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Abstract: A first synoptic and trans-domain overview of plankton dynamics was conducted across the aquatic sites belonging to the Italian Long-Term Ecological Research Network (LTER-Italy). Basing on published studies, checked and complemented with unpublished information, we investigated phytoplankton and zooplankton annual dynamics and long-term changes across domains: from the large subalpine lakes to mountain lakes and artificial lakes, from lagoons to marine coastal ecosystems.
This study permitted identifying common and unique environmental drivers and ecological functional processes controlling seasonal and long-term temporal development. The most relevant patterns of plankton seasonal succession were revealed, showing that the driving factors were nutrient availability, stratification regime, and freshwater inflow. Phytoplankton and mesozooplankton displayed a wide interannual variability at most sites. Unidirectional or linear long-term trends were rarely detected but all sites were impacted across the years by at least one, but in many case several major stressor(s): nutrient inputs, meteoclimatic variability at the local and regional scale, and direct human interventions at specific sites. Different climatic and anthropic forcings frequently co-occurred, whereby the responses of plankton communities were the result of this environmental complexity.

Overall, the LTER investigations are providing an unparalleled framework of knowledge to evaluate changes in the aquatic pelagic systems and management options.

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Dear Editor,

We are pleased to submit the paper entitled “Plankton dynamics across the freshwater, transitional and marine research sites of the LTER-Italy Network. Patterns, fluctuations, drivers”, by Morabito et al, to “Science of the Total Environment”, for the "ILTER" special issue.

We are sorry for these few days of further delay, respect to the deadline of August 31st.

The paper is the fruit of a real teamwork from all the researchers involved in the LTER-Italy aquatic sites. It was “coordinate” by the first (Giuseppe Morabito) and the last Author (myself, acting also as corresponding Author).

As you probably already know from Peter Haase, Giuseppe passed over on July 12th. We wish to dedicate this work to him. I did not write yet any sentence on the paper, just not to influence in anyway the reviewers. However, if the work will be considered for publication, we will ask you to add it, possibly on the front page.

Thank you so much.

Yours sincerely,

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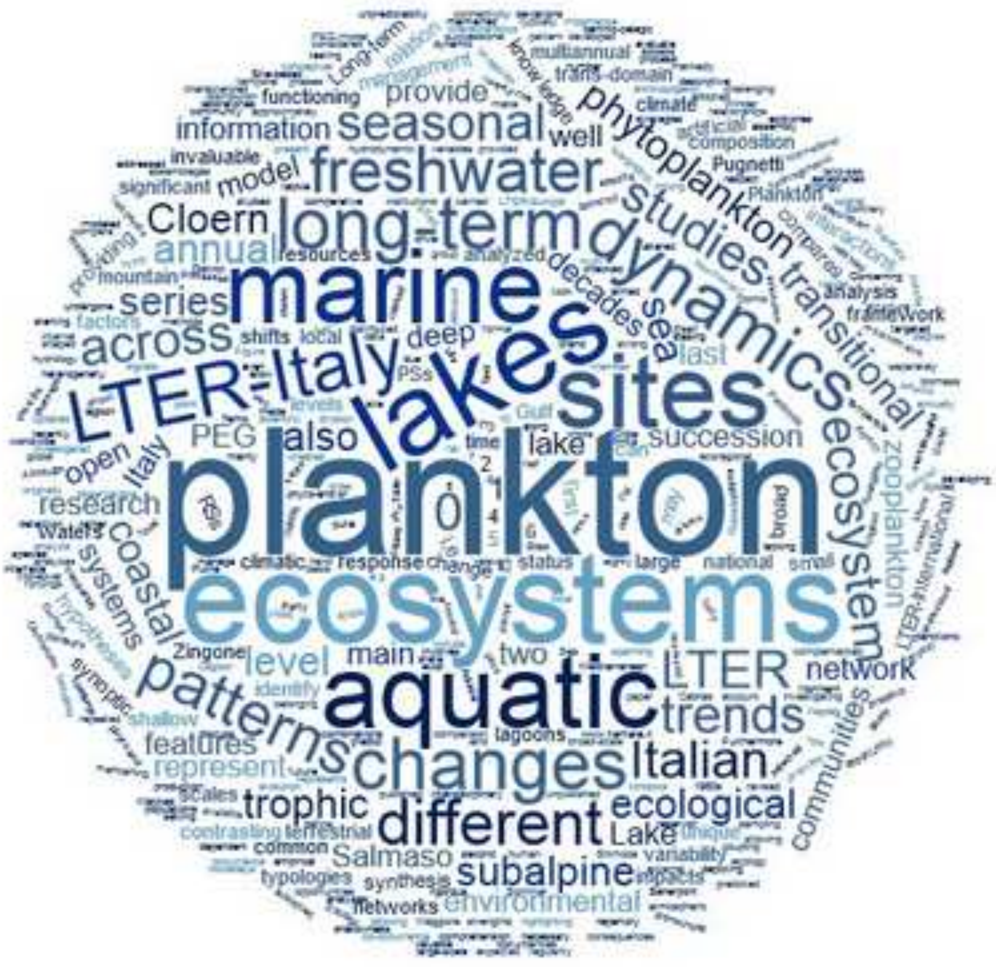
*Graphical Abstract



Highlights

- This is the first synoptic study on plankton dynamics in LTER-Italy aquatic sites
- We adopted a trans-domain approach, considering lakes, lagoons and coastal sea
- We based our review on published studies, complemented with unpublished information
- The plankton seasonal cycles presented site-specific patterns and commonalities
- The long-term changes were mainly driven by climatic and anthropogenic drivers

Plankton dynamics across the freshwater, transitional and marine research sites of the LTER-Italy Network. Patterns, fluctuations, drivers

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ABSTRACT

A first synoptic and trans-domain overview of plankton dynamics was conducted across the aquatic sites belonging to the Italian Long-Term Ecological Research Network (LTER-Italy). Basing on published studies, checked and complemented with unpublished information, we investigated phytoplankton and zooplankton annual dynamics and long-term changes across domains: from the large subalpine lakes to mountain lakes and artificial lakes, from lagoons to marine coastal ecosystems.

This study permitted identifying common and unique environmental drivers and ecological functional processes controlling seasonal and long-term temporal development. The most relevant patterns of plankton seasonal succession were revealed, showing that the driving factors were nutrient availability, stratification regime, and freshwater inflow. Phytoplankton and mesozooplankton displayed a wide interannual variability at most sites. Unidirectional or linear long-term trends were rarely detected but all sites were impacted across the years by at least one, but in many case several major stressor(s): nutrient inputs, meteoclimatic variability at the local and regional scale, and direct human interventions at specific sites. Different climatic and anthropic forcings frequently co-occurred, whereby the responses of plankton communities were the result of this environmental complexity.

Overall, the LTER investigations are providing an unparalleled framework of knowledge to evaluate changes in the aquatic pelagic systems and management options.

Keywords

LTER-Italy, aquatic ecosystems, phytoplankton, mesozooplankton

1. Introduction

Plankton communities are at the base of aquatic ecosystem functioning. Across freshwater, transitional and marine ecosystems, phyto-and zooplankton have a broad and different repertory of seasonal patterns, multi annual trends and shifts. An in-depth comprehension of plankton dynamics is necessary not only to manage aquatic resources, but also to predict and tackle future environmental changes. Long-term series of plankton provide unique and precious datasets for depicting reliable patterns of average annual cycles while detecting significant changes, occurrence of shifts and trends of populations and communities in response to global or local impacts. Moreover, sites of long-term ecological research may represent *in situ* laboratories that allow testing hypotheses about plankton ecology.

The seasonal succession of plankton is an annually repeated process of community assembly, shaped by changes in external factors and internal interactions. In the 1980s, the Plankton Ecology Group (PEG) developed a descriptive model, providing a conceptual framework for the description of seasonal dynamics in temperate lake plankton communities, recently revised and updated (Sommer et al., 2012). De Senerpont Domis et al. (2013) took the PEG model as the basis to analyze and discuss the effect of climatic changes on seasonal patterns of plankton successional phases and trophic relationships in different freshwater systems. Other studies analyzed long-term plankton trends in shallow (Mooij et al., 2005) and deep (Shimoda et al., 2011) lakes and the effects of climate variability on seasonal pattern of plankton, showing that the response of each ecosystem is strongly dependent on its ecological characteristics (trophic status, mixing regime, hydrology and food web structure). Although originally targeted for lake ecosystems, the PEG model was also adopted by marine plankton ecologists. As in lakes, a relatively small number of environmental factors typically drive the seasonal plankton cycle in the open sea, so that the annual succession of plankton biomass and species composition shows some regularity, which can be assessed, modeled and even predicted (Rubao et al., 2010; Mackas et al., 2012). In the open sea and in lakes, the PEG-model can therefore represent a valuable starting point to describe and compare the planktonic succession across different aquatic systems and to identify deviations from expected patterns. On the contrary, at the land-sea interface, that is, in marine coastal and transitional waters, plankton dynamics are characterized by a pronounced degree of unpredictability, making it harder to define "baselines" against which to evaluate the role of local and large-scale changes as well as multiannual trends (Cloern and Jassby, 2008, 2010; Zingone et al., 2010a; Carstensen et al., 2015; Cloern et al., 2016).

