ORIGINAL ARTICLE

Synoptic results on the potential impacts of the Lake Maggiore water management strategy on freshwater littoral ecosystems and invertebrate biocoenosis (NW, Italy)

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ABSTRACT

The first results of the application of the integrated multidisciplinary protocol to study the effects of water level management on the Lake Maggiore littoral habitats and biocoenosis are presented. The "Parchi Verbano Ticino" project (2019-2021, ID: 481668) was the driving force to fine-tune the monitoring and management system of multidisciplinary information (chemistry, hydro-morphology, macro- and meio-fauna monitoring). The study reveals that water level fluctuations in Lake Maggiore, sometimes characterized by measurable changes in water levels, have remarkable effects on littoral habitats and on the structure and function of macro- and meio-faunal assemblages living there. Overall, this study provides insights into the potential impacts of Lake Maggiore water management strategy on freshwater littoral ecosystems during late spring-early summer, and emphasizes the need for a comprehensive understanding of the lake ecosystem dynamics. Thanks to the results achieved, publicly endorsed water management rules will be stated, for the late spring-early summer period, considering frequency and amplitude of water level fluctuations as crucial factors in management plans to mitigate their impacts. The endorsed rules turn out to be a negotiated compromise between the maintenance of ecosystem services and the protection of littoral life below water.

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Key words: water chemistry; lake habitat survey; lakeside; macro- and meio-faunal bioindicators; morpho-functional traits; water fluctuation control.

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INTRODUCTION

Lake Maggiore and its benthic macro-meio-faunal bioindicators of ecosystem quality were used as a case study within the activities of the Interreg Project ParchiVerbanoTicino (from here on PVT, ID: 481668). This is an Interreg Italy-Switzerland Project launched in 2019 (Boggero *et al*., 2022) with the aim of verifying the onset of impacts on the conservation status of the littoral habitats through the evaluation of the changes occurring in the structural and functional littoral biodiversity as a result of lake water level management. Indeed, Lake Maggiore provides prime opportunities for recreation and tourism, due to numerous protected areas and beaches along its shores, with a number of environmental benefits influencing our everyday life quality, and for the economy of the Po Valley as an invaluable water resource. Compared with the other deep subalpine lakes, Lake Maggiore has the largest watershed, able to deliver considerable water amounts to the River Po and the surrounding natural landscapes, thus becoming fundamental for economy and society in Northern Italy.

Water levels' alterations induce a different functioning of lake ecosystems, above all in the riparian, littoral and semi-aquatic areas (Evtimova and Donohue, 2016; Mammides, 2020). The frequency and duration of high levels, together with the artificial modification of the hydro-morphological features of lakes, can cause severe impacts on physical processes and biological productivity with cascading effects on the health and the integrity of ecosystems (Leira and Cantonati, 2008; Evtimova and Donohue, 2016;

Mammides, 2020). Pronounced water level fluctuations has proved to favour cyanobacterial blooms in Lake Maggiore as a result of nutrient pulses (Callieri *et al*., 2014). Finally, high water levels decrease the resilience and increase the vulnerability of the structure and function of lake ecosystems (You *et al.*, 2022). However, the impact of water levels, whether natural or human-induced, on the functionality of littoral benthic communities in freshwater lakes remains understudied (Leira and Cantonati, 2008; Evtimova and Donohue, 2016; Cifoni *et al.*, 2021).

To obtain impact indices aimed at evaluating the effects of water levels imposed by the regulation of the Miorina dam (constructed at the lake-mouth down of Sesto Calende municipality) on the littoral areas of Lake Maggiore, macroinvertebrates and meiofaunal assemblages were used as bioindicator taxa. Since decades, they have been frequently recommended for assessing aquatic ecosystem health, because they are subject to both water and sediments environmental modification (Majdi *et al.*, 2020; Rosenberg and Resh, 1993; Boggero *et al*., 2020). Invertebrates also respond strongly to hydrological modifications such as droughts and floods (Reich *et al*., 2023). They, therefore, have been used in bio-monitoring programs to verify the effects of toxic substances, to predict anthropic-induced impacts, to assess the efficacy of conservation measures, or, as in the present case, the effectiveness of water resources management (Coull and Chandler, 1992; Majdi *et al.*, 2020; Rosenberg and Resh, 1993; Allan and Castillo, 2007; Boggero *et al*., 2020).

In particular, an integrated multidisciplinary standard method, encompassing the application of the Lake Habitat Survey to highlight hydro-morphological changes, the characterization of the water chemical composition and the macro- and meio-faunal assemblages to identify changes in water quality and biological structure, was applied to assess the water-level management stress on the littoral areas of a temperate large lake (Boggero *et al*., 2022). With the application of this methodology, our main aims were to evaluate: i) if and how water levels influence the structure and function of littoral macro-meiofauna in sites with similar sediment texture and chemical-physical conditions but subjected to different level excursions, ii) which are the best macro- and meio-faunal candidate taxa to predict water level effects, iii) which quality indices using macro-meiofauna are the most suitable to define the effects of water level alteration. These main aims represent part of the final goals of the project, which will foster the definition of feasible, sustainable, shared and exportable environmental water management strategies to reduce the conflicts of water use among stakeholders (agricultural, industrial, civil use) and the negative effects of climate change to safeguard biodiversity and ecosystem health. The project was especially focused on areas of community interest, natural Parks, or Natura 2000 sites in Italy and on Emerald protected areas in Switzerland where the potential negative effects of poor water level management may cause major damage to biodiversity and to the conservation status of the sites themselves.

METHODS

Study area

Lake Maggiore is a pre-Alpine lake of fluvio-glacial origin located south of the central Alps (Piedmont and Lombardy Regions, Fig. 1) (Boggero *et al*., 2022). It extends for about 65 kilometres from north (Locarno bay) to south (Sesto Calende), and its watershed is shared between Switzerland and Italy. Since 1942, Lake Maggiore water levels are regulated through the Miorina Dam (placed at the River Toce outflow), built to maintain water levels in the range of -0.50/+1.00 m at Sesto Calende gauge station (Boggero *et al.*, 2021). The regulation supported water managers to satisfy agricultural and industrial needs, but it was also useful in controlling floods and drought periods. In the 1960s, the regulation limits were raised to +1.50 m in winter (November to March) to have sufficient water for the greater demands in summer. In 2014, water managers asked for the extension of the +1.50 m water level also to the late spring-summer period (Boggero *et al*., 2021). Thus, the needs for the assessment of potential impacts of late spring–summer human-induced water levels on the littoral macro- and meio-fauna.

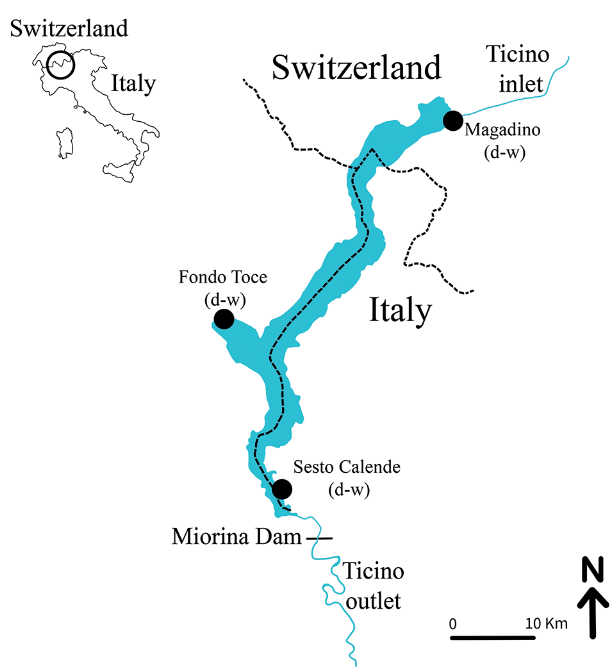

Fig. 1. Lake Maggiore: sampling sites and habitats. d, dry; w, wet (see text for details); dashed line, Italy-Switzerland border.

