Cladocera paleocommunity to disentangle the impact of anthropogenic and climatic stressors on a deep subalpine lake ecosystem (Lake Iseo, Italy)

Barbara Leoni · **Martina Patelli** · **Veronica Nava** · **Monica Tolotti**

Abstract In big lakes with strong anthropogenic pressure, it is usually difficult to disentangle the impacts of climate variability from those driven by eutrophication. The present work aimed at the reconstruction of change in the species distribution and density of subfossil Cladocera in Lake Iseo (Italy) in relation to climate and anthropogenic pressure. We related subfossil Cladocera species composition and density in an 80-cm sediment core collected in the pelagic zone of Lake Iseo to long-term temperature trends and phosphorus concentration inferred by diatoms frustules. The Cladocera remains detected in Lake Iseo sediment reflected the species composition and density of modern pelagic Cladocera assemblages. Cladocera rapidly respond to environmental change, and that climate change combined with eutrophication can induce changes in community composition and species density. At the beginning of twentieth century,

when global warming was not yet so accentuated, the nutrient increase in water resulted as the principal driver in determining the long-term development of plankton communities and pelagic food web structure. Moreover, catchment-related processes may decisively affect both species composition and density of the lake planktonic communities due to the decrease of lake water transparency induced by input of inorganic material from the catchment area to the lake. The paleolimnological investigation, through the combined study of biotic and abiotic factor, allowed clarifying the synergic effects of the most important drivers of change in lake ecosystems, suggesting that climatic factors should be considered with nutrient availability as determinant element in controlling the temporal development of plankton communities and pelagic food web structure.

Keywords Zooplankton · Paleolimnology · Multiple stressors · Environmental change · Sediments · Eutrophication

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Introduction

Multiple anthropogenic and natural stressors can compromise lake ecological quality and ecosystems services. Although it is widely accepted that eutrophication is still one of the most impacting problems for

lake water quality, in the last decades, it has become evident that also climate change can strongly influence lake ecosystem and lake water quality (Adrian et al. 2009; Perga et al. 2015). In deep lakes affected by multiple and strong anthropogenic pressures, it is usually difficult to disentangle the impacts driven by climate from that driven by eutrophication, as these impacts may often produce additive or synergic effects on lake ecology.

Cladocera (Crustacea) are key organisms in the pelagic food web of deep lakes, as they represent the link between bottom-up factors (nutrient and phytoplankton) and top-down regulators (fish and other invertebrate predators) (Leoni 2017). Moreover, zooplanktonic organisms are particularly sensitive to environmental stressors, such as climate change and nutrient variations (Vadadi-Fülöp and Hufnagel 2014). The chitinous bodies of Cladocera organisms can be well preserved in lake sediments and present some typical morphological characteristics useful for the identification at species level. Therefore, they are considered to be a good proxy for reconstructing lake responses to environmental changes (Zawisza and Szeroczyńska 2007; Alric et al. 2013; Cheng et al. 2020) and they have been widely used to track historical changes in lake either alone or in combination with other paleolimnological proxies (Tolotti et al. 2016; Caballero et al. 2020). Recent studies highlighted that the best way to track different aspects of past ecological responses to overlapping stressor is the multi-proxy approach, combining the analysis of paleolimnological biotic (e.g., subfossil cladoceran and diatoms frustules) and abiotic (e.g., inorganic and organic content) proxies and measured long-term data (e.g., air temperature, teleconnection indices) (Milan et al. 2015; Perga et al. 2015; Tolotti et al. 2018). Furthermore, sediment records can be useful to disentangle the effects of climate change and nutrient enrichment in deep lakes, because they span over secular time periods, that reach the time before the beginning of major human disturbance (Battarbee et al. 2012; Milecka et al 2020) and to help predicting future scenarios through the "past-forward" principle (Tolotti et al. 2018). Indeed, the present environmental and socioeconomic context makes the need for better capacity to predict future lake development increasingly urgent, especially in relation to the crucial need to understand the role of superimposed climate

variability in modulating lake response to nutrients (Tolotti et al. 2018).

Surprisingly, the information on past lake trophic status and definition lake reference conditions for deep lakes of perialpine districts, with the exception of the Savoyan lakes, are far away from being exhausted and could be further exploited to address modern ecological and management issues, as well as lake changes in hydrology, thermal regime and biodiversity related to present climate variability (Tolotti et al. 2018).

The present work aims at reconstructing changes in the species composition and density of subfossil Cladocera in eutrophic Lake Iseo (the fourth largest lake in Italy) in relation to combined eutrophication and climate change. In order to study the effects of these stressors on lake biological communities, we relate subfossil Cladocera recorded in an 80-cm sediment core, collected in the pelagic zone of Lake Iseo, to measured air temperature trends, climatic proxies, such as teleconnection indices, and nutrients, mainly phosphorus concentration inferred by diatoms frustules.

We strive to: (1) highlight long-term differences in Cladocera species composition and density along a century; (2) relate possible changes to historical limnological and climatic variability; and (3) discriminate between the lake's responses to nutrient enrichment and climate change through the comparison between Cladocera results and data from other sediment biological proxies (i.e., sediment organic content, diatom-inferred lake TP concentrations).

Lake Iseo appeared to be an ideal site to conduct this kind of paleolimnological investigation thanks to the high sedimentation rate due to the high ratio between catchment area and lake surface area (Leoni et al. 2019). Moreover, on Lake Iseo a monitoring limnological campaign has been carried out since the beginning of 1990s and this allows the interpretation and comparison of paleolimnological results in light of those provided by the decadal freshwater investigations.

Methods

Study area

Lake Iseo (Site LTER_EU_IT_008 "Southern Alpine Lakes"; http://www.lter-europe.net) is located in

northern Italy, in the Alpine foothills (190 m a.s.l.) at the lower end of a large populated prealpine valley (Val Camonica). The inflow and outflow of water in the lake are from the River Oglio. Lake Iseo has a surface area of 61.8 km², water volume of 7.6 km³, a maximum depth of 258 m and an average depth of 124 m (Nava et al. 2017). The surface area of the watershed, including the lake, is 1842 km², with a mean altitude of 1429 m a.s.l and a maximum of 3554 m a.s.l (Garibaldi et al. 2003). Water temperatures of deep subalpine lakes typically do not drop below 4 °C, so they are commonly classified as "warm monomictic," as they are characterized by complete water circulation once a year in late winter and stable stratification from spring season (Leoni 2017). Nevertheless, due to the great depth of Lake Iseo, late winter vertical mixing occurs only during harsh and windy winters. During the last 25 years, complete winter mixing occurred only in 2005 and 2006, so the lake is to be regarded as holo-oligomictic.