In these ecotones the analysis of long-term trends in plankton dynamics is rather challenging, not only due to the co-occurrence of climate change and human disturbances, but also to the interactions of atmospheric, terrestrial and open sea forcings. Some features of these ecosystems, such as shallowness, benthic-pelagic coupling and connectivity to both land and sea, markedly affect plankton composition and distribution on both spatial and temporal scales (Winder and Cloern 2010; Zingone et al., 2010a; Paerl et al., 2015; Cloern et al., 2016).

Site-based studies on plankton have been maintained worldwide for decades; considered jointly, they may provide an invaluable opportunity to assess common or contrasting patterns of variability, to understand how those patterns change at different scales and to hypothesize about causes and consequences.

The importance and the challenge in maintaining long-term series have been addressed and sustained, in the last decades, by setting up long-term ecosystem research (LTER) sites and networks, nowadays well established at the international (LTER-International), regional (LTER- Europe) and national (e.g. LTER-Italy) level. The LTER site networks provide unique insights for developing a framework for ecological synthesis, which creates new knowledge through innovative combinations of information and integrating long-term series with broad-scale comparison of patterns.

The Italian LTER network, LTER-Italy (www.lteritalia.it), is a formal member of LTER-Europe and LTER-International since 2006. It involves several national scientific institutions that manage a group of twenty-five "parent sites" (PSs), belonging to terrestrial, freshwater, transitional and marine ecosystems. The PSs encompass a total of seventy-nine “research sites” (RSs), which represent the main ecosystem typologies of Italy and give to the network a strong interdisciplinary brand. Forty RSs, i.e. more than half of the network sites, are aquatic ecosystems. They include the most common Italian lake typologies (large and deep subalpine lakes, small and shallow mountain lakes and reservoirs), the main Italian lagoons and relevant marine coastal ecosystems (Fig. 1). The LTER-Italy aquatic sites are distributed along the whole Peninsula, spanning the two main ecoregional division levels of Italy (Blasi et al., 2014), the Temperate and the Mediterranean.

Long-term time series on plankton (phyto-and/or zooplankton) dynamics have been collected during the last forty years at the LTER-Italy aquatic sites, providing an invaluable empirical and rigorous knowledge for the sustainability and management of aquatic resources. In the last decades, aquatic ecosystems in Italy have undergone significant changes that have been studied mostly in isolation from each other. Concerning lakes, a few synoptic studies considered the subalpine Lake District, comparing deep Italian subalpine lakes with respect to their trophic status and evolution (Salmaso et al., 2007), their response to climatic drivers (Salmaso et al., 2014) and their phytoplankton assemblages (Salmaso et al., 2003, 2006). For the LTER-Italy coastal transitional waters, the level of integration of observations across systems has been analyzed only at a broad and general level, highlighting strengths and opportunities (Pugnetti et al., 2013). Unfortunately, trans-domain (i.e., freshwater vs. marine ecosystems) comparative analyses are lacking. As far as we know, only two studies exist that compares Italian freshwater and marine ecosystems (Pugnetti et al., 2006; Pulina et al., 2016). The first analyzes the state of the art of phytoplankton production in one freshwater (Lake Maggiore) and two marine ecosystems (the Northern Adriatic Sea and the Gulf of Naples); the second compares multiannual phytoplankton dynamics from a reservoir (Lake Temo), a lagoon (Cabras Lagoon) and a marine ecosystem (Gulf of Olbia) in Sardinia, in relation to selected environmental variables.

In this paper we aimed at a first synoptic and trans-domain overview of plankton dynamics across the LTER-Italy aquatic sites, from the large subalpine lakes to mountain lakes and artificial lakes, from lagoons to marine coastal ecosystems (Fig. 1 and Table 1). Basing on published studies, checked and complemented with unpublished information, we aimed at investigating phytoplankton and zooplankton annual dynamics and long-term changes across sites. The LTER sites have different specific functioning processes, mainly related to morphometric, hydrodynamic and trophic features, and different levels of anthropogenic impacts. Furthermore, sampling methods and strategies, data analysis, time windows investigated and level of details provided are quite heterogeneous. Taking into account the limits tied to this heterogeneity, here we present a synthesis of the information available in order to identify common or contrasting ecological signals across LTER-Italy aquatic ecosystems.

2. Materials and methods

In this section we describe the criteria and the process that we used to collect information we considered relevant. Sampling and analytical methods used at each LTER site to generate time series of plankton and abiotic parameters, as well as a thorough description of each site, can be found in the published literature. Moreover, information for each site, data sets, staff and relevant publications can be searched through the metadata documentation and retrieval system DEIMS (Drupal Ecological Information Management System), set up within LTER-Europe (http://data.lter-europe.net/deims/).

It is outside the aim of this study to make any assessment of the comparability of the observational methods and approaches used at the LTER-Italy sites. However, the published time series are quite heterogeneous (Table 1): (i) they have different lengths, the longest starting in the 1960s and the shortest in the 2000s, and (ii) they are not continuous at most of the LTER sites and present many gaps, owing to changes in the availability of financial and human resources. Conspicuous differences were found among sites concerning the sampling strategies, i.e., the sampling frequency, which spanned from weekly to seasonal, and the sampling depth, which includes the whole euphotic zone (most southern alpine lakes), the whole water column or only the surface layer (marine and transitional waters and shallow lakes).

LTER-Italy has twelve aquatic PSs, most of them include multiple RSs, for a total of forty RSs (Figure 1). Twenty-one RSs are freshwater ecosystems: the Southern Alpine Lakes (six RSs), the Mountain Lakes (eight RSs), the Lake Ecosystems of Sardinia (six RSs) and Lake Trasimeno. Transitional waters are represented by nine RSs: the Lagoon of Venice, the Po River Delta Lagoons (two RSs), the Marine ecosystems of Sardinia (three RSs), the Mar Piccolo of Taranto and the Lagoons of Salento (two RSs). Ten RSs are coastal marine ecosystems: the Northern Adriatic Sea (four RSs), the Gulf of Naples (two RSs), the Marine ecosystems of Sardinia (two

RSs) and the Ligurian Sea (two RSs).

Plankton communities are the main focus of LTER activities at all RSs sites but four. For this study we made a further selection of the remaining thirty-six RSs, based on available information from published studies, on their representativeness for each PS, and according to their suitability to address the topics of this review: (i) recurrent seasonal patterns of plankton and (ii) long-term changes in the plankton communities. After this selection, twenty-two RSs remained (Fig. 1 and Table 1), equally distributed between lacustrine and marine/transitional waters and including at least one RS from each PS.

The literature we considered mainly spanned the last fifteen years, although it contained references to older papers, dating back, in a few cases, to the first half of the last century. The most relevant papers for our work were those published most recently, i.e., 2010-2017. Plankton studies date back, in a few cases, to the sixties or seventies: however, most of the sites have been investigated since the 1990s, although with some gaps (Table 1).

For the transitional and marine sites, a total of one hundred and twelve papers were analyzed, almost half of them published in the period 2010-2017. Publications were slightly more abundant for marine ecosystems (sixty-seven) than for transitional waters (forty-five) and this ratio remained similar for the most recent period (2010 onwards). The papers focused on all the issues relevant to our work: long-term trends, seasonal succession, structure and diversity of plankton communities. For freshwater sites, a total of forty papers published in 2010-2017 were examined: twenty-eight focus on the deep subalpine lakes, five on mountain lakes, and seven on the reservoirs of Sardinia. All papers focus on long-term studies: the effects of climate change and the trophic evolution of the ecosystems were the primary research topics.

For comparative purposes, we focused on a small set of substantial information, available at all sites (Table 2). The general features of the sites were outlined based on: (i) average depth, for morphometric features, (ii) prevalent stratification/mixing regime, for hydrodynamics and (iii) chlorophyll *a* (chl; Table 2), for trophic state, phytoplankton biomass, water quality, and carrying capacity.

3. Results and discussion

3.1 Overall morphometric and hydrodynamic features and trophic state of RSs

The geographical distribution and large variety of the LTER-Italy aquatic ecosystems are presented in Fig. 1 and Table 1.

The sites' average depth spans two orders of magnitude (Fig. 2A): from 1 m (Lagoon of Venice and Acquatina) to 178 m (Lake Maggiore). As expected for sites not including deep offshore marine stations, the deepest sites (> 100 m) were the deep subalpine lakes. The water column was always fully mixed only at the 7 sites with mean depths below 5 m, all the other 15 sites showed stratification, thermal (lakes) or thermohaline (marine ecosystems), from spring to autumn (Fig. 2A). Mean annual chl concentrations below 4 μg l^{-1} characterized most subalpine lakes, all the marine ecosystems and most lagoons (Fig. 2B), which can therefore be considered oligo- to mesotrophic environments. Only 4 LTER sites showed mean chl concentrations higher than 10 μg l^{-1}, with the two reservoirs of Sardinia, Lake Trasimeno and the Lagoon of Cabras attaining the highest values. The variability of chl concentrations was quite wide at both seasonal and multi-annual scales at each site with large differences among sites (Table 2). The range of average annual chl across the years was prevalently between 2- and 5- fold. This range of interannual variability can be the result of stochastic fluctuations or trends (see below). The annual mean concentration range at individual sites (Table 2) gives indications about the amplitude of the annual phytoplankton cycle: it was highly variable among sites, ranging between 3-fold (e.g. Lake Tovel) to 2 orders of magnitude (Lagoon of Venice). For most of the sites it ranged between 10- and 30-fold. At most sites, average minimum chl was less than 0.5 μg l^{-1}, while maximum values were much more variable across sites. Intra-annual variability in chl is reported to range up to 4 orders of magnitude (Zingone et al., 2010a; Winder and Cloern, 2010) and marked differences in seasonal chl cycles are usually observed in temperate and Mediterranean waters (Cloern and Jassby, 2008; Winder and Cloern 2010; Zingone et al., 2010a; De Senerpont Domis et al., 2013; Lürling and De Senerpont Domis, 2013).

