (POPs) from agriculture, urban and industrial areas (Guzzella et al., 2018), as well as “new” pollutants, such as microplastics (Faure et al., 2012; Imhof et al., 2013) and drugs inducing antibiotic resistance (Di Cesare et al., 2015), currently represent the most widespread contamination threat. Alien species, which easily spread also in relation to tourist transfer (Gherardi et al., 2008), are becoming a crucial issue for the conservation of biodiversity and ecosystem services of LDPL.

Nevertheless, the sensitivity of LDPL to climate change currently represents a hot issue due to the tight relation existing between LDPL physiography, their peculiar thermal dynamics (i.e. holomixis with complete thermal circulation only after cold and/or windy winters, Ambrosetti et al., 2003), and major atmospheric circulations (Salmaso et al., 2014). These factors together represent key drivers of transport processes in water and sediments, and of water chemistry, nutrient availability, water transparency, and biological dynamics of LDPL (e.g. Manca et al., 2000; Straile et al., 2003;

69 Jankowski et al., 2006; George, 2010; D'Alelio et al., 2011). Water temperature is increasing in many lakes of the
70 northern hemisphere, including perialpine lakes (O'Reilly et al., 2015), but the evidence that global warming is more
71 pronounced in mountain regions (Gobiet et al., 2014) is of particular concern, as the LDPL catchments extend to the
72 glacial Alpine ranges. The progressive Alpine deglaciation and the changing precipitation pattern predicted for the 21st
73 century (Beniston, 2006; IPCC, 2013; Radić et al., 2014) have the potential to strongly affect the hydrological regime of
74 perialpine lake catchments, and to produce negative ecological and socio-economic effects related to water scarcity.
75 The present context of multiple stressors and superimposed global warming is challenging the sustainable management
76 of LDPL, especially in connection to the insufficient knowledge of the complex interactions between local human
77 impacts and climate variability, and of the related lake ecological responses. On the other hand, the present
78 environmental and socio-economic context of LDPL makes the need for better capacity to predict future lake
79 development increasingly urgent. According to the EU Water Frame Directive (European Commission, 2000), current
80 lake ecological quality and restoration targets have to be defined as the degree of deviation from good pre-impact
81 quality, i.e. from ecological reference conditions (European Commission, 2003), which characterizes less or not
82 impacted reference lakes or past periods in the development of a certain lake. However, due to the variety and spatial
83 distribution of human perturbations on lacustrine ecosystems, reference lakes are in reality rare or scarcely
84 representative for the majority of lake categories (Buraschi et al., 2005). Furthermore, high quality long term
85 limnological data are available only for a few key perialpine lakes, such as for lakes Lucerne and Constance since the
86 early 20th century (Wolff, 1966; Grim, 1968), L. Geneva since 1957 (Monod et al., 1984), lakes Maggiore and Lugano
87 since 1973 (<http://www.cipais.org/index.asp>). Smaller lakes usually received attention only after symptoms of cultural
88 eutrophication became evident in the 1960s-1970s (e.g. Alefs & Müller, 1999; Garibaldi et al., 1999). Although the
89 decadal-scale data are crucial for lake quality control and management, as well as for understanding ecological
90 processes, this lack of long temporal perspective hampers the definition of lake-specific reference conditions and
91 restoration targets, as well as the prediction of future lake ecological trends (Bennion et al., 2011).

92 Paleolimnology - the reconstruction of past lake environmental conditions and ecological status based on the study of
93 proxies stored in lake sediments - represents the most powerful tool, in mutual complementarity with limnological
94 surveys, to close the knowledge gaps between present and past lake ecological conditions. Paleolimnological
95 reconstructions allow using each lake as a reference site for itself, while the extension of the limnological perspective
96 back to pre-impact periods, when lake dynamics were mainly controlled by climate, can help discriminating between
97 natural and anthropogenic variability (Mills et al., 2017). The comparison with lake conditions during past stages of
98 major climate change (such as the Little Ice Age or the Holocene Climatic Optimum) can help disentangling climate

99 effects from other impacts, and can sustain the prediction of future trends within a context of climate change (Battarbee
100 et al., 2012).

101 The present review paper aims at providing a synthetic summary of the contribution of paleolimnological research to
102 the knowledge of LDPL responses to human stressors at secular scale, and to the assessment of perialpine lake
103 sensitivity to present and future human impacts. By pinpointing spatial and temporal differences in paleolimnological
104 research conducted in the different Alpine countries, this work has the additional objective of identifying knowledge
105 gaps in the study of lacustrine sediment in the perialpine area, and of exploring the potential of modern methodological
106 approaches to answer open basic and applied limnological research questions.

107 According to geography and bedrock geology five major sub-groups of LDPL are recognized (Fig. 1): 1) Savoyan lakes
108 (F) located on calcareous bedrock and with waters of middle hardness; 2) Lakes of the Swiss plateau (CH, D, A)
109 receiving waters from the crystalline mountain ranges of the Central Alps; 3) Lakes of the Southern Alps (I, CH) mainly
110 located at lower altitude (average = 245 m a.s.l., Table 1) in calcareous regions and with watershed basins extending in
111 the crystalline Central Alps; 4) Bavarian (D), and 5) Salzkammergut (A) lakes located at altitudes between ~400 and
112 500 m a.s.l. in calcareous watersheds. The present contribution focuses on the 20 largest and deepest perialpine lakes,
113 with $Z_{\max} \geq 100$ m and lake area ≥ 10 km² (Fig. 1 and Table 1). Four additional perialpine lakes shallower than 100 m
114 have also been included in the review as hotspots of extensive limno- and paleolimnological research (Table 1).

115 The review of the paleolimnological literature was mainly based on papers published on international journals indexed
116 on Web of Science (ISI-WoS, Thomson Scientific's Institute for Scientific Information,
117 <http://www.webofknowledge.com>) and Scopus (<http://www.scopus.com>) from 1975 to April 2017. The databases were
118 searched for each selected lake (keywords: "lake name" AND "sediment" NOT "geology") as a topic (word included at
119 least in title, abstract, or keywords), and contributions on surface lake sediment, geology or sedimentology were then
120 manually eliminated. Papers published in not indexed journals and unpublished PhD theses were identified through a
121 final search in Google Scholar (<https://scholar.google.com>) using the same key words. The paleolimnological
122 achievements are organized in four major thematic sections: sedimentology, past lake chemical conditions, past climate
123 variability, and past lake ecological conditions. Finally, most recent and novel paleolimnological approaches potentially
124 contributing to the advance of large lake ecosystem science are discussed.

125

126 **Sedimentology**

127

128 *a) Geophysical and sedimentological studies*

129

130 The earliest studies of LDPL sediments aimed at the physical characterization of deep sediment deposits, while
131 ecological implications were considered marginally. Typical sedimentological approaches were applied to the Swiss
132 lakes (Fig. 2; Müller & Gees, 1970; Schindler, 1976; Niessen et al., 1992), where Hsü & Kelts (1985) first studied
133 sediment turbidites from a limno-geological point of view, and to a few subalpine Italian lakes (Finckh et al., 1984; Bini
134 et al., 2007). More recent sedimentological studies rely on high resolution seismic profiling of lake bottom sediments
135 (Müller, 1999; Beck et al., 2001; Schnellmann et al., 2005), and aim at studying processes visible on the lake floor
136 morphology, such as mass movements and moraine ridges (Hilbe et al., 2014; 2016).

137

138 *b) Sediment chronology*

139

140 Tightly related to sedimentological investigations is the development of methods for the establishment of reliable
141 chronologies and the estimation of sedimentation rates on the basis of varve counts (Lambert & Hsü, 1979; Wolff et al.,
142 2006), magnetic susceptibility (Thompson & Kelts, 1974; Creer et al., 1975), and radioactive isotopes such as ^{210}Pb and
143 ^{137}Cs (Fig. 3; Dominik et al., 1981; Lister et al., 1984; Von Gunten et al., 1987). The majority of these studies were
144 conducted on lakes of the Swiss Plateau (Fig. 2). Of particular interest is the artificial radioisotope ^{137}Cs , which
145 attracted the interest of European scientists after the nuclear accident of Chernobyl in 1986, when huge amounts of this
146 highly toxic metal isotope and other radioactive elements were released in the atmosphere. After the accident, numerous
147 studies were conducted all over Europe in order to determine dynamics and ranges of atmospheric transport of
148 radioactive caesium and its deposition on soils and aquatic environments (e.g. Santschi et al., 1988). The studies
149 conducted on sediments of those perialpine lakes which received higher amounts of Cs fallout due to contingent
150 atmospheric circulation patterns (Irlweck, 1991; Schuler et al., 1991; Bollhöfer et al., 1994; Putyrskaya et al., 2009)
151 contributed to the validation and improvement of the ^{210}Pb based dating of lakes sediment records by pinpointing the
152 sedimentary ^{137}Cs peaks marking 1963 (when stratospheric testing of nuclear weapons was banned) and 1986, the
153 Chernobyl accident (Fig. 3).