Lake Iseo experienced a relatively rapid eutrophication process since the 1970s that was mainly attributed to nutrient loading from the inflows (Leoni et al. 2019). The increase in nutrient loadings brought the lake to a meso-eutrophic condition, as total phosphorus concentrations in the water column increased from approximately 60 μgP/L in the 1990s to 80 μgP/L between 2006 and 2016 (Rogora et al. 2018).

The contemporary zooplankton is largely dominated by copepods, mainly *Copidodiaptomus steweri*, but Cladocera and rotifers are significantly abundant from spring to autumn (Leoni et al. 2019).

Sediment coring, chronology and lithological parameters

An 80-cm-long sediment core was collected in the deepest point of Lake Iseo (45°43′11″N; 10°03′46″E) using a Kajak gravity corer (UWITC, Austria) in late June 2014. The core was vertically extruded and sliced in the laboratory: the first 30 cm of the core was sliced at 0.5 cm contiguous intervals, while from 31 cm to the bottom at 1 cm intervals. Sediment visual aspects, i.e., color and texture presence of macroscopic remains, were annotated during slicing. The core chronology, from the surface to 74 cm, was established through radiometric analysis of ^{210}Pb and ^{137}Cs,

[226]Ra and [241]Am (Appleby 2005) by Ensis Ltd. (University College London, UK).

For all the subsamples, we determined the wet density, water content (measured by drying the sediment at 105 °C for at least 12 h) and the organic matter content (measured as Loss On Ignition—LOI) after heating the sample at 550 °C in a furnace for three hours (Heiri et al. 2001).

Diatom-inferred phosphorus

In order to analyze diatom frustules preserved in the sediment, around 0.75 g of wet sediment from each subsample was treated with H_2O_2 (30%) and HCl (10%) according to standard procedures (Battarbee et al. 2001). The cleaned diatom suspensions were permanently mounted using Naphrax® resin (refraction index = 1.7). For each slide, at least 500 valves were counted under a light microscope (Leica DM2500) at 1000 × magnification and using Nomarski interference contrast. Lake total phosphorus concentrations were inferred based on diatom taxa reaching relative density of 0.5% in each sediment subsample (diatom-inferred total phosphorus—DiTP) using the Swiss-TP calibration set—including a set of low- to medium-altitude lakes mainly located in the Swiss Plateau (Lotter et al. 1998)—and a weighted-average regression with inverse deshrinking (TP CH WA-INV). This calibration set was preferred over the others available for Europe (i.e., Central Europe, combined European, Northwest European) based on its capacity to provide better estimations of the lake TP concentrations determined since the beginning of the monitoring of Lake Iseo in the 1960s. In fact, the alternative calibrations set clearly underestimated both the maximum and present lake TP concentrations.

Subfossil Cladocera

Cladocera remains were analyzed in 72 of the 110 subsample sliced from the core. The samples have been treated in order to clean and concentrate the subfossil remains following the method described by Szeroczyńska et al. (2007). About 2.5 cm³ of wet sediment was heated in KOH (10%) and then treated with HCl (10%); after the treatment, the subsample was washed through a mesh of 35 μm and concentrated in falcon tubes. One–two drops of a safranin–

glycerol mixture were added to the cleaned subsamples in order to facilitate the identification of the remains under an optical microscope (100 × or 400 × magnification). Taxonomical identification of Cladocera remains was based on Szeroczyńska and Sarmaja-Korjonen (2007). Cladocera remains (headshield, shell, postabdomen, postabdominal claw, mandible) were counted and converted to a number of individuals following Frey (1986). From three to six slides for each sample were counted in order to obtain a minimum of 100 individuals (Milan et al. 2016); however, this number had not been reached in a few samples characterized by very scarce density of remains.

Data elaboration and analysis

In order to detect general changes in Cladocera community, the total pelagic species density (Total Pelagic), the total littoral species density (Total Littoral) and the total Cladocera density (Total) were calculated. Additionally, the percentage of pelagic species above the total (Pelagic %) was computed in order to detect the proportion between pelagic and littoral taxa.

Starting from sedimentation rates (provided by the radiometric dating) and the percent organic content of each sediment layer (LOI%), the inorganic sedimentation rate (InSedRate) has been calculated. This parameter has been used as a proxy of the inorganic materials carried from the catchment area.

Homogenized monthly mean air temperatures provided by the HISTALP data set (Auer et al. 2007) for Torbole-Riva station (c.a. 60 km away from the coring point) were used as proxy for climate variability at Lake Iseo, covering the ages between 1908 and 2010. In particular, the average values of temperature from March to September (representing the vegetative period) and in winter season (December–February) have been calculated. The presence of significant trend in temperature data was evaluated using the nonparametric Mann–Kendall test, and the slope was estimated using the Sen's slope estimator. Similarly, average values of East Atlantic pattern (EA) from March to September and from December to February have been calculated for the ages 1950–2014. The values of the teleconnection index East Atlantic pattern (EA), computed by the National Oceanic and Atmospheric Administration-Climate Prediction

Centre (NOAA-CPC, www.cpc.ncep.noaa.gov), were considered to outline possible relations between ecological dynamics and global atmospheric circulation patterns. We choose to use East Atlantic pattern because several studies verified the effectiveness of this atmospheric mode of variability in representing meteoclimatic variation and the influence on limnological characteristic and zooplankton phenology in the deep subalpine lakes (Leoni et al. 2018a; Rogora et al. 2018).

A Pettitt test (Mallakpour and Villarini 2016) was performed on the total pelagic Cladocera density in order to detect changing points in Cladocera community development.

A Spearman correlation analysis was performed in order to explore relations between the principal Cladocera taxon density and to detect intra-species relation, and between the principal Cladocera taxon density and LOI% and InSedRate aiming at clarifying the relations between the density and the load of organic and inorganic materials to the Lake Iseo ecosystem.