During the study period, Lake Maggiore water levels were continuously measured by three gauge stations placed near the biological sampling stations (namely, Locarno near the Bolle di Magadino Nature Reserve, Verbania Pallanza near Fondo Toce Nature Reserve, and Sesto Calende gauge near Sesto Calende Nature Reserve). These three gauge stations show different littoral slopes and geographic position; therefore, the measured lake levels influence the ecological status of the sampling stations differently. To define the different water level scenarios during the biological sampling periods, the average, maximum and minimum daily levels were calculated for the reference period 1951-2018, (representing the scenario before the study: pre-project) on which the levels measured in the biological sampling dates were entered. The water level scenarios were thus defined as below pre-project average (low levels: September 2019 and August 2020), average (medium levels: August 2019 and September 2020), and above pre-project average (high levels: July 2020 and July 2021). On average, the daily excursion in lake level is between -3 cm and +6 cm over the whole year. During floods or after prolonged drought periods, the lake level rise can be faster, up to 1.09 m in one day during floods and down to -5 cm in one day or even to -20 cm in a month during drought periods. Although the artificial raising and lowering are not so sudden, they however, are larger than the average natural variations, above all with respect to water ramping.

In detail, we consider three biological sampling stations representing two areas adjacent to river deltas (River Ticino inlet – Bolle di Magadino area, and River Toce - Fondo Toce area) enriched by lotic species, and one totally lacustrine station (Sesto Calende) composed only by lentic fauna. The sampling stations have been selected according to the following criteria: i) they belong to protected areas (Switzerland: Bolle di Magadino Nature reserve - Canton Tessin; Italy: Fondotoce Nature Reserve - Piedmont; Bruschera Nature Reserve - Lombardy), all located along the shore of the lake; ii) they are distributed in different parts of the lake (northern, central and southern) subject to different water levels during the regulation period (from March to September) by the Miorina dam; iii) they represent different habitats under dry conditions during the low water levels ("d"), and permanently wet ("w") throughout the year; v) they are all characterised by the occurrence of sandy sediments where the meiofauna inhabits the first oxygen- and nutrient-rich littoral centimeters (Majdi et *al.*, 2020).

Sampling

For sampling and sorting methods and protocol for the identification of taxa and functional traits of the macro- and meio-faunal assemblages of the littoral zone of Lake Maggiore, the reader should refer to the protocol published in this Special Issue (Boggero *et al*., 2022). However, to ease reading, a brief summary of the methods is hereafter reported.

Field methodology

The taxonomic and functional composition of the macro- and meio-faunal assemblages of Lake Maggiore littorals were analyzed in the three sampling stations: Bolle di Magadino in Switzerland (Md: 46.150444 N, 8.857072 E, Mw: 46.160131 N, 8.854477 E), and Fondo Toce (FTd: 45.936286 N, 8.490822 E, FTw: 45.93500 N, 8.492969 E) and Sesto Calende (SCd: 45.753622 N, 8.591364 E, SCw: 45.751619 N, 8.593186 E) in Italy. At each station, two littoral habitats were sampled: namely, wet (w) always underwater throughout the year, and dry (d) drought-stressed as lake level drops for six times between 2019 and 2021, during periods of low (September 2019 and August 2020), medium (August 2019 and September 2020) and high water levels (July 2020 and 2021) were taken. In each habitat, three spatial replicates were taken along a cross-shore transect to a maximum depth of 1.2 m and at fixed distances from the shore. The distances of the three spatial replicates from the shore varied among 3-5, 10, and 20-25 m, taking as a reference point, a plant, a trunk, or other stable objects on the shore (for sampling details, see Boggero *et al.*, 2022). Macro-fauna was sampled through a handled net (24×24 cm) equipped with a 250 μm opening mesh net (Boggero *et al.*, 2011), while meio-fauna through a handled net equipped with a 60 μm opening mesh net (Malard *et al.*, 2002). Once collected, the biological samples were fixed with 80% ethanol and bottled for further laboratory analysis (sorting, identification to the minimum taxonomic resolution level - genus or species (Tab. 1), photography under a microscope or stereoscope, measurements of length, width and body weight, counting of individuals, biomass estimation).

In total, 100 samples for macro- and 100 for meio-fauna were collected. On some occasions, we were unable to sample sites nearest to the shore due to extremely low water levels, which resulted in completely dry beaches with no faunal records. Similarly, sites farther from the shore were also not sampled because of excessively high lake levels, which posed safety risks. At each of the six sampling points (corresponding to "w" and "d" habitats of each station) and on each sampling date, water temperature was measured and water samples collected for chemical analyses. For details on the analytical methods and the data quality controls, see Boggero *et al.* (2022).

Hydro-morphology

To characterize habitats and potential changes of natural banks and shore zones, the LHS method was applied (Boggero *et al.*, 2022). Forty-four total hab-plots were typified collecting information on riparian, bank, shore and littoral zones, vegetation occurrence and type, beaches and substrate composition (Fig. 2). Any other relevant information,

Tab. 1. Number of individuals and of taxa (in brackets) sampled for each site and taxonomic group, and total values. Numerical order on the total. The rankings of taxonomic groups (taxa) represented the traditional target of limnological studies and groups with homogeneous ecological characteristics.

Taxa	Magadino	Fondo Toce	Sesto Calende	Total ind/(taxa)
Chironomidae	3777 (19)	3228 (27)	408(16)	7413 (31)
Oligochaeta	1198 (15)	339 (15)	735 (15)	2272 (20)
Ceratopogonidae	122 (1)	279 (1)	377 (1)	778 (1)
Bivalvia	501 (2)	120 (3)	83 (2)	704 (4)
Heteroptera	270 (1)	17 (2)	23 (1)	310 (2)
Gastropoda	106 (4)	1 (1)	6 (1)	113 (4)
Ephemeroptera	1 (1)	35 (2)	15 (1)	51 (2)
Trichoptera	4 (2)	45 (2)	1 (1)	50 (2)
Coleoptera	10 (2)	0	3 (2)	13 (2)
Odonata	0	0	4 (1)	4 (1)
Amphipoda	0	3 (1)	0	3 (1)
Platyhelminthes	0	0	1 (1)	1 (1)
Hirudinea	1 (1)	0	0	1 (1)
Total	5990 (48)	4067 (54)	1656 (42)	11713 (72)