154

155 *c) Catchment processes*

156

157 Lake catchment processes are affected essentially by: 1) internal geodynamics phenomena including earthquakes and
158 volcanic eruptions; 2) climate-related factors, such as the action of meteoric waters and winds on rock weathering, soil

erosion and transport, bio-geochemical cycles, and land cover (see further down); 3) human-related activities able to modify land cover and hydrology within the lake's catchment, such as deforestation and land clearance, agriculture, urbanization, water diversion and hydroelectric exploitation (Fig. 4).

The study of effects of casual geodynamic events on past LDPL conditions, which is tightly related to the sedimentological approach, put high attention to the effects of earthquakes. In fact, seismic activity can reduce underwater slopes stability and induce mass movements and anomalous accumulations, which in turn interfere with the chronology of lake sediment records (Chapron et al., 1999; Brauer & Casanova, 2001; Fanetti et al., 2008). These mass movement records were used to reconstruct past seismic activity in the Alpine region (Siegenthaler et al., 1987; Beck, 2009; Strasser et al., 2013), and as a model for understanding stability of submerged lacustrine slopes (Strupler et al., 2017) and ocean margins in regions of high seismic activity (Strasser et al., 2007). In addition, it has been shown that major past earthquakes in the Alpine region started landslides, which induced tsunami-like waves when reaching perialpine lakes. The extensive study of these pre-historical and historical catastrophic events in Swiss and French LDPL (Fig. 2) contributed to highlight the risk for tsunamis in the perialpine area (Chapron et al., 1996; Schnellmann et al., 2006; Kremer et al., 2012; 2014).

Not surprisingly, studies aimed at tracking effects of past volcanic activity are rare in the Alpine region, with the exception of the studies by Moscariello & Costa (1987), Wessels (1998), and Schnellmann (2004) which revealed ash layers (tephras) of the Laacher Volcano (Eifel Mountains, Germany) in sediments of western Perialpine lakes during the Late Glacial.

Similarly to many other lakes in fertile European regions (Dubois et al., 2017), the majority of the LDPL have a long history of human presence, which dates back at least to the Neolithic Age (ca. 5900-4500 cal Yr BP, Menotti, 2004). However, impacts of human activities on lake catchments remained negligible for most of the Holocene thanks to the size-related buffering capacity of LDPL, which tends to absorb and minimize moderate external perturbations. Effects of early human activities, such as pile dwellings on lakeshores, agriculture development and the related soil clearance, were demonstrated for L. Constance (Rösch, 1993), but especially for smaller LDPL, such as Mondsee since the Late Neolithic (Swierczynski et al. 2013a) and L. Bourget since the Bronze Age (Jacob et al., 2009).

Human activities increased rapidly since the Industrial Revolution and at enhanced velocity since the economic and demographic boom after World War II (WWII). During the last century, the establishment of hydroelectric power plants represented, together with urbanization, one of the major anthropogenic impacts on LDPL catchments. Between the 1930s and the 1950s, the hydrological regime of many LDPL was modified due to construction of reservoirs, impoundments, water diversions and plants for forced water pumping aimed at power production (Wüest et al., 2007;

189 Lappi, 2008). Reservoirs and impoundment decreased the input of suspended material of riverine origin to LDPL
190 (Anselmetti et al., 2007), as was revealed by the increasing proportion of organic material deposited in sediments of
191 some lakes (e.g. Milan et al., 2015). This may erroneously suggest an early increase in lake productivity, while in other
192 lakes, as in L. Brienz, the reduced input of riverine material decreased the allochthonous nutrient input, thus inducing
193 the lake's oligotrophication (Wüest et al., 2007; Thevenon et al., 2013).

195 **Past lake chemical conditions**

196
197 Natural chemical composition of surface waters largely depends worldwide on the geology of watersheds. Nowadays,
198 rivers and lakes receive a great variety of anthropogenic contaminants, including nutrients and numerous non-nutrients
199 pollutants, such as heavy metals, organic synthetic chemicals, pharmaceuticals, hormones, or radionuclides. Toxicity,
200 transport, persistence, and accumulation of contaminants in water, sediments and organisms depend on their intrinsic
201 chemical properties and on complex interactions between pollutants and natural lake chemical and biological
202 components, which are still far from being completely understood (Nellier et al., 2015).

204 *a) Eutrophication: reconstructing the evolution of anthropogenic lake nutrient enrichment*

205
206 Paleolimnological studies of perialpine lakes were triggered during the 1980s by the symptoms of cultural
207 eutrophication, which became evident in numerous temperate lakes of the Alpine region during the 1960s. Several
208 works explored the possibility to track effects of lake nutrient enrichment on lake productivity through the study of
209 sediment aspect (Nipkow, 1920) and biogeochemical indicators, such as the sediment content of organic matter and
210 algal pigments (Ravera & Parise, 1978; Guilizzoni et al., 1982), stable isotopes (Giger et al., 1984), biogenic silica
211 (Schelske et al., 1987), or lipids (Buchholz et al., 1993). These early eutrophication studies concentrated on lakes that
212 were the main study object of Research Institutes and Universities and were considered as reference lakes at country
213 level (e.g. Geneva, Zürich, Constance, Mondsee, and Maggiore).
214 As the relation between organisms and lake nutrient level was already known for long (e.g. Kolkwitz & Marsson,
215 1908), the studies rapidly focussed on the use of lacustrine species composition and diversity as qualitative indicators of
216 eutrophication symptoms. Cyanobacteria were the first biological indicators used, in relation to the early recognition
217 that their occurrence in perialpine lakes is related to and exacerbated by nutrient increase (De Candolle, 1825). Past
218 abundance of cyanobacteria in LDPL has been usually inferred from concentrations of taxonomically specific subfossil

219 pigments preserved in sediments (Neukirch, 1990; Züllig, 1956; 1989; Guilizzoni et al., 1983), although different
 220 degradation rates related to both molecular structure and lake environmental conditions can hamper the estimation of
 221 original abundance (Leavitt, 1993; Milan et al., 2015). In recent years the quantification of endospore (akynetes) formed
 222 by Nostocales provided reliable information on lake colonization by cyanobacterial populations and lake trophic
 223 development (Wunderlin et al., 2014; Salmaso et al., 2015).

224 Remains of other aquatic organisms, such as Cladocera, revealed great potential as qualitative indicators of past trophic
 225 condition of perialpine lakes (e.g. Nauwerck, 1988; Hofmann, 1998), but diatoms were widely preferred (e.g. Klee &
 226 Schmidt, 1987; Schmidt, 1991; Alefs & Müller, 1999; Wessels et al., 1999), due to their ubiquitous abundance and
 227 good preservation in lake sediments, as well as to their reliability as trophic indicators (Hall & Smol, 2010).

228 Statistical models for quantitative reconstruction of past total phosphorus (TP), and secondarily of photosynthetic
 229 pigments, which represent the most widely used variables for lake trophic classification (Vollenweider & Kerekes,
 230 1982), developed during the 1980s, in parallel with tools for the inferring of lake acidification in N-Europe and N-
 231 America (Smol, 2008). However, as the direct determination of phosphorus concentration in lake sediment is not
 232 reliable due to a set of complex chemical interactions (Engstrom & Wright, 1984), models aimed at an indirect
 233 reconstruction of past lake TP based on biological proxies, especially subfossil diatoms (Birks, 2010). Sediment records
 234 from numerous perialpine lakes were used to quantify ecological optima and tolerance of diatom species, which were
 235 combined with species abundances to develop transfer functions for inferring past TP in Alpine and perialpine lakes
 236 (Wunsam & Schmidt, 1995; Lotter et al., 1998). The development of these statistical tools is considered as a sort of
 237 “Rosetta stone” (Smol, 2008), as it allowed extending the temporal perspective provided by lake surveys from decades
 238 to centuries.

239 Although regional studies are still rare (e.g. Berthon et al., 2013) and no supra-regional integrated study has been
 240 conducted yet, the available diatom-based reconstructions outline a coherent secular-scale evolution of the lake trophic
 241 status in perialpine lakes north and south of the Alps. The majority of the lakes remained in oligo- to mesotrophic
 242 conditions until the late 1940s, while TP levels increased very rapidly in the 1960s in relation to the input of untreated
 243 waste waters originating especially from the rapidly expanding resident and tourist population during the post-war
 244 economic boom. The lake nutrient enrichment was accompanied by the substitution of small oligotrophic centric
 245 diatoms (i.e. *Cyclotella* spp. (Kützing) Brébisson) by colony forming pennate taxa (primarily *Fragilaria crotonensis*
 246 Kitton, *Asterionella formosa* Hassall, *Tabellaria flocculosa* (Roth) Kützing), which prefer mesotrophic conditions
 247 (Marchetto & Bettinetti, 1995; Wessels et al., 1999; Marchetto et al., 2004; Berthon et al., 2013; Milan et al., 2015).