3.2 Seasonal patterns

Assessing the seasonal patterns of plankton is crucial for evaluating the extent of future changes and their consequences for communities and ecosystems. Multiple processes, interplaying and acting at different time scales, drive the seasonal patterns of plankton (Sommer et al., 2012). For example, the climate-driven annual cycle is frequently masked by different factors that affect population variability, including human disturbance, exceptional and abrupt meteorological events and trophic coupling between phytoplankton and zooplankton.

Here we present the most relevant patterns of plankton seasonal succession in the aquatic LTER-Italy sites, showing that the main drivers are nutrient availability, stratification and mixing regime, and freshwater inflow.

3.2.1 Phytoplankton

We used phytoplankton biomass (chl) to examine annual average phytoplankton seasonal cycles. Three main patterns can be observed (Table 3): (i) one main biomass peak per year, typically in summer, (ii) two main peaks, in spring and summer or autumn, (iii) several peaks per year. For some sites, the pattern is not stable across years, showing shifts that hinder the description of a "typical" template. The above patterns are not characteristic of any specific ecodomain; instead, examples of each one are found in lake, marine and transitional waters.

The first pattern of one peak per year is observed in 5 environments: 3 lakes (1 alpine, 1 lowland lake and 1 artificial lake), 1 lagoon and 1 marine coastal site (Table 3). The amplitude of the seasonal cycle is different among these sites and is determined by very diverse, site-specific, controlling processes. We select the Lagoon of Venice and Lake Tovel to exemplify this type of seasonal cycle. The Lagoon of Venice (Northern Adriatic Sea) is the largest (550 km^2) Italian lagoon. It is a polyhaline, turbulent, permanently nutrient-enriched environment, openly connected to land and sea. The high nutrient availability in the Lagoon results in the seasonal climate cycle becoming the main driver of phytoplankton biomass, apparently weakening the influence of nutrient limitation on phytoplankton growth. A recurrent unimodal seasonal pattern of phytoplankton biomass is observed across the years (Bernardi Aubry et al., 2013, 2017), fairly well tuned to that of temperature and irradiance, with minor monthly fluctuations related to the additional effect of climatic and local events occurring on shorter time scales. This pattern is characteristic of temperate enclosed coastal ecosystems, with shallow depths and permanently high nutrient concentrations (Cebrian and Valiela 1999).

Lake Tovel (1177 m a.s.l., Italian Central Alps) is an oligotrophic, dimictic, temperate mountain lake of glacial origin. A high catchment-to-lake area ratio contributes to fast water renewal, mainly in spring and early summer during snowmelt. The main factor structuring the seasonal succession of plankton in the lake actually is water residence time (Obertegger et al., 2007, 2010): snowmelt and strong flushing result in low phytoplankton biomass in spring, while one or more peaks are typically observed in summer, modulated by water residence time, water temperature and turbulence of the upper layers (Cellamare et al., 2016).

The second phytoplankton pattern, i.e. a prevalently bimodal cycle (Table 3), is reported for all the deep subalpine lakes, some mountain lakes and some marine sites. The two main annual peaks can occur in early spring and in summer (subalpine lakes and Gulf of Naples), in early and late summer/autumn (Lake Santo and Scuro) and in late winter and autumn (Gulf of Trieste). This pattern is prevalently associated with seasonal changes of stratification and mixing intensity, which modulate nutrient availability. It is quite stable over the years in the subalpine lakes, while it shows a wider variability at the coastal marine sites, mainly related to their intrinsic dynamics, and in small, dimictic lakes of the Northern Apennines, due to the interannual variability in ice cover formation and breakup and in the duration of the mixing phases.

The subalpine lakes (SLs) are holo-oligomictic, because of their large depth. A stable stratification from spring to early autumn is followed by a late winter mixing that is usually partial, with complete circulation occurring only after exceptionally harsh and windy winters. The SLs share some common morphological features: they are narrow, elongated and delimited by steep sides, with a generally flat bottom (Ambrosetti and Barbanti, 1997). Nutrient loads and climate are the two most important factors controlling the basic limnological variables and plankton. Synoptic studies on these lakes (Salmaso et al., 2003, 2006, 2012, 2014) show coherent and comparable phytoplankton structure and patterns. The shared physiographic characteristics play a key role in the selection of common phytoplankton compositional features, whereas biomass is mainly determined by different nutrient loads (Salmaso et al., 2003, 2006). Their similar morphology and hydrology probably constitute standardizing factors, forcing the phytoplankton succession pattern towards a limited number of outcomes (Morabito et al., 2002, 2012). The regular annual cycles in the SLs are favored by a complex of drivers which include seasonal climate variability, vertical mixing of the water column from late autumn to early spring, formation of extended and stable epilimnetic layers, and high inertial characteristics typical of large lakes, which minimize the effects of local and stochastic perturbations (meteorological events, hydrological inputs). The prevalent annual cycle, which is basically characterized by two main growing phases in early spring and summer, can show deviations from year to year, mainly due to meteorological events that can modify the time course of phytoplankton succession. This is well documented in Lake Maggiore, where particularly mild and rainy winters may trigger an early growth phase, especially for diatoms (Morabito et al., 2012), which may bloom at the end of the winter.

In contrast to these unimodal and bimodal patterns, the dominant trait of the phytoplankton of the Northern Adriatic Sea (NAS) is a marked variability, mainly related to river discharge dynamics and its associated nutrient input. The NAS is a shallow basin (mean depth 35 m), which is influenced by the inputs from several rivers, with the Po, Adige and Isonzo as the main contributors. At its southeastern boundary, it receives highly saline and oligotrophic waters from the Southern Adriatic Sea. A trophic gradient, decreasing from northwest to southeast, is typically observed with nutrient rich waters coming from the rivers mainly spreading southward and eastward from the Italian coast. A prevalent bimodal pattern is reported only for the Gulf of Trieste, in the eastern part of the NAS. At this LTER site, the late winter and spring bloom, triggered by an increase of light, temperature and water stratification, is followed by a collapse in summer, mainly due to nutrient depletion, until the fall growth phase, tied to mixing and nutrient regeneration (Cabrini et al., 2012). In the western part of the NAS, the phytoplankton pattern is mainly driven by the nutrient inputs from the Po and other minor rivers, flowing southward along the western Adriatic Current (WAC). In the Senigallia LTER station, crossed by the WAC, the largest annual peak occurs in winter and is strongly dominated by the colonial diatom *Skeletonema marinoi*. Other smaller and multispecies diatom blooms occur in spring and autumn with an irregular pattern related to the rain regime, while during the annual minimum in summer, dinoflagellates and large-sized diatoms are the main contributors to biomass (Zoppini et al., 1995; Totti et al., 2005). In the Gulf of Venice, the seasonal phytoplankton pattern appears even more irregular: the main late winter bloom is followed by minor irregular peaks throughout the whole summer and autumn, in relation to the variability of the Po river inflow and to the spreading of the plume, eastward and northward, in stratified conditions (Bernardi Aubry et al., 2012).

A notable seasonal variability in the water column structure is also observed in the Gulf of Naples-MC, which reflects the dynamic character of this coastal site, exposed to the influence of both littoral and offshore water masses (Ribera d'Alcalà et al., 2004). Despite its vicinity to the coast (2 nautical miles), the rather deep (ca 75 m) Gulf of Naples-MC site is also affected by the large-scale processes taking place in the Tyrrhenian Sea. The overall seasonal pattern of the water column structure at Gulf of Naples-MC is typically driven by the seasonal cycle of heat flux, which interplays with municipal freshwater inputs from coastal runoff. The pronounced irregularity of these inputs generates abrupt changes in the mixed layer depth, especially in the winter months. The first part of the phytoplankton annual cycle, which culminates in the early spring blooms, undergoes different phases (Zingone et al., 2010b). Phytoplankton, mostly small flagellates, start accumulating in the winter mixed water column, with occasional intense peaks of diatoms associated with runoff events. Then the large colonial diatoms take over during the initial onset of stratification. A second phytoplankton peak in May is confined to surface layers, whose stability is enhanced by the annual salinity minimum and often related to runoff events (Ribera d'Alcalà et al., 2004). Summer is characterized by intense, irregular and short-lived blooms in surface waters, still related to inputs from coastal water (Zingone et al., 1990). A more regular increase in phytoplankton biomass occurs in October in a water column still stratified down to 40-50 m, mainly sustained by several species of colonial diatoms and coccolithophores.

