Continental Shelf Research 294 (2025) 105547

Contents lists available at ScienceDirect

Continental Shelf Research

journal homepage: www.elsevier.com/locate/csr

Silent survivors: diatom resilience in Mediterranean Temporary Ponds

Davide Taurozzi [a,*], Massimiliano Scalici [a,b]

[a] Department of Sciences, University of Roma Tre, Viale G. Marconi 446, 00146, Rome, Italy
[b] National Biodiversity Future Center (NBFC), Università di Palermo, Piazza Marina 61, 90133, Palermo, Italy

ARTICLE INFO

Keywords:
Freshwater
Ephemeral waters
Hydroperiod
Vernal pools
Ecological guilds
Bioindicators

ABSTRACT

Mediterranean Temporary Ponds (MTPs) are ephemeral freshwater habitats hosting a large number of aquatic and terrestrial organisms. Among these, diatoms represent the bioindicators that contribute mostly to Earth's global primary production. Herein, we focused our attention on the role of seasonality and hydroperiod on benthic diatoms of MTPs. We analyzed the diatom community turnover along one year in two MTPs in the Latium region, Italy. The two MTPs showed different levels of anthropogenic pressures. Our results demonstrated that hydroperiod length and seasonality showed a moderate influence on diatom richness of MTPs; in particular, although the highest number of species was found during spring, taxonomic diversity remained stable at seasonal and inter-annual level despite strong changes in community composition and hydroperiod length. Overall, sampling sites showed different ecological conditions and chemical drivers: protected site was dominated by species occurring in minimally impacted oligo- to mesotrophic waters; unprotected site with high EC and ORP was dominated by species occurring in euryhaline brackish waters. Moreover, physicochemical parameters showed a low influence on diatom assemblages in the protected site and a strong influence in the unprotected site. No significant correlation between diatom ecological guilds and physicochemical parameters emerged. While for all the seasons the dominant guild was the motile guild, no inter-season variations emerged: diatom communities and ecological guilds in MTPs are resilient to seasonal variations. To provide novel insights, future research should focus on additional environmental drivers such as nutrient availability, sediment composition, and hydrological variability, including long-term monitoring plans.

1. Introduction

Mediterranean Temporary Ponds (hereafter MTPs) are ephemeral freshwater habitats considered biodiversity hotspots and habitats of some biological importance because they can host a considerable number of rare and endemic species (de Necker et al., 2025). The definition of ponds is actually challenging researchers; here, we adopted the most recent definition by Richardson et al. (2022): small (<5 ha) and shallow (<5 m depth) water bodies with a maximum of 30 % emergent vegetation coverage. The appellative "Mediterranean Temporary Ponds" was firstly used in the scientific literature since the adoption of the Habitats Directive (Bagella, 2023): these ponds were categorized as priority habitats (Natura code: 3170*) included in Annex I of the Directive 92/43/EC (Dimitriou et al., 2009). MTPs are present in five biogeographical regions, mainly located in the Mediterranean biome, below 1500 m a.s.l. (Boix et al., 2016). MTPs are located in semi-arid and transitional regions (Pulido et al., 2020) with hot, dry summers and mild, wet winters. These habitats may experience seasonal fluctuations in water availability, with periods of drought and low water levels in the summer months (Koren et al., 2023). The term "temporary" refers to the hydroperiod of these ecosystems (Fernández-Zamudio et al., 2016). Hydroperiod, the length of aquatic phase, is a crucial environmental variable for these ecosystems (Taurozzi and Scalici, 2024a): MTPs show a significant variability regarding the length of their hydroperiod and the beginning of their inundation period (Zacharias and Zamparas, 2010). Furthermore, they play a significant role in the provision of ecosystem services, such as nutrient sinks, water sources for wildlife, reservoirs of biodiversity and cultural elements (Krivtsov et al., 2022).

MTPs are not isolated systems, but they actively interact with terrestrial environments (Fehlinger et al., 2023). MTPs host a large number of different aquatic and terrestrial organisms (Dimitriou et al., 2006), from viruses and bacteria to consumers and predators, showing strong and complex trophic interactions (Pille et al., 2023). However, despite an improving public sensibility to these habitats over recent years, they are still overlooked and exposed to threats or destruction

* Corresponding author.
E-mail address: davide.taurozzi@uniroma3.it (D. Taurozzi).

https://doi.org/10.1016/j.csr.2025.105547
Received 5 May 2025; Received in revised form 24 July 2025; Accepted 9 August 2025
Available online 13 August 2025

(Boix et al., 2016). MTPs show an alarming rate of loss and degradation, and biodiversity rarefaction (Olmo et al., 2022). Vascular plants, amphibians, many microorganisms and macro invertebrates and phytoplankton are constantly threatened by numerous human activities (Zacharias et al., 2007): degradation and biodiversity loss (Beja and Alcazar, 2003), wastewater discharge and acidification (Zacharias and Zamparas, 2010), solid and liquid waste disposal (Yadav and Goyal, 2022), introduction of alien species (Van den Broeck et al., 2015) and climate change (Zacharias and Zamparas, 2010). Increased water temperature can decrease pH and dissolved oxygen (DO) concentration, as well as increasing levels of available phosphorous, of which could be stressful to pond inhabitants (Earl et al., 2023). In this sense phytoplanktic communities play an important ecological role, increasing primary production, providing oxygen and absorbing CO2, counteracting the effects of climate change (Widigdo et al., 2020; Häder and Gao, 2017).

Phytoplankton in temporary ponds are dominated by fast-growing, single-celled r-strategists and opportunists, which are adapted to variable conditions in rapidly changing environments (Celewicz and Gołdyn, 2021; Padisak and Naselli-Flores, 2021). Under climate change pressures, phytoplankton can show dramatic changes in population density (Diana et al., 2017), generating important shifts in distribution of species and compositional diversity (Domis et al., 2013; Hays et al., 2005). Among phytoplanktic communities, diatoms represent the group which contributes mostly to Earth's global primary production (20–40 %) (Rousseaux and Gregg, 2013); this characteristic make them fundamental for supporting global life forms, being primary producers and an important source of oxygen (Taurozzi and Scalici, 2024a). Diatoms are widespread in all the aquatic ecosystems and represent excellent indicators of environmental changes (Lobo et al., 2016): their response through compositional alteration was already applied in the understanding and management of lakes' surface water eutrophication and acidity, rivers' salinization studies (Stenger-Kovács et al., 2023) and water level change in wetlands (Wolin and Duthie, 1999). However, diatoms represent an important biological model largely used in aquatic permanent habitats but underused in ephemeral waters: the response of diatoms to multiple stressors (hydroperiod length, seasonal changes, physicochemical variations, droughts) in temporary ponds has received much less attention (Taurozzi et al., 2024a).