248 The maximum eutrophication stage, which was usually reached in the 1970/1980s, was characterized by high
249 proportions of *Stephanodiscus parvus* Stoermer & Håkansson and *Aulacoseira* spp..
250 Paleolimnological reconstructions corroborate and underscore the neo-limnological evidence of a heterogeneous trophic
251 development of LDPL in the last few decades, in relation to different timing and success of restoration measures,
252 catchment features, lake size and morphology, or local economic issues. Several lakes north of the Alps (e.g. Berthon et
253 al., 2013, Jochimsen et al., 2013, Dokulil & Teubner, 2005) and L. Maggiore (Mosello et al., 2010) represent examples
254 of particularly successful lake restoration, which are now tending to pre-1960s trophic status (Table 1). Other lakes still
255 show enhanced trophic status due to secondary internal P-load, such as Zürich and Lugano (Lepori & Roberts, 2017), or
256 to incomplete and/or late restoration measures, such as Iseo and Garda (Salmaso & Mosello, 2010; Tolotti, unpublished
257 data). Despite the general stimulus that the EU FWD provided to sediment studies in Europe since the 2000s (Bennion
258 et al., 2011), sediment-based reconstructions of past lake TP still remain rather heterogeneous for the LDPL. Research
259 concentrated on a few key lakes, while the definition of reference conditions continues to be mainly based on historical
260 limnological data and expert judgment. At present, past trophic development has not yet been reconstructed at secular
261 scale for some Swiss lakes, while sediments of the Italian subalpine lakes have been investigated only after 2010 (Milan
262 et al., 2015).

263 Furthermore, the quantitative approach to infer past lake TP is currently undergoing a stage of critical revision, as it
264 shows some biases which are mainly related to the set of ecological and statistical assumptions involved in
265 paleoenvironmental reconstructions (Juggins, 2013). In particular, the models for diatom-base lake TP reconstruction
266 show scarce spatial replicability in relation to the strong geographical connotation of the training sets, and the inclusion
267 of numerous taxa without significant relations to TP (e.g. many benthic TP-tolerant Fragilariaceae). The relation
268 between diatom and TP may be strongly affected or confounded by secondary variables, such as water chemistry, depth
269 and climate conditions (Juggins et al., 2013). Finally, LDPL are strongly under-represented in the existing European
270 calibration sets. Only four LDPL (i.e. Ammersee, Attersee, Como, and Garda) are included in the Central European
271 dataset, which was calibrated on 86 lakes south and north of the Alps (Wunsam & Schmidt, 1995), while the Swiss
272 dataset (Lotter et al., 1998) includes only small lakes. This situation often results in poor estimates of TP concentrations
273 measured in the lake water column, or in the necessity to rely on more general calibrations sets (such as the Comb-EU
274 TP, Battarbee et al., 2001), or on sets calibrated to different European regions, as reported for example by Milan (2016).
275 Another critical aspect regards the general scarcity of long monitoring records, which hampers the validation of trophic
276 reconstructions based on comparison between paleo-and neo limnological data. In the Alpine area, this has been
277 possible for Mondsee (Bennion et al., 1995; Dokulil & Teubner, 2005), Maggiore (Manca et al., 2007) and Geneva

278 (Berthon et al., 2013). The reliability of the taphonomic diatoms assemblages represents a further important issue for
 279 reconstructions based on biological remains. Comparison between living and sediment communities aimed at outlining
 280 diagenetic processes has been conducted only in a few lakes (Marchetto & Musazzi, 2001; Jankowski & Straile, 2003;
 281 Berthon et al., 2013).
 282 Possibly also in connection to these issues, the existing diatom-based transfer functions did not undergo any updating
 283 process after their development in the 1990s, so that they still rely on a taxonomical stand, which is out of date and does
 284 not take in account recent taxonomical revisions and new autoecological knowledge. As a result, although diatom-based
 285 TP reconstructions still represents a fundamental and common step for sediment investigations, paleolimnology is
 286 currently moving on towards more comprehensive and ecological approaches (see below).
 287 Subfossil photosynthetic pigments represent an alternative proxy for inferring past lake TP in perialpine lakes. Due to
 288 higher post-depositional degradation rates of pigments relative to diatoms, pigment-inferred TP often underestimate
 289 diatom-inferred nutrient levels (Fig. 5), especially in oligotrophic well-oxygenated lakes (Guilizzoni et al., 2011).
 290 However, pigment-inferred TP values are usually sufficiently robust to provide a reliable reconstruction of major past
 291 lake nutrient trends, and are especially useful when subfossil diatoms are dominated by nutrient-tolerant taxa, or when
 292 no other suitable trophic indicators are contained in the lake sediments (Marchetto & Musazzi, 2001; Guilizzoni et al.,
 293 2012).
 294 Subfossil Cladocera remains have also been successfully used as quantitative indicator of lake trophic level. As
 295 *Daphnia* has strong stoichiometric requirements for P, changes in its past abundance could be directly related to
 296 changes in lake TP level and a *Daphnia*-inferred TP transfer function was developed for the Savoyan LDPL (Berthon et
 297 al., 2013). *Daphnia*-inferred TP has been shown to track early enrichment in TP below 10 $\mu\text{gP L}^{-1}$ that were so far
 298 undetectable from diatom-based methods, but becomes inefficient for TP concentrations > 100 $\mu\text{gP L}^{-1}$ (Bruehl et al., *in*
 299 *press*). However, as the growth of aquatic animals is strongly affected by both bottom-up and top-down factors,
 300 Cladocera response to nutrients may be difficult to discriminate from the response to fish predations or climate
 301 variability (Tolotti et al., 2016). Globally, subfossil Cladocera are used to validate diatom-based TP reconstructions, and
 302 are considered as more powerful to reveal effects of multiple human impacts on LDPL ecological dynamics and food
 303 webs (e.g. Boucherle & Züllig, 1990; Jankowski & Straile, 2003; Manca et al., 2007; Perga et al., 2010; Alric et al.,
 304 2013). Furthermore, subfossil Cladocera remain less extensively investigated in LDPL than in smaller productive lakes
 305 with hypolimnetic anoxia, which ensures better remain preservation in the sediments (e.g. Szeroczyńska & Sarmaja-
 306 Korionen, 2007).

307 As lake hypoxia or hypolimnetic anoxia are usually caused by enhanced oxygen consumption in lakes following
 308 increases in productivity (Jenny et al., 2016), sediment based reconstructions of past lake oxygenation provided indirect
 309 information on the trophic development of some perialpine lakes particularly affected by deep anoxia, such as L. Zürich
 310 (Naeher et al., 2013), Geneva and Bourget (Giguët-Covex et al., 2010; Jenny et al., 2013), and Lugano (Bechtel &
 311 Schubert, 2009). As for phosphorus, the reconstruction of past lake oxygenation is indirect, and based on abiotic or
 312 biological (animal) proxies. Beside varve formation and geochemical composition (Jenny et al., 2013), the ratio Fe:Mn
 313 has been particularly used (Naeher et al., 2013), due to the relation between solubility of these ions and water redox
 314 potential (Engstrom & Wright, 1984). Chironomid head capsules are the preferred animal remains in the studied LDPL
 315 (Marchetto et al., 2004; Millet et al., 2010; Frossard et al., 2013), due to the high tolerance of several species to low
 316 oxygen concentrations and to the good preservation of the larval head capsules in deep sediments (Walker, 2001).
 317 Ostracods and Oligochaets also showed good capability at tracking changes in lake oxygenation at millennial scale
 318 (Niessen et al., 1992; Newrkla & Wijegoonawardana, 1987).
 319 Climate change can interact with anthropogenic nutrient enrichment in complex ways, and these interactions may
 320 modify the behaviour of lake ecosystems to a point where historically defined restoration targets may become difficult
 321 or even impossible to achieve (Bennion et al., 2011). This implies the need of resetting quality/restoration targets and
 322 re-defining boundaries between water quality classes. As a consequence, most of the recent paleolimnological studies
 323 on perialpine lakes in France and Italy aimed at understanding how climate variability modulates lakes response to
 324 nutrients (Berthon et al., 2014; Milan et al., 2015; Tolotti unpublished data). For instance, Jenny et al. (2016) showed
 325 that if the appearance of bottom hypoxia has been triggered by early nutrient enrichment in the first half of the 20th
 326 century in three large LDPL, further expansion of the hypoxic volume is now under climate control. Besides, responses
 327 of different pelagic biological compartments to climate warming are conditioned, in magnitude and type, by the local
 328 concentrations in TP (Perga et al., 2015). Milan et al. (2017) showed that climate variability represents the primary
 329 driver for Cladocera under low nutrient conditions, while the climate effect tends to be overridden under nutrient
 330 enrichment conditions.