A lack of a repeatable pattern across the years is found in two lagoons (i.e., Cabras and Alimini), which are characterized by high meteo-climatic and hydrologic variability, and at those sites affected by regular (i.e., artificial lakes) or sporadic (i.e., Mar Piccolo) management. Artificial lakes are strategic water resources in the Mediterranean region, which is one of the most vulnerable to the impacts of climate change, particularly for the expected significant decrease in water resources (Giorgi, 2006; García-Ruiz et al., 2011; EEA, 2012). In Mediterranean reservoirs, phytoplankton is affected by the strong climatic seasonality of both rainfall regime and operational procedures. In particular, these lakes are subject to considerable water level fluctuations, with an abrupt increase during the rainy season and a strong reduction during drought periods. Water level decrease can be accompanied by a break in thermal stratification in summer, which generates rapid changes in nutrient availability. The impact of water level variations is reflected by the lack of a clearly identifiable phytoplankton seasonal pattern at Lake Sos Canales, a mesotrophic and warm monomictic reservoir of Sardinia (Mariani et al. 2015a). It has been affected by intense water level fluctuations throughout the years (Fadda et al., 2016), with alternating empty low-water level phases during the drought season (summer–autumn) to re-filling (winter–spring) and high water level phases (spring-beginning summer) during the rainy season. Further, wide interannual variations are observed due to multiannual periods of more or less intense drought. All these hydrological changes affect phytoplankton, its seasonal succession and multiannual dynamic in the lake, where phytoplankton has been dominated by dinophytes in some years and cyanobacteria in others (Sechi and Lugliè, 1996).

In the Mar Piccolo (Taranto, Ionian Sea) major man-made changes occurred between 2000 and 2005, when one quarter of the urban sewage outfalls were relocated, with the aim of improving water quality and defending the mussel consumers' health. The Mar Piccolo is an enclosed ecosystem strongly exploited for intensive commercial fishery of mussel and impacted by industrial, agricultural, and sewage inputs (Caroppo et al., 2012). These changes are the main cause of the marked interannual variability of the phytoplankton pattern: while a main peak can typically be observed in spring (April), secondary peaks occur, without clear regularities, in winter and in summer (Caroppo et al., 2016).

3.2.2 Mesozooplankton

Mesozooplankton are investigated at sixteen LTER sites (Table 1) where they show, as common and prevalent seasonal pattern of the abundance, a main peak that may occur, with a good repeatability within each site, in different seasons (Table 3).

A main mesozooplankton peak in spring is typically recorded in the Subalpine Lakes and at one marine site (Portofino). In the SLs, numerous interplaying causal factors drive spring nutrient concentration, algal development and zooplankton phenology. These factors include large-scale atmospheric circulation patterns, winter air temperatures, cooling of hypolimnetic waters, deep water renewal, vertical distribution of oxygen, and epilimnetic replenishment of phosphorus at spring overturn (Salmaso et al., 2014). In Lake Iseo warmer winters stimulate, after the winter pause, early development of most zooplanktonic crustaceans, primary as well as secondary consumers (Leoni et al., submitted). The extent of vertical mixing can also affect the reproduction and abundance of cladocerans and cause the increase the population of *Daphnia* spp., a key zooplankton taxa, which is also influenced by food quality (Leoni et al., 2014). Manca et al. (2015) proposed a food-mediated response of *Daphnia* to climate forcing as the main driver of the spring peak, at least in Lakes Maggiore and Garda but, very likely, also in the other SLs. They hypothesized that the increase of algal nutrients in the trophogenic layers, triggered by cold winters and specific patterns in the atmospheric modes of circulation, were directly responsible of an increased fecundity and therefore of the *Daphnia* spring density peak. Temperature also indirectly affected the timing of *Daphnia* growth by enhancing egg production, through its effects on mixing depth and algal carrying capacity (Manca et al., 2015). In mountain lakes, mainly hydrological and meteoclimatic conditions strongly affect the mesozooplankton summer peak, influencing both timing and community composition. In Lake Tovel, water residence time (WRT), which summarizes different hydrological aspects such as inflow, water-level fluctuations, precipitation, and evaporation, determines the mesozooplankton community composition and succession (Obertegger et al., 2007, 2010). High WRTs, associated with lower turbulence and higher temperatures, tend to favor crustaceans, while low WRT values, associated with higher turbulence and lower temperatures, tend to favor zooplankton with faster generation times, i.e. rotifers. Furthermore, rotifer vertical distribution and trait patterns are related to ultraviolet radiation and competition for food (Obertegger and Flaim, 2015; Obertegger et al., 2008). In lakes Santo and Scuro mesozooplankton show quite stable seasonal cycles, though anomalies in phenology and voltinism are recorded, mainly related to local meteoclimatic factors, in particular temperature and onset and duration of stratification (Mazzola, 2013).

Similarly to what is observed in freshwater environments, the mesozooplankton dynamic at the marine sites is mainly related to meteoclimatic conditions and food availability. The spring peak is typically dominated by copepods at Portofino (Ligurian Sea), a nitrogen-limited system (Rivaro et al., 2000, Schiaparelli et al., 2007). The amount of yearly precipitation is the main factor driving nitrogen inputs and phytoplankton biomass, which consequently affect the mesozooplankton community (Povero et al., 2002; Ruggieri, 2005). In the Gulf of Trieste the atmospheric conditions show their indirect effects on mesozooplankton abundance, through their influence on river inputs and stratification dynamics, which are the main bottom up factors controlling phytoplankton availability (Kamburska and Fonda Umani, 2009; Piontovski et al., 2011). A similar mechanism seems to underlay also the mesozooplankton dynamic in the Gulf of Venice (Bernardi Aubry et al., 2012). The total abundance of copepods generally shows a bimodal annual cycle with a larger spring maximum and a second smaller peak in autumn (Kamburska and Fonda Umani, 2009). Nevertheless, when also cladocerans are considered (Piontovski et al, 2011), the principal peak of total mesozooplankton takes place in summer.

In the Gulf of Naples-MC, the mesozooplankton seasonal cycle is characterized by a main peak in summer, mainly sustained by cladocerans and copepods, and by a secondary peak in spring due to the latter group (Mazzocchi and Ribera d’Alcalà, 1995). Notably, in spite of the remarkable variability of local conditions, robust and persistent associations in the zooplankton community have been identified across seasons (Mazzocchi et al., 2011). In particular, the dominant group of copepods appears persistent in its seasonal dynamics, providing evidence of resilience (Mazzocchi et al., 2012).

Mesozooplankton show peaks in summer in the Lagoon of Venice (Camatti et al. 2006; Solidoro et al., 2010) and in Acquatina (Belmonte et al., 2009) and in autumn in Mar Piccolo (Belmonte et al., 2013). At all these three sites, the high environmental variability seems to select zooplankton species with short life cycles (e.g. species belonging to the genus *Acartia, Paracartia* and *Pteriacartia*) able to cope with the environmental instability and to the rapid onset of unfavorable conditions. This seems to be a unifying concept in hydrological dynamic systems, both marine and freshwater ((Flaim et al., 2006; Obertegger et al., 2007, 2010).

3.3 Interannual variability and trends

Phytoplankton and mesozooplankton show a wide interannual variability at all LTER-Italy aquatic sites, but unidirectional or linear long-term trends are rarely detected (Table 4). However, some features and issues shared by most of the sites or by groups of them can be highlighted (Table 4). Here we will briefly discuss a selection of the most relevant traits. All sites were impacted across the years by at least one, but in many case several major stressor(s): trophic state, meteoclimatic variability at the local and regional scale, and direct human interventions at specific sites. The different climatic and anthropic forcings frequently co-occur so that the responses of plankton communities are intrinsically the result of this environmental complexity.

3.3.1 Water temperature, trophic state and phytoplankton

A common trait in the marine sites and in the largest lakes is the increase in water temperature documented in the last decades. On a global scale, the most recent IPCC report (IPCC, 2015) documented an increase of water temperature by 0.11 °C per decade in the upper 75 m over the period 1971 to 2010. From 1982 to 2012, different basins of the Mediterranean Sea showed an increase of surface water temperatures between 0.33 and 0.45 °C decade^{-1} (Giani et al., 2012; Shaltout and Omstedt, 2014). Similarly, with the exception of a few localized regions, lake warming was documented all over the world. In a study based on the analysis of 235 globally distributed lakes, O'Reilly et al. (2015) reported an average increase in the summer surface water temperatures of 0.34 °C decade^{-1}. In the most recent survey, based on satellite measurements recorded between 1986 and 2015 and calibrated with field data recorded in the lakes Maggiore, Como, Iseo and Garda, Pareeth et al. (2017) found a warming trend at a rate between 0.17 and 0.20 °C decade^{-1}. At most LTER marine sites, an increase in sea surface temperature (SST) is reported, though a comparison among the sites is not straightforward because of differences in the reference periods. According to Giani et al. (2012) a marked increase of SST up to about 5°C occurred in the Northern Adriatic basin, in all seasons during the 1990s, with respect to the period 1911-1987 (Russo et al., 2002). Differences were more pronounced in the western part of the basin (Solidoro et al., 2009). In the Gulf of Naples, SST increased significantly between 1984 and 2013, mainly in spring and early summer (Castellani et al., 2016). The Ligurian Sea also shows an increase of SST, starting from the 90s (Cattaneo-Vietti et al., 2010, 2015), mainly in late spring and autumn in the last 15 years (Stirnimann, 2015**.** In the Gulf of Olbia, instead, there was no significant temperature trend over time, even considering the single seasons (Pulina et al. 2016).

At the marine sites, a process of oligotrophication (mainly: reduction of nutrients and of chl) is also reported up to the middle 1990s/early 2000s, followed by stabilization or a new increase. This trend is well exemplified by the Gulf of Naples-MC, where a marked chl reduction was recorded between the first (1984-1990) and the second period (1995-2002) of the time series, followed by a slow positive trend from 2003 (Mazzocchi et al., 2012). This pattern was also accompanied by a reduction of the mean phytoplankton size, evident up to early 2000 (Ribera d'Alcalà et al., 2004), followed by a reversal in recent years (Sarno and Zingone pers. comm.). Size variations were not related to changes in the main taxonomic groups, but rather to changes in single species, i.e.: shift, across the years, in the magnitude of blooms by larger (e.g. colonial *Chaetoceros*) and smaller diatoms (e.g. *Skeletonema pseudocostatum* and *Chaetoceros tenuissimus*).