Performing several tests on the same set of data may result in an increased risk of type I statistical error, i.e., the rejection of the null hypothesis of no difference between the zooplankton taxa densities and/or core lithological variables due to mere chance. A high conservative approach to reduce the risk of type I errors is to adopt Bonferroni correction of significance of statistical tests (Rice 1989). However, there is no general consensus on the procedure of application of Bonferroni correction (Nakagawa 2004), partially because the application of this high conservative approach may lead to considerably reduced power of the tests and consequently to increased risk of type II statistical errors, whereby the null hypothesis being tested is unduly accepted (Nakagawa 2004). In addition, several studies on relationships between actual zooplankton predator and prey, as well as among actual limnological characteristics and zooplankton population development, supported the existence of many direct correlations between the tested parameters in this study. Considering the well-known relationships mentioned above and the absence of a clear theoretical framework for how to apply correction of significance to data of this nature, we decided to consider the uncorrected p values < 0.05 as significant. However, we have also applied a Bonferroni correction and we highlighted

relationships that were significant according to this procedure.

The data analysis and environmental variable graphical elaboration have been performed with R (version 3.6.1), using the packages "base," "trend." The graphical elaboration of the stratigraphic data has been performed using the software C2 version 1.7.7 (Juggins 2007).

Results

Sediment core analysis

The ^{210}Pb- and ^{137}Cs-based core chronology spanned from 1922 ± 13 at depth 73.5 cm and 2014 on the surface with an average error of ± 6 year. Sediment accumulation rate (Fig. 1a) presented an average value of 0.39 g/cm^2 year from the sediment top down to the beginning of the 1980s, and then, it decreased
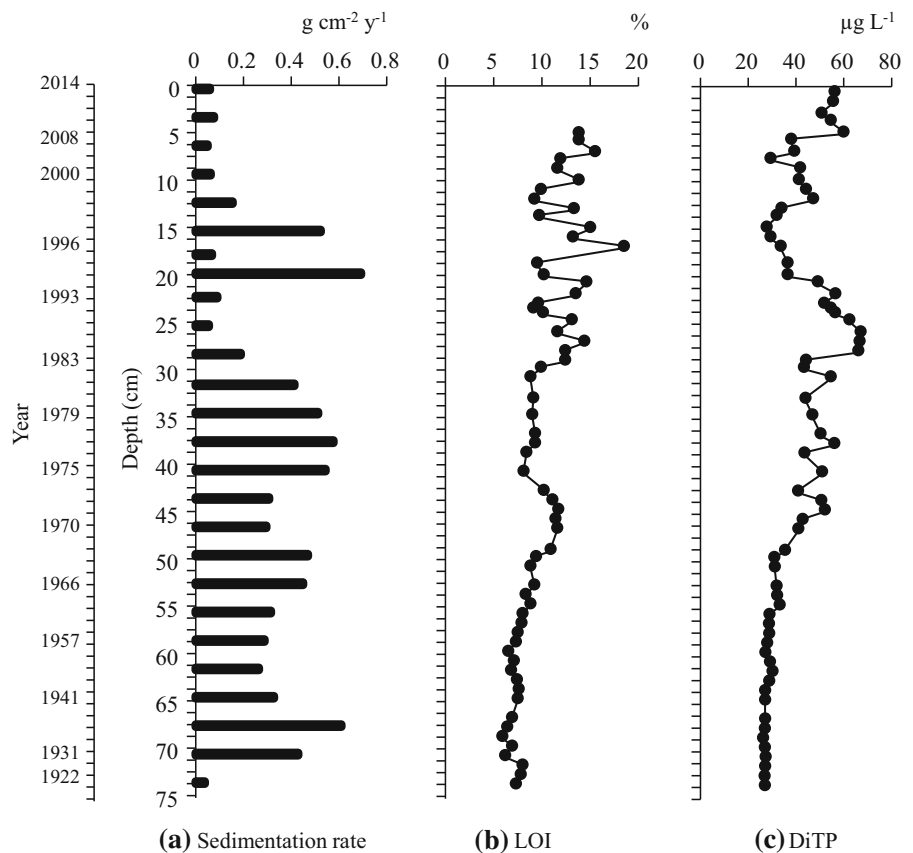
under 0.2 g/cm^2 year, with the exception of two peaks over 0.5 g/cm^2 year in 1995 ± 4 and in 1998 ± 3.

Organic matter content presented as a percentage of LOI showed minimum values in the deeper layer of the core and gradually increased in the upper layer (Fig. 1b). The minimum and the maximum recorded values were, respectively, 4.2% at 76.5 cm depth and 18.5% at 16.75 cm. In the upper layers, from the beginning of 1980s until 2014, it was possible to observe a particularly accentuated variability, with values spanning from 8.8% to 18.5%.

Diatom-inferred total phosphorus

Subfossil diatoms (Tolotti, unpublished data) are characterized by the dominance of planktonic taxa through the whole sediment core and by a pronounced dominance up to 80% of the total diatom density of the oligotraphentic *Cyclotella comensis* group from the beginning of the twentieth century until the early 1940s, when colony-forming pennate taxa

Fig. 1 Parameters scaled by depth from the sediment core taken within Lake Iseo: **a** sedimentation rate; **b** percentage of loss on ignition (LOI%); **c** phosphorus inferred by diatoms (DiTP)

(a) Sedimentation rate **(b)** LOI **(c)** DiTP

Asterionella formosa and *Fragilaria crotonensis* started to increase. These meso-traphentic taxa reached their highest density in the first half of the 1980s, when they were accompanied by eutraphentic taxa, such as *Stephanodiscus parvus*. The proportion of *C. comensis* partially recovered in the 1990s, while the sediment layers deposited since the early 2000s show a new increase of the meso- and eutraphentic taxa. The values of total phosphorus inferred by diatoms largely reflect this taxonomic alternation and present an increasing trend from the deeper to the surface layers (Fig. 1c). In particular, a constant total phosphorus concentration of 28 µgP/L was estimated from the core bottom until 48.5 cm (year 1968 ± 7). From 48.5 to 20.5 cm, the total phosphorus concentration increased, reaching a maximum of 67 µg/L at 25.75 cm (year 1993 ± 4). In the surface layers, i.e., from 25.75 until the core surface, total phosphorus variability was quite high spanning from a minimum of 28 µgP/L at 14.75 cm (year 1998 ± 3) to a maximum concentration of 62 µgP/L at 24.5 cm (year 1989 ± 6).