331

332 *b) Pollution: reconstructing the history of human driven lake contamination*

333

334 Lake anthropogenic contaminants (other than nutrients) can be differentiated in two major groups: metals and
 335 industrially synthesized chemicals. Metals are naturally present in lake waters in small quantities, which originate from
 336 physical and chemical weathering of the catchment bedrock and reach the lakes through runoff or atmospheric

deposition. Although essential for many metabolic processes, metals become toxic or even lethal when exceeding specific thresholds, a condition which often occurs for metal contaminants of anthropogenic origin.

First sediment evidence of metals contamination of European lakes dates back to the development of technologies for extraction of copper ~4000 years BC (Mighall et al., 2002), and then of lead since the Roman period (Renberg et al., 2001). To date, few records of ancient anthropogenic metal contamination are available for LDPL, due to the scarcity of paleolimnological investigations at millennial scales. Nevertheless, those sediment records reaching pre-industrial times show low metal concentrations in comparison to the high modern levels of contaminants related to industrial emissions and fossil fuels, which dramatically increased in the early 20th century (Wessels et al., 1995; Arnaud et al., 2004; Liechti, 2015). Stable isotopes of lead ($^{208}\text{Pb}/^{207}\text{Pb}$ and $^{206}\text{Pb}/^{207}\text{Pb}$) in perialpine lake sediments were particularly useful for the detection of pollution sources, deposition rates, and pre-industrial metal contamination of lakes (Moor et al., 1996; Kober et al., 1999; Monna et al., 1999), the latter as possibly related to past mining activity, as observed for L. Lucern during the High Middle Age (Thevenon et al., 2011).

Industrially synthesized chemicals are usually defined as persistent organic pollutants (POPs), as they are organic, often halogenated, toxic compounds, which are scarcely soluble in waters but highly volatile, so that they can be transported for long distances, persist for long time in the environment, and bioaccumulate in the food webs. Among the variety of POPs, polychlorinated biphenyls (PCBs) and polycyclic aromatic hydrocarbons (PAHs) are particularly relevant due to their large diffusion and their significant negative effects on human health and other organisms (Lallas, 2001). In comparison to metal contamination, POPs emission in the environment is relatively young, as it started worldwide with the massive use of DDT (dichloro-diphenyl-trichloro-ethane) as an insecticide, and with the increasing emission of PAHs from gasoline combustion since the ~1930s. The negative effects of DDT on human and environmental health led to its ban in most of the industrialized countries in the 1970s, but the evidence that water and soil contamination was steadily increasing in industrialized districts during the 1980s and 1990s stimulated studies aimed at tracking the contaminant fate in aquatic environments, including LDPL sediments. The majority of studies regarded the most impacted LDPL in Switzerland, France and Italy (Fig. 2, <http://www.cipais.org/html/lago-maggiore-pubblicazioni.asp>; Guzzella et al., 2018; Naffrechoux et al., 2015). Some studies provided methodological improvements of extraction and detection of heavy metals and POPs (Müller, 1984; Arnold et al., 1998), while the majority gathered information on pollutants origin, dispersal and residence in lake ecosystems, where the sediments play an important role in sequestration and mobilization processes (Wakeham et al., 1980; Czuczwa et al., 1985; Wang et al., 1986; Provini et al., 1995; Wessels et al., 1995). For example, these studies demonstrated significant correlations between legacy contaminants of common origin, such as Cr, Zn, Pb, Cd, Cu (e.g. Monticelli et al., 2011) and PAHs from combustion of

367 fossil fuels, in particular coal (Müller et al., 1977; Kober et al., 1999). As Hg contamination never represented a major
 368 issue in the Alpine region, only a few studies focussed on Hg contamination sources and methodological issues in
 369 LDPL (e.g. Ciceri et al., 2008).

370 Recent studies on contamination of perialpine lake sediments tracked pollution timing and trends (Bogdal et al., 2008)
 371 in order to check the success either of the ban of certain compounds (Becker-van Slooten & Tarradellas, 1995), or of
 372 remediation strategies, such as the implementation of wastewater treatment plants (Thevenon & Poté, 2012; Vignati et
 373 al., 2016). Several of these studies revealed a coherent decrease in deposition rates and sediment concentrations of lead
 374 and related metals since the ban of leaded fuels in Europe in the mid-1980s, while DDT and related PCBs decreased in
 375 lake waters and sediments after their European ban (79/117/CEE, Council of the European Communities, 1979). On the
 376 contrary, sediment records of other metals and POPs are much variable due to local factors, such as industrialization,
 377 urbanization, and long range atmospheric transport following the major atmospheric circulations (Jung et al., 2008;
 378 Poma et al., 2014). Several recent studies aimed at identifying possible factors responsible for persisting high level of
 379 some POPs in perialpine lakes, as in L. Thun (Bogdal et al., 2008; 2010). Naffrechoux et al. (2015) demonstrated that
 380 the different historical records of recent PCBs sediment concentrations in the three major French-Swiss perialpine lakes
 381 (Geneva, Bourget and Annecy) is related to a combination of different lake catchment and hydrological features,
 382 pollution sources, as well as to differing dynamics of atmospheric transport and deposition. Bettinetti et al. (2016)
 383 recently demonstrated that melting of Alpine glaciers is contributing to maintain high levels of DDT in the sediments of
 384 L. Como, a legacy first revealed by Bogdal et al. (2009) in a small high alpine lake in Switzerland.

385 Despite the amount of studies addressing spatial and temporal distribution of sediment contamination in LDPL, only a
 386 few paleolimnological works focus on long term effects of pollutants on lake organisms. An exception is represented by
 387 L. Orta, Italy, which experienced high levels of metal pollution from local industry since the late 1920s and subsequent
 388 acidification since 1960 (Fig. 6). The effects of pollution on the lake biota were so dramatic (summarized in Manca &
 389 Comoli, 1995) that first wastewater treatment started already in the late 1950s. The lake was then limed to mitigate
 390 acidification in the late 1980s. Numerous paleolimnological studies tracked the pollution and recovery of L. Orta
 391 (Guilizzoni & Lami, 1988; Guzzella, 1996; Vignati et al., 2016), but especially demonstrated long term pollution-driven
 392 changes in species composition and diversity of phytoplankton (Ruggiu et al., 1998; Guilizzoni et al., 2001),
 393 techamoebs (Asioli et al., 1996), oligochaetes (Bonacina et al., 1986), cladocerans (Manca & Comoli, 1995), and
 394 rotifers (Piscia et al., 2012; 2016). Other studies demonstrated the contamination-driven onset of diatom teratology
 395 (Ruggiu et al., 1988; Cantonati et al., 2014), and of changes in the size distribution of the lake biota (Cattaneo et al.
 396 1998). The sediment studies of L. Orta underscore the knowledge gaps regarding effects of pollutants on the lake biota,

397 and envisage the future potential development of paleolimnological investigations addressing wide range atmospheric
398 contamination of water ecosystems.

399

400 **Past climate variability**

401

402 Ecosystem processes are influenced to varying degrees by climate conditions, which change due to a set of natural
403 forcings operating at centennial or millennial scale, such as variations in the Earth orbit, solar activity, volcanic
404 emissions, and ocean/atmospheric interactions. Although climate directly affects lake water temperature, seasonal and
405 annual variability of the resulting thermal dynamics (i.e. water stability, mixing, ice-cover) are those playing the
406 principal role in modulating lake environmental conditions, as well as chemical and biological processes (Adrian et al.,
407 2009). Moreover, many effects of climate on lake ecosystems are mediated by climate-driven hydrological variability in
408 the lake catchment and its vegetation cover (Leavitt et al., 2009).

409 The influence of human activities on the Earth's carbon cycle has been growing so intensively and rapidly during the
410 last ~two centuries, i.e. since the beginning of the Industrial Revolution, that humans are currently considered the main
411 driver of climate variability. In addition, human modification of lake catchments (due to agriculture, deforestation,
412 urbanization, hydroelectric exploitation) often exacerbates climate-driven catchment processes. This poses the necessity
413 to rely on long term climate records in order to understand both the natural range of climate variability and the extent of
414 human impacts on water ecosystems (Mills et al., 2017). Although meteorological records are usually longer than
415 limnological data and of better quality, they are mainly limited to a few major cities in Europe and North America and
416 to the last ca. 150 years. For example, the HISTALP database, which includes recorded and statistically extrapolated air
417 temperature and precipitation data for the "Greater Alpine Region", covers the period since ~1850 (Auer et al., 2007).
418 As lakes accumulate records of past environmental and climatic conditions in their sediments, the paleolimnological
419 approach can effectively extend information on past climate and on direct and indirect effects of climate variability on
420 lake ecosystems.