The diatom communities of MTPs are still overlooked; only a few studies considered the species temporal and spatial turnover of diatoms (Liu et al., 2025; Blanco et al., 2020; Remmer et al., 2019; Hill et al., 2017), none in MTPs consider a one-year monitoring. Different factors may affect species diversity at different spatial scales (Blanco et al., 2020). The scientific literature on this topic is highly contrasting. Some studies suggest that physicochemical water parameters do not play a fundamental role, unlike hydroperiod, which appears to be more influential (Blanco et al., 2020). Conversely, other research highlights the significant role of factors such as pH (Potapova and Charles, 2002) and electrical conductivity (Pestryakova et al., 2018). Similarly, Ferdoushi et al. (2023) demonstrated that temperature had a stronger influence on diatom diversity than pH and dissolved oxygen. Liu et al. (2025) further showed that the composition and relative abundance of dominant species varied significantly across seasons, with notable seasonal differences also observed in alpha and beta diversity, as well as in the relative influence of physicochemical parameters on both species- and trait-based communities. Examining elevational trends in diversity is crucial for identifying broad-scale distribution patterns (Soininen, 2007). Therefore, understanding the relative influence of various environmental factors on taxa diversity and their connection to different scale gradients is essential (Zaharescu et al., 2016).

Herein, we focused our attention on the responses of benthic diatoms to seasonal and hydroperiod variations in MTPs of Central Italy, one of the most threatened freshwater ecosystems of the Mediterranean region. For our purpose, we selected two MTPs located on different landscapes, altitudes and subject to different anthropogenic disturbances, focusing on the study of diatom communities along a one-year sampling. In our research, we considered anthropogenic disturbances as all directly or indirectly human-related activities that can alter ecological conditions (Battisti et al., 2016). This definition is based on the concept proposed by Pickett et al. (1985), where anthropogenic disturbances are defined as "environmental changes or disruptions directly or indirectly caused by human activities, which affect the structure, function, or composition of ecosystems". We further expanded this definition to include biological forms of disturbance. Specifically, we grouped under this term activities directly linked to human presence, such as vehicular traffic, tourism (White et al., 2000), and direct pollution, as well as biologically mediated processes (*sensu* Sousa, 1984), including agricultural practices and grazing. In this study, we acknowledge the presence of such disturbances based on direct qualitative observation, although we did not attempt to quantify them. These anthropogenic disturbances are conceptually and ecologically distinct from natural physical disturbances such as droughts, which in our case are interpreted as seasonal phenomena rather than being directly influenced by human activity.

Our aim was to explore.

i) whether benthic diatom richness responds to seasonal variations;
ii) the capacity of MTPs to host Red List species among different seasons;
iii) which physicochemical factors represent the main drivers for diatom diversity in MTPs;
iv) whether alpha and beta diversity indices and functional metrics (i.e. ecological guilds and life-forms) could be influenced by seasons and relative ecological and biological variations in MTPs, including droughts.
v) the influence of protection measures on diatom diversity.

Based on the scientific literature supporting our study, we hypothesize that both taxonomic and functional diatom communities respond significantly to seasonal variations, affecting both alpha and beta diversity, with a marked influence of the environmental variables considered. Moreover, following ISPRA (2014), we expect a higher number of species included in the Red List during the spring and summer months, which coincides with the peak of diatom floristic development. The variable related to the different management regimes of the two pond systems represents a novel aspect of this study. In the absence of directly comparable literature, we can hypothesize that protected and undisturbed sites will host a higher number of diatom species, as the absence of anthropogenic stressors (such as vehicular traffic, grazing, and tourism) allows diatom communities to structure themselves naturally, without external disturbances.

2. Materials and methods

2.1. Study area

The study focused on Central Italy, in Latium region. The ponds were identified using GEE images and field surveys, while their temporary nature was analyzed with the use of the GEE historical imagery tool, following Taurozzi and Scalici (2024b) (Fig. 1a).

- MTP(A): The first pond is included in the Castelporziano Presidential Estate (41°42′12"N, 12°23′45"E), a nature reserve along the Tyrrhenian coast near Rome and one of the residences of the Italian Republic President (Tinelli et al., 2012), covering an area of 59 km^2 (Sbarbati et al., 2022). The access is forbidden to the public and no direct anthropogenic threats are present (Taurozzi et al., 2024a). This pond will be considered the "protected site"
- MTP(B): The second pond is included in a grazing land in the Altipiani di Arcinazzo (41°50′39"N, 13°12′16"E), a typically alpine-looking plateau 60 km south-east Rome, included in an agricultural and grazing pattern (Taurozzi et al., 2024b). The pond is used