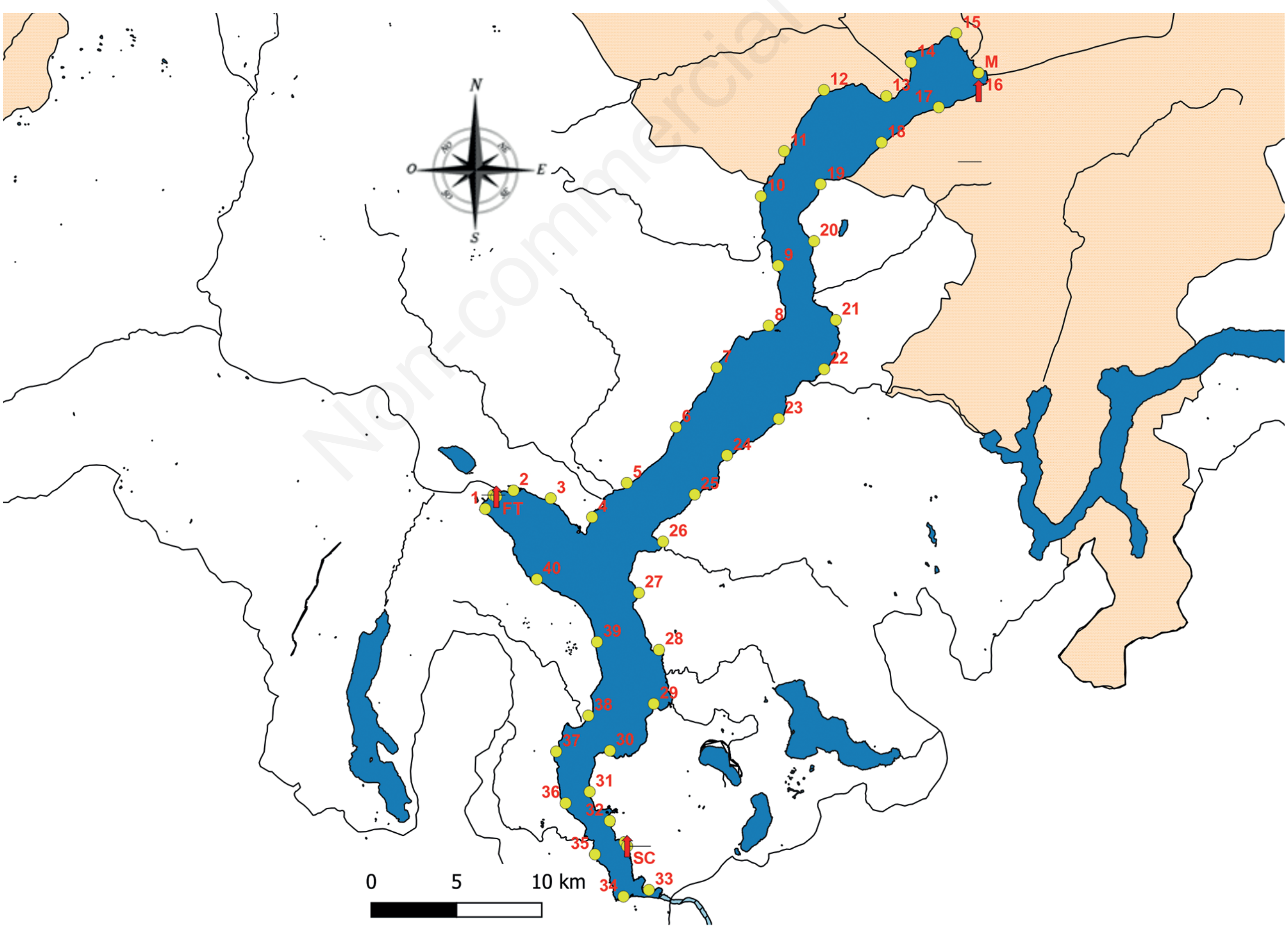

Fig. 2. Number of hab-plots evaluated through LHS application along Lake Maggiore shores and their distribution; arrows, LHS applied to biological sampling stations.

such as human activities, artificializations, and habitat types, were also collected in-between hab-plots. Forty hab-plots out of forty-four were placed in the same places as previous applications (summer 2011) to keep hab-plot points intact. Four hab-plots were placed in the same sites of biological sampling to gather site-specific information. Since the sampling sites were too close to carry out two different LHS applications, only four hab-plots instead of six (such as the number of biological sampling sites) were evaluated. Then, two indices were estimated (LHQA - Lake Habitat Quality Assessment, and LHMS - Lake Habitat Modification Score; Boggero *et al.*, 2022) for the whole lake, and habitat information was extrapolated for each of the four biology-based hab-plots. LHS application was performed with the lowest lake level of the study period (range: 192.72-193.30 m asl) and at high water level (between 194.10-194.25 m) to verify the potential impacts of various levels on the riparian/littoral habitats.

LHS application (Rowan *et al.*, 2006) enabled to separate riparian, littoral and shore zones as follows: i) riparian zones: lands occurring along the edges of rivers, streams, lakes, or other water bodies. The zone is characterised by herbaceous, shrub, and tree vegetation, different land uses, alien plant species occurrence, bare ground or artificial elements. ii) Shore zone: extends from the waterline to the bank edge, so that its width varies with WFLs. Its characterization is based on bank face features and beach features such as height, width, slope, material, vegetation cover and structure, and erosion, which can alternate in both bank face and beach. iii) Littoral zone: near-shore shallow waters where light penetrates to the bottom. The zone includes features such as substrate, woody debris, type and structure of aquatic vegetation. In Tab. 2 are reported the parameters that contribute to the calculation of LHMS and LHQA indices. In detail, LHMS is the sum of the maximum values obtained by the presence of shore modifications (*e.g.*, impoundments, hard bank engineering, floating and tethered structures, moorings, recreational beaches, etc), the shore uses (commercial, residential, roads or railways, parks, gardens, camping and caravans), the hydrological features (maximum lake level, presence of dams, etc) and the maximum sedimentation percentage (hab-plots and delta sedimentation or shore erosion). LHQA index score is the result of the sum of the riparian scores (given by the sum of the vegetation complexity and longevity, natural land cover types, and bank top features), the shore scores (given by the sum of habitat diversity, bank and beach naturalness) the littoral scores and the sum of the whole lake final score (see Tab. 2 in Boggero *et al.*, 2022 for calculation items details).

Laboratory methodology

Water chemistry

Chemical analyses were performed on water samples to measure conductivity, pH, alkalinity, sulphate, chloride and major nutrients (phosphorus and nitrogen compounds, silica), following standard methods for freshwater analysis (APAT, CNR-IRSA, 2003; APHA, AWWA, WEF, 2012). In total, 36 samples were characterised from the chemical point of view (*Tab. S1* SM). Internal and external quality controls were regularly performed to assess data quality (Boggero *et al.*, 2022 for details).

Macrofauna

Once in the laboratory, the 100 samples taken were sorted into the main taxonomic groups without subsampling, identified at the lowest taxonomic level (genus or species) using identification keys specific to each group (chironomids: Andersen *et al.*, 2013; oligochaetes: Timm, 2009; other faunistic groups: AA VV, 1977-1985), and all specimens counted. Subsequently, body length, dry and wet weights were measured for chironomids only, given their dominant role in freshwater lakes (see Boggero *et al.*, 2022 for method details). Taxonomic parameters: number of taxa, presence/absence and relative abundance of each taxon were analyzed. The relative abundances for each taxon recorded at the three spatial replicates per sampling date and station were pooled together in order to grasp the impact of different water levels on macroinvertebrates. Morphological parameters such as chironomid total body

Tab. 2. Results of LHS application: values represent alterations (LHMS) and habitat quality (LHQA) indices as total value (**bold**), and as value per each category at low and high water levels (see Tab. 2 in Boggero *et al.*, 2022 for calculation details).

LHMS	Low	High	LHQA	Low	High
Total score	**36**	**36**	**Total score**	**80**	**72**
Shore modifications	8	8	Riparian score	14	10
Shore uses	8	8	Shore score	13	13
In-lake pressures	8	8	Littoral score	22	18
Hydrology	4	4	Whole lake final score	31	31
Sediment	4	4			
Nuisance species	4	4			

length, and wet and dry weights of single specimens of different chironomid species were used as functional traits to evaluate the potential effects of different water levels.

Meiofauna

In the laboratory, all the samples were sorted, and all the collected individuals were identified and counted. Then, the percent occurrence of five different functional traits, which, based on literature, may be affected by water levels, were evaluated: body size, body shape, locomotion and substrate relation, diet and feeding habits (Cifoni *et al.*, 2021, 2022). We identified different functional categories in each of these traits, as in Tab. 4 in Boggero *et al.* (2022). The taxonomic and functional composition of the faunal assemblages of the three stations were analyzed by using, first, an overall multivariate approach (*i.e.*, all taxa simultaneously) and, subsequently, by focusing our investigations on copepods, which represented one of the dominant littoral taxa of Lake Maggiore, and more in general of freshwater lake littorals. Functional traits were attributed to individuals based on literature descriptions and direct observations carried out in preliminary investigations. Traits were assigned at the class/order level relative to the whole meiofaunal assemblage and at the species level to copepods (Di Lorenzo *et al.*, 2021; Cifoni *et al.*, 2022). The trait profile of each sample was obtained by weighting the individual trait class of each taxon (or species, in the case of copepods) by its abundance in the sample and reporting it to 0-100%.

