

Literature-based insights into phytoplankton ecology at the Long-Term Ecological Research - Italy site Venice Lagoon

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ABSTRACT

Since 1998, phytoplankton communities have been systematically studied at five stations in the northern and central parts of the Venice Lagoon (VL). The long-term maintenance of this phytoplankton data series, alongside similar datasets for other communities (e.g., zooplankton, macrozoobenthos, and macrophytes), has contributed to the inclusion of the VL as a site in the Italian Long-Term Ecological Research (LTER) network. In this paper, we synthesize key insights into the phytoplankton ecology of the VL's LTER stations, based exclusively on published studies. Specifically, we provide an overview of phytoplankton taxonomic composition, morphological traits, seasonal succession, long-term trends and interactions with the other components of the planktonic communities.

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Context and aims

The Venice Lagoon (VL) (Figure 1) has an intrinsic ecological complexity due to its large size, marked habitat heterogeneity and hydrodynamics. It is one of the most important Transitional Water Ecosystems (TWE) (European Union, 2000; Elliot and McLusky, 2002) in the Mediterranean. Microtidal and polyhaline, it is located in the north-western sector of the Adriatic Sea. Covering an area of approximately 550 km², about 85% of the lagoon has depths of less than two meters, while about 10% consists of channels deeper than five meters. The VL is connected to the sea through three port inlets (Lido, Malamocco, and Chioggia) where water exchange is governed by the Adriatic tides, with amplitude ranges between 20 and 100 cm, during neap and spring tides respectively. Freshwater inflow into the lagoon originates from twelve main tributaries, with seasonal peaks occurring in spring and autumn. The VL is heavily influenced by urbanization, intensive industrial and port activities, and significant maritime traffic.

The spatial and temporal dynamics of phytoplankton in TWE is affected and modulated by a wide range of local and regional factors (Cloern and Jassby, 2008; Winder and Cloern, 2010). Notable TWE's features, such as shallow depths, close benthic–pelagic coupling and connectivity to both land and sea, significantly impact on the composition and distribution of phytoplankton across spatial and temporal scales (Cloern and Jassby, 2010). Understanding phytoplankton community structure and its fluctuations is essential for environmental management, as phytoplankton is a key water quality indicator in TWE under the European Water Framework Directive (WFD) (WFD 2000/60/ EC).

Research on phytoplankton in the VL has been conducted since the mid-20th century with relevant but sporadic studies, covering different areas with irregular sampling frequency and limited time span, driven by heterogeneous targets and purposes. Systematic monthly surveys of hydrochemical parameters and phytoplankton were initiated only in 1998 at five stations located in the northern and central areas of the VL (Figure 1) (Bianchi *et al.*, 2003). These stations were strategically selected to represent distinct environmental conditions

and anthropogenic impacts, influenced by the interaction between marine and fresh inputs, as well as by urban, industrial and agricultural pollution.

Like other TWEs, the primary producer's community in the VL is highly diversified, comprising several functional levels, including phytoplankton, benthic microalgae, aquatic angiosperms and macroalgae. However, in the selected areas as well as in other extensive regions of the VL, phytoplankton is the prevalent primary producer and play a crucial role in the lagoon's ecosystem functioning (Acri *et al.* 2004; Sfriso *et al.* 2005; Bernardi Aubry *et al.*, 2013).

This paper aims to summarize key insights into the phytoplankton ecology of the VL based on published literature from 2003 - the year of the first publication on the five stations - to 2024, derived from regular observations at these LTER stations. Specifically, we provide an overview of phytoplankton taxonomic composition, morphological traits, seasonal succession, long-term trends, as well as its interactions with other planktonic communities.

Overview of the phytoplankton in the Venice Lagoon: taxonomic composition, seasonal succession, and morphological traits

For general context, the chlorophyll *a* (chl), nutrient concentration, and phytoplankton abundances are reported in Table 1.

Among the various seasonal phytoplankton cycles observed in TWE, the annual pattern of phytoplankton abundance in the VL exhibits features typical of temperate, enclosed coastal ecosystems with shallow depths and permanently high nutrient concentrations (Cebrian and Valiela 1999). Specifically, phytoplankton abundance follows a unimodal pattern, peaking in summer (July and August) (Bernardi Aubry *et al.*, 2013, 2021, 2022). In the VL nutrient availability does not appear to be a limiting factor throughout the year; instead, the seasonal variations of temperature and light are the main driver of the yearly phytoplankton growth.