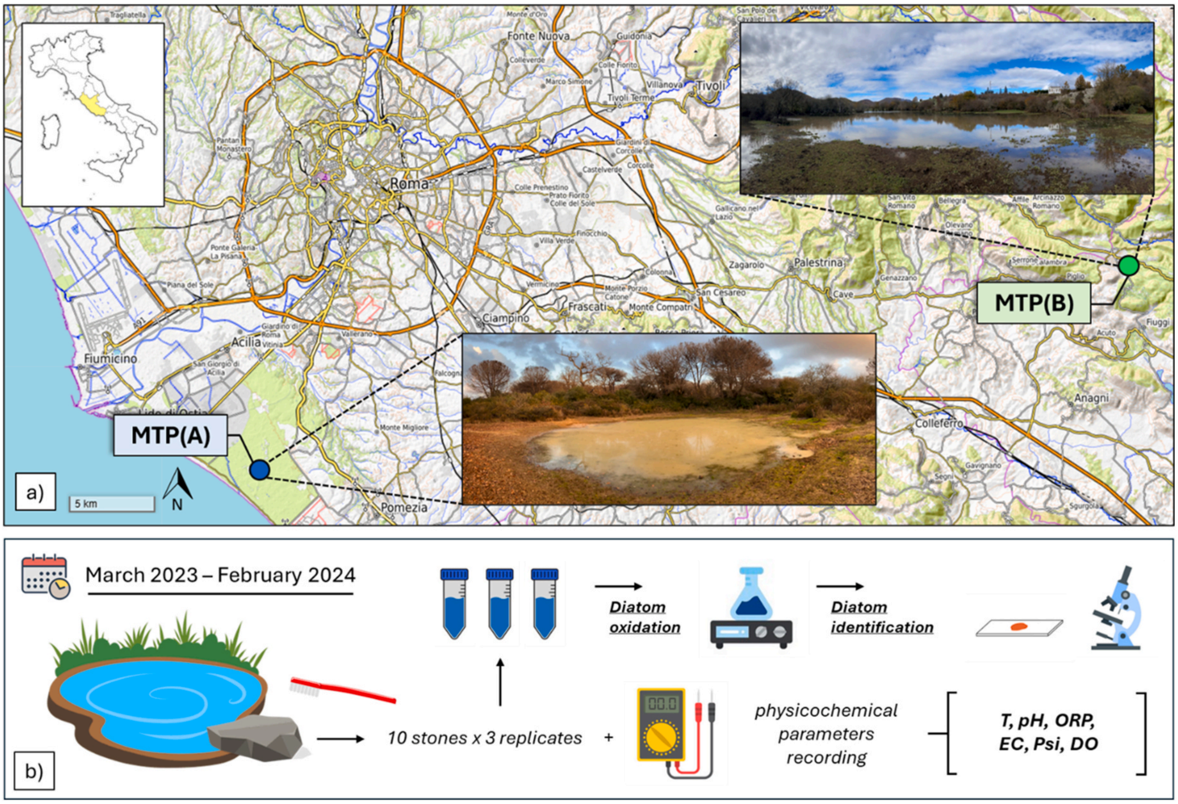

Fig. 1. a) Study area and sampling sites. MTP(A) is located inside the Castelporziano Presidential Estate; MTP(B) is located on the Altipiani di Arcinazzo plateau. b) Sampling activities and laboratory analysis.

daily for watering cattle. This pond will be considered the "unprotected site", where direct anthropogenic disturbances are present.

2.2. Sampling activities

The samplings were performed each month, one sampling per month, for one year, from March 2023 to February 2024. Samplings were performed by the same operator at the same hour of the day (±30 min) to avoid discrepancies in sampling methodologies. Diatom sampling was carried out according to ISPRA (2014) guidelines, with adaptations for pond environments as described in Taurozzi et al. (2024a). Samples were collected at multiple points and depths within each pond. For each sample, at least 10 stones (dimensions between 64 mm and 256 mm) were scraped using a commercial toothbrush (taking care to use a new toothbrush for each sampling site); then, the toothbrush was immersed in a 50 ml Falcon containing 70 % diluted ethanol and distilled water (Fig. 1a). Diatom oxidation operations followed in the laboratory (Fig. 1b). For each site, three different replicates were performed as suggested by Maitland et al. (2020). Before performing diatom sampling activities, 6 physio-chemical parameters of ponds were recorded using a multiparametric probe Hannah® HI98194 following Taurozzi et al. (2024a) Temperature (T °C), pH, Oxygen Reduction Potential (ORP, mV), Electrical conductivity (EC, µS/cm), Pressure (Psi), Dissolved oxygen (DO, ppm).

The oxidation method used was taken from Taurozzi et al. (2024a) and Beltrami et al. (2007) for freshwaters: through the use of hydrogen peroxide, the organic matter was digested, and diatoms were mounted on permanent slides using Naphrax® (high resin power of refraction) to fix the coverslip. The morphological identification of diatom species was conducted under a microscope at 1000 × magnification (Leica), using taxonomic guides (DREAL Languedoc Roussillon, 2021; Bahls et al., 2018; ISPRA, 2014; Ector and Hlúbiková, 2010; Taylor et al., 2007a; Krammer et al., 2002; Krammer and Lange-bertalot, 1991b; Krammer and Lange-bertalot, 1991a; Krammer and Lange-bertalot, 1988; Krammer and Lange-bertalot, 1986). For each slide, the analysis was considered completed when identification at the species level of 400 valves was achieved (ISPRA, 2014). Counting 400 valves provides a reliable estimate of relative abundances, especially for detecting rare taxa and ensuring species richness and diversity indices are stable and representative of the true community. As reported in Battarbee (1986) and Taylor et al. (2007b), counting 400 valves is generally satisfactory for the calculation of relative abundance of diatom species.

2.3. Statistical analysis

Normality, homogeneity of variance and independence were tested before performing statistical analysis. Given all the assumptions checked, we performed both parametric and no-parametric tests in our analysis. Here, we considered two factors for our analysis: "season", expressed as division of the year based on changes in weather, ecology, and the number of daylight hours in a given region (spring, summer, autumn, winter) and "protection", considering the protected Nature of MTP(A), included in the Castelporziano Estate (expressed as the absence of potential direct anthropogenic disturbances following Taurozzi and Scalici, 2024a).

The hydroperiod of each pond was determined through in situ visual assessment, based on the detection of water presence and availability.

2.3.1. Physicochemical variables

Permutational Multivariate Analysis of Variance (PERMANOVA) is a non-parametric test of significant difference between two or more groups, based on any distance measure; here, physicochemical variables differences between sites and seasons were tested using one-way PERMANOVA with stratification: this tests whether diatom community composition differs by month, while only permuting within each pond. That respects the non-independence of samples from the same pond.

Ordinary least squares regressions were performed to highlight significative correlations between physicochemical parameters among seasons.

2.3.2. Diatom overview and Red List species

Repeated-measures analysis of variance (ANOVA) test, a statistical method that simultaneously compares means across several groups to determine if observed differences are due to chance or reflect genuine distinctions, was used to analyze significant differences in the number of species across seasons.

Here, we also considered Diatom Red Lists which provide an account of the diatom flora of a geographic area pointing out the distribution and threat status of individual species as determined by environmental factors and impacts (Cantonati et al., 2022). The presence of endangered diatom species was evaluated following diatom's Red List from Hofmann et al. (2018); for this purpose, 7 classes of risk were considered.

a) Endangered (EN)
b) Vulnerable (VU)
c) Near Threatened (NT)
d) Rare (RA)
e) Least Concern (LC)
f) Data Deficient (DD)
g) Not Evaluated (NE)

The repeated-measures ANOVA test was used to analyze differences between the distribution (number of species and relative code) of Red List species between sites. PERMANOVA tests with stratification were performed to highlight significant differences in Red List species abundances between seasons.

2.3.3. Environmental factors associated with diatom community variability

Redundancy Analysis (RDA) is a method to extract and summarize the variation in a set of response variables that can be explained by a set of explanatory variables, summarizing linear relationships between components of response variables that are "redundant" with a set of explanatory variables. Here, RDA was run to test statistical significance of each environmental variable in explaining species data structure and seasonal distribution of sampling sites.

2.3.4. Diatom alpha and beta diversity

Alpha diversity was calculated through the a) number of species and b) the Shannon diversity Index (H).