Statistical approaches

First, both for macro- and meio-faunal assemblages, percent abundances and traits of organisms belonging to three spatial replicates in each habitat (wet and dry) were averaged.

Macrofauna

Then, following the taxonomic approach, a canonical-correlation analysis (CCA – ter Braak and Šmilauer, 2002) was performed on biological (square-root -transformed percent abundance to reduce data variability) and abiotic (sampling sites, sampling dates, log-transformed chemical and physical variables) parameters. Only species with a minimum number of individuals ≥ 5 (relative abundance higher than 0.04 %) were considered, whereas species with lower relative abundance (< 0.04%) were considered rare and then excluded. Due to the high correlation among the 11 environmental variables analysed, a Monte-Carlo permutation test (Hope, 1968) calculated by randomly sampling 999 permutations under a reduced model was carried out to estimate the significance of every single parameter and exclude closely related variables. The selected variables were: temperature, pH, conductivity, ammonium ($N\text{-}NH_4$), and total phosphorus (TP). All statistical analyses were performed using R project software version 4.2.0 (R Development Core Team, 2022) and the vegan package 2.6-2 (Oksanen *et al*., 2022).

Considering the functional approach, the two-way ANOVA test (Statistica, StatSoft 2003) was used to compare the effects of two factors: water level (high, medium and low water levels) and type of habitat (dry and wet habitats) on the functional traits of chironomids (total body length and dry mass).

Meiofauna

Concomitantly, multivariate permutational analyses of variance (PERMANOVA; Anderson, 2001) based on Bray-Curtis resemblance matrices were used to assess the effect of water levels on the taxonomic and functional composition of the littoral meio-faunal assemblages. Three fixed and orthogonal factors were used to explore the data variability across the three sampling stations, two habitat types, and three water levels. Permutation test (999 permutations), type III sum of squares, and permutation of residuals under a reduced model (Anderson, 2001) were used. When appropriate, pairwise permutational post-hoc tests were performed (Anderson, 2001). Before the analyses, the PERMDISP routine was used to check for homogeneity of variances (Anderson, 2001), which is analogous to Levene's test. Data distribution related to body shape, locomotion and substrate relation were non-homoskedastic concerning the habitat type. Therefore, those two traits were examined through a reduced PERMANOVA test consisting of two fixed factors (water level and sampling stations) instead of three. Abundance data were log(x + 1)-transformed to reduce the effect of a skewed distribution, while percent traits were not transformed. The statistical significance was set at $\alpha = 0.05$ since permutational tests do not require additional corrections for multiple comparisons (Anderson, 2001). To improve the comprehension of the results through data visualization, we employed nMDS plots to display mean abundances and barplots to represent morphological traits of littoral meiofaunal taxa across three water levels. Multivariate analyses were performed first on overall meiofaunal assemblages (all taxa simultaneously) and then on copepods.

RESULTS

Water chemistry

Results for all the chemical variables (11 in total) are reported in *Tab. S1*. The main chemical characteristics were quite similar at Fondo Toce and Sesto Calende (conductivity 130-145 µS cm^{-1}, alkalinity about 0.80 meq L^{-1}, low concentrations of reactive and TP), while Magadino showed a higher solute content (conductivity 150-200 µS cm^{-1} and alkalinity close or above 1 meq L^{-1}) and higher nutrient concentrations, mainly of phosphorus. At Fondo Toce and Sesto Calende, the two habitats (w and d) showed similar chemical composition, with slightly higher P and N-NH_4 contents in Fondo Toce. The two habitats at Magadino differed quite markedly, with the d habitat showing higher levels of phosphorus, N-NH_4 and total nitrogen. Conversely, nitrate (N-NO_3) showed higher concentrations in Fondo Toce and Sesto Calende. Differences among stations and habitats were more relevant in 2019 and in the summer 2020, while in September 2020 and July 2021 the chemical features were more homogenous (*Tab. S1*).

Macrofaunal assemblages

Taxonomic diversity

Overall, a total of 11713 specimens and of 62 taxa were collected, and the biodiversity (total number of taxa) representing each site was: 48 in Magadino, 54 in Fondo Toce and 42 in Sesto Calende. The results in Tab. 1 highlighted the high specific and numerical diversity at Magadino and Fondo Toce compared to Sesto Calende. The captured taxa belonged mainly to Insecta (Ceratopogonidae, Chironomidae, Coleoptera, Ephemeroptera, Heteroptera, Odonata, Trichoptera) and Oligochaeta. Then, Hirudinea, Platyhelminthes, Molluscs (Bivalvia, Gastropoda), Amphipoda followed. For detailed information on occurrence data of chironomids and oligochaetes in each sampling station and season, see https://doi.org/10.15468/sh5kzm easily accessible via GBIF.org (Zaupa *et al*., 2022).

All three sites were dominated by chironomids (63% of the whole assemblage), followed by oligochaetes (19%), ceratopogonids (7%) and bivalve molluscs (6%). The other fauna showed very low relative abundances (<5%) and was represented by a small number of specimens for each taxon. The same pattern was evident when analysing macroinvertebrate abundance per single sampling site. Magadino and Fondo Toce showed a similar assemblage structure, with chironomids prevailing (63 and 79%, respectively) on oligochaetes (20 and 8%). Sesto Calende showed the opposite situation, with oligochaetes predominating (44%) on chironomids and ceratopogonids with similar percentages (25 and 23%). The other fauna was represented by relative abundances lower than 6% or even much lower (<2%). Considering only the dominant groups, chironomids and oligochaetes, 7413 chironomid specimens were identified to genus/species level for a total amount of 31 taxa. Frequent and common taxa to all sampling stations were: *Ablabesmyia longistyla* and *Procladius* sp. (Tanypodinae), *Cladotanytarsus* sp., *Cryptochironomus* sp., *Demicryptochironomus vulneratus*, *Microchironomus tener*, *Polypedilum bicrenatum, P. nubeculosum*, *P. scalenum*, and *Stictochironomus pictulus* (Chironominae), *Orthocladius* sp., and *Psectrocladius sordidellus* (Orthocladiinae). Among Oligochaetes, 2272 specimens belonging to 21 taxa were collected, but at each station a maximum of 14 taxa was reached. Six species/taxa are common to all sites: *Psammoryctides barbatus, Tubifex ignotus* (Tubificidae), *Nais communis, Nais pseudobtusa, Uncinais uncinata* (Naididae) and the family Enchytraeidae.

Taking into consideration the percent abundance of the most common species in relation to water levels (Fig. 3), it is quite evident that *Cladotanytarsus* sp. and *Polypedilum bicrenatum* decreased progressively in number from low to high water levels. Just the opposite pattern was manifested by *Cryptochironomus* sp., *Polypedilum nubeculosum, Psectrocladius sordidellus* and especially by *Stictochironomus pictulus* whose relative abundances increased significantly from lower to higher water levels. The same tendency was observed within oligochaetes: *Limnodrilus hoffmeisteri* and *Nais* sp. showed a decrease in abundance as water level increased, whereas a reverse pattern was observed for *Psammoryctides barbatus*, which seemed to increase in abundance with lake water levels (Fig. 4). CCA results pointed out all the selected variables as drivers of macroinvertebrates assemblage structure (Fig. 5). The first four axes altogether explained 57% of the total variation in assemblage structure. The main environmental gradient (axis 1: represented by pH

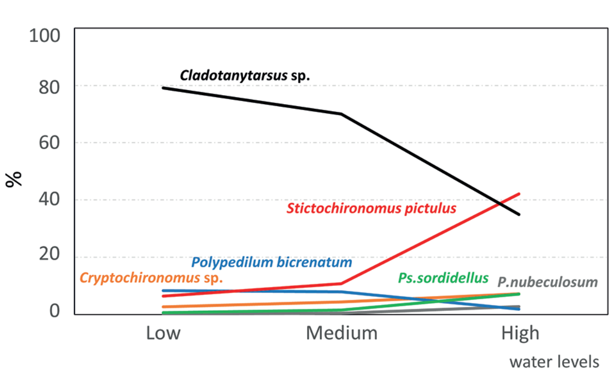

Fig. 3. Percent total abundance of common chironomid taxa per different water levels (high, medium and low).