A notable decrease in chl was observed for the late winter peaks, which are strictly controlled by physical and meteorological conditions (Zingone et al., 2010b). Surface winter blooms were frequent until 2000 and mostly caused by colonial diatoms, after which they have become more modest and caused by small flagellates and small non-colonial diatoms. The negative chl trend is significant in both winter and non-winter conditions (Zingone et al., 2010b).

A reduction in size is also reported, starting from the years 2000s, for the Gulf of Olbia (Pulina et al., 2016) where, however, it was prevalently caused by changes of the main taxonomic groups, with a shift from a diatom dominated community (during the 1990s) to undetermined small (~ 5 μm) coccoids and flagellates and, more recently, cryptophytes. A significant chl decrease was also recorded during the same years, despite a significant nutrient increase. Pulina et al. (2016) hypothesize that a combination of bottom-up and top-down controlling factors affect phytoplankton dynamics on a multiannual scale, with intensive mussel and clam farming acting as the prevalent driver.

A decreasing chl trend in the 2000-2007 period was also observed in the NAS (Bernardi Aubry et al., 2012; Cabrini et al., 2012) and in the Lagoon of Venice (Bernardi Aubry et al., 2013), followed by stabilization and a marked increase in the following decade (Totti, unpublished data; Bernardi Aubry, unpublished data). This pattern appears to be mainly determined by climatic factors, in particular by reduced precipitation since the early 2000s, causing a reduction of freshwater inputs and, consequently, of nutrient loading from inflowing rivers, which are the main regulating factors of the basin. This period was characterized by very severe droughts (Zanchettin et al., 2008), with an estimated decrease of nutrient discharge in the sea of 50% -70 % with respect to previous years (Cozzi et al., 2012). A decrease in chl is also reported for the Lagoon of Cabras. Here, Pulina et al. (2016) describe a simultaneous decreasing trend in nutrients - mainly related to a reduction of the human population in the catchment area and to improvement of wastewater treatment - and in phytoplankton chl and size, starting from the beginning of the 2000s. At Cabras, a salinity decrease since the early 2000s, resulted in a shift in phytoplankton community composition, which became dominated by cyanobacteria (Pulina et al. 2012). Salinity changes were mainly due to the precipitation regime and inputs of freshwater from the watershed, which increased in relation to the increased frequency of exceptional climatic events (Pulina et al., 2016).

At the other transitional water sites (i.e. Lagoons of Alimini and Acquatina), irregular phytoplankton fluctuations across the years are observed, with no clear directional trends (Vadrucci et al., 2004). In the Mar Piccolo, notwithstanding a reduction of nutrients caused by wastewater diversion during the early 2000s (Caroppo et al., 2012), phytoplankton chl did not show significant variations over the years. However, other relevant changes occurred such as a reduction of community size, due to a shift of dominance from diatoms to nanoflagellates, an increased duration of secondary blooms (beside the spring one, see above), and the appearance of a diversified dinoflagellate community, recorded both in plankton (Caroppo et al., 2016) and in sediment samples (cysts) (Rubino et al., 2016; Ferraro et al., 2017). An increase of the pico-sized autotrophic component has also been recently detected (Karuza et al., 2016).

Interannual changes of climate during the winter months are the main factors which regulate, to varying degrees in each lakes, deep mixing dynamics, hypolimnetic oxygenation, and fraction of nutrients recycled from the deeper hypolimnetic layers (Manca et al., 2000; Salmaso et al., 2003; Simona, 2003). As observed at the marine sites, also most SLs underwent a process of re-oligotrophication, starting from the end of the eighties of the last century, with different intensities and responses in the various basins (Salmaso et al., 2014). Trophic changes are widely documented, particularly for lakes Maggiore and Garda, and concern not only nutrient status, but also changes in plankton taxonomic composition, and functional aspects. The analysis of long-term datasets has provided increasing evidence of the combined effects of climate change and meteoclimatic events on biota and lake trophy. Synoptic studies have been therefore carried out to identify the most temperature- and eutrophic-sensitive algal groups (Salmaso et al., 2012) and the influence of teleconnection indices to the thermal structure and deep mixing dynamics of the lakes (Salmaso et al., 2014; Manca et al., 2015). Based on long-term datasets, concurrent effects of temperature fluctuations and trophic status on the development of some algal groups (chlorophytes, charophytes, dinophytes and, partly, cyanobacteria) have been highlighted. By contrast, for other relevant groups, such as cryptophytes and diatoms, the action of other important variables, such as grazing or sinking, appeared equally or more relevant (Marti et al., 2016). Concerning diatoms, a study carried out in Lake Maggiore (Morabito et al., 2012) clearly shows the need for robust long-term datasets to analyze the effect of trophic vs climatic constraints and how their interplay changes across years, leading to different and overlapping controlling factors. Climatic variables started to play a significant role in the lake after the process of re-oligotrophication. Under nutrient limitation, some deep mixing events became important in sustaining an abundant growth of diatoms, favored by the turbulence of the water column as well as by the higher than usual silica supply (Morabito et al., 2012). Winter climate, thermal structure, mixing regime and vertical redistribution of oxygen and nutrients in the SLs appear to be mainly controlled by two modes of atmospheric circulation relevant for the Mediterranean area, i.e., the East Atlantic pattern (EA) and the Eastern Mediterranean Pattern (EMP) (Salmaso et al., 2014). The interactions between climate and trophic status are deeply affected by the physiography of the lake, the strength of vertical nutrient gradients and mixing depth in spring. Vertical redistribution of nutrients in the water column represents an important source of recycled nutrients to the epilimnetic layers in this group of lakes.

Among the SLs, Lake Orta represents a unique and specific case as one of the world's largest acidic lakes, following industrial pollution in the late 1920s (Rogora et al., 2016). Prior to pollution, Lake Orta supported a rich and diversified phytoplankton community dominated by diatoms, cyanobacteria and dinoflagellates. The taxonomic composition was comparable to that of nearby Lake Maggiore, which provides a useful reference comparison. After acidification, Lake Orta was so acidic and contaminated with trace metals that only a few tolerant phytoplankton species persisted, together with sudden and short-living outbursts of occasional colonists (Morabito et al., 2001). A successful liming intervention was performed in the lake in 1989-1990. The positive effects of the liming on the chemistry and biology of the lakes have been described in several publications (see Bonacina, 2001). In particular, many phytoplankton species that inhabit Lake Maggiore are now re-appearing in Lake Orta. However, the phytoplankton assemblages still have a peculiar structure, only partially resembling the taxonomic and functional composition of nearby Lake Maggiore (Morabito, 2016).

At the two Mediterranean artificial lake sites, Lake Sos Canales and lake Bidighinzu, multiple signals of changes are observed, which cause a strong interannual variability of basic limnological parameters and phytoplankton (Sechi and Lugliè 1996; Lugliè et al., 2001; Mariani et al., 2015a, 2015b; Fadda et al., 2016), rather than a directional trend. Local drivers, such as operational water management, modification of anthropogenic activities in the watershed, wastewater diversion, as well as global drivers, such as warming and modification of precipitation regime, are affecting phytoplankton in complex ways (Mariani et al., 2015a), resulting in a high year to year variability of chl, total cell density and biomass (Mariani et al., 2015a).

In Lake Trasimeno, the change in the phytoplankton assemblage has likely been continuous, but not regular, in the last fifty years. An increase in density of cyanobacteria and green algae, accompanied by a reduction in biodiversity (as equipartition), can be taken as representing the most general long-term trend in the phytoplankton of this lake (Ludovisi and Taticchi, 2006; Elia et al., 2011). Hypotheses about the causes of these changes deal with direct and indirect effects of meteoclimatic changes. From 1991 to 2012, Lake Trasimeno experienced a drought period (Ludovisi et al., 2013), which rapidly increased salt concentration (Ludovisi and Gaino, 2010), affecting many phytoplankton species. On the other hand, an increase in temperature observed in the same period, concomitant to the reduction in the water level, has likely favored summer blooms of filamentous cyanobacteria. It is worth mentioning that no significant changes in the trophic condition were observed in that period (Ludovisi and Gaino 2010). Since meteorology drives a number of important and interacting mechanisms in the lake, any long-term trend must be considered ephemeral. In fact, after 2014, the lake has experienced a period of high water level, which has newly modified the water quality and the whole lake biocoenosis (Ludovisi, unpublished data).