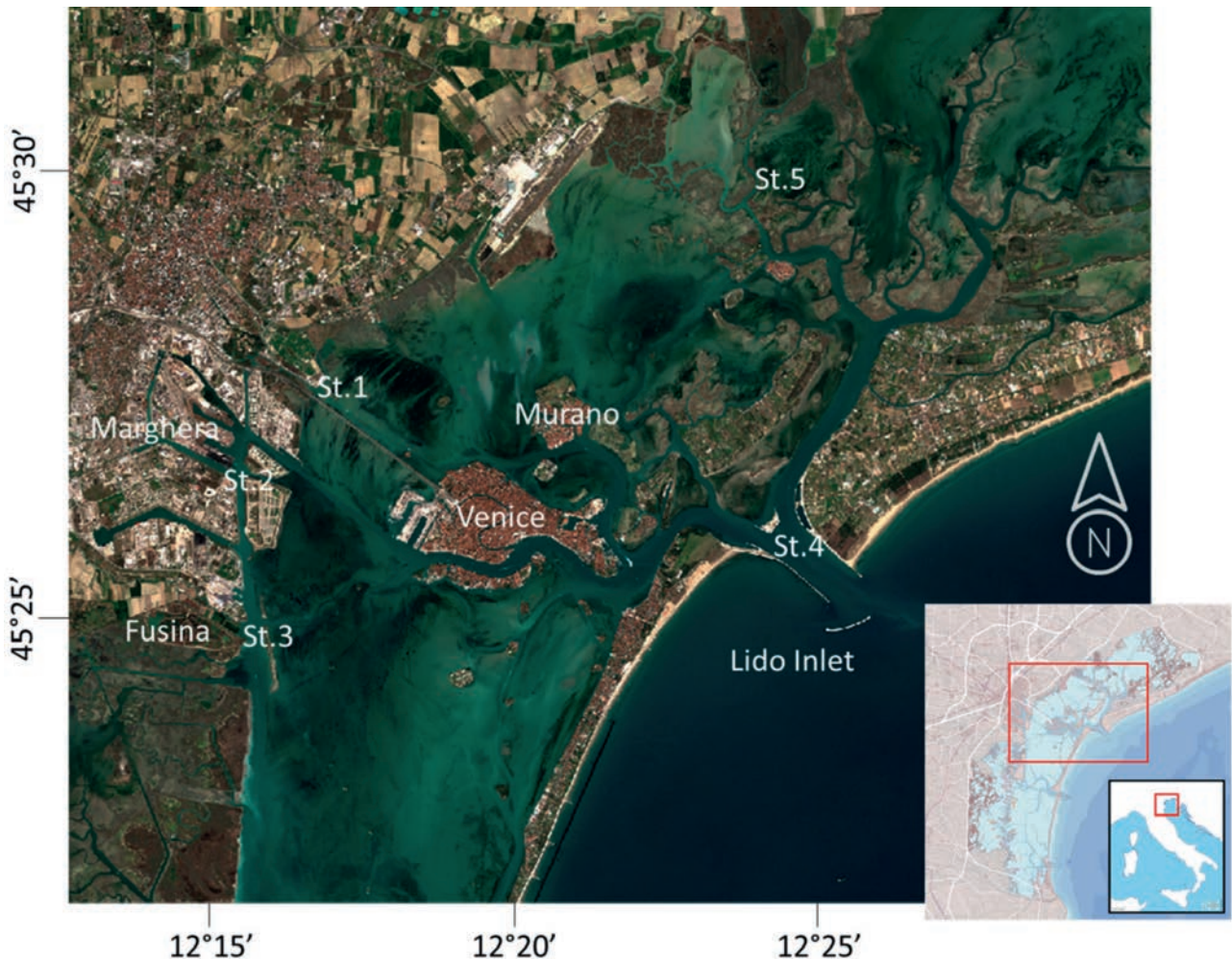


Figure 1. The Venice Lagoon and the location of the five LTER sampling stations (Bernardi Aubry *et al.*, 2021).

Table 1. Averages (Avg) and standard deviations (SD), minimum (min) and maximum (max) values, and number of observations (n) for the main abiotic parameters in the 20-year period 1998–2017 (Bernardi Aubry *et al.*, 2021).