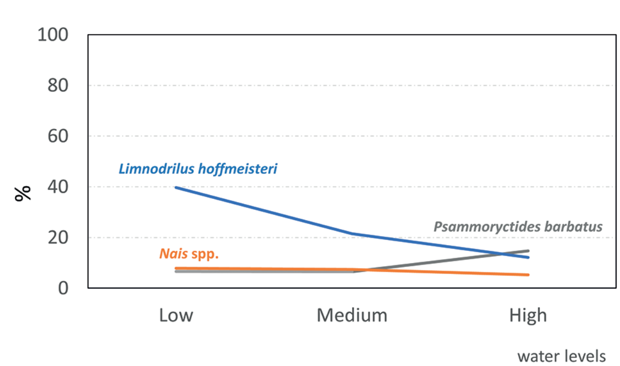

Fig. 4. Percent total abundance of oligochaeta taxa per different water levels (high, medium and low).

and temperature) explained 22% of the total variance, whereas CCA axes 2 (defined by conductivity, TP and N-NH_4 and representing a condition of nutrient enrichment) explained 16%. Most sites and taxa are related to axis 2, whereas a few of them to axis 1 (Aug_19_FT, Sep_19_FT, Aug_20_FT, July_20_SC, Aug_20_SC, July_21_SC, Sep_20_M). Among them *Cladotanytarsus* sp., *Corbicula fluminea, Stylaria lacustris, Tubifex ignotus* (or the dominant chironomids, molluscs, oligochaetes) seemed to be related to nutrient enrichment (CCA axis 2), while other fauna such as *Baetis* sp., *Caenis* sp., Trichoptera seemed to respond to water temperature and pH (CCA axis 1).

Functional diversity of chironomids

The results of two-way ANOVA on the variance of two functional traits of chironomids: body length (size diversity across several chironomid species) and dry weight in relation to water levels and type of habitat (dry and wet) showed that medium water level privileged organisms with larger body size with no difference at dry and wet habitats (Fig. 6a) and slowest growth compared to low and high water levels (Fig. 6b), suggesting more favorable conditions. Smaller organisms with faster growth rates predominate at low water levels compared to medium and high water levels (Fig. 6b). Dry habitats manifested more pronounced effects of water level scenarios on total body length than permanently wet habitats (Fig. 6a) with less significant variations in body length.

Our results suggest medium water levels are more favourable for the fauna inhabiting the littoral areas, both as diversity and as growth rate. Larger and negative effects where found under drought conditions (low water levels) on chironomid functional traits (faster growth and smaller chironomid individuals), exacerbated by higher temperatures recorded along the littorals. Unfortunately, we are unable to counteract or mitigate the effects of water scarcity

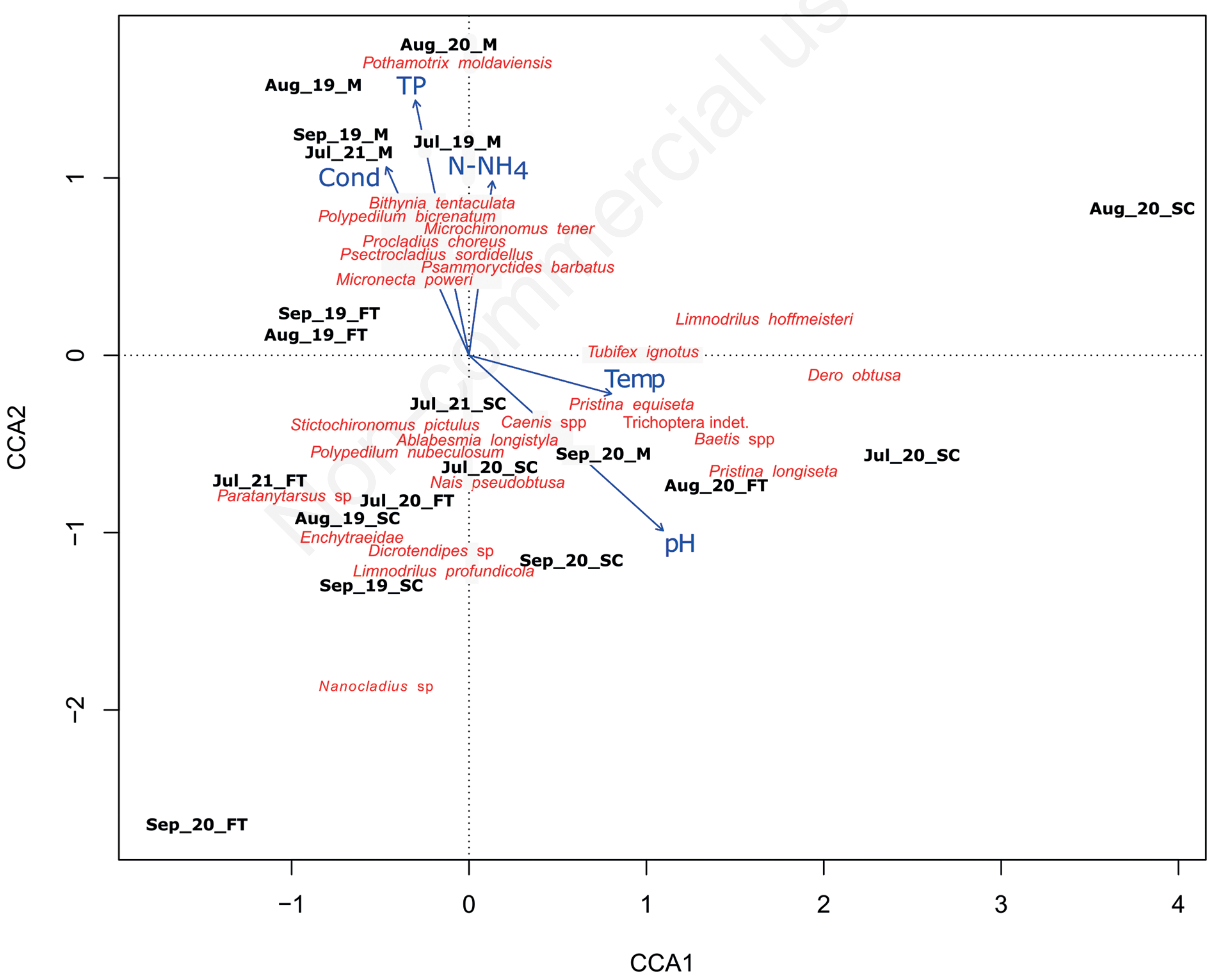

Fig. 5. Canonical correspondence analysis (CCA) plot showing the influence of main environmental parameters (blue arrows) and sampling periods month and year/sites on macroinvertebrates; Jul, July; Aug, August; Sep, September; 19, 2019; 20, 2020; 21, 2021; M, Magadino; FT, Fondo Toce; SC, Sesto Calende.

related to climate change. Other impacts, but of minor importance, were found at high-water levels when chironomid growth rate is lower and individuals are larger. In this case, we are able to propose mitigation actions (a different water level management) in support of chironomids (and of the whole food web structure) to counteract this impact.