3.3.2 Mesozooplankton

Life cycles and seasonal dynamics in lakes located at higher latitudes and/or altitudes are strongly affected by the timing and duration of ice cover and by climatic conditions (Hampton et al., 2015; Flaim et al., 2010). In lake Tovel, although directional trends have not been reported yet, any change in precipitation appears to produce cascading effects on the lake ecosystem through the interplay of temperature, nutrient availability, plankton composition and succession (Borghi et al., 2006; Cellamare et al., 2016). As stated above, WRT and temperature are the most important plankton community structuring forces, evidenced mainly in relation to zooplankton (Flaim et al., 2006; Obertegger et al., 2007, 2010). Crustacean biomass appears directly controlled by WRT, whereas rotifer biomass responds to exploitative competition with crustaceans for phytoplankton (Obertegger et al., 2007). WRT also determines the temperature evolution of the lake and, therefore, the influence of temperature on zooplankton is an indirect effect of WRT. Thus, physical processes seem to set the scene for biological interactions. For Lakes Santo and Scuro there is no evidence of directional long-term changes. Some in-depth analyses of interannual variability have been carried out, correlating the main environmental variables with phenological indices of both phytoplankton and zooplankton (Mazzola, 2013; Bertani et al., 2016). A functioning model has been proposed which could be useful to understand and forecast limnological and biotic long-term changes. This model correlates, at both lakes, large scale climatic fluctuations with the inter-annual local climatic variability, evidencing the direct or indirect (through the surface and epilimnic temperature) effects on the development of plankton communities. In particular, the EA (spring value for Lake Santo, winter and spring values for Lake Scuro) is the climatic index that best explains the interannual variability of plankton phenology. These results are coherent with what observed for the deep subalpine lakes (Salmaso et al., 2012; see above), confirming the EA as a suitable index for lakes of the Mediterranean area. At the ecosystem level Bertani et al. (2016) provided a conceptual model for Lake Scuro, forecasting the effects of heat waves on shallow oligotrophic lakes, where the main driver is the reduction of water level, possibly enhancing the development of benthic macroalgae, with cascading effects on the whole trophic web, through both engineering and demographic effects and ecological interactions.

The application of the two climatic indices EA and EMP also proved to be suitable for the assessment of interannual variability of mesozooplankton in the SLs (Manca et al., 2015). The main changes in the mesozooplankton community of Lake Maggiore are a general increase of the total biomass, an increase of cladocerans, in particular of *Daphnia*, and a decrease of colonial rotifers (Manca et al., 2007, 2008; Manca, 2011). Among cladocerans, Manca (2011) highlights the re-emergence of the predator *Bytotrephes*, which, during the re-oligotrophication phase of the lake, increased its abundance and showed an earlier and longer growing season. Also at Lake Iseo a shift in cladoceran predators occurred (Leoni, 2016; Leoni et al., submitted.): *Bythotrephes longimanus* postponed its appearance and persisted for a longer time, while the presence of *Leptodora kindtii* was anticipated. These changes are prevalently ascribed to an increase in winter temperatures, which stimulated the early development of most zooplanktonic crustacean (Leoni et al., submitted). From a functional aspect, rotifers in Lake Maggiore also underwent a change from microphagous species to raptorial species linked to re-oligotrophication and climate change (Obertegger and Manca, 2011).

In Lake Orta, zooplankton diversity has increased after liming, but most of the new taxa are rotifers, while many calanoids and the large cladoceran predators (*Bythotrephes* and *Leptodora*), that are common in nearby Lake Maggiore, are still absent. In particular, the unusually high annual presence of rotifers in Lake Orta in comparison to Lake Maggiore is related to the absence of top-down control from cladocerans predators. The persistent abundance of rotifers is not a sign of recovery;

rather, it suggests a transient state brought on by unusually low predation pressure in the absence of both planktivorous fish (Volta et al., 2016) and predatory cladocerans (Piscia et al., 2016).

An increase in the relative abundance of cladocerans, the dominant summer group, is reported for the Gulf of Naples-MC for the years 1995-2006, together with a decrease in copepods, dominant during the rest of the year, which appear particularly constant and relevant since 2011 (Mazzocchi, pers.comm.). Total mesozooplankton abundance shows a positive and significant increasing trend, notwithstanding marked interannual variability and fluctuations, with the alternation of high and low abundances. In particular a decreasing trend was observed, since 1995, for the two most abundant spring copepods (*Acartia clausi* and *Centropages typicus*), which show an anticipation of the end of the season in relation to summer temperature anomalies (Mackas et al., 2012; Mazzocchi et al., 2012). The copepods *Calocalanus* spp., and the Appendicularia and Chaetognata groups are, on the contrary, increasing significantly.

Similarly, at the other Tyrrhenian site, Portofino, there is an increase of total mesozooplankton abundance, characterized by a slight reduction of the percentage contribution of copepods and an increase of cladocerans. In particular, *C. typicus* decreased and of small-size copepods (0.5-1 mm) increased, together with Appendicularia (Licandro and Ibanez, 2000; Stirnimann, 2015). Whether these similar patterns in the southern and northern Tyrrhenian Sea are responses to basin-wide processes has still to be assessed. The most recent changes at Portofino seems to suggest an increase of the detritivorous and microbic components, with intensification of recycling processes and a shift towards a microbial loop dominated ecosystem (Stirnimann, 2015).

Long-term variations of the copepod community in the Gulf of Trieste, available since 1970s, have been thoroughly investigated in many papers (Conversi et al., 2009; Kamburska and Fonda Umani, 2006, 2009; Conversi et al., 2010; Piontovski et al., 2011). Ecosystem-wide changes were evidenced, starting at the end of the 1980s-early 1990s. Contrary to what observed for the Tyrrhenian Sea sites, total copepod abundance more than doubled. However, the community as a whole shifted toward smaller species (e.g. *Oncaea* spp.) and toward species that previously had a more southern distribution (i.e., *Diaixis pygmaea*, *Paracalanus parvus*), at the expenses of cold-water species (i.e., *Pseudocalanus elongatus*). The changes in copepod abundance and community composition in the Gulf of Trieste have been related to the basin-wide changes, namely, the general increase in the SST and the changes in the Mediterranean circulation that began at the end of the 1980s and affected the whole basin in the following years, as part of the phenomenon called the Eastern Mediterranean Transient. Warming and circulation changes are not mutually exclusive as driving factors, and they interplay as well with specifically endogenous factor, such as changes in the species phenology. Piontovski et al. (2011) evidence a pronounced response of the thermal characteristics of the upper surface layer of the Gulf of Trieste to the North Atlantic Oscillation (NAO): the SST was positively correlated with the NAO index and high NAO years have been accompanied by maximum total copepod abundance, with up to one year lags. Mesozooplankton in the Gulf of Venice, though based on more scanty and irregular surveys, show an increase in copepod abundance, in particular during winter and spring, together with an increase of small-size taxa (e.g., Poecilostomatoida copepods*, Oncaea* spp. and *Diaixis pygmaea*) (Camatti et al., 2008; Bernardi Aubry et al., 2012).

The Lagoon of Venice was affected, starting from the 1990s, by significant alterations in trophic condition. Marked changes in species also occurred, such as a drastic decrease of the copepods *Acartia margalefi* and *Paracartia latisetosa* and the appearance and massive development, mainly in the inner areas of the lagoon, of *Acartia tonsa* (Acri et al., 2004). In very recent years new copepod species have been recorded: *Pseudodiaptomus marinus* and *Oithona davisae (*Camatti, personal communication).

*S*pecies re-arrangement and enrichment, starting from the second half of 2000s, is recorded for Mar Piccolo (Belmonte et al., 2013) and at the other two Apulian lagoons, Alimini and Acquatina, where, however, year to year fluctuations are evidenced without any indication of trends. In Mar Piccolo, the study of Belmonte et al. (2013) on samples collected in 2005-06, proposed a different interpretation. The well-known existence of a cyst bank in the bottom sediments of that site (Belmonte et al., 1995), and the consequent high resilience of planktonic populations, could justify changes in the water column. The presence of resting stages in the life cycle of coastal species (also phytoplankton), and the existence of cyst banks in the sediments, richer in taxa than the waters above, could be an intrinsic element for the functioning of this system

4. Concluding remarks

This study represents the first synoptic trans-domain overview of phytoplankton and mesozooplankton dynamics, at the annual and multi annual level, across the LTER-Italy aquatic sites. Though exclusively based on a selection of the most relevant scientific literature, this synoptic study allowed identifying the common and unique environmental drivers and ecological functional processes controlling the seasonal and long-term temporal development in different freshwater and marine ecosystems of the LTER-Italy network. A general conceptual framework emerged, connecting the large and small scale in a chain of events: from large climatic events, through local meteoclimatic fluctuations, affecting the structure of the water column and modulating nutrient inputs, to direct/indirect effects on phytoplankton and direct or food mediated effects on mesozooplankton. Response of the plankton depended mainly on the trophic state of the ecosystems and on the strength of local disturbance. A common trait in the marine sites and in the largest lakes is the marked increase in water temperature over the last decades. Though based on different temporal periods, these results concur to confirm the significant warming of Italian marine and freshwater LTER sites, in line with the outcome of measurements recorded at the global scale. Effects of global warming on biotic communities have been documented or suggested both in marine (Poloczanska et al., 2013) and freshwater environments (Landkildehus et al., 2014). Nevertheless, while the results documenting the warming of aquatic ecosystems are undeniable, much uncertainty remains on the long-term effects caused on biotic communities in Italian LTER sites. A few cases however were proposed, including, e.g., shifts of invertebrate predators in deep lakes (Manca and DeMott, 2009) and the appearance and range expansion of many thermophilic organisms in the Mediterranean Sea (Conversi et al., 2010; Occhipinti-Ambrogi and Galil, 2010; Corriero et al., 2016). In freshwater environments, besides the direct and indirect effects on biota, the increase of water temperature and changes in stratification patterns significantly affect biogeochemical cycles and nutrient inputs from the watershed, thus contributing to generate combined effects that are difficult to disentangle (Hamilton et al., 2016). As a matter of fact, most of the long-term changes in plankton communities identified in the marine and lacustrine sites were linked to nutrient loads and/or environmental drivers, indirectly connected to climate change and land and coastal zone use.