Linear multivariate multiple regressions were applied to test significant correlation between alpha diversity indices and physicochemical values. Multivariate linear regressions were applied to test for significant correlation between alpha diversity indices and the number of days after droughts. Beta diversity analysis, i.e. the comparison of dissimilarity in community composition between each pair of sites, was calculated using Bray-Curtis and Jaccard dissimilarity, based on occurrence data (abundance). One-way PERMANOVA with stratification based on Bray-Curtis and Jaccard dissimilarity matrices were set to investigate community differences among sampling sites. Two-way PERMANOVA with stratification was run to test variations in community composition among sampling sites and seasons and also for testing the influence of season and protection factors on diatom alpha diversity.

2.3.5. Diatom functional ecology

Then, three diatom ecological guilds were considered following Passy (2007).

- Low profile: species associated with environments characterized by low nutrient levels and high flow rates (Liu et al., 2025);
- High profile: larger species that tend to form colonies, and do not resist turbulence well but are enhanced by nutrient enrichment (Gelis et al., 2020);
- Motile: fast moving species not sensitive either to resource limitation or to disturbance (Stenger-Kovács et al., 2013).

The repeated measures ANOVA tests were performed to determine differences in species distribution among guilds and seasonal fluctuations. Polynomial regressions were performed to evaluate significant correlations between diatomic guilds abundances and physicochemical parameters.

Statistical tests were considered significant when p-value was <0.05. Statistical analysis were computed in PAST 4.02 software (Hammer et al., 2001), GraphPad Prism version 8.0.0 and R software (version 4.4.2) (R Core Team, 2021).

3. Results

3.1. Physio-chemical parameters

Ponds' hydroperiod was monitored throughout the year with 1 sampling per month. MTP(A) was facing 5 months of complete dryness (August, September, October, November, December), while MTP(B) was facing 1 month of dryness (July). Physicochemical parameters recorded were reported in Table S1 and Fig. S1.

PERMANOVA based on physicochemical values showed that abiotic characteristics statistically differed among the two sampling sites considering the protection variable ($F = 5.9$, $p = 0.02$), while no differences emerged between seasons ($F = 0.6$, $p = 0.7$).

For MPT(A) and MTP(B), PERMANOVA showed no significant differences between physicochemical parameters among seasons emerged ($F = 1.3$, $p = 0.3$ and $F = 1.4$, $p = 0.2$, repsectively). For MTP(A), significant correlations emerged between T and DO ($R^2 = 0.9$, $p = 0.008$) during spring, pH and EC ($R^2 = 0.9$, $p = 0.04$), pH and DO ($R^2 = 0.9$, $p = 0.006$), EC and DO ($R^2 = 0.9$, $p = 0.04$) during summer and between pH and DO ($R^2 = 0.9$, $p = 0.01$) during winter. For MTP(B), significant correlations emerged between pH and EC ($R^2 = 0.9$, $p = 0.006$) during summer, pH and ORP ($R^2 = 0.9$, $p = 0.03$) during winter and EC and DO ($R^2 = 0.9$, $p = 0.02$) during autumn.

3.2. Diatom overview and Red List species

The benthic diatom diversity in the two MTPs was represented by 146 species belonging to 44 genera, of which 24 genera were shared both from MTP(A) and MTP(B): in MTP(A) 93 species were found, in MTP(B) 115 species. The highest number of species was found in March ($n = 36$) and May ($n = 34$) for MTP (A) and in April ($n = 38$) and November ($n = 34$). Among 146 species, a total of 5 diatom taxa were classified as dominant (>5 %): *Achnathidium eutrophilum*, (number of valves counted, $n = 4045$), *Nitzschia palea* ($n = 2075$), *N. frustulum* ($n = 1406$), *Eunotia minor* ($n = 1139$) and *Navicula trivalis* ($n = 1113$) represent 45 % of the total number ($n = 21600$) of individuals counted ($n = 9778$).

Overall, 66, 52, and 38 species were identified in spring, summer and winter, respectively, in MTP(A); ANOVA test showed no significant differences in the number of species across seasons ($F = 1.4$, $p = 0.24$). 62, 42, 57, 43 diatom species were identified in spring, summer, autumn, winter, respectively, in MTP(B); ANOVA test showed no significant differences in the number of species across seasons ($F = 0.6$, $p = 0.63$).

Considering the Red Lists codes, MTP (A) hosted 70 % of LC species, 13 % NE, 9 % NT, 3 % VU, 3 % RA, 2 % DD and 1 % EN; MTP(B) hosted 70 % of LC species, 19 % NE, 4 % RA, 3 % NT, 2 % DD, 1 % VU, 1 % EN. Furthermore, no differences emerged between the distribution (number of species and relative code) between sites from ANOVA test ($F = 1.3$, $p = 0.29$). PERMANOVA showed that abundances for red list codes did not differ among seasons for MTP(A) ($F = 1.9$; $p = 0.13$) and for MTP(B) ($F = 0.2$, $p = 0.82$).

3.3. Environmental factors associated with diatom community variability

Statistical analyses conducted using the RDA method revealed statistically significant correlations between environmental factors and the structure of diatom assemblages (F = 1.7, p = 0.004) (Fig. 2). The RDA analysis showed that the first axis explained 23.7 % of the fitted variation, two axes explained 32.5 %, three axes accounted for 38.8 %, and four axes explained 44.1 %. The most statistically significant influence on the differentiation of diatom assemblages was attributed to Pressure (p = 0.001), explaining 9.1 % of the variability, followed by temperature (p = 0.011; 8.4 %). The influence of pH, ORP, EC and DO ions on the differentiation of diatom assemblages was smaller (p = 0.2–0.6; 5–3 %), and these factors were not also statistically significant. Temperature showed a very strong positive correlation with DO (r = 0.6, p = 0.003); this parameter correlated with the occurrence of, among others: *Gomphonema exillissimum*, *Gomphonema gracile*, *Nitzschia frustulum*, *Stauroneis phoenicenteron*. Electrical conductivity also demonstrated a weak negative correlation with Temperature (r = −0.4, p = 0.06), which in turn correlated with the occurrence of *Cocconeis placentula* and, to a lesser extent, *Anomoeoneis sphaerophora*. ORP demonstrated a strong negative correlation with pH (r = −0.5, p = 0.02), which in turn correlated with the occurrence of *Gomphonema pumilum*, *Fragilaria biceps* and, to a lesser extent *Denticula tenuis*, *Fragilaria capucina*, *Geissleria decussis*.

