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

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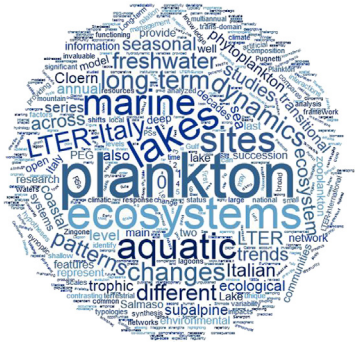
HIGHLIGHTS

- 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- We based our review on published studies, complemented with unpublished information.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.

GRAPHICAL ABSTRACT



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Dedicated to Giuseppe Morabito, beloved colleague and friend, who passed away during the drafting of this article.

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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). Based on published studies, checked and complemented with unpublished information, we investigated phytoplankton and zooplankton annual dynamics and long-term changes across domains: from the large subalpine lakes to mountain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 course. 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, meteo-climatic variability at the local and regional scale, and direct human activities 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.

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 observations 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 model that provided a conceptual framework for the description of seasonal dynamics in temperate lake plankton communities, which has recently been 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 the 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, modelled 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) levels (Mirtl et al., in this issue). The LTER networks provide unique opportunities 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 (Haase et al., 2016; Haase et al., 2018).

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 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 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