Subfossil Cladocera remains

The subfossil Cladocera assemblage of Lake Iseo sediment core featured 29 taxa (Table 1), including 8 pelagic and 21 littoral taxa. The identified taxa belonged to the families *Leptodoridae*, *Daphniidae*, *Bosminidae*, *Cercopagidae* and *Chydoridae*. The Cladocera belonging to the first four families consist of open water zooplankton (pelagic), while taxa belonging to *Chydoridae* are characteristic of the littoral zone. The Cladocera densities are presented in Figs. 2 and 3; in the last, nine littoral and two pelagic species are not represented as they were detected in only one sediment level each and with scarce density. The pelagic species prevailed over littoral ones and represented for most of the layers the total density, while only in the layers deeper than 61.5 cm (year 1950 ± 10) pelagic species were less than 50% of the total remains. The Cladocera density was particularly low in the deeper layers of the core, from 79.5 to 64.5 cm depth, that were deposited from the early twentieth century until 1941 ± 12, while are quite swinging in the upper layer but considerably higher.

A Pettit test applied on the total of the pelagic species pointed out three significant changing points in the pelagic density, in 1941 ± 12 years

(*p* value < 0.001), in 1969 ± 8 years (*p* value < 0.001) and in 1993 ± 4 years (*p* value < 0.05).

The first section (Figs. 2 and 3—zone 1), from 79.5 to 64.5 cm, was characterized by scarce Cladocera density and a number of taxa spanning from 1 to 5 per layer. The most relevant among the pelagic are *Bosmina (Eubosmina) longispina* group (from here on out *B. longispina*), *Bosmina (Bosmina) longirostris* (from here on out *B. longirostris*), *Daphnia longispina* group (from here on out *D. longispina*) and the zooplanktivorous *Bythotrephes longimanus* (Fig. 3). The second section (Figs. 2 and 3—zone 2), from 64.5 to 48.5 cm, showed higher density of both pelagic and littoral taxa and higher species variability. In particular, *B. longispina* and the littoral species *Chydorus sphaericus* and *Graptoleberis testudinaria* appeared here for the first time. The third section (Figs. 2 and 3—zone 3), from 48.5 to 21.75 cm, was characterized by swinging density, as the pelagic species prevailed in some layers while in others prevailed the littoral ones. It was possible to observe two peaks, i.e., 19,000 ind/g DW and 16,000 ind/g DW, respectively, in pelagic species density at 45.5 and at 27.75 cm, corresponding to years 1971 ± 7 and 1984 ± 4, respectively (Fig. 3). Conversely, at 36.5-cm depth it was possible to observe a general decline in the identified subfossil Cladocera remains, with a total density of 91 ind/g DW. The high density of the pelagic species was particularly due to *Bosmina (Eubosmina)* spp., *D. longispina* group and the two zooplanktivorous *B. longimanus* and *Leptodora kindti* (Fig. 3). On the contrary, *C. sphaericus* resulted as the most abundant littoral taxa. The most recent core section (Figs. 2 and 3—zone 4), from 21.75 cm to the core surface, is characterized by the prevalence of pelagic species that represented more than 95% of the total density (Fig. 2—zone 4). However, periods of high Cladocera density alternated with phases characterized from lower levels, with a minimum of 393 ind/g DW at 18.5 cm (1995 ± 4) and a maximum of 16,900 ind/g DW at 0.5 cm (2014). In this core section, it was possible to observe the increase in *Bosmina (Eubosmina) coregoni* group (Baird, 1857) (from here on out *B. coregoni*) density and a decreased density of *B. longirostris*, the latter being identified only in six layers (Fig. 3—zone 4). Included in the most abundant pelagic species there were also *B. longimanus*, *L. kindti* and *D. longispina*.

Table 1 List of all taxa identified in the core with indication of authority and habitat (based on Szeroczyńska and Sarmaja-Korjonen [2007])

N	Taxon name	Authority	Habitat
1	*Acroperus harpae*	(Baird, 1835)	Littoral
2	*Alona affinis*	(Leydig, 1860)	Littoral
3	*Alona costata*	Sars. 1862	Littoral
4	*Alona guttata*	Sars. 1862	Littoral
5	*Alona intermedia*	Sars. 1862	Littoral
6	*Alona quadrangularis*	(O. F. Müller, 1785)	Littoral
7	*Alonella excisa*	(Fischer, 1854)	Littoral
8	*Alonella exigua*	(Lillijeborg, 1853)	Littoral
9	*Alonella nana*	(Baird, 1843)	Littoral
10	*Chydorus sphaericus* s.l	(O. F. Müller, 1785)	Littoral
11	*Coronatella rectangula*	(Sars, 1861)	Littoral
12	*Disparalona rostrata*	(Koch, 1841)	Littoral
13	*Eurycercus (Eurycercus) lamellatus*	(O. F. Müller, 1785)	Littoral
14	*Graptoleberis testudinaria*	(Fischer, 1848)	Littoral
15	*Monospilus dispar*	Sars. 1862	Littoral
16	*Paralona pigra* (formerly *Chydorus piger*)	(Sars. 1862)	Littoral
17	*Pleuroxus (Peracantha) trucatus*	(O. F. Müller, 1785)	Littoral
18	*Pleuroxus (Pleuroxus) leavis*	Sars. 1861	Littoral
19	*Pleuroxus (Pleuroxus) uncinatus*	Baird, 1850	Littoral
20	*Pleuroxus (Pleuroxus) trigonellus*	(O. F. Müller, 1776)	Littoral
21	*Pseudochydorus globosus* (formerly *Chydorus globosus*)	(Baird, 1843)	Littoral
22	*Bosmina (Bosmina) longirostris*	(O. F, Müller, 1785)	Pelagic
23	*Bosmina (Eubosmina) longispina* group	Leydig, 1860	Pelagic
24	*Bosmina (Eubosmina) coregoni* group	Baird, 1857	Pelagic
25	*Bythotrephes longimanus*	Leydig, 1860	Pelagic
26	*Camptocercus* sp	Baird, 1843	Pelagic
27	*Ceriodaphnia* spp.	(Dana, 1853)	Pelagic
28	*Daphnia longispina* group	O. F, Müller, 1785	Pelagic
29	*Leptodora kindti*	(Focke, 1844)	Pelagic