Based on the RDA findings, two distinct groups of sites were observed because of differences in species composition. The first group consisted of the protected site - MTP(A) - which is characterized by high dissolved oxygen, high temperature, high pressure and low pH. This site was dominated by diatom cosmopolitan species such as *Frustulia vulgaris, Gomphonema gracile, G. parvulum, G. zellense, Nitzschia frustulum, Pinnularia gibba*. The second group - MTP(B) - was composed of an agricultural and grazing site that was characterized by very low electrical conductivity and low Oxidation-Reduction Potential amounts. *Anomoeoneis sphaerophora, Cocconeis placentula, Denticula tenuis, Fragilaria biceps, F. capucina, Geissleria decussis, Gomphonema pumilum, Nitzschia filiformis, N. linearis* diatom species were abundant in this site.

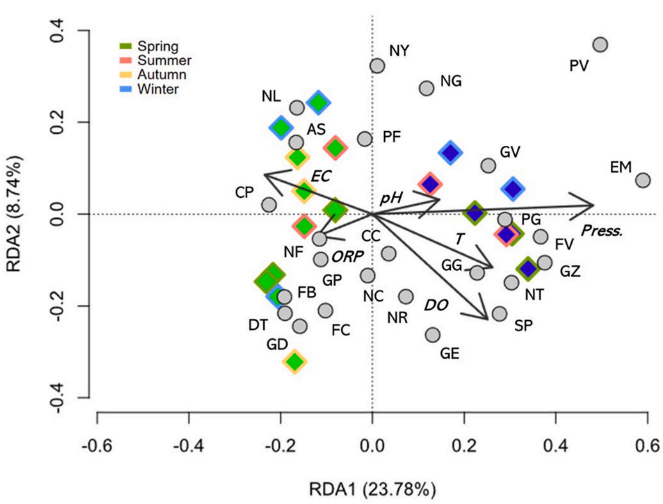

Fig. 2. Redundancy analysis (RDA) ordination showing environmental variables correlated with RDA1 and RDA2. Physicochemical parameters are shown in italic. Diatom species are shown with abbreviations and grey dots. (AS = *Anomoeoneis sphaerophora*; CC = *Craticula cuspidate*; CP = *Cocconeis placentula*; DT = *Denticula tenuis*; EM = *Eunotia minor*; FB = *Fragilaria biceps*; FC = *Fragilaria capucina*; FV = *Frustulia vulgaris*; GD = *Geissleria decussis*; GE = *Gomphonema exillissimum*; GG = *Gomphonema gracile*; GP = *Gomphonema pumilum*; GV = *Gomphonema parvulum*; GZ = *Gomphonema zellense*; NC = *Navicula capitatoradiata;* NF = *Nitzschia filiformis*; NG = *Navicula gregaria*; NL = *Nitzschia linearis*; NR = *Navicula reichardtiana*; NT = *Nitzschia frustulum*; NY = *Navicula cryptocephala*; PF = *Planothidium frequentissimum*; PG = *Pinnularia gibba*; PV = *Pinnularia viridiformis*; SP = *Stauroneis phoenicenteron.* Blue rhombuses represent MTP(A); Green rhombuses represent MTP(B). T = Temperature (°C), ORP = Oxygen Reduction Potential (mV), EC = Electrical conductivity (μS/cm), Press. = Pressure (Psi), DO = Dissolved oxygen (ppm).

3.4. Diatom alpha and beta diversity

Overall linear multivariate multiple models applied on alpha diversity indices and physicochemical values did not show significant correlations for MTP(A) (F = 1.6, p = 0.5), while showed significant correlations for MTP(B) (F = 3.7, p = 0.04). Moreover, the overall effect of each independent physicochemical parameter was not significant (ANOVA, p > 0.05). The number of species in MTP(B) was mainly influenced by T (R^2 = 0.0004, p = 0.04), pH (R^2 = 0.08, p = 0.01), ORP (R^2 = 0.02, p = 0.01), Press (R^2 = 0.06, p = 0.02) and DO (R^2 = 0.06, p = 0.01); Shannon index was influenced by DO (R^2 = 0.5, p = 0.01). Multivariate linear regressions applied on alpha diversity indices and the number of days after droughts did not show significant correlations both for MTP(A) and MTP(B) (p > 0.05).

One-way PERMANOVA based on Bray-Curtis dissimilarity showed that diatom structure differed among the sampling sites (F = 4.7, p = 0.001). Similar results emerged from one-way PERMANOVA based on Jaccard dissimilarity (F = 2.4, p = 0.0003). Two-way PERMANOVA highlighted that there was also seasonal variation in diatom community composition between the studied sites for Bray-Curtis dissimilarity (F = 1.9; p = 0.0032) but not for Jaccard dissimilarity (F = 1.1, p = 0.06). However, the interaction between seasonal and protection variables in defining diatom variation was not statistically significant (PERMANOVA, F = 0.5; p = 0.72). Furthermore, the influence of seasonal and protection variables on diatoms was reflected on species richness: two-way PERMANOVA highlighted the influence of protection factors on diatom alpha diversity (F = 9.8, p = 0.008) but not for season (F = 0.8, p = 0.6). Moreover, the interaction between seasonal and protection variables in defining diatom diversity was statistically significant (PERMANOVA F = 2.6; p = 0.04).

3.5. Diatom functional ecology

In this study, all categories of the diatom ecological guilds, including motile, low-profile, and high-profile were observed (Table 1). 25 among the 146 different species identified belong to the low-profile guild, 37 to the high-profile guild and 84 to the motile guild (Fig. 3a and b).

The results highlighted that the motile guild predominated among the diatom guilds (MTP (A), H = 7.2, p = 0.02; MTP(B), H = 8.1, p = 0.01) and displayed insignificant seasonal fluctuations (MTP(A), H = 0.5, p = 0.8; MTP(B), H = 1.2, p = 0.7). Polynomial regressions showed significant correlations between the number of species of high-profile guild and T (F = 6.4, p = 0.009), EC (F = 7.5, p = 0.005) and DO (F = 5.2, p = 0.01) (Fig. 3c, d and 3e).

Table 1
Frequencies (expressed in percentage %) of diatom guild for each season in the two ponds analyzed.