Meiofauna

Taxonomic diversity

In total, 13,650 specimens belonging to 13 taxa were examined. Chydorids (cladocerans) represented the dominant group (27% of total abundance), followed by copepods (22%), nematodes (20%), and chironomids (10%). Oligochaetes and ostracods showed abundances of 7% and 6%, respectively, while other taxa (rotifers, tardigrades, bivalves, mites, early larval stages of ephemeropterans, plecopterans, and collembolans) accounted for ≤3%. During the survey period, mean abundances varied significantly as a function of water levels, while they were unaffected by sampling stations and habitat type (*Tab. S2*). In detail, mean abundances varied significantly between high and low, and between high and medium water levels, but not between medium and low water levels (*Tab. S2*). Six out 13 collected taxa, namely copepods, ostracods, mites, and chironomids, showed the highest abundances in high water level period (Fig. 7). In the meantime, oligochaetes and nematodes were highly abundant during medium and low levels (Fig. 7). Chydorids, the most abundant taxon, did not vary significantly among water levels.

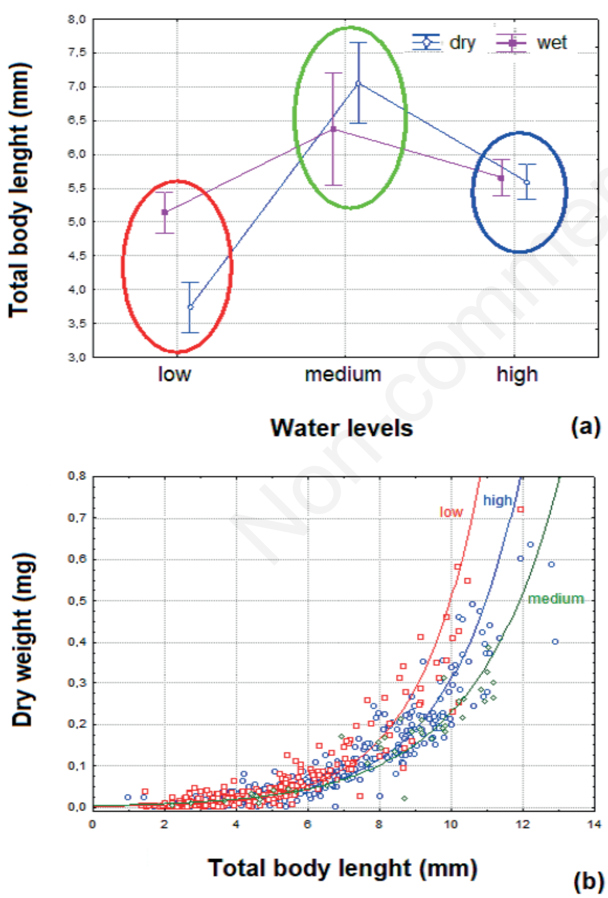

Fig. 6. Chironomid functional traits variation. a) Two-way analysis of variance (ANOVA) of total body length by lake water levels (low, medium, high) and habitat type (dry and wet), p=0.00001; bars: 0.95 confidence interval. b) Total body length-dry weight relationships per water level; red, low; green, medium; blue, high.

Functional diversity

Locomotion and diet (feeding habit) traits did not show significant variations due to water levels (*Tab. S3*). Diet varied significantly with habitat type and with the interaction of habitat and sampling stations. The other two functional traits (*i.e.*, body size and shape) differed considerably with water levels, with significant differences between high and low levels and between high and medium levels, but not between medium and low levels (*Tab. S3*). In detail, organisms with intermediate body sizes were more abundant in high water levels, whereas the smallest and largest specimens were collected during medium and low levels (Fig. S1). Cylindrical specimens were more abundant during high water levels, while streamlined and flattened ones dominated medium and low water levels (Fig. S1). Spherical organisms were always low-abundant, regardless of water level.

Taxonomic diversity of copepods

Overall, 2259 copepods at copepodite and adult stages were identified (Cifoni *et al*., 2022; Tabilio Di Camillo *et al*., 2022). Thirteen copepod species were identified. Seven species belonged to the order Cyclopoida: *Acanthocyclops robustus robustus* (Sars G.O., 1863), *Paracyclops fimbriatus fimbriatus* (Fischer, 1853), *Eucyclops (Macrurocyclops) macrurus* (Sars G.O., 1863), *Eucyclops serrulatus serrulatus* (Fischer, 1851), *Mesocyclops leuckarti leuckarti* (Claus, 1857), *Macrocyclops albidus albidus* (Jurine, 1820), *Eucyclops* cf. *lilljeborgi* (Sars G.O., 1918). Six species belonged to the order Harpacticoida: *Bryocamptus echinocamptus echinatus* (Mrázek, 1893), *Attheyella (Attheyella) crassa* Chappuis, 1929, *Bryocamptus (Bryocamptus) minutus* (Claus, 1863), *Nitokra hibernica hibernica* (Brady, 1880), *Bryocamptus (Echinocamptus) hoferi* (Van Douwe, 1908) ed *Epactophanes richardi richardi* Mrázek, 1893. The dataset of copepod abundances, along with georeferenced occurrence records, is available on GBIF (Global Biodiversity Information Facility) at https://www.gbif.org/dataset/78e81992-16c2-4644-9820-4b0dbe19f2a2 (Tabilio Di Camillo *et al*., 2022).