The Spearman correlation between Cladocera taxa densities outlined some positive and significant relations between the pelagic species (Table 2a). In particular, it is possible to notice a positive and significant correlation between *B. coregoni* and *B. longispina* and between *B. coregoni* and *D. longispina*. Both the latter species resulted to be positively correlated with the main predators *B. longimanus* and *L. kindti*. In addition, a positive and significant correlation was found between the littoral species *C. sphaericus* and the pelagic *B. coregoni* and *B. longispina* groups.
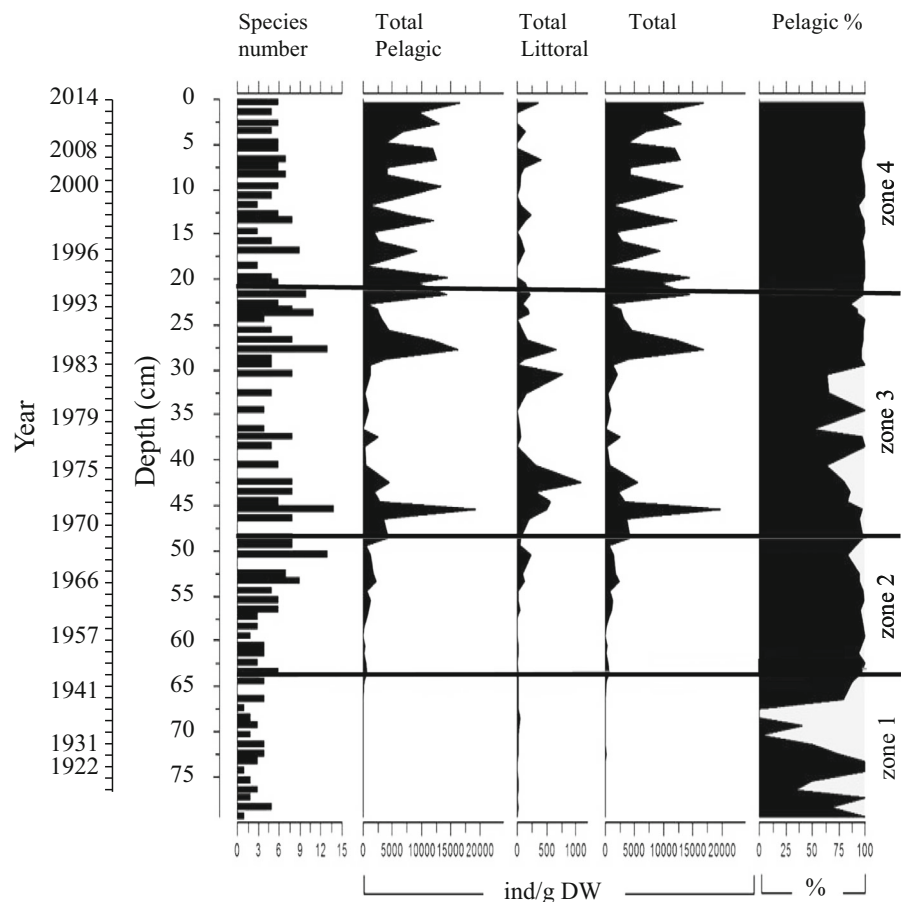
The Spearman correlation between Cladocera density and InSedRate pointed out positive and significant relationship between InSedRate and *B. longirostris*, *C.*

sphaericus and the total littoral density, while negative relation existed between InSedRate and *B. coregoni* and *L. kindti*. Conversely, the organic matter content (LOI%) had positive and significant relation with *B. coregoni* group, *D. longispina*, *L. kindti* and the total pelagic density (Table 2b).

Environmental variables

The mean air temperature from March to September has increased since the beginning of the twentieth century (Fig. 4a). In the first 20 years of the century (1900–1920), the average air temperature was 16 ± 0.67 °C, while it was 18 ± 0.53 °C from 1990 to 2010. The Mann–Kendall test highlighted a

Fig. 2 Depth profiles of subfossil Cladocera. "Number of Species": number of species identified in every layer; "Total Pelagic": total pelagic taxa density (ind/g dry weight); "Total Littoral": total littoral taxa density (ind/g dry weight); "Total": total Cladocera density (ind/g dry weight); "Pelagic %": percentage of pelagic Cladocera over the Total. The horizontal lines identify the significant changing points pointed by the Pettitt test performed on the total pelagic densities

significant positive trend for temperature data (*p* value < 0.001) at a rate of (Sen's slope) 0.022 °C/year (lower and upper bounds of the 95% trend's confidence interval equal to 0.017 °C/year and 0.026 °C/year), which is equivalent to 2.27 °C increase over the study period. Winter air temperatures (calculated from December to February) follow a similar pattern, with a significant positive trend (Mann–Kendall test, *p* value < 0.001; Fig. 4b). The rate of the increase was equal to 0.017 °C/year (lower and upper bounds of the 95% trend's confidence interval equal to 0.010 °C/year and 0.024 °C/year).

In addition, the average value of East Atlantic pattern from March to September and in winter (Fig. 4c and 4d) showed an increasing trend (Mann–Kendall test, *p* value < 0.001), with a rate (Sen's slope) of 0.015/year (95% CI[0.008, 0.020]) and 0.025/year (95% CI[0.013, 0.036]), respectively. Since the second half of the 1990s, EA showed high

inter-annual variability in particular in winter, spanning from − 1.64 in 2005 to 1.60 in 2014.