		Winter	Spring	Summer	Autumn
MTP (A)	Motile	63.1	69.7	53.9	–
	Low profile	13.1	7.5	15.4	–
	High profile	23.8	22.8	30.7	–
MTP (B)	Motile	74.4	50.0	69.0	59.7
	Low profile	13.9	17.7	9.6	8.7
	High profile	11.7	32.3	21.4	31.6

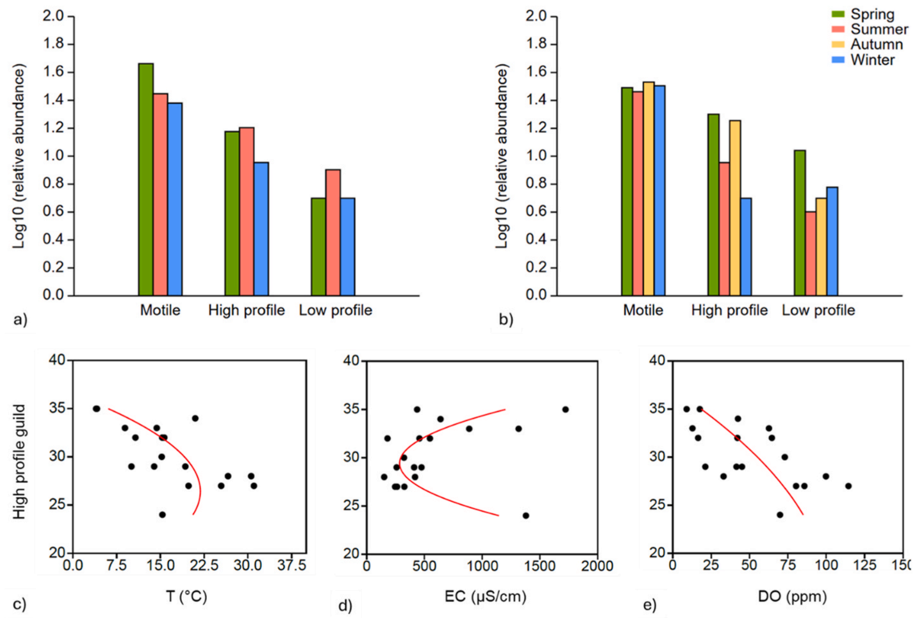

Fig. 3. Seasonal changes in the composition and relative abundance of the benthic diatom ecological guilds for a) MTP(A) and b) MTP(B); Polynomial regression for number of species of high-profile guild and c) Temperature (T), d) Electrical Conductivity (EC) and e) Dissolved oxygen (DO).

4. Discussions

This research represents, to the best of our knowledge, the first investigation of diatom community turnover and ecological responses to seasonality and hydroperiod fluctuations in MTPs. Our study demonstrated that hydroperiod length and seasonality showed, respectively, a low and moderate influence on diatom richness of MTPs.

4.1. Diatom overview and red list species

The highest number of species was found during spring months, March, April and May (for the northern hemisphere), confirming previous studies (Villa-Alfageme et al., 2024; Sassenhagen et al., 2023), while no significant differences emerged in the number of species across seasons, unlike our initial hypothesis. This is in accordance with Taurozzi and Scalici (2024a) and Virta et al. (2020), where taxonomic diversity remained stable at seasonal and inter-annual level despite strong changes in community composition and hydroperiod length. Hydroperiod can represent an important limit factor for many aquatic lifeforms (Pires et al., 2021; Schriever et al., 2014). Water availability can directly and indirectly affect seasonal assemblages of aquatic communities (Mdidimba et al., 2021): amphibians can show complex responses for survival and growth to variations in hydroperiod length (Thompson and Popescu, 2021), while macroinvertebrates communities can show important changes mainly due to physicochemical variations (Coccia et al., 2021). Here, we demonstrated that diatom richness was not affected by hydroperiod length and seasonal variations. This observation is consistent with the study by Ma et al. (2023) who showed that seasonal differences in planktic diatoms were more pronounced than those in benthic diatoms. Adhesion to the substrate leads to benthic diatoms to be more prone to resist dryness than planktic ones (Falasco et al., 2018). Then, we hypothesize that benthic diatoms respond to droughts with resistance cists (Kooistra et al., 2007), regenerating the same community during wet periods. Very few studies have investigated the relationship between ponds' hydroperiod and diatom communities. Cantonati et al. (2023) highlighted that the composition of diatom assemblages can provide information on the hydroperiod and waterflow variability; Blanco et al. (2020) demonstrated that diatomic diversity changes with hydroperiod. In our study we revealed that variations in diatom communities of MTPs are independent from hydroperiod length. Moreover, our findings suggest that MTPs are particularly suitable for hosting threatened species included in the Red List of diatom species (Padula et al., 2021). At the same time, no differences emerged between sites regarding the number of endangered species, raising awareness about the relative effect of protection measures on diatom communities and the consequent benefits for endangered species. In this sense, our study revealed that MTPs host similar Red List species regardless of the level of protection differently from our hypothesis. However, many variables could contribute to this homogeneity: aerial dispersion of diatoms (Stenger-Kovács and B-Béres, 2024), similarity in physicochemical conditions between sampling sites, dispersion through ectozoochory of freshwater diatoms via adherence to waterfowl feathers (Manning et al., 2021). For these reasons, considering the novelty of the research topic, further studies are necessary to deeply understand the potential biotic and abiotic influences on diatom communities and distribution of threatened species.

4.2. Environmental factors associated with diatom community variability

Based on RDA grouping of sites, physicochemical variables were determinant factors for diatom community structure for both MTP(A) and MTP(B). Sampling sites showed different ecological conditions and chemical drivers: our study revealed that substantial variation in physicochemical parameters emerged between samplings sites. Protected site with high Press., T and DO was dominated by *Frustulia vulgaris, Gomphonema gracile, G. parvulum, G. zellense, Nitzschia frustulum, Pinnularia gibba* species during the wet season. These species also occurred in minimally impacted oligo-to mesotrophic waters enriched with oxygen concentrations, with medium-low conductivity. Unprotected site with high EC and ORP was dominated by *Anomoeoneis sphaerophora, Cocconeis placentula, Denticula tenuis, Fragilaria biceps, Fragilaria capucina, Geissleria decussis, Gomphonema pumilum, Nitzschia filiformis, N. linearis* species during the wet season. These species also occurred in euryhaline, fresh and brackish waters with low to moderate concentrations of organic pollution. Our results align with previous studies that documented similar species assemblages in relation to physicochemical gradients. For instance, *Frustulia vulgaris*, *Gomphonema gracile*, and *Pinnularia gibba* have been commonly associated with well-oxygenated, oligotrophic to mesotrophic conditions in protected or minimally impacted aquatic environments (Cantonati et al., 2012; Rimet and

Bouchez, 2012). Similarly, *Anomoeoneis sphaerophora*, *Cocconeis placentula*, and *Fragilaria capucina* are known to occur in more disturbed habitats characterized by elevated conductivity and organic enrichment, including euryhaline and brackish systems (Lavoie et al., 2009).