		Avg	Min	Max	SD	n
Transparency	m	1.4	0.1	6.6	1.0	1169
Temperature	°C	18.2	0.6	33.9	7.5	1220
Salinity		28.62	8.63	37.05	4.79	1218
Relative Oxygen	%	105	38	204	18	1217
N-NH ₃	μM	8.74	0.01	69.23	9.30	1215
N-NO ₂	μM	1.49	0.02	11.93	1.11	1215
N-NO ₃	μM	32.49	0.01	211.14	28.51	1215
DIN	μM	42.71	0.52	242.97	33.74	1215
Si-SiO ₄	μM	33.20	0.83	294.15	30.99	1215
P-PO ₄	μM	0.79	0.01	17.19	0.96	1215
N/P		118	1	1889	161	1215
Chlorophyll-a	μg L ⁻¹	5.23	0.02	124.64	10.86	1214
Total Phytoplankton	Cells L ⁻¹	4,471,079	92,293	115,496,858	9,706,009	1202

Table 2. List of main phytoplankton taxa in VL for each season in the period 1998–2017. For each taxon, we also indicate the divisions to which they belong. Taxa are listed in order of decreasing importance of abundance and frequency in each season (re-arranged from Bernardi Aubry *et al.*, 2021).

Division	Species	Division	Species
WINTER		Diatoms	<i>Chaetoceros</i> spp. (small)
Diatoms	<i>Skeletonema marinoi</i>	Diatoms	<i>Phaeodactylum tricornutum</i>
Coccolithophorids	<i>Emiliana huxleyi</i>	Diatoms	<i>Leptocylindrus minimus</i>
Diatoms	<i>Gyrodinium fasciola</i>	Diatoms	<i>Skeletonema tropicum</i>
Diatoms	<i>Navicula tripunctata</i>	Chlorodendrophyceans	<i>Tetraselmis</i> spp.
Diatoms	<i>Pseudo-nitzschia</i> spp.	Dinoflagellates	<i>Blixaea quinquecornis</i>
Diatoms	<i>Melosira nummuloides</i>	Pyramimonadophyceans	<i>Pyramimonas</i> spp.
Diatoms	<i>Melosira</i> spp.	Diatoms	<i>Cyclotella caspia</i>
Diatoms	<i>Amphora lineolata</i>	Diatoms	<i>Pseudo-nitzschia galaxiae</i>
Euglenophyceans	<i>Eutreptia globulifera</i>	Diatoms	<i>Cerataulina pelagica</i>
Chrysophyceans	<i>Dinobryon coalescens</i>	Diatoms	<i>Proboscidea alata</i>
SPRING		Diatoms	<i>Pseudo-nitzschia multistriata</i>
Diatoms	<i>Navicula</i> spp.	Dinoflagellates	<i>Protoperidinium bipes</i>
Diatoms	<i>Navicula cryptocephala</i>	Diatoms	<i>Chaetoceros calcitrans</i>
Dinoflagellates	<i>Prorocentrum minimum</i>	Diatoms	<i>Chaetoceros compressus</i>
Diatoms	<i>Cyclotella</i> spp. (small)	Chlorophyceans	<i>Scenedesmus quadricauda</i>
Dinoflagellates	<i>Prorocentrum gracile</i>	Diatoms	<i>Thalassiosira rotula</i>
Chlorophyceans	<i>Ankistrodesmus</i> spp.	Dinoflagellates	<i>Prorocentrum rhathymum</i>
Dinoflagellates	<i>Prorocentrum triestinum</i>	Trebouxiophyceans	<i>Chodatella</i> spp.
Diatoms	<i>Halaphora hyalina</i>	Coccolithophorids	<i>Michaelsarsia adriatica</i>
Diatoms	<i>Licmophora gracilis</i>	Diatoms	<i>Chaetoceros diversus</i>
SUMMER		AUTUMN	
Diatoms	<i>Cylindrotheca closterium</i>	Diatoms	<i>Cocconeis</i> spp.
Diatoms	<i>Thalassiosira</i> spp. (small)	Diatoms	<i>Craticula cuspidata</i>
Diatoms	<i>Nitzschia frustulum</i>	Coccolithophorids	<i>Calciosolenia murrayi</i>
Dinoflagellates	Und. naked dinoflagellates <20 μm	Diatoms	<i>Placoneis elginensis</i>
Diatoms	<i>Thalassiosira pseudonana</i>	Diatoms	<i>Sellaphora pupula</i>
Dinoflagellates	<i>Gymnodinium</i> spp.	Diatoms	<i>Coscinodiscus</i> spp.