Discussion

Zooplankton plays a pivotal role in the biogeochemical cycles, and it is a key component transferring energy and matter from primary producers to higher trophic levels (Karpowicz et al. 2020). Small-bodied species, such as small cladocerans, are mainly regulated by the "bottom-up" process, while larger species are mostly regulated by "top-down" control by fish (Gliwicz 2003). Large-bodied zooplankters are more efficient at grazing on phytoplankton than their smaller competitors, which can only consume small particles. In the pelagial area of deep lakes, vertical environmental gradients (light, temperature, oxygen, food, predation pressure) prevail creating niches for different organisms (Karpowicz et al. 2019). Pelagic
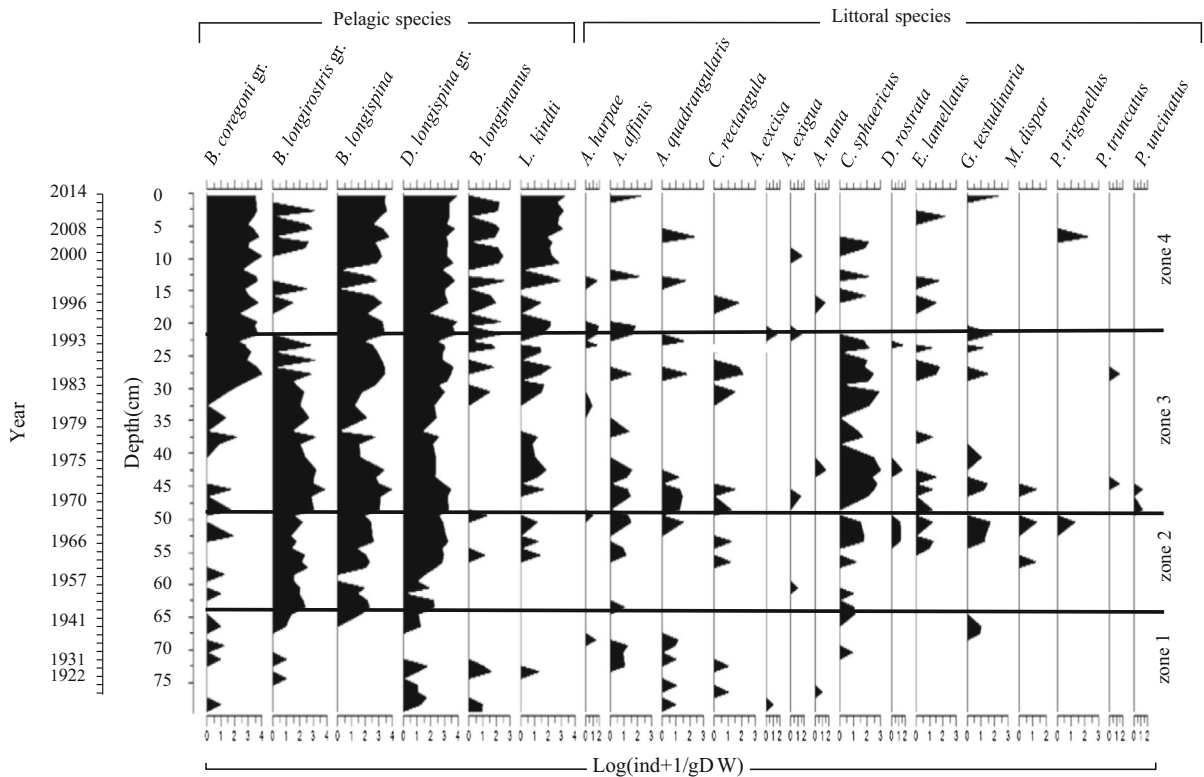
Fig. 3 Diagram of the density of the principal Cladocera species identified in the core collected from Lake Iseo sediments. Nine littoral and two pelagic species are not represented in the diagram as they were detected in only one sediment level each and with scarce density. Cladocera full taxonomic names are reported in Table 1

zooplankton species richness and community structure is important for ecosystem functioning, food web complexity and ecosystem stability, and they are widely used as indicators of the ecological status of lakes (Pociecha et al. 2018; Karpowicz et al. 2019). Planktonic crustaceans, particularly the cladocerans, are highly sensitive to environmental changes and represent good sentinels to anthropic and climatic impacts (Berthon et al. 2014). The Cladocera remains detected in Lake Iseo sediment reflected the species composition and density of modern pelagic Cladocera assemblages (Leoni 2017; Leoni et al. 2018a), and this confirms the potential of these biological proxies for paleoecological reconstructions, as previously reported in several studies on different lake types (Milan et al. 2017; Pociecha et al. 2020). A relation between the principal pelagic species has been pointed out, highlighting that the density of predators, as *B. longimanus* and *L. kindti*, is related to the density of their principal prey, *Bosminidae* and *D. longispina*. These two species of predators are potentially

competitor; however, in deep lakes, it has been verified that the coexistence of *B. longimanus* and *L. kindti* is possible thank to the temporal and spatial separation of their ecological niches, with shift in population seasonal cycles and vertical distribution on the water column (Manca et al. 2007; Manca 2011).

From the combined study of subfossil Cladocera remains, diatom-inferred total phosphorus, content of organic matter, inorganic sedimentation rate and some climate proxies (such as air temperature and East Atlantic pattern), we could identify several stages in the ecological evolution of Lake Iseo during the twentieth century. From the beginning of the twentieth century to the early 1960s, Lake Iseo resulted characterized by low organic matter content and scarce density of Cladocera, with the prevalence of littoral species on the pelagic ones. The concentrations of phosphorus inferred by diatoms frustules < 30 µg/L suggest that Lake Iseo was in mesotrophic conditions in the beginning of the twentieth century. This contrasts with the oligotrophic original condition

Table 2 Results of the correlation between (a) Cladocera species density and (b) the Cladocera and the organic content (LOI %) and inorganic sedimentation rate (InSedRate) of each layer

		r-Spearman
(a)		
B. coregoni gr	*B. longispina* gr	**0.65*****
B. coregoni gr	*D. longispina* gr	**0.74*****
B. coregoni gr	*B. longimanus*	**0.51*****
B. coregoni gr	*L. kindi*	**0.66*****
B. longirostris	*B. longispina* gr	0.3*
B. longirostris	*C. sphaericus*	**0.49*****
B. longispina gr	*D. longispina* gr	**0.84*****
B. longispina gr	*B. longimanus*	**0.36****
B. longispina gr	*L. kindi*	**0.7*****
B. longispina gr	*C. sphaericus*	0.3*
D. longispina gr	*B. longimanus*	**0.45*****
D. longispina gr	*L. kindi*	**0.73*****
B. longimanus	*L. kindi*	**0.52*****
(b)		
InSedRate	*B. coregoni* gr	− 0.28*
InSedRate	*B. longirostris*	0.29*
InSedRate	*L. kindi*	**− 0.39****
InSedRate	*B. longimanus*	− 0.24+
InSedRate	*C. sphaericus*	0.36**
InSedRate	Total littoral	0.36**
LOI%	*B. coregoni* gr	**0.46*****
LOI%	*D. longispina* gr	0.29*
LOI%	*L. kindi*	0.29*
LOI%	Total pelagic	**0.36****
LOI%	Total	0.35*