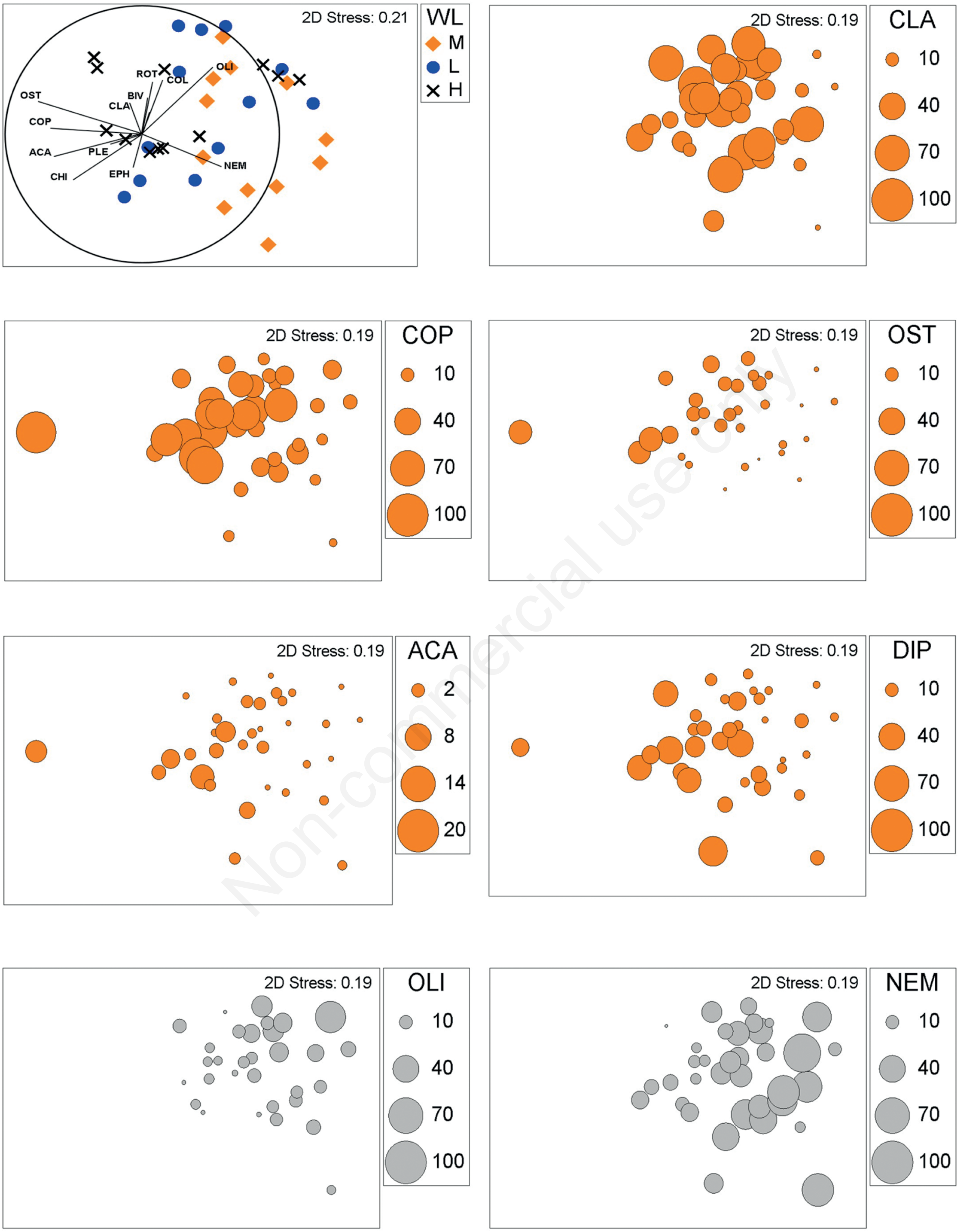

Fig. 7. nMDS plots of mean abundance of littoral meiofaunal taxa of Lake Maggiore during high (H), medium (M) and low (L) water levels (WL). Circle sizes are proportional to mean abundances (number of individuals); ACA, mites; CLA, cladocerans; COP, copepods; DIP, chironomids; NEM, nematodes; OLI, oligochaetes; OST, ostracods.

Mean copepod species abundance varied significantly with lake levels, sampling stations, and the interaction of the two factors (*Tab. S2*). However, the post-hoc tests showed that differences were significant only between high and medium water levels, while non-significant variations were detected between low and medium levels, and between high and low levels (*Tab. S2*). Variations were mainly due to 2 copepods, namely: *P. fimbriatus* and *A. crassa*. *Paracyclops fimbriatus* was highly abundant during high and low levels, whereas *A. crassa* during low water levels (Fig. S2).

Functional diversity of copepods

Copepod biomass, and locomotion/substrate relation and body shape traits seemed to be affected by water levels only (*Tab. S3*). Differences were mainly due to swimming and spherical copepods, which were less abundant during high levels than in the other periods (*Tab. S3*). None of the three factors controlled significantly the body size (*Tab. S3*), but water level had a considerable influence on diet and feeding habits; however, these traits also varied among sampling stations (*Tab. S3*). During high water levels, copepods detritus-feeders were more abundant at Magadino, and during medium water levels, omnivores and scraping herbivores prevailed at Fondo Toce than in the other two water levels and stations.

Hydro-morphology: habitat and alteration indices

Tab. 2 reported LHMS and LHQA indices results for the whole lake. LHMS values showed high shore alterations due to hard bank engineering, mooring, floating and tethered structures, residentials, roads and railways, parks and gardens, docks, recreational activities, beaches, and commercial activities. In-lake pressures were also high due to overall commercial and sport fishing, fish stocking, navigation, dredging, motorboat activities, surface oil film, and many others. Hydrology also appeared impacted because of lake level regulation. During both applications, the final evaluation gave similar results (36 as the total score). LHQA represents the presence and complexity of natural vegetation, *i.e.* woods, shrubs, grasslands, and also aquatic and semi-aquatic plants, peat bogs, marshes, rocks and dunes. The presence of delta deposits of high naturalistic value should also be noted. At high water level, LHQA value was 72, due to a lower abundance of vegetated and unvegetated habitats (habitat homogeneization). Only wet woodland was highly represented at this water level. At low water level, the same index shows a value of 80, an indication of higher littoral quality and habitat diversification. For the habitats of the biological hab-plots, the riparian, shore and littoral scores extrapolated from LHQA specific-index were used (Tab. 3). These values were very similar among biological sampling stations. Comparing the mean values of the riparian, shore and littoral zones (mean score calculated for riparian, shore and littoral zones using LHQA index) of the biological stations and the same score considered for the whole Lake Maggiore, the three biological stations represented the 34.7% of the naturalness of the whole lake, and in particular, the 26.2% of the riparian, the 61.5% of the shore and the 24.2% of the littoral zone scores. These values represent the number of natural features detected in the three biological study areas with respect to the natural features detected in the riparian, shore and littoral zones at the whole lake level. Comparing the percent values of riparian, shore and littoral zones of the three biological hab-plots to the ones of the whole lake, they are high and characteristics of a high habitat diversification. This condition is due to the low anomalous levels related to the prolonged 2021 drought, which led to a vertical decline of approximately 1.5 m of horizontal littoral exposure.

DISCUSSION

Overall, Lake Maggiore displayed a quite complex situation (physical, chemical and biological) as typical for the littoral area of large and deep lakes (Kaufmann *et al*., 2014).

The water chemistry variability during the survey period was rather limited, as confirmed by conductivity stability, a proxy for solute content. Nutrients were more variable in space and time, with systematically higher values of total phosphorus in Magadino strongly related to a cormorant colony occurring at the Ticino river-delta. Nitrate, the dominant fraction of total nitrogen, showed some seasonal and inter-annual variability, mostly in relation to precipitation events, being atmospheric deposition the main source of nitrogen in Lake Maggiore area (Rogora *et al*., 2016).

From a structural point of view, the lake is characterized

Tab. 3. Habitat scores for riparian, shore and littoral zones for the three biological sampling stations are shown. Total score and relative cover at the whole lake scale are also added (**bold**).

	Fondotoce	Sesto Calende	Magadino	% whole lake
Total score	**14**	**22**	**15**	**34.7**
Riparian	3	4	4	26.2
Shore	6	12	6	61.5
Littoral	5	6	5	24.2

by several river-delta systems such as those of the rivers Ticino and Toce here considered, defined by the encounter between the dynamic solid transport of the river and the lake water mass and combined alluvial ecological processes with marshes, and by more lentic areas providing refuges to prey, substrates for macrophytes growth, and food source (Sass *et al*., 2006). Water level fluctuations in the lake, naturally linked to high pluviometric periods, but also anthropogenically induced by the Miorina dam, have changed our perception of lake morphology, littoral slopes and their habitats, especially when littoral areas remained uncovered and biocoenosis most likely undergoes changes in its structure and functions (Evtimova and Donohue, 2016).

Hydro-morphological features related to lake water bodies, habitats and human infrastructures along the banks/shores and littoral zones, are strongly related to the lake ecological quality (Strayer and Findlay, 2010; Zaupa *et al*., 2017). LHS covers all the features of Italian lakes, both at low and high lake levels, and allowed to define which habitats are permanent, which are only present during low levels, which one occurred only at high water levels, and their percentage extents. In particular, during low lake levels the more represented habitats are the natural ones used by benthic organisms as nursery, shelter, and climate adaptation zones. Different habitats cause different benthic invertebrates assemblage structures (Smilikov *et al.*, 2005), thus the greater naturalness experienced by the lake at low level supports the ecosystem services, improving biodiversity and their function. On the contrary, a habitat highly represented during high lake levels such as wet woodlands could act as nursery, shelter, and climate adaptation zone but it remains one of the few habitats present, which therefore provides an idea of monotony of the environment. Hence, when human activities and artificializations are found in the riparian area, a loss of biodiversity can occur as stated by Thomaz *et al.* (2007). In both river-deltas it is worth saying that not only the biodiversity, but also macroinvertebrate abundances were high (at Magadino, abundance was 1.5 fold higher compared to Fondo Toce and almost 3.5 times higher compared to Sesto Calende) and constituted spectacular examples of active river-delta systems.