The main ecological characteristics of the VL - turbulence, nutrient enrichment, and connectivity with surrounding systems such as land, sea, and sediments - play a more significant role in shaping phytoplankton communities than the specific attributes of each individual station (Bernardi Aubry *et al.*, 2013). Consequently, the most abundant phytoplankton taxa are common across all the five LTER stations, regardless of their unique envi-

ronmental conditions. The key phytoplankton taxa are listed in Table 2 (Bernardi Aubry *et al.*, 2021). Diatoms dominate the VL phytoplankton community year-round and across all stations (Bernardi Aubry *et al.*, 2013, 2021, 2022) and are the group that contribute to most phytoplankton blooms in the lagoon, which is consistent with the characteristics of permanently nutrient-rich and turbulent environments (Margalef 1978). Early winter is pri-

marily characterized by resuspended species, such as *Gyrosigma fasciola* and *Melosira* spp. In late winter, *Skeletonema marinoi* is dominant, followed in spring by resuspended diatoms such as *Navicula* spp., *Halamphora hyalina*, *Licmophora gracilis*, and *Cyclotella* spp. The summer diatom peaks are driven by a diverse assemblage, comprising *Cylindrotheca closterium*, *Thalassiosira pseudonana*, *Nitzschia frustulum*, *Phaeodactylum tricornutum*, various *Chaetoceros* spp., *Pseudo-nitzschia* spp., and *Leptocylindrus minimus*. In autumn, benthic diatoms such as *Placoneis elginensis*, *Navicula* spp., and *Cocconeis* spp. characterize the season's low abundance. Due to the strong benthic–pelagic coupling, benthic resuspension plays a fundamental role in VL diatom dynamics. Indeed, many of the taxa identified in the lagoon waters belong to the microphytobenthos and are resuspended from sediments. Notably, some diatom species responsible for summer blooms, such as *Nitzschia frustulum* and *Thalassiosira pseudonana*, are frequently found in benthic habitats and appear to thrive in both sediments and the water column (Facca *et al.*, 2002; Facca and Sfriso, 2007). Other key diatom taxa, such as *Skeletonema marinoi*, *Thalassiosira* spp., *Chaetoceros* spp., are euplanktonic and also found in the adjacent Adriatic coastal waters. Actually, the VL and the Gulf of Venice, another LTER Italy site, form a complex, interconnected system. A comparative analysis of the two environments (Bernardi Aubry *et al.*, 2022) revealed that they share several generalist taxa, although local environmental factors play a predominant role in structuring their respective phytoplankton communities.

The second most abundant phytoplankton group in the VL consists of taxonomically diverse undetermined flagellates (nanoflagellates) smaller than 10 μm . These organisms are a constantly present and significant component throughout the year, with peaks in spring and summer. A similar feature has been observed in other transitional ecosystems (Glibert *et al.*, 2010; Bec *et al.*, 2011; Durante *et al.*, 2013; Pachés *et al.*, 2014; Leruste *et al.*, 2016) and in the Adriatic Sea (Bernardi Aubry *et al.*, 2012; Cabrini *et al.*, 2012; Mozetic *et al.*, 2012; Neri *et al.*, 2022). The taxonomic identification of nanoflagellates using light microscopy remains a major limitation in routine long-term phytoplankton monitoring. Metabarcoding analyses of VL planktonic protist communities (Armeli Minicante *et al.*, 2020) have revealed a greater diversity within this group than previously recognized, identifying taxa such as *Picochlorum* and *Micromonas* for the first time.

Dinoflagellates, representing less than 2% of the total abundance, are most prevalent in spring (*Prorocentrum* spp.) and summer (*Gymnodinium* spp., *Blixaea quinquecornis*, *Protoperidinium bipes*, and *Prorocentrum rhathymum*). Coccolithophorids accounted only for a 0.2% average contribution to total abundance, with *Emiliania huxleyi* dominating, especially in September and winter, while summer and autumn samples are also characterized by the presence of *Michaelsarsia adriatica* and *Calciosolenia murrayi*, respectively. Some freshwater taxa are recorded sporadically and in very low abundance. In winter, these included the euglenophycean *Eutreptia globulifera* and the chrysophycean *Dinobryon coalescens*; in spring, *Ankistrodesmus* spp. (chlorophyceans); in summer *Tetraselmis* spp. (chlorodendrophyceans), *Pyramimonas* spp. (pyramimonadophyceans), *Scenedesmus quadricauda* (chlorophyceans), and *Chodatella* spp. (trebouxiophyceans).