Only significant and marginally not significant relations are presented in the table: *p value < 0.05; **p value < 0.01; ***p value < 0.001; +*p* value < 0.06. The values that resulted significant after Bonferroni correction are presented in bold. Cladocera full taxonomic names are reported in Table 1

theorized for deep subalpine lakes (Ambrosetti et al. 1992; Tolotti et al. 2018). This may be due to the fact that the Swiss calibration set assigns a higher TP optimum to the taxon that was dominant in the deep core section (*C. comensis*) in comparison with the discarded calibration sets. Alternatively, it seems reasonable that Lake Iseo was not in oligotrophic in the early 1900s, similarly to what reconstructed for other more productive subalpine lakes exposed to

intense early human impacts (Rapuc et al. 2019), such as Lake Lugano (Barbieri and Mosello 1992; Lepori et al. 2018). Nonetheless, it is relevant that the profile of diatom-inferred lake TP concentration agrees with both the pronounced increase in lake productivity since the postwar economic boom and with the increase in TP level since there.

In addition, that period was characterized by lower air temperature and EA value. East Atlantic pattern has been shown to drive climate patterns over the Mediterranean basin impacting on the limnological characteristics of deep subalpine lakes and on zooplanktonic communities (Manca et al. 2015; Leoni et al. 2018a). In particular, since negative and lower value of EA are associated with colder temperature in the Mediterranean region (Leoni et al. 2018a; Salmaso et al. 2018), the lower density of Cladocera in the deepest core layers can be also due to overall unfavorable conditions for the development of zooplankton community. Indeed, scarce food availability and lower winter air temperature are known to negatively affect lake primary productivity and zooplankton fecundity and growth rate (Zawisza and Szeroczyńska 2007; Manca et al. 2015). This result is consistent with those found in other studies on deep subalpine lakes, where the deepest layers are characterized by low species diversity and density (Milan et al. 2015). From the beginning of the 1960s, diatom-inferred phosphorus concentrations began to increase. The increasing trend is confirmed by several studies that observed a period of strong eutrophication affecting the principal deep subalpine lakes, including Lake Iseo (Rogora et al. 2018). Cladocera community seems to react to the higher nutrient availability; indeed, a progressive increase of planktonic species densities and richness, indicators of warm and nutrient-rich water, was observed. In this phase, species such as *B. longirostris*, *B. longispina* and *D. longispina* became dominant. In particular, *B. longirostris* is considered as a typical indicator of eutrophication (Zawiska et al. 2014; Milan et al. 2017). The increase of pelagic taxa in times of high nutrient availability was an expected result following the bottom-up mechanisms reported in the literature and verified in other lakes (McQueen et al. 1989). In deep lakes, phosphorus availability controls the density and the composition of the phytoplankton community, affecting food availability and quality for primary consumers. A higher biomass of zooplankton, due to high
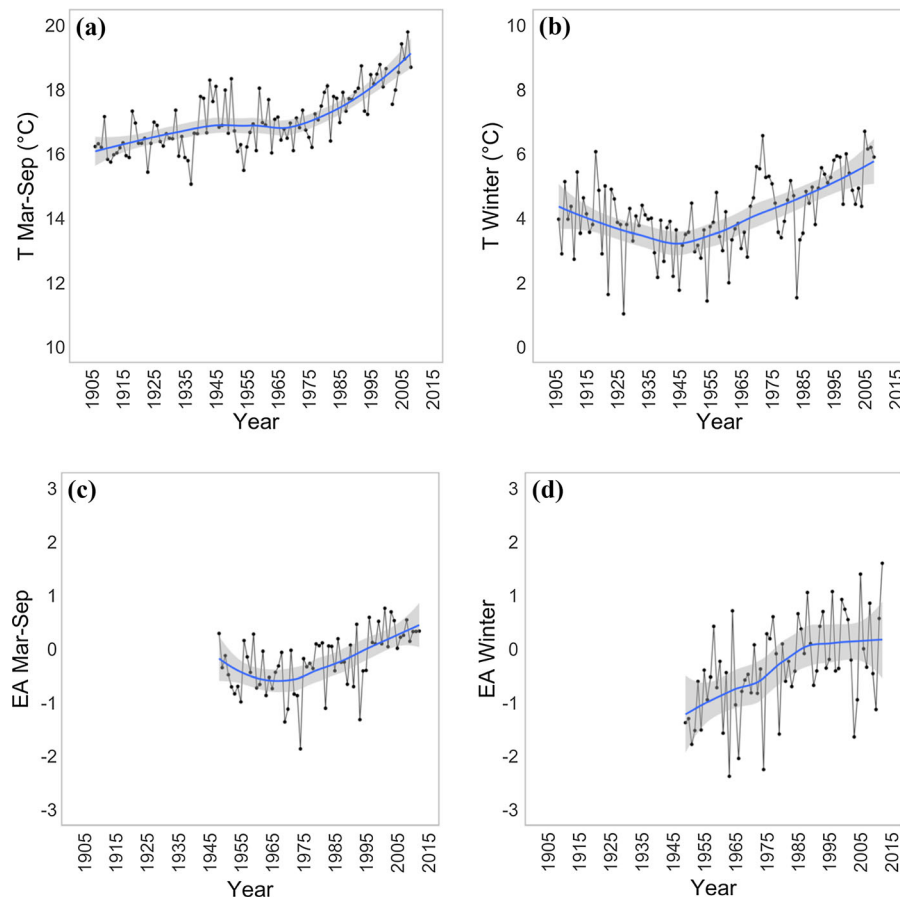
Fig. 4 Temporal trend of climatic proxies: **a** Air temperature from March to September ($T_{MAR-SEP}$). **b** Winter air temperature, from December to February (T_{WINTER}). **c** East Atlantic pattern from March to September ($EA_{MAR-SEP}$). **d** Winter East Atlantic pattern, from December to February (EA_{WINTER}). Blue curves indicate the LOESS smoothing and gray area the confidence interval (95%) around smooth. (Color figure online)

phosphorus concentration, is usually associated with higher biomass of primary producers (Leoni et al. 2014; Manca et al. 2015). Furthermore, the importance of food quality (i.e., presence of certain phytoplankton taxa, diatoms, and green algae), in particular for planktonic taxa with relatively high P requirements, is well supported in the literature (Gulati and DeMott 1997; Weers and Gulati 1997). The increase in the density of primary consumers is known to positively affect their predators, and this triggers the entire pelagic food web through a bottom-up mechanism (primary producers).