A re-oligotrophication process was identified in many marine and freshwater Italian LTER sites, although the periods showing a decrease in nutrient loads and/or chl and the environmental drivers differed among sites. In most marine sites, the decrease of phytoplankton biomass was observed in different periods during the 1990s and 2000s, and was followed by a positive trend or stabilization. These long-term patterns were linked to a variety of stressors, differently identified or hypothesized in physical and meteorological conditions, combination of bottom-up and top-down (mussel and clam farming) controlling factors, reduction of the human population and improvement of wastewater treatment and by reduced precipitations and nutrient loading from inflowing rivers. Conversely, the long-term decrease in phytoplankton biomass observed in the large lakes south of the Alps was deemed to be determined exclusively by the decrease of nutrient loads (particularly phosphorus), caused by improvement and increase in the number of wastewater treatment plants and/or construction of ring trunk sewers (Boscaini, 2009; Mosello et al., 2010, 1997; Salmaso et al., 2007). Generally, these changes were followed by strong modifications in plankton community structure, and in particular by a decrease of cyanobacteria (Fastner et al., 2015; Hamilton et al., 2016). The interannual fluctuations in plankton biomass superimposed on these long-term changes were controlled through a chain of causal factors driven by specific modes of atmospheric circulation relevant for the Mediterranean area. A few LTER sites showed peculiar long-term changes linked, in the case of Lake Orta, to a well-known and documented pollution history. The assessment of the severity of the impact on the lake ecosystem and the successive degree of recovery was only possible by evaluating the lake conditions before, during and after the impact and by comparing the biological communities with those studied in other nearby deep lakes where long-term scientific monitoring was available. In line with the majority of investigations, LTER studies carried out in Mediterranean reservoirs showed high, irregular year-to-year fluctuations due to operational water management. Similarly, irregular interannual phytoplankton fluctuations without clear directional trends were described in some transitional water sites.

One clear result of the comparison among different sites was the evidence of the heterogeneity of plankton studies at the LTER-Italy sites, for what concerns series lengths, survey schemes, focus and level of details in the results, and quantitative and statistical analysis applied. Indeed methodological heterogeneity is a crucial issue in most LTER networks, at least at the European level. It intrinsically stems from the most frequent procedure applied in the establishment of national networks, which is based on a bottom up process that makes the best use of the existing long-term ecological activities and facilities, without any prior harmonization. Obviously long-term series are much valuable beyond their local use as a source of information for cross-system analysis, in particular within a network. Therefore harmonization is a priority, and it is fostered and sustained in the LTER-Europe network as well as in other contexts concerned with long-term studies on plankton, such as the SCOR working group 137 (Klais et al., 2015) on global phytoplankton dynamics in coastal ecosystems the IOC-UNESCO International Group on Marine Time Series (IGMETS http://igmets.net/) and Working group to investigate Climate Change and Global Trends of Phytoplankton in the Ocean (Trends PO, http://trendspo.net/).

Strictly related to the methodological harmonization issue is that of the availability of the long-term datasets that must be tackled with appropriate data management, exchange and sharing procedures. The Open Access and the Open Science principles (Raymond, 1999) in the field of ecology have become a matter of interest and discussion only in quite recent years and still in restricted groups (Hampton et al., 2015). For LTER, data quality, consistency and integrity are obviously crucial to identify reliable trends (e.g. Zingone et al. 2015), which could really make the difference for a scientifically sound management of ecosystems. Broadening access to data and findings requires a shift in researchers' attitude as well as tools and best practices to enable it: a process that is actually going on within the LTER networks, at the European and national level, according to the LTER data specificity. The national LTER communities are stimulated towards the target of collegiality and fostered to adopt the aspects of open science that are currently feasible in the different research groups.

The information collected in the LTER-Italy sites provides a necessary base to identify specific environmental drivers acting on these peculiar systems and to evaluate their effects on the aquatic biota, establishing an unparalleled framework of knowledge to evaluate changes and management options. Results of the comparative approach applied in this overview indicate the value of these observational activities beyond their local use and call for more intense efforts towards the harmonization and the wider availability of the data and of the information on long-term variations of the planktonic system.

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Figure Caption

Figure 1 – Map of the LTER-Italy aquatic sites. The color of the dots indicates the different ecosystem typologies: blue=marine, light blue=freshwater, green=transitional. The red circles evidence the 22 sites selected for the present study. The numbers refer to the DEIMS codes (see Table 1).

Figure 2 – (A) Mean depth and (B) mean chl of the LTER-Italy aquatic sites. The asterisks indicate the sites with always-mixed water columns. The acronyms of the site names are reported in Table 1, the colors of the histograms indicate the ecosystem typology as in Figure 1.

Table 1 – List of the LTER – Italy aquatic sites (extended names and acronyms) of the present work. The name of the parent site, the EUNIS classification, the DEIMS reference (http://data.lter-europe.net/deims/), the community under study (phyto- or zooplankton) and the years of LTER series are indicated.

LTER-Italy Parent Site	**LTER-Italy Research site**	**Acronym**	**Ecosystem typology**	**EUNISS classification**	**DEIMS Reference**	**Phytoplankton**	**Zooplankton**	**Long-term series**
Southern Alpine lakes	**Lake Orta**	LOR	Deep subalpine lake	C1.1	LTER_EU_IT_042	X	X	1963-2017; gaps in the first decades.
Southern Alpine lakes	**Lake Maggiore**	LMA	Deep subalpine lake	C1.1	LTER_EU_IT_045	X	X	1970-2017
Southern Alpine lakes	**Lake Como**	LCO	Deep subalpine lake	C1.2	LTER_EU_IT_087	X	X	2000-2017
Southern Alpine lakes	**Lake Iseo**	LIS	Deep subalpine lake	C1.2	LTER_EU_IT_102	X	X	1993-2016; gaps
Southern Alpine lakes	**Lake Garda**	LGA	Deep subalpine lake	C1.2	LTER_EU_IT_044	X	X	1991-2015; gaps
Mountain lakes	**Lake Tovel**	LTO	Alpine lake	C1.1	LTER_EU_IT_090	X	X	1995-2017;
Mountain lakes	**Lake Santo Parmense**	LSaP	Appennine lake	C1.1	LTER_EU_IT_046	X	X	1950-2012; gaps
Mountain lakes	**Lake Scuro Parmense**	LScP	Appennine lake	C1.1	LTER_EU_IT_047		X	1986-2012; gaps
-	**Lake Trasimeno**	LTR	Shallow lake	C1.2	LTER_EU_IT_096	X	X	1970-2014; gaps
Lake Ecosystem of Sardinia	**Lake Bidighinzu**	LBI	Reservoir	C1.3	LTER_EU_IT_048	X		1978-2015; gaps
Lake Ecosystem of Sardinia	**Lake Sos-Canales**	LSC	Reservoir	C1.3	LTER_EU_IT_052	X		1978-2013; gaps
Northern Adriatic Sea	**Gulf of Trieste**	GTR	Mediterranean Shelf and sea	A7	LTER_EU_IT_056	X	X	Phytoplankton: 1986-2017; Zooplankton: 1970-2017:
Northern Adriatic Sea	**Gulf of Venice**	GVE	Mediterranean Shelf and sea	A7	LTER_EU_IT_057	X	X	Phytoplankton: 1999-2016, gaps; Zooplankton: 1991-2006
Northern Adriatic Sea	**Senigallia**	SNG	Mediterranean Shelf and sea	A7	LTER_EU_IT_059	X		1988-2017
Ligurian Sea	**Portofino Promontory**	PPR	Mediterranean Shelf and sea	A7	LTER_EU_IT_015		X	2002-2017
Marine Ecosystems of Sardinia	**Gulf of Olbia**	GOL	Mediterranean Shelf and sea	A7	LTER_EU_IT_063	X		1995-2015; gaps
Gulf of Naples	**Marechiara**	MC	Mediterranean Shelf and sea	A7	LTER_EU_IT_061	X	X	1984-1990; 1995-2015.
-	**Lagoon of Venice**	LVE	Coastal lagoon	X02 X03	LTER_EU_IT_016	X	X	1998-2015; gaps for zooplankton
Marine Ecosystem	**Lagoon of Cabras**	LCA	Coastal lagoon	X03	LTER_EU_IT_064	X		1999-2017; gaps

s of Sardinia								
-	**Mar Piccolo of Taranto**	MPT	Coastal lagoon	X02	LTER_EU_IT_095	X	X	1991-2014; gaps
Lagoons of Salento	**Alimini**	ALI	Coastal lagoon	X03	LTER_EU_IT_105	X		1998-2009; gaps
Lagoons of Salento	**Acquatina**	ACQ	Coastal lagoon	X03	LTER_EU_IT_104		X	1985-2009; gaps

Table 2

Table 2 – Basic characteristics of LTER-Italy aquatic sites. Mean depth, mean and standard deviations of chl (whole time series), mean seasonal range of chl (range of the mean minimum and maximum seasonal values), range of chl across the years (range of the mean minimum and maximum annual values) and hydrological regime.