Physicochemical variables are generally the main drivers of diatom species richness in lotic systems (Shibabaw et al., 2021). This study confirmed electrical conductivity, dissolved oxygen, T, and pressure were important in determining diatom community structure also in MTPs (Dalu et al., 2022). DO direct relationship with diatom richness is consistent with other studies (Shibabaw et al., 2021). However, our findings contrast with those of Guo et al. (2020) and Al-Imari et al. (2023) who reported that hydrology plays a primary role over physicochemical parameters in shaping diatom communities; on the contrary, our findings agree with Novak and Zelnik (2021) and Shetty and Gulimane (2023), where ecological conditions like temperature, pH, dissolved gases, were found to impact the growth and abundance of diatoms. pH was identified as a key factor for diatoms, significantly affecting their growth through direct physiological stress (Shibabaw et al., 2021). In the same study, electrical conductivity (EC) and dissolved oxygen (DO) also emerged as important predictors for diatom community composition. Similarly to Shibabaw et al. (2021), who compared urban and agricultural sites, we can draw parallels between our two study sites: a protected (=urban-equivalent) site and an unprotected (=agricultural-equivalent) site. Our protected site exhibited mean values of 8.52 for pH, 294 μS/cm for EC, and 69.3 mg/L for DO. In contrast, the unprotected site averaged 7.82 for pH, 760.7 μS/cm for EC, and 40.6 mg/L for DO. Notably, Shibabaw et al. (2021) reported quite different values: their urban site had a mean pH of 6.6, EC of 132.7 μS/cm, and DO of 3.29 mg/L, while their agricultural site had a mean pH of 7.5, EC of 99.2 μS/cm, and DO of 6.72 mg/L. These discrepancies may be attributed to the different aquatic environments studied (streams/rivers vs. our pond sites).

The importance of pH and conductivity for diatom communities was likewise highlighted by Della Bella et al. (2007) in their analysis of wetlands. However, even in their study, the mean values for pH (8.02) and conductivity (3.56 μS/cm) were lower than those observed in our sites. This suggests that diatom assemblages in freshwater ecosystems can respond differently to a broad spectrum of environmental conditions, which may influence community structure across diverse habitats (Soininen, 2007).

Given the absence in literature of studies involving MTPs as sampling sites, we could hypothesize that diatom communities are both influenced by hydrology, water availability and physicochemical parameters in many ways: the exact magnitude of these influences could be different for each pond considered, given the contemporary influence of different biotic and abiotic factors (Kumar et al., 2020).

4.3. Diatom alpha and beta diversity

Diatom alpha diversity indices did not show significative correlations with physicochemical parameters for MTP(A), while significative correlations emerged for MTP(B). Physicochemical parameters showed a low influence on diatom assemblages in the protected site: we could hypothesize that biotic and spatial factors may override the effect of physicochemical factors (Blanco et al., 2020), especially in anthropogenic disturbances-free environments. Differently, MTP(B) diatom communities resulted highly influenced by physicochemical parameters: all the parameters significantly influenced the number of species, with DO which was confirmed as one of the most important abiotic factors for shaping diatom communities (Schuch et al., 2015). Shannon diversity index was also driven by DO. These results are in line with previous studies reporting DO as a major environmental driver of taxonomic diversity in freshwater diatoms (Cui et al., 2023; B-;Béres et al., 2016). In addition, conductivity and redox potential (ORP), which significantly influenced assemblage structure in MTP(B), have also been identified as relevant predictors of diversity in various aquatic systems (Stenger-Kovács et al., 2023; Soininen, 2007), particularly in temporary or fluctuating habitats. Our study confirms the importance of seasonality as an important structuring force for diatom communities (Sun et al., 2022): however, protection factor showed a greater influence on diatom diversity. In fact, significative results for seasonality emerged only including the protection factor. The absence of anthropogenic stressors (vehicular traffic, grazing, tourism disturbances) lead to diatom communities to be structured without external disturbances. Comparable studies also showed similar patterns in diversity indices. For example, B-Béres et al. (2016) reported that in temporary or semi-permanent ponds, alpha diversity tends to be more variable in unprotected or human-influenced sites, where environmental filtering is stronger. This supports our findings, where MTP(B) sites, exposed to more variable and stressful conditions, showed significant correlations between alpha diversity indices and abiotic parameters such as dissolved oxygen.

Disturbed freshwater ecosystems generally show different diatom communities (Falasco et al., 2012), which differ from isolated ones (Blanco et al., 2020). Our results show this tendency: by comparing beta diversity, the two sampling sites showed different community assemblages, with MTP(A) showing general better water quality with high oxygen concentrations. The patterns of alpha and beta diversity observed in our study are consistent with those described by B-Béres et al. (2017) and Soininen (2007), who found that environmental heterogeneity and disturbance intensity can lead to high beta diversity via species turnover, especially in fragmented or temporary aquatic systems. This suggests that while local environmental filtering may be weak in protected areas, it becomes a stronger driver of diatom assemblage structure in more impacted or variable habitats. Moreover, the seasonal effect is amplified while comparing diatom communities, underlying the fundamental role of climatic and seasonal biotic and abiotic variations on diatom assemblages.

4.4. Diatom functional ecology

Our results were not consistent with Liu et al. (2025): although the ecological guild allows us to determine the magnitude of the change in the values of the investigated parameters, our research did not highlight the correspondence between diatom ecological guild and physicochemical parameters. While for all the seasons the dominant guild was, as expected, the motile guild, no inter-season variation emerged. Motile guild species are very sensitive to unfavorable ecological conditions, and very common in temporary ponds, given their ability to move to most suitable habitats (Passy, 2007). Their broad presence among all seasons reflects the unstable conditions of MTPs, often subject to alternating phases of floods and droughts (Van den Broeck et al., 2015). However, these results did not reveal a higher sensitivity of diatom ecological guilds to variations in physicochemical variations; high profile guild, sensitive to physical disturbance, including hydrological stress, showed, as hypothesized, a negative correlation with temperature and the relative DO, which represent the two main factors involved during MTPs droughts. These results imply that the diatom communities and the ecological guilds in the MTPs are resilient to seasonal variations. Furthermore, given the novelty proposed by our research, future investigations are therefore necessary to analyze the seasonal dynamics of diatom communities in MTPs.