The massive presence of *B. longirostris* group reversed at the end of the 1980s, when the most abundant species of *Bosminidae* became *B. coregoni* group that required less eutrophic but warmer waters (Stenson 1976). In this phase, inferred total

phosphorus decreases but it is possible to observe an increase in air temperature and in EA values, corresponding to warmer climate. We hypothesize that the warmer climate combined with the reduced phosphorus concentration favored the development of *B. coregoni* instead of *B. longirostris*. It is known that most of the subalpine lakes, after the strong phases of eutrophication that peaked between 1960 and 1980s, faced a phase of re-oligotrophication. However, in Lake Iseo the process was not so marked and the lake is still in meso-eutrophic condition (Leoni et al. 2018a; Rogora et al. 2018), despite the partial reduction of epilimnetic phosphorus concentration. Indeed, from the second half of 1980s the first measures to reduce nutrient loading to freshwater were taken, like, for instance, the development of the first wastewater collectors and treatment plants (Garibaldi et al. 1999).

Another factor that contributed to the partial reduction of the spring phosphorus concentration after the 1980s is the decrease of the late winter vertical mixing depth. Indeed, a reduction in the depth reached by water turnover in late winter, connected with the increase in winter air and water temperature, has been observed in all the subalpine lakes. In deep oligomictic lake, as Lake Iseo, water turnover in late winter represents a key factor in determining spring phosphorus concentration in the epilimnetic layers, because it favors the vertical transfer from the hypolimnion and the replenishment of phosphorus in the epilimnion, while shallow mixing has the opposite effect (Leoni et al. 2018b; Rogora et al. 2018).

A generalized increase in all the pelagic species (including the predators *L. kindti* and *B. longimanus*) was observed in the upper layers of the core concomitantly with the increased density of *B. coregoni* group. This can be due to the increased water temperatures related to the warmer climate, as suggested by the air temperature trend and East Atlantic pattern. Moreover, several recent studies reported increases in water temperature, and in particular, Pareeth et al. (2017) reported an increase in surface water temperature of 0.017 °C/year in the last 30 years (1986–2015). This period corresponded to the highest density and the major species variability recorded in Lake Iseo sediment core, and the co-occurrence of not limited phosphorus concentration and warmer water favored the development of lake primary and secondary production (Schalau et al. 2008). As verified in other deep lakes, higher temperature positively influenced the development of zooplanktonic and phytoplanktonic organisms, their primary food resource, in some cases miming the effects of eutrophication (Lepori et al. 2018).

Interestingly, in Lake Iseo the total cladoceran density along the core showed pronounced oscillations, with alternating phases of high density to phases of very low density, in particular of the pelagic species. Lake Iseo is characterized by a high sedimentation rate, in particular if compared to other deep subalpine lakes like, for instance, Lake Garda. As a consequence, the 80-cm-long sediment core retrieved from Lake Iseo covers around 100 years, while a shorter core (48 cm) collected from Lake Garda covered around seven centuries according to the radiocarbon dating, with the bottom layer dating back at 1418 ± 30 AD (Milan et al. 2015). The high

sedimentation rate points out the strong impact that catchment area dynamics can have on lake ecological characteristics. A pattern similar to that of Lake Iseo, with periods of high density alternated to strong decreases in pelagic taxa density, was detected by Milan et al. (2016) in Lake Ledro. In this lake, characterized by a high ratio between catchment area and surface area as Lake Iseo, these shifts could be imputed to the effect of hydrological variability and in particular to flood events. In Lake Iseo, a similar hypothesis can be plausible (Rapuc et al. 2019) and high amounts of inorganic material coming from the catchment area through flood events can negatively affect lake production increasing water turbidity and nutrient availability and leading to unfavorable conditions for pelagic community development (Adrian et al. 2009). Indeed, in Lake Iseo it was possible to observe a negative correlation between the inorganic sedimentation rate and some vulnerable pelagic species as *B. coregoni* and *L. kindti*. Moreover, the littoral species *C. sphaericus* and the high adaptable *B. longirostris* (Milan et al. 2017) increased in phases characterized by high sedimentation rate. This relation can be due to a major material transportation from the littoral zone to the centre of the lake, caused by high hydrological variability in the catchment area. An increase in sediment resuspension, due to the increase of inorganic material input, may increase water turbidity and negatively affect lake primary production (Graham and Vinebrooke 2009; Morabito et al. 2018) and promote detritivorous taxa development. However, we cannot exclude that periodical floods could directly transport littoral species and Cladocera remains in the pelagic zone.

In the current context of global climate changes, the intensification of catastrophic events, such as floods, is expected in European regions and mountainous areas (Hirabayashi et al. 2013) and the study of these extreme events represents a great issue for natural hazards assessment, water resources management and freshwater ecosystem services protection. However, tendencies at the regional and local scales are still uncertain, and the use of geological paleoclimate records associated with paleobiological information can be useful tools to develop for understanding the past variations of these events in contrasting climatic contexts and forecast future scenarios.

Conclusions

The present paleolimnological investigation of Lake Iseo allowed identifying some environmental factors that likely played a key role in driving the changes in the structure and composition of pelagic zooplankton during the last century. In particular, the results suggest that climatic factors should be considered together with nutrient availability as key factors in controlling the temporal development of plankton communities and pelagic food web structure. In the period characterized by stable trophic condition and not-limiting nutrient level, climatic variation, and in particular increased temperature, became the most important driver of lake ecological characteristics. Moreover, this study provides the basis for understanding the combined effect of climate and eutrophication over deep lake ecosystems and to interpret possible future changes.

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