421

422 *a) Direct and indirect reconstruction of paleoclimate based on lacustrine proxies.*

423

424 In general, LDPL are characterized by a pronounced thermal inertia (Straile et al., 2010), which slows and smooths
425 effects of temperature changes. However, increasing lake thermal stability due to temperature increase is responsible for
426 prolonged summer stratification and reduced winter mixing of LDPL, which in turn strongly affect nutrient distribution

427 along the lake water column and plankton growth (e.g. Straile et al., 2003; Dokulil, 2013; Salmaso et al., 2014). On the
 428 other hand, effects of global warming may be blurred for temperate lakes at middle to low altitude, which are typically
 429 subject to multiple stressors often prevailing over climate signals. As a consequence, past temperature reconstructions
 430 based on sediment proxies are relatively scarce for LDPL.

431 Subfossil organism remains preserved in lake sediments have been used to infer past climate trends after determining
 432 their species optima and tolerance to certain climate variables (Birks, 1998). In particular, chironomids, and to a lesser
 433 extent Cladocera, provided direct quantitative temperature reconstructions along Alpine altitudinal gradients (revised by
 434 Heiri & Lotter, 2005) thanks to the fact that their life cycles are more affected by temperature than that of vegetal
 435 organisms. Among algae, chrysophytes stomatocysts were successfully used as proxy to infer spring and winter
 436 temperature only in smaller perialpine and Alpine lakes (Kamenik & Schmidt, 2005; De Jong & Kamenik, 2011).
 437 However, the relations between organisms and temperature are usually not straightforward, as organisms
 438 simultaneously respond to a variety of environmental factors, which are often interconnected and affected by climate
 439 variability. As a result, organisms-inferred past temperatures are better in providing insight in climate trends rather than
 440 in absolute values. In addition, some taxonomic groups may have better capacity to track variables that are only
 441 indirectly related to climate, such as water thermal stratification, oxygenation, or chemistry, rather than water
 442 temperature directly. Therefore, sediment-based reconstructions of past climate variability often adopt a multiproxy
 443 approach (Birks & Birks, 2006), which involves the coupled study of biotic and abiotic sediment proxies related to
 444 climate variability. Sediment carbon and silica content, oxygen isotopes in calcite (CaCO_3) and silica (SiO_2), organic
 445 matter or biological remains (such as lipids, ostracod shells and diatoms frustules), have been successfully combined to
 446 reconstruct past climate variability in lakes Mondsee (Drescher-Schneider & Papesch, 1998), Lugano (Niessen et al.,
 447 1992), and Constance (Hanisch et al. 2009; Schwalb et al., 2013). As carbonate shells or silicate frustules are secreted
 448 over a short time, their isotopic composition can store information on past lake environmental conditions. The $^{18}\text{O}/^{16}\text{O}$
 449 ratio of ostracods and molluscs shell CaCO_3 applied to long sediment records spanning over millennia allowed the
 450 reconstruction of paleotemperatures during the Late Glacial (ca. 14700-11500 years BP) and the first half of the
 451 Holocene (ca. 11500-6000 y BP) of some LDPL north of the Alps (e.g. Von Grafenstein et al., 1992; 1994; 1998;
 452 Lister, 1988; Anadon et al., 2006). Temperature-inferring based on the oxygen isotopic composition of diatoms
 453 frustules has been developed more recently, but with promising results for application on subfossil records (Crespin et
 454 al., 2010).

455 More recently, Blaga et al. (2013) inferred temperatures from L. Lucerne during the last deglaciation (14600-
 456 10600 cal. yr B.P.) using the “organic geochemical paleothermometer TEX_{86} ” (TetraEther index of archaeal isoprenoid

457 Glycerol Diakyl Glycerol Tetraethers (GDGTs) membrane lipids with 86 carbons (Fig. 7). The L. Lucern TEX₈₆
458 paleotemperature record reveals remarkable resemblance with the Greenland ice (NGRIP) $\delta^{18}\text{O}$ and Ammersee
459 (Germany) ostracods shells $\delta^{18}\text{O}$ records, and suggests that temperature changes in continental Europe were dominated
460 during the last 15000 years by large-scale reorganizations in the northern hemispheric climate system.

461

462 *b) Paleoclimate reconstruction based on climate-driven catchment processes*

463

464 Regional patterns of atmospheric precipitation are strongly dependent on large scale climate dynamics and local
465 physical features, and represent the primary driver for catchment and lake hydrological variability, which in turn can
466 control land vegetation, soil erosion, transport and accumulation of allochthonous clastic and organic material in lakes.
467 These materials can increase lake water turbidity, thus affecting the development of plankton and fish, and can transport
468 nutrients and pollutants, which enter the food webs (Leavitt et al., 2009). Due to these cascade effects, much effort has
469 been recently dedicated to the study of perialpine catchment processes as driven by climate variability. The frequency
470 and intensity of past floods have received special interest as a proxy of past climate dynamics. Flood sediment records
471 typically consist of thick sediment layers (turbidites, Fig. 4), which can be discriminated from “normal” sediment layers
472 by their texture, geochemical composition, and organism remains, the latter being often scarce due to dilution by clastic
473 material. In addition, flood layers can be distinguished from underwater slumps especially on the basis of their peculiar
474 geochemical content (e.g. Revel-Rolland et al., 2005; Kremer et al., 2015).

475 Paleohydrological studies were typically conducted on long cores spanning over large portion of the Holocene, or even
476 including records of the Late Glacial, with the objective to understand natural (i.e pre-human impact) climate
477 variability. Studies on ancient flood records in French LDPL could demonstrate the relation between natural climate
478 variability and solar activity (Magny et al., 2010; Czymzik et al., 2016). Sediments of L. Maggiore provided a detailed
479 reconstruction of past flood frequency through the application of an integrated approach combining instrumental
480 monitoring data and sediment analyses. Microfacies analyses on thin sediment sections combined to μ -XRF element
481 scanning allowed detecting even thin flood layers (Kämpf et al., 2012). Long cores from LDPL in France (e.g. Chapron
482 et al, 2002; 2005; Debret et al., 2010; Arnaud et al., 2012) and in the NE Alps (e.g. Czymzik et al., 2010; Swierczynski
483 et al., 2013b, Fig. 2) allowed linking changes in frequency and intensity of runoff events and debris floods to
484 precipitation and glacier fluctuations during the Holocene. Several of the most recent works were carried out within
485 supra-regional projects (e.g. DecLakes: Decadal Holocene and Late Glacial variability of the oxygen isotopic
486 composition in precipitation over Europe reconstructed from deep-lake sediments), and joined research clusters (e.g.

PROGRESS: Potsdam Research Cluster for Georisk Analysis, Environmental Change and Sustainability, REKLIM, Topic 8: Rapid climate change derived from proxy data) aimed at detecting coherent trends in long term climate variability at European or Alpine level (Lauterbach et al., 2012; Kämpf et al., 2015). Past climate variability has been successfully reconstructed also based on sediment records of lake water level related to precipitation or glacial thawing. However, since sediment signals of water level fluctuation may not be straightforward or easy to recognize, this approach usually rely on combined information from multiple proxies, such as lacustrine terraces indicating past higher lake-level, seismic profiles, sediment particle-size and geochemistry, pollen of terrestrial and aquatic plants (e.g. Magny, 2004; Magny et al., 2009; Girardclos et al., 2005; Gauthier & Richard, 2009). It is important to pinpoint that palynological studies aimed at reconstructing past climate through the changes in vegetation cover over the LDPL catchments are quite scarce. In fact, since pollen can be transported over long distances, palynological studies are useful to track regional-scale changes, but are rarely valuable to reconstruct changes within a singular watershed (Bennet & Willis, 2001). This aspect is particularly limiting for those LDPL with heavily perturbed catchments, where pollen analyses could successfully track vegetation and climate changes only during the Late Glacial and the early Holocene (e.g. Vernet & Favarger, 1982; Lauterbach et al., 2012). Human impacts on the lake catchment occur at a much shorter time scale than natural climate changes and are often more intense, but human- and climate driven effects are often comparable to each other, as they principally affect hydrology, soil erosion, and land vegetation cover. Some recent studies tried to discriminate catchment changes driven by climate from those caused by pre-historical human activities (Hanisch et al., 2009; Gauthier & Richard, 2009; Thevenon & Anselmetti, 2007), while others aimed at understanding the effects of past hydrological variability on the pre-historic human settlements around the LDPL (e.g. Magny 2004; Magny et al., 2012; Swierczynski, 2013a). Nevertheless, a holistic study approach has progressively developed during recent years in relation to the increasing relevance for lake management of combined climate and human driven catchment processes able to affect lake abiotic and biotic responses.