Despite the taxonomic diversity of the VL phytoplankton,

a limited number of dominant morphological types can be recognized (Bernardi Aubry *et al.*, 2017). Seven morphological shapes are consistently widespread across space and time, following two main adaptive strategies: (i) a high surface area-to-volume ratio (S/V) combined with a low Greatest Axial Linear Dimension (GALD), and (ii) a low S/V together with high GALD. Certain morphological traits, particularly those contributing to high S/V (ranging from 0.8 to >1), remain relatively constant: (i) small size (GALD < 15 μm), especially in round-shaped organisms, and (ii) elongated forms with high GALD, observed both within individual species and across different taxa. This morphological structure aligns with the characteristics described by Reynolds (1994 and 2003) for kinetic lakes, where species assemblages are strongly influenced by frequent mixing. Two primary and coexisting ecological strategies indeed emerge: Type I (r or C)—small, unicellular nanoplanktonic algae capable of rapid, opportunistic growth when nutrients are available and waters are well-mixed, and Type II (w or R)—mostly non-motile species with elongated or irregular shapes that enhance light and nutrient acquisition but require water turbulence for suspension.

Long-term trends in the VL water quality based on phytoplankton

Published analyses (Acri *et al.*, 2020; Bernardi Aubry *et al.*, 2020) of long-term phytoplankton changes at the five LTER stations currently cover the first 20 years of monitoring (1998–2017). These studies indicate an overall improvement in the lagoon's water quality, particularly a reduction in the trophic state. This trend is primarily attributed to decreased inputs of dissolved inorganic nitrogen from the watershed, following the implementation of the Council Directive 91/676/EC, which introduced restrictions on the application of nitrogen-rich farm waste. Additionally, increased water transparency and higher dissolved oxygen levels have been observed, largely due to the resurgence of macroalgae and seagrasses, whose biomass has grown following regulations on clam fishing.

The general water quality improvement, however, was not directly reflected in phytoplankton abundance, which showed a declining trend that was not statistically significant (Bernardi Aubry *et al.*, 2021). Instead, it was more effectively captured using the Multiparametric Phytoplankton Index (MPI), which integrates multiple indicators: Menhinick's Diversity Index (measuring species richness; Menhinick, 1964), Hulburt's Dominance Index (assessing community evenness; Hulburt *et al.*, 1963), bloom frequency, and chl concentrations. Developed specifically for the VL to assess water quality (Facca *et al.*, 2014), the MPI has demonstrated its reliability, leading to its official adoption by the Italian Ministry of Ecological Transition (formerly the Ministry of the Environment) to fulfil the requirements of the Water Framework Directive (WFD 2000/60/EC). Over the 20-year monitoring period, MPI trends indicate a shift in water quality from "moderate" to "good" conditions: during the first 12 years, moderate water quality was predominant, but from 2014 to 2017 the frequency of good water quality levels increased. A significant decrease in bloom frequency was recorded over the 20-year study, despite no

major changes in the composition of the phytoplankton community. The dominant taxa within different groups remained largely consistent over the years (Bernardi Aubry *et al.*, 2021). In particular, diatom blooms, regardless of intensity, were consistently composed of the same few species: *Skeletonema marinoi* in late winter, *Thalassiosira* spp. and *Cyclotella* spp. in spring, and *Cylindrotheca closterium*, *Chaetoceros* spp., and *Nitzschia frustulum* in summer.