Based on the provided results, it is evident that we achieved the first aim of our study. Water levels proved to have significant effects on the structure and function of littoral macro-meiofauna in sites with similar sediment texture and chemical-physical conditions but subjected to different level excursions. Further, the following macro- and meio-faunal candidate taxa may be suggested as potential indicators for predicting water level management effects, following the second aim of our study: i) chironomids and oligochaetes and ii) copepods, such as *P. fimbriatus* and *A. crassa,* which exhibit significant variations in abundance with water levels; iii) functional traits related to body size and shape in macro- and meio-fauna. The abundances of both chironomids and oligochaetes at different lake levels showed the chironomids *Cladotanytarsus* sp. and to lower extent *P. bicrenatum,* together with the oligochaete *L. hoffmeisteri* prefer warmer, shallower habitats because they are considered to be more or less resistant to desiccation (Slavevska-Stamenković, 2012). By contrast, the abundances of *S. pictulus*, *P. nubeculosum, P. sordidellus* and *Cryptochironomus* sp. (chironomids) (Rossaro *et al*., 2022), and *P. barbatus* (oligochaetes) increase (more or less significantly) with depth (in relation to higher water levels) and cooler waters. Further, the analysis of functional traits (body length and dry weight) highlighted a significant stress of low, but also of high water levels, although less significant, on chironomid growth and growth rate (faster growth compared to medium water levels) exacerbated by higher temperatures recorded along the littorals during the study period. These results are in agreement with studies on within-lake variability of chironomid assemblages underlining water depth as a key factor in chironomid distribution modifications (Heiri, 2004; Engels and Cwynar, 2011). Therefore, both assemblage structure of chironomids and oligochaetes also provide insights on the level fluctuations impacts on macroinvertebrates as a whole in terms of occurrence, abundance and growth rate of specific taxa.

CCA results should shed light on the assemblages-environment relationships, whereas the analysis of functional traits on the ecosystem functioning, thus acquiring a more complete picture than the one provided by taxonomic approaches alone on the variability of littoral communities (Brodersen *et al*., 1998; Brauns *et al*., 2007). CCA relationships suggested that total phosphorous, ammonium, temperature and pH, strongly influence macroinvertebrate assemblages. Total phosphorous and ammonium are here strongly related to a cormorant colony occurring at the Ticino river-delta having cascading effects on macroinvertebrate richness and abundance thanks to the huge quantities of guano produced (Marmen *et al*., 2017; Grant *et al*., 2022). Temperature and pH are well known physicochemical parameters affecting macroinvertebrates distribution and abundance (Trichkova *et al*., 2013; Bonacina *et al*., 2023) mainly along the littoral areas of lakes under climate change forcing.

Lake Maggiore littoral areas also harbor well-diversified meio-faunal and copepod assemblages, which presented peaks of taxonomic and functional abundances during the high water levels and comparatively reduced abundances in the low-medium levels in late spring-early summer in 2019-2021. Our data on chydorids are in agreement with previous studies (Adamczuk, 2014), where invariable chydorid abundances were found in the littoral zones of oligotrophic lakes with scarce vegetation. Our results on ostracod and mite assemblages appear to be in line with Traunspurger *et al.* (2012), who highlighted the preference of ostracods for high lake water levels, and Mastrantuono *et al.* (2008), who came to the same conclusion regarding mites. The preference of early larval stages of chironomids for high water levels has also been assessed by Shcherbina (2013). We observed variations in the abundances of nematodes and oligochetes as a function of water levels, as also previously observed by Vidakovic *et al.* (2001) and Furey *et al.* (2006). We assessed variation in body size of meiofaunal taxa due to water levels as also observed for diatoms (Leira *et al.*, 2015), macroinvertebrates (Spoljar *et al.*, 2021), and chydorids (Mezquita and Miracle, 1997), in previous studies, where the changes in biomass were attributed to the higher habitat heterogeneity occurring during the high water levels compared to the low ones.

The variations in the abundances of copepod species and functional traits observed in this study were in line with Cifoni *et al.* (2022) and seemed unrelated to the species phenologies (Sarvala, 1979; Fefilova, 2007). *Paracyclops fimbriatus* and *A. crassa* showed high abundances also during low water levels, as observed in previous studies (*e.g.*, Gaviria, 1998). The two species seemed to be more resistant than others to water turbulences induced by increased wave intensity during low water level periods (Särkkä, 1996; Sarvala *et al.*, 1998; Dole-Olivier *et al.*, 2000). Accordingly, omnivorous, deposit feeder and opportunist copepods, which can resist habitat disturbance better than non-generalist species (Death and Winterbourn, 1995) by exploiting a broad range of potential food sources, were more abundant during the low water level than in the high one, as also observed by Evtimova and Donohue (2016) for other benthic invertebrates in the littoral zone of lakes. Nevertheless, copepod biomass was significantly higher during the high water level than in the medium/low ones, as also observed in other studies (Palomäki, 1994; Cifoni *et al.*, 2021).

Finally, to define water level management effects using macro-meio-fauna, we considered several quality indices that reflect different aspects of assemblage structure and function, following the third aim of our study. Based on the provided results, we can conclude that abundance- and functional-based indices would be suitable. Our results provided a better understanding of the potential consequences of the water management strategy of Lake Maggiore during the late spring-early summer period. Likely, publicly endorsed water management rules will be developed to strike a balance between human uses and the preservation of the lake ecosystem. The study's outcomes may play a role in guiding decision-makers to develop sustainable strategies that ensure the ecological health and biodiversity of Lake Maggiore's littoral zone are protected for the benefit of both the environment and the local community.

CONCLUSIONS

Key findings of the present work allow us to highlight and conclude that a more in-depth knowledge of the main hydro-morphological, physico-chemical conditions and of the ecological response of Lake Maggiore may be essential for its water management. Because lakes showed an equilibrium among variations in water levels, wave patterns and physical and biological features of their shorelines, the artificial raising of the lake level must take into account the seasonal evolution of the littoral biocenoses to be ineffective on the biocoenosis itself and must be variable over time. Thus, the obtained data may support mitigation actions of impacts improving the ecological status of the lake.

Our results reveal that water levels, or rather, the changes in the water level occurring over relatively short time periods in Lake Maggiore, most likely cause ephemeral environments inducing modifications in the composition and functionality of the littoral macro- and meio-faunal assemblages. Organisms need longer periods of adaption to significant variations in water levels (low/high), but also to their extension in time (how long these conditions last). Moreover, an increase in water level has as a consequence the erosion, washing, and rolling of the littoral substrate that pose macro- and meio-faunal assemblages under stress. Therefore, these temporary ecosystems host specific coenosis associated with pronounced impacts on the whole food web only when they recur over time with a certain frequency (Beca, 2008), even under "up-regulation" (high levels) of the water levels, although less significant than those produced by "down-regulation" or lower levels.

During low water levels, drying may occur depending on bathymetry, and it is more frequent in river-deltas where the littoral slope is gentler. These river-deltas habitats are very rare throughout Europe, therefore the importance of their conservation is pivotal, as well as the management plans in support of water level changes in frequency and amplitude mitigations. More studies are needed also on habitat features at different levels of the lake, both in natural and non-natural areas, to verify the biocoenosis ability to adapt and undergo changes in environmental conditions, and ecosystem services modifications under projected climate and current water management.

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Online supplementary material:

Tab. S1. Results of the chemical analyses performed on the 36 samples collected at the different sites within 2019-2021.

Tab. S2. Pseudo-Fs and p-values of the PERMANOVA performed on the overall abundance of littoral meiofaunal taxa and copepods of Lake Maggiore, and t-values and p-values of the permutational post-hoc t-tests.

Tab. S3. p-values of the main tests of PERMANOVAs and pairwise post-hoc t-tests performed on functional traits of littoral meiofaunal and copepod assemblages of Lake Maggiore.

Fig. S1. Barplots of mean percentages of body size and body shape traits during high, medium, and low levels.

Fig S2. nMDS plot of mean abundance of littoral copepod species of Lake Maggiore during high, medium and low water levels.