Past lake ecological conditions

Lake ecosystems are simultaneously affected by interacting anthropogenic stressors, which can increase the overall vulnerability of lake ecosystems to external perturbations by making them less resistant and less resilient (Dong et al., 2012). Global warming can interact with almost all anthropogenic impacts making environmental problems increasingly complex and trans-boundary, and lake management less efficient because of the difficulty in predicting future trends.

517 The necessity of addressing the complexity posed by interlaced stressors has required a perspective change of
518 paleolimnological studies of LDPL, which are progressively focussing on effects of natural and human-driven
519 environmental changes on features of the lake biota and on ecological responses of perialpine lakes.
520 Several of the recent paleoecological studies adopt a multiproxy approach (Birks & Birks, 2006), since the simultaneous
521 study of different biological indicators characterized by different sensitivity toward environmental variables allows
522 outlining different timing and magnitude of ecological responses (as shown in Fig. 8), thus increasing both the
523 diagnostic potential and the predictive reliability of sediment studies (Bennion et al., 2015; Perga et al., 2015).
524 The multiproxy approach provided insight in the effects of climate change as superimposed over nutrients in Subalpine
525 and Savoyan lakes (Guilizzoni et al., 2012; Jenny et al., 2014), and allowed discriminating the response to climate
526 change and nutrients by different organisms (Fig. 8), such as diatoms (e.g.; Berthon et al., 2014; Milan et al., 2015),
527 cladocerans (Manca & Comoli, 1995; Alric et al., 2013; Milan et al., 2017), chironomids (Frossard et al., 2013), and
528 ostracods (Namiotko et al., 2015). The comparative study of biological and abiotic (i.e. sediment geochemistry) proxies
529 outlined that lake and catchment size can modulate the effects of combined climate variability and human driven
530 catchment processes (i.e. hydropower exploitation) on the biota of perialpine lakes (e.g. Milan, 2016).
531 The multiproxy approach is putting increasing attention to the combination of data from sediment studies and
532 limnological surveys, respectively, aiming not only at validating sediment-based reconstructions, but also at improving
533 process understanding and prediction potential. Multivariate statistical approaches combining nutrient (either sediment-
534 reconstructed or from monitoring records) and climatic factors allow discriminating ecological responses that can be
535 attributed to local human activities from those due to climate change (e.g. Mosello et al., 2010; Guilizzoni et al., 2012;
536 Milan et al., 2015). In that matter, the varved nature of the sediments of some LDPL is a clear asset as it provides the
537 opportunity for high-resolution dating up to an annual accuracy (Alric et al., 2013; Jenny et al., 2013; Frossard et al.,
538 2013).
539 Studies addressing organism responses to multiple stressors are increasingly focussing on biogeography of key
540 lacustrine taxa and on colonization by alien species. Biodiversity, geographical distribution and dispersal, evolution,
541 and development trajectories of ostracods were extensively studied in Mondsee (Danielopol et al., 2008; Namiotko et al.
542 2015), while colonization patterns of Cyanobacteria were reconstructed for lakes Geneva (Wunderlin et al., 2014) and
543 Garda (Salmaso et al., 2015). These studies benefit from the rapid evolution of the high-throughput sequencing
544 techniques applied to bulk sediments, which allow the quantification and identification of subfossil DNA and RNA. For
545 example, the application of molecular techniques to sediment records allowed investigating the development of
546 cyanobacteria population in relation to lake trophic and environmental changes in lakes Bourget (Savichtcheva et al.,

2011; 2015; Domaizon et al., 2013) and Zürich (Monchamp et al., 2016). In a study on 10 peri-alpine lakes, Monchamp et al. (2018) suggested that the cyanobacterial communities became more homogenous across lakes due to raised temperatures strengthening the thermal stratification, which favoured cyanobacterial taxa able to regulate buoyancy. On the other side, the microsatellite analysis of subfossil Cladocera resting eggs allowed reconstructing the invasion history of *Daphnia pulicaria* Forbes in Lower L. Constance (Möst et al., 2015). A similar approach using allozymes, applied already in the 1990s, allowed tracking changes in genetic architecture of *Daphnia* spp. in Upper Lake Constance due to nutrient enrichment (Weider et al., 1997). These studies suggest that original species composition and genetic architecture were not restored after the lake environmental conditions were reestablished after peak eutrophication during the 1970-1980s (Brede et al., 2009). The microsatellite characterization of subfossil Cladocera resting eggs from the Savoyan perialpine lakes related hybridization and different evolutive trajectories of synoptic *Daphnia* species with lake nutrient level and change in fish predation pressure (Alric et al., 2016). However, studies using cladoceran resting eggs as a tool need to be aware that ephyppia production is species-specific and may change in response to environmental change (Jankowski & Straile, 2003).

Sediment studies focussing on organisms producing cysts (Cyanobacteria, Chrysophyta) or resting eggs (Rotifera, Cladocera) can take great advantage from resurrection ecology techniques (Kerfoot et al., 1999), where vital propagules preserved in lake sediments are hatched in order to obtain pure cultures. These pure lineages can be used for genomic analyses and laboratory experiments with the objective of investigating adaptation and evolutionary dynamics during different stages of environmental change. Although the potential of combining descriptive and experimental paleolimnology is not being fully exploited yet, it has been extensively applied to investigate the evolutionary response of Cladocera and Rotifera to pollutants (Piscia et al., 2015; Sommer et al., 2016; Zweerus et al., 2017), and of *Daphnia* to toxic cyanobacteria (Hairston et al., 1999), as well as to quantify past population densities and to genetically confirm the taxonomic identity of the cyanobacterium *Dolichospermum lemmermannii* (Richter) Wacklin, Hoffmann & Komárek (Salmaso et al., 2015).

Another innovative paleoecological approach consists in the use of stable isotope composition aimed at tracking past changes in the lake food web or carbon cycling as affected by human impacts and climate variability. At L. Annecy $\delta^{15}\text{N}$ of sediment organic matter was shown to be significantly correlated to lake trophic changes during the last century (Perga et al., 2010). Changes in carbon and nitrogen stable isotopes have been recently studied in chironomid remains (head capsules) of Savoyan lakes in order to reconstruct spatial and temporal differences in the contribution of methanotrophic bacteria to the benthic secondary production in relation to changes in lake deep oxygenation (Frossard et al., 2015). The $\delta^{13}\text{C}$ values of subfossil cladoceran remains were shown to quantitatively track changes in the summer

577 CO₂ surface concentrations of LDPL, showing that nutrients and climate have considerably modified the C exchanges
578 between perialpine lakes and the atmosphere over the last century (Perga et al., 2016). A further example is the
579 measurement of $\delta^{15}\text{N}$ in bulk sediment and in hydrolysable sediment amino-acids in Swiss LDPL of contrasting trophic
580 conditions, which allowed tracking changes in heterotrophic microbial metabolism in relation to lake nutrient level
581 (Carstens et al., 2013), or comparing the development of lake food webs (Bechtel & Schubert, 2009).

582

583 **Research gaps and future perspective**

584

585 Although numerous paleolimnological studies of LDPL exist, the present review puts in evidence several spatial and
586 temporal heterogeneities. The main objectives of sediment research have been unevenly distributed in the different
587 countries since the very beginning. Sediment studies were conducted more extensively on LDPL next to Research
588 Institutes and Universities, while research topics are distributed rather heterogeneously according to different academic
589 specializations and local environmental problems (Fig. 2). The majority of the early studies on sedimentology and past
590 catchment processes were concentrated on lakes of the Swiss Plateau (including the transboundary L. Constance),
591 studies on lake pollution are concentrated on Swiss and subalpine lakes, while reconstruction of paleoclimate and past
592 lake ecological conditions are more numerous for the Savoyan and Swiss lakes. Surprisingly, reconstruction of past lake
593 nutrient level received scarcer attention (Fig. 2), with the result that information on past lake trophic status and
594 definition lake reference conditions are still to be completed , or updated, for the majority of the perialpine lake
595 districts, with the exception of the Savoyan lakes.

596 Also the focus of sediment studies of perialpine lakes evolved over time, moving from the quantification of past
597 changes in lake environmental features (e.g. sedimentation rate, water level, temperature) and impacts (e.g. nutrients,
598 pollutants) towards the understanding of effects of human- driven environmental changes and superimposed climate
599 change on lake ecological features and functions. These heterogenities, besides pointing out the necessity to complete
600 the picture at regional level, indicate that the potential of sediment investigations of LDPL is far away from being
601 exhausted , but could be further exploited to address modern ecological and management issues.

602 Despite the efforts to reduce nutrient inputs to lakes from urban and productive effluents, eutrophication still represents
603 the most common water quality problem for the densely populated and highly productive areas of the world (Smith &
604 Schindler, 2009), which includes the perialpine region. As a consequence, sediment studies addressing nutrient
605 enrichment and re-oligotrophication of LDPL are still topical, especially in relation to the crucial need to understand the
606 role of superimposed climate variability in modulating lake response to nutrients.