Phytoplankton and the trophic plankton web

Studies conducted in the early 2000s, based on a few seasonal samplings, explored the relationships between phytoplankton and other components of the planktonic trophic web. Regarding planktonic biomass (Coppola *et al.*, 2006, 2007), autotrophic communities were dominated by pico- and nanoplanktonic fractions, while heterotrophic communities were primarily composed of picoplankton (bacteria). The overall ratio of autotrophic to heterotrophic planktonic biomass indicated a predominance of heterotrophic biomass. By analysing the spatial and temporal co-occurrence of phytoplankton, heterotrophic protists, and metazooplankton in relation to biogeochemical properties, Bandelj and colleagues (2008) identified five multitrophic plankton assemblages in the VL. Seasonality played a significant role in structuring these communities: autotrophy dominated from late winter to spring in the inner lagoon, while heterotrophy prevailed from late summer to early winter, especially near the inlets.

The strength of the coupling between phytoplankton and bacterial communities was also investigated (Pugnetti *et al.*, 2010) by analysing Dissolved Primary Production (DPP) vs Bacterial Carbon Demand (BCD), Bacterial Carbon Production (BCP) vs Phytoplankton Production (PP), and Community Respiration (CR) vs PP. Results suggested that phytoplankton and bacterial communities were largely uncoupled, with BCD exceeding PP, and BCP often surpassing PP. This indicates that bacterial metabolism relies on additional organic carbon sources beyond phytoplankton production. During periods when CR exceeded PP, the planktonic system is primarily sustained by stored or imported organic matter. A recent study by Loschi and colleagues (2023), although focused only on summer assemblages, further highlights detrital resuspension as a crucial factor in maintaining the lower trophic levels in the VL. Sediment resuspension allowed bacteria to sustain high densities even when phytoplankton-derived carbon was insufficient. Bacteria thriving on detritus significantly influenced the food web by serving as a major food source for protozoa, which were then consumed by higher trophic levels.

Conclusions “without a conclusion”

This literature review has provided an overview of the current knowledge on phytoplankton communities in the VL, based on data collected from the five LTER stations, which have been sampled monthly since 1998. These sustained observational efforts have provided a valuable temporal framework to detect ecological trends and assess phytoplankton dynamics in a highly variable coastal system. Looking ahead,

maintaining these long-term studies, while strategically expanding research into key areas, will be crucial to deepen our understanding of the phytoplankton ecology and the whole lagoon's ecosystem functioning.

Future investigations in the VL should be informed by three intersecting dimensions: (i) the broader European context, where the European Long-Term Ecosystem Research Infrastructure (eLTER-RI) is being developed (Mirtl *et al.*, 2021; Mollenhauer *et al.*, 2018; Ohnemus *et al.*, 2025; Zacharias *et al.*, 2025), offering a comprehensive conceptual and methodological framework; (ii) the main on-going research activities and priorities emerging from other LTER-Italy aquatic sites (Capotondi *et al.*, 2021), which enable cross-site comparisons and shared analytical frameworks; and (iii) the local context, including site-specific scientific questions, existing research efforts, and infrastructural capacity within the lagoon.

At the intersection of these levels, we identified four key research directions, aligning with core themes of eLTER-RI, reflecting broader ecological challenges and incorporating activities and perspectives of other LTER-Italy sites.

Carbon cycling and allocation

Understanding the role of phytoplankton in the carbon cycle requires a detailed examination of their interactions with other trophic compartments across lagoon zones that differ in hydrodynamics and nutrient regimes. Investigating carbon fluxes will enhance our capacity to model ecosystem metabolism and assess the lagoon's role in coastal carbon budgets.

Molecular approaches to biodiversity

The application of high-throughput molecular techniques, such as DNA metabarcoding and imaging flow cytometry, will provide finer taxonomic resolution and improved insight into the structure and dynamics of protistan communities. Particular attention should be directed toward nanoflagellates, a key yet understudied component of the lagoon plankton, whose diversity and ecological roles remain largely unknown.

Modelling of environmental and ecosystem change

Strengthen the link between existing and newly developed hydrodynamic models and phytoplankton distribution patterns will improve the understanding of spatial and temporal variability, allowing the analysis to be extended to broader areas of the lagoon.

Remote sensing for phenological monitoring

The use of remote sensing technologies offers novel opportunities to track spatial and temporal patterns in phytoplankton dynamics and environmental drivers. These approaches can complement *in situ* observations and enable high-resolution, large-scale monitoring of ecosystem changes over time.

Together, these research lines provide a roadmap for advancing phytoplankton ecology in the VL and strengthening its integration within the national and European LTER frame-

works. Emphasizing interdisciplinary approaches and methodological innovation will be pivotal in addressing emerging environmental challenges in transitional and coastal ecosystems.

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