LTER-Italy site	**Mean depth (m)**	**Mean and stdev of chl (mg l^{-1})**	**Mean seasonal range of chl (mg l^{-1})**	**Mean range of chl across the years (mg l^{-1})**	**Stratification/mixing regime**
Lake Orta	71	2.0 ± 1.8	0.4 - 6.4	1.0 - 2.6	monomictic, apr-sept
Lake Maggiore	178	3.0 ± 2.2	0.3 - 3.4	2.8 - 3.2	monomictic, apr-sept
Lake Como	154	3,7 ± 3	1.5 – 7.2	1.1 – 8.7	monomictic, apr-sept
Lake Iseo	123	6.1± 1	1.8 - 14.1	3.8 - 7.4	monomictic, apr-sept
Lake Garda	133	3.0 ± 1.6	1.3 - 6.4	2.2 - 4.0	monomictic, apr-sept
Lake Tovel	19	1.9 ± 0.5	1.0 - 3.3	0.8 - 3.0	dimictic
Lake Santo Parmense	22.5	1.6 ± 1.5	0.2 - 5.5	0.5 - 2.7	dimictic
Lake Scuro Parmense	9	2.1 ± 2.1	0.3 - 7.0	1.0 - 3.7	dimictic
Lake Trasimeno	4.5	6.5 ± 3.9	1.1 - 20.2	2.3 - 14.4	polimictic
Lake Bidighinzu	7.3	20.6 ± 22.1	4.1 - 71.7	11 - 26	monomictic, apr-sept
Lake Sos Canales	13.2	12 ± 13.2	2.6 - 37.3	7.5 - 21	monomictic, apr-sept
Gulf of Trieste	17	0.9 ± 0.7	0.1 - 3.5	0.1 - 6.5	thermohaline stratification, march-nov
Gulf of Venice	28	1.2 ± 1.1	0.2 - 4.8	0.6 - 3.0	thermohaline stratification, march-nov
Senigallia	28	2.8 ± 3.1	0.4 - 11.6	1.02 - 4.4	thermohaline stratification, march-nov
Portofino Promontory	80	0.30 ± 0.1	0.1 - 0.6	0.2 - 0.4	thermohaline stratification, apr-nov
Gulf of Olbia	5	2.7± 3.0	0.2 - 16.3	1.1 - 4.3	always mixed
Marechiara	75	1.9 ± 0.6	0.2 - 7.5	0.8 - 3.1	thermohaline stratification, may-oct
Lagoon of Venice	1	5.6 ± 11.0	0.3 - 45.1	2.3 - 16.9	always mixed
Lagoon of Cabras	1.5	47 ± 66.7	11.6 -141.1	19 - 127	always mixed
Mar Piccolo	12	1.8 ± 0.6	0.9 - 2.6	1.02 - 2.3	always mixed
Alimini	1.5	3.1 ± 1.8	0.58 - 10.9	0.75 - 6.4	always mixed
Acquatina	1.2	1.7 ± 0.7	0.1 - 5.1	1.0 - 2.4	always mixed

Table 3 - Main seasonal patterns of phytoplankton and zooplankton and timing of the annual peak. 1= 1 peak per year, 2= 2 peaks per year

LTER-Italy site	**Main annual Pattern - phytoplankton**	**Main annual Pattern - zooplankton**
Lake Orta	2 - spring and summer	1 - spring
Lake Maggiore	2 - spring and summer	1 - spring
Lake Como	2 - spring and summer	1 - spring
Lake Iseo	2 - spring and summer	1 - spring
Lake Garda	2 - spring and summer	1 - spring
Lake Tovel	1 – summer or autumn	1 – summer or autumn
Lake Santo Parmense	2 – early and late summer or autumn	1 - summer
Lake Scuro Parmense	2 – early and late summer or autumn	1 - summer
Lake Trasimeno	1 – late summer or early autumn	1 - summer
Lake Bidighinzu	1 – summer or autumn	-
Lake Sos-Canales	Unstable	-
Gulf of Trieste	2 – spring and autumn	1 - summer
Gulf of Venice	Several peaks per year	1 - summer
Senigallia	Several peaks per year	-
Portofino Promontory	-	1 - spring
Gulf of Olbia	1 - summer	-
Marechiara	2 – spring and late summer	1 - summer
Lagoon of Venice	1 - summer	1 - summer
Lagoon of Cabras	Unstable	-
Mar Piccolo Taranto	Unstable	1 - autumn
Alimini	Unstable	-
Acquatina	-	1 - summer

Table 4 – Summary of the main changes occurred at the LTER-Italy aquatic sites. NA: Not Available; + and – unidirectional increase or decrease across the years; +/- and -/+: increase followed by decrease (or viceversa) across the years; N=No change; Y: irregular changes occurred

LTER-Italy site	Water temperature	Trophic State (nutrients)	Chl	Mesozooplankton abundance
Lake Maggiore	+	-	-	+
Lake Como	+	-	-	NA
Lake Iseo	+	N	N	Y
Lake Garda	+	-	-	+
Lake Tovel	+	NA	NA	NA
Lake Santo Parmense	N	N	N	N
Lake Scuro Parmense	N	N	N	N
Lake Trasimeno	+	N	N	NA
Lake Bidighinzu	N	-	-/+	NA
Lake Sos-Canales	NA	-	+/-	NA
Gulf of Trieste	+	-/+	-/+	-/+
Gulf of Venice	+	-/+	-/+	+/-
Senigallia	+	-/+	-/+	NA
Portofino Promontory	+	NA	-/+	+
Gulf of Olbia	+	+	-	NA
Marechiara	+	-/+	-/+	+
Lagoon of Venice	N	-	-	-
Lagoon of Cabras	N	-	-	NA
Mar Piccolo Taranto	N	Y	Y	Y
Alimini	N	N	N	NA
Acquatina	N	N	NA	N

Figure 1


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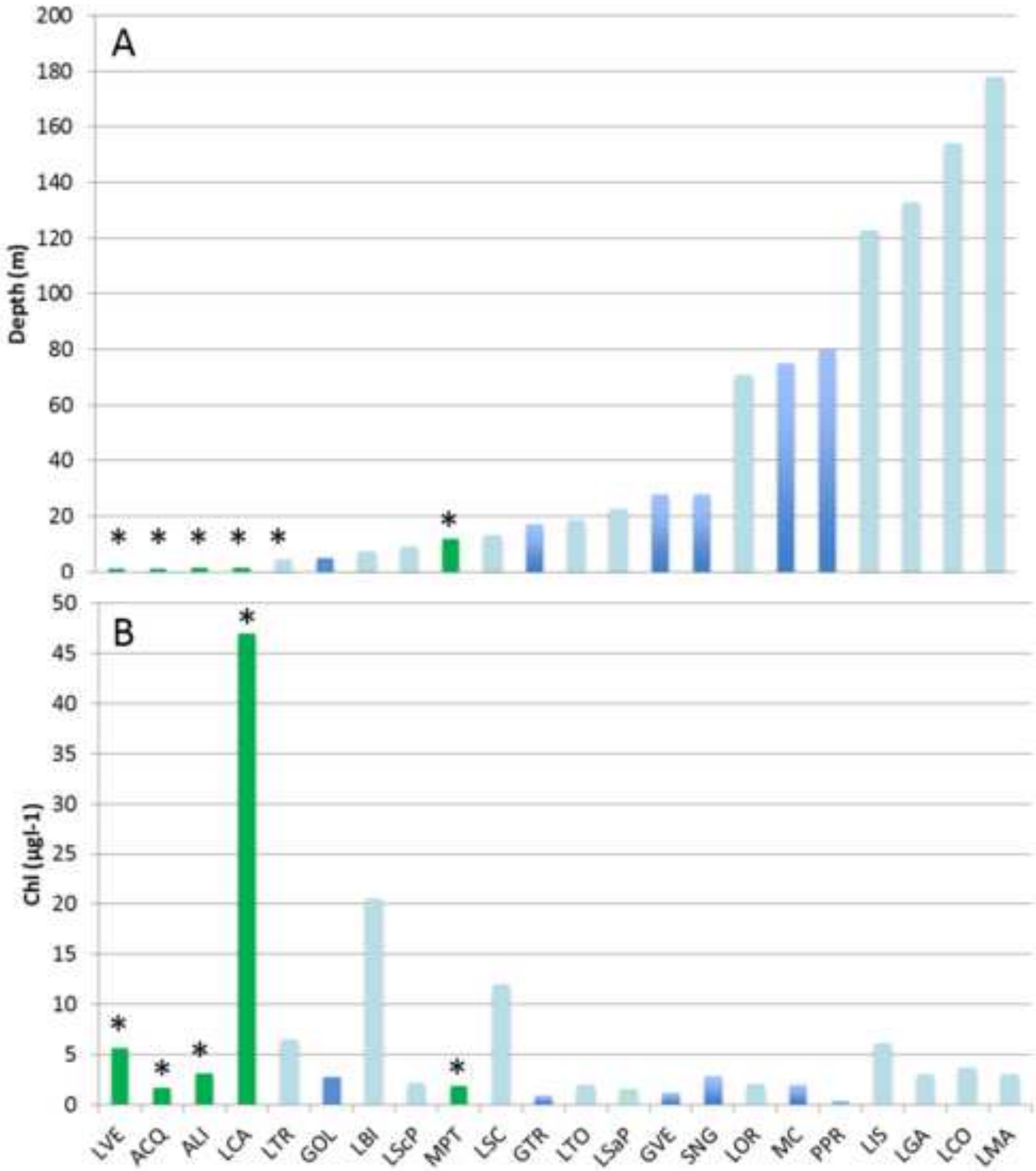
Italian Long-Term Ecological Research Network

Figure 2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