607 Since present climate conditions are approaching those of the Holocene Optimum (IPCC, 2013), paleoecological studies
 608 of LDPL at millennial scale could provide the reconstruction of lake ecological conditions during past warmer periods,
 609 thus improving the prediction of future lake scenarios based on the study of past analogue climate stages. Alpine
 610 glaciers are predicted to strongly retreat, if not completely disappear, within the next few decades (Radić et al., 2014).
 611 This will substantially impact the hydrological regimes of LDPL, with serious consequences for agriculture,
 612 hydropower production, drinking water, tourism, and navigation. Paleolimnology may support prediction of future lake
 613 trends and a conscious lake management by revealing LDPL responses to major stages of glacier reduction and scares
 614 precipitations during the Holocene.

615 Although numerous LDPL are directly or indirectly exploited for hydropower production, a systematic study of the
 616 resulting lake changes in hydrology, thermal regime and biodiversity is still missing. Sediment studies can provide
 617 information for a direct comparison of lake ecological condition before and after the human driven modification of lake
 618 hydrological regime.

619 The increasing importance of diffuse and long ranging human impacts over lake ecosystems suggests the opportunity to
 620 intensify supra-regional sediment studies (which at present are still scarce) in order to outline temporal and spatial
 621 coherence/difference between LDPL in relation to environmental and impact gradients. The adoption of a holistic
 622 ecoregional vision may increase the strength of lake management within the relatively socio-economically
 623 homogeneous Alpine region. Such supra-regional comparisons appear to be particularly relevant when considering that
 624 lake biological and ecological responses to climate change tend to be idiosyncratic, in contrast to more coherent
 625 physical and chemical response, in relation to local factors, and can hardly be extrapolated from one lake to another
 626 (Dokulil, 2013).

627 The unexploited potential of sediment studies on LDPL strongly emerge when considering the recent methodological
 628 developments in paleolimnology. The multidisciplinary and multiproxy approach already appears to be indispensable to
 629 address the study of multiple stressors within the current context of climate warming. The investigation of stable
 630 isotopes in subfossil biological and biochemical remains represents a powerful method to investigate changes in the
 631 lake food webs, from microbes to fishes. New approaches, such as those exploiting the structural composition of the
 632 sediments (e.g. Jenny et al., 2016), enable to evaluate the consequence of environmental changes on lake functioning
 633 (e.g. hypoxia, carbon cycle).

634 Vegetal and animal resting stages preserved in the sediment allow the application of experimental paleolimnology to
 635 track past changes in biodiversity, to reconstruct colonization and invasion processes by species of interest, and to
 636 understand micro-evolutionary trajectories and life strategies of key lacustrine organisms.

637 The study of subfossil genomic material preserved in lake sediments currently represents one of the most promising
638 developments of paleoecology. Although this approach still needs methodological improvements and is prone to
639 degradation of subfossil DNA and RNA, especially under peculiar chemical conditions, it already allowed investigating
640 organisms that do not leave remains in sediments (such as the majority of cyanobacteria and protists). This widens the
641 palette of biological information that can be retrieved through sediment studies. At present the metagenomic approach is
642 mainly aimed at the characterization and quantification of past lake bacterial populations, but very recent developments
643 are targeting planktonic unicellular eukaryotes (Capo et al., 2015; 2016). This approach has the great potential to
644 substantially strengthen the knowledge of past lake biodiversity and ecological processes through detailed information
645 on entire ecosystem compartments.

646 Although regime shifts are considered as typical for shallow lakes (Scheffer, 1998), there is yet some evidence that
647 especially benthic and littoral compartments have crossed critical tipping points very early during the eutrophication
648 process (at lake TP levels $<10 \mu\text{gL}^{-1}$, Jenny et al., 2016, Bruel et al., *in press*) in some LDPL. Theoretically, the LDPL
649 context of high local human alterations and climate warming, which is already twice the global average (Auer et al.,
650 2007), makes climate-driven shifts more probable (Scheffer et al., 2015), even in nutrient-restored lakes (Moreno-
651 Mateos et al., 2017). Because the richness of sediment archives of perialpine lakes allows reconstructing the dynamics
652 of both forcings and responses, LDPL offer the unique opportunity to quantitatively document their response dynamics
653 and to reconsider their past and current vulnerability to regime shifts.

655 **Conclusions**

656

657 Paleoecological reconstructions represent a powerful tool, in mutual support with limnological surveys, to close the
658 knowledge gaps between present and past lake ecological conditions. In addition, paleoecological studies can help
659 predicting future scenarios through the “past forward” principle, which consists in reconstructing past lake responses to
660 conditions comparable to those present or to come. Albeit climate change increases the ecosystem variability and makes
661 prediction more difficult, the most recent methodological developments of sediment studies appear to have the potential
662 to cope with this complexity. The present work pinpoints that paleolimnological studies of LDPL represent a research
663 field having the potential to produce innovative information, which can be crucial to tune future management and
664 sustainable use of Alpine waters, likely the most precious natural resource of the Alps, to future climate and local socio-
665 economic scenarios.

666

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 1309

1310 Tables

1311 Table 1. Geographical position, key morphometric features, current thermal regime and trophic condition of the 20 large
 1312 and deep perialpine lakes (LPL) included in this study (with maximum depth ≥ 100 m and lake area ≥ 10 km²) and of
 1313 four smaller lakes (not numbered, but indicated by a code), which have been additionally included since they represent
 1314 key sites for the development of sediment studies on perialpine lakes. Length (L) and width (W) are intended as the
 1315 maximum dimensions of each lake. $Z_{\max}$ and Z_{mean} = maximum and mean lake depth, respectively, C. A. = catchment
 1316 area, t_w = estimated retention time, Mix. = mixing regime, mo = monomictic, di = dimictic, ol = oligomictic, me =
 1317 meromictic. T. S. = trophic status, o = oligotrophic, m = mesotrophic, o-m = oligo-mesotrophic, m-e = meso-eutrophic,
 1318 e = eutrophic. The information reported in table has been collected from the literature cited in the text, data for L. Idro
 1319 as in Viaroli et al., [submitted, this issue](#); data for Mondsee as in Ficker et al., 2017. Numbers for L. Constance refers to
 1320 Upper Lake Constance.

1321

N	Ac	Lake	Country	Altitude m a.s.l.	L Km	W Km	$Z_{\max}$ m	Z_{mean} m	Area Km ²	C. A. Km ²	Vol Km ³	t_w y	Mix.	T. S.
1	G	Geneva (Léman)	F-CH	372	72.0	13.0	310	153	582	7975	89	11.4	me-ol	o-m
2	B	Bourget	F	232	18.0	3.5	145	80	42	560	3.6	10.0	mo	o-m
	An	Annecy	F	447	14.6	3.2	82	41	27	251	1.1	n.a.	mo	o
3	Th	Thun	CH	558	18.3	3.8	217	135	48	2404	6.4	1.8	ol	o
4	Br	Brienzen	CH	564	14.2	2.8	259	173	30	1108	5.2	2.6	ol	o
5	L	Lucern (Vierwaldstättersee)	CH	434	39.2	3.3	214	104	114	2124	11.8	3.5	ol	o
6	Zu	Zug	CH	414	14.6	4.3	198	83	38	212	3.2	17.0	me	e
7	Z	Zürich (lower)	CH	406	40.6	3.8	136	51	65	1757	3.4	1.4	ol	m
8	Wa	Walzen	CH	419	15.4	2.0	145	105	24	1037	2.5	1.5	me	o
9	C	Constance (Bodensee)	CH-D-A	539	63.0	14.0	252	101	493	10900	48.0	4.7	ol	o
10	O	Orta	I	290	13.1	2.5	143	72	18	116	1.3	8.9	mo	o
11	M	Maggiore	I	193	64.4	10.0	370	178	213	6599	37.5	4.1	ol	o
12	Lu	Lugano	I-CH	271	35.0	4.3	288	171	28	297	4.69	12.4	me	m-e
13	Co	Como	I	198	45.7	4.3	410	154	146	4508	22.5	4.5	ol	o-m
14	I	Iseo	I	186	25.0	4.4	251	123	62	1842	7.6	4.1	me	m-e
15	Id	Idro	I	368	8.3	1.9	124	77	11	617	0.9	1.2	me	o-m
16	Ga	Garda	I	65	51.9	17.5	350	133	368	2290	49.0	26.6	ol	o-m
	Am	Ammer	D	533	16.2	5.3	81	38	46.6	993	1.8	2.7	mo	m
17	S	Starnberger	D	584	20.2	4.7	128	53	56	315	3.0	21.0	mo	o-m
	Ch	Chiem	D	518	12.8	6.2	73	25	80	1399	2.1	1.4	mo	m
	Mo	Mondsee	A	481	11.0	1.5	68	36	14	247	0.5	1.7	di-mo	o-m
18	W	Wolfgang	A	538	10.3	2.0	114	47	14	123	0.7	3.6	di	o

19	A	Atter	A	469	20.1	3.3	171	85	46	464	3.9	7.1	di	o
20	T	Traun	A	422	12.2	2.9	189	91	26	1417	2.3	1.0	ol	o

1322

1323

1324 Figure captions

1325

1326 Fig. 1: Map of the Alpine region with the large and deep perialpine lakes (LDPL) considered in this paper, with
1327 indication of the geographical latitude and longitude (Greenwich). The lakes included in different, often transnational,
1328 districts are indicated with different colours. Green: Savoyan lakes; orange: lakes of the Swiss Plateau; blue: subalpine
1329 lakes; white: Bavarian lakes; violet: lakes of the Salzkammergut region.

1330

1331 Fig. 2: Total amount, and absolute and percent distribution (histogram and pie plots, respectively) of sediment studies
1332 conducted on the 24 perialpine lakes selected for the present contribution (see Fig. 1), as resulting from the literature
1333 survey conducted for the period 1975-April 2017. The studies include both ISI and not indicized papers and are
1334 distributed according to the lake districts indicated in Fig. 1, and to eight major thematic categories. SA: Savoyan lakes;
1335 SP: Swiss Plateau; SU: subalpine lakes; BA: Bavarian lakes; SK: Salzkammergut lakes. The low number of studies
1336 conducted on German lakes depends on the fact that Lake Constance (D, CH, A) has been considered as geographically
1337 belonging to the Swiss Plateau.

1338

1339 Fig. 3: Fallout radionuclide concentrations in the cores collected from the deepest point (350 m depth) of L. Garda in
1340 2009 and from L. Lugano (Melide, ca. 180 m depth) in 2015. Left, central and right panels show, respectively, total
1341 ^{210}Pb activity, unsupported ^{210}Pb activity, and ^{137}Cs and ^{241}Am concentrations versus sediment depth (analyses
1342 performed by Handong Yang at Ensis Ltd, University College London, UK). The ^{210}Pb method relies on the fact that the
1343 gas ^{226}Ra produced in the U decay series escapes to the atmosphere where it naturally decays to ^{210}Pb (Appleby and
1344 Oldfield, 1978). Unsupported ^{210}Pb consists in atmospheric particle-reactive ^{210}Pb attached to aerosol, which are
1345 deposited over the lake catchments and incorporated into the sediments. As most lake sediments contain U and ^{226}Ra ,
1346 ^{210}Pb is also naturally produced in situ (“supported” ^{210}Pb). Total ^{210}Pb activity and the supporting ^{226}Ra reach
1347 equilibrium depth at ~35 cm the Garda core, and at ~50 cm in the Lugano core. Unsupported ^{210}Pb activities, calculated
1348 by subtracting ^{226}Ra activity from total ^{210}Pb activity, decline irregular with depth in both cores. The sharp dips in
1349 unsupported ^{210}Pb activities around 20 cm (L. Garda) and 27 cm (L. Lugano) suggest stages of rapid sediment

1350 accumulation from floods or slumpings. The ^{137}Cs activity showed two well-resolved peaks in both cores, with the
1351 deepest one marking the termination of the atmospheric tests of nuclear weapons in the Pacific in 1963, and the upper
1352 one the Chernobyl accident in 1986. The shallower depth of the ^{137}Cs peaks in L. Garda reflects the lower sedimentation
1353 rate in this less productive lake respect to the meso-eutrophic L. Lugano.

1354

1355 Fig. 4: Schematic representation of a perialpine lake and its catchment, with indication of major climate and human
1356 related catchment processes, which can directly or indirectly affect lake ecological dynamics (drawing by M. Tolotti).
1357 Principal physical and chemical processes (i.e. sliding, resuspension, bioturbation, re-dissolution) occurring in the lake
1358 sediments are shown. The schematic sediment cores indicate the normal sequence of seasonal biochemical and clastic
1359 varvae, as well as perturbations by volcanic activity (thephas), and turbidites due to major hydrological events (floods,
1360 slumps).

1361

1362 Fig. 5: Comparison of sediment profiles of lake total phosphorus (TP) concentrations during the 20th century inferred
1363 based on subfossil diatoms (red) and pigments (blue) in lakes of decreasing depth, i.e., L. Maggiore (Pallanza basin,
1364 $z_{\text{max}} \sim 100$ m), L. Garda (shallower Bardolino basin, $z_{\text{max}} = 81$ m), and L. Ledro (a small lake located close to L. Garda
1365 at 652 m a.s.l, $z_{\text{max}} = 49$ m). C-TP and DI-TP = lake total phosphorus concentration inferred, respectively, from
1366 subfossil carotenoid concentrations and diatom species composition and abundances. The profiles clearly indicate that
1367 pigment-inferred TP values are useful to reconstruct past lake phosphorus level, but tend to underestimate the highest
1368 TP values during nutrient enrichment stage. Pigment-based reconstruction of past TP level performs better in shallower
1369 lakes, where pigment degradation during sedimentation may be less pronounced than in deep lakes.

1370

1371 Fig. 6: Age profiles of major contaminants in L. Orta (Italy) during the 20th century. Cu-sed and Hg-sed indicate,
1372 respectively, Hg and Cu concentrations measured in a sediment core collected from the lake in 2007. Other profiles
1373 indicate average concentrations recorded in water samples collected since 1925. The Cu profile reflects the
1374 contamination since the 1930s by a textile factory established on the lake shore in the 1920s. The Cu-sed profile clearly
1375 indicates the persistence of Cu in the lakes sediments also after the termination of industrial contamination. The pH
1376 values dropped since the 1960s due to concomitant contamination by ammonium sulphate, $(\text{NH}_4)_2\text{SO}_4$ and recovered
1377 after the lake liming in 1989/90. Cr, Ni, and Hg profiles reflect the relation between contaminants concentration and
1378 water pH.

1379

1380 Fig. 7: Comparison of the TEX₈₆ record (5-pt moving average) from sediments of L. Lucern (plotted against depth) with
1381 the $\delta^{18}\text{O}$ records (5-pt moving average) of the NGRIP ice core (Rasmussen et al., 2006) across the Late Glacial
1382 Interstadial, Younger Dryas and onset of the Holocene. TEX₈₆ values were converted into temperature (lower scale)
1383 using the lake calibration of Powers et al. (2010). Chronological tie points are provided by the Laacher See Tephra
1384 (LST, identified in the magnetic susceptibility record at 752 cm) and a fossil leaf at 650 cm depth. Figure redrawn from
1385 Blaga et al. (2013).

1387 Fig. 8. Compared dynamics of major environmental forcing and ecological responses in L. Bourget during the period
1388 1850-2010. a. TP concentrations as inferred from diatoms (Alric et al., 2013) and *Daphnia* (Berthon et al., 2013). Subtle
1389 changes occurred already in the 1920s, with a significant post WWII acceleration of eutrophication. TP levels are
1390 currently getting close to their initial levels. b. atmospheric temperature anomalies over the study period (HISTALP,
1391 Auer et al., 2007). Vertical lines points the threshold across which detected ecological changes are due to TP (vertical
1392 green line) and warming (vertical orange line). Benthic responses include changes in lake hypoxic volumes (c., Jenny et
1393 al., 2016) and in subfossil chironomid communities at maximal (d), intermediate (e) and mid-depths (f), summarized by
1394 scores on the first principal component of PCA analyses. At greater depths, responses to eutrophication occurred 20
1395 years earlier than at shallower depths. Pelagic responses include: subfossil diatom (g., Berthon et al., 2014) and
1396 cladoceran communities (i., Alric et al., 2013), which are both summarized by scores on the first PCA component,
1397 contribution of *Synechococcus* spp. *Nägeli* (Domaizon et al., 2013) and *Planktothrix rubescens* (Savichtcheva et al.,
1398 2014) to total cyanobacterial sediment DNA (h.), and reconstructed lake surface CO₂ concentrations (j., Perga et al.,
1399 2016). The responses to eutrophication occurred in the 1920s for diatoms and CO₂, but appeared only in the 1940s, at a
1400 higher lake TP level, for cyanobacteria and cladocerans. The absence of reversal trajectories for all the studied
1401 compartments, except diatoms, despite the successful reduction in lake TP level, was interpreted as related to significant
1402 direct or indirect effects of climate warming over the last 3 decades.

Sediment studies on large and deep perialpine lakes

Lake Garda (Brenzone, 350 m depth) - 2009

Lake Lugano (Melide, 180 m depth) - 2015

L. Maggiore

L. Garda

L. Ledro

L. Orta

MAIN FORCINGS

BENTHIC RESPONSES

PELAGIC RESPONSES