4.5. Limitations of the study

Despite the robust design and analytical approach, our study has some limitations. First, the relatively small sample size and spatial extent may limit the generalizability of our findings to broader MTPs. Unfortunately, the restricted hydroperiod allowed us to sample the protected pond only for 7 months. It was not possible to collect data outside this period due to drought conditions. Second, although we included a range of physicochemical variables, other important ecological drivers such as nutrient concentrations (e.g., P, N), or biotic interactions were not explicitly considered due to lack in instrument and fundings to perform such analysis. No water samples have been collected for nutrient and cation analysis, which are very important parameters for diatoms and for the spatio-temporal dynamics of the benthic diatom communities. The collection of these water samples would also indicate the effect of agriculture and urban wastewater treatment plants, with higher values of sulphates, nitrates and phosphates in the water. However, we used the same protocols adopted in other studies, analyzing an even higher number of valves (400), compared to many other studies that limit the count to 200 or 300 valves. Therefore, our study is fully replicable and follows established methodological standards. Finally, our analysis focused on a single year; temporal variability could influence community dynamics and diversity patterns, particularly in highly seasonal temporary ponds.

5. Conclusions

Our study confirms that benthic diatoms are reliable bioindicators for detecting both natural and anthropogenic disturbances in MTPs. The proposed research represents the first investigation of diatom community turnover among seasons, comparing protected and disturbed Priority Habitats. In particular, the results showed that diatoms were not affected by hydroperiod length and seasonal variations in benthic diatom richness were not statistically significant. However, MTPs have proven to be particularly suitable for hosting Red List species, although their unstable ecological and hydrological conditions. Temperature, dissolved oxygen and electrical conductivity emerged as the primary environmental drivers influencing the seasonal dynamics of the species-based diatom community. Furthermore, physicochemical parameters emerged as not significant for structuring benthic diatom communities in protected MTPs, while they represent the main driver for disturbed MTPs. Alpha and beta diversity described a complex community, with significant differences between sampling sites in function of anthropogenic and grazing disturbances. Moreover, protection and undisturbed MTPs showed different diatom assemblages, with alpha, beta and ecological diversity deeply influenced by the protection and, to a lesser extent, by seasonality. These findings are consistent with previous research highlighting the sensitivity of diatom communities to environmental gradients such as oxygen availability and conductivity. Importantly, we provide new insights into seasonal turnover and the differential impact of protection status on diatom diversity, expanding knowledge on ephemeral habitats in the Mediterranean region. Quantification of the disturbance levels and their effects on diatom communities is the main limit of our research: we therefore suggest, for future research, to integrate further studies taking into consideration precise data regarding the anthropogenic impacts in MTPs. As proposed by Salafsky et al. (2008), a structured system for classifying and evaluating threats to conservation should be based on two pillars: a standardized taxonomy of threats (e.g., pollution, land use, biological harvesting, etc.) and a systematic approach to quantifying each threat, considering three parameters: scope, severity, and timing. For quantifying and ranking anthropogenic disturbances on MTPs, with diatom as main target, for future research we suggest adopting a combination of field-based observations (e.g., signs of trampling, pollution sources, debris, or excessive algal growth), expert-based scoring systems (ranking the scope, severity, and timing of each threat or the creation of a composite disturbance index combining multiple stressor scores), GIS-based land use analysis and detection of nearby infrastructures or changes in pond hydrology. For this reason, this research should be understood as a starting point for analyzing diatom temporal turnover and ecological response in peculiar ephemeral ecosystems such as MTPs.

CRediT authorship contribution statement

Davide Taurozzi: Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Data curation, Conceptualization. **Massimiliano Scalici:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Consent to participate

Not applicable.

Ethics approval

Not applicable.

Funding

This research was supported by the Grant of Excellence Departments, MIUR-Italy (ARTICOLO1, COMMI 314–337 LEGGE 232/2016). This research was supported by NBFC at the University of Roma Tre.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors acknowledge the support of NBFC to University of Roma Tre, funded by the Italian Ministry of University and Research, PNRR, Missione 4 Componente 2, "Dalla ricerca all' impresa", Investimento 1.4, Project CN00000033.

We would like to thank the Castelporziano Presidential Estate for supporting our research. We are grateful to the General Secretariat of Presidency of the Italian Republic and to the Direction of Castelporziano Presidential Estate for the hospitality and the possibility to set up the research.

We thank the anonymous reviewers for their constructive comments and suggestions which substantially improved the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.csr.2025.105547.

Data availability

Data will be made available on request.

References

Al-Imari, T.J.K., Lengyel, E., Korponai, J., Padisák, J., Stenger-Kovács, C., 2023. Lake morphology as an important constraint for benthic diatoms in temperate, humic forest ponds. Ecol. Indic. 155, 110939. https://doi.org/10.1016/j.ecolind.2023.110939.

Bagella, S., 2023. Which perspectives for mediterranean temporary ponds in the european union in the third millennium? Biodivers. Conserv. 32 (3), 839–849. https://doi.org/10.1007/s10531-023-02549-3.

Bahls, L., Boynton, B., Johnston, B., 2018. Atlas of diatoms (bacillariophyta) from diverse habitats in remote regions of Western Canada. PhytoKeys 105, 1–186. https://doi.org/10.3897/phytokeys.105.23806, 2018.

Battarbee, 1986. Diatom analysis. In: Berglund, B.E. (Ed.), Handbook of Holocene Paleoecology and Paleohydrology. John Wiley & Sons Ltd., Chichester. Great Britain, pp. 527–570.

Battisti, C., Poeta, G., Fanelli, G., 2016. An Introduction to Disturbance Ecology. Springer, Cham, pp. 13–29.

B-Béres, V., Török, P., Kókai, Z., Lukács, V., T-Krasznai, E., Tóthmérész, B., Bácsi, I., 2017. Ecological background of diatom functional groups: comparability of classification systems. Ecol. Indic. 82, 300–312. https://doi.org/10.1016/j.ecolind.2017.07.007.

B-Béres, V., Lukács, Á., Török, P., Bácsi, I., 2016. Combined eco-morphological functional groups are reliable indicators of colonisation processes of benthic diatom

assemblages in a lowland stream. Ecological indicators. https://doi.org/10.1007/s10750-014-1929-y.
Beja, P., Alcazar, R., 2003. Conservation of mediterranean temporary ponds under agricultural intensification: an evaluation using amphibians. Biol. Conserv. 114 (3), 317–326. https://doi.org/10.1016/S0006-3207(03)00051-X.
Beltrami, M.E., Bernabei, S., Bona, F., Cappelletti, C., Ciutti, F., Della Bella, V., et al., 2007. Protocollo di campionamento e analisi delle diatomee bentoniche dei corsi d'acqua. https://hdl.handle.net/2318/48661.
Blanco, S., Olenici, A., Ortega, F., Jiménez-Gómez, F., Guerrero, F., 2020. Identifying environmental drivers of benthic diatom diversity: the case of mediterranean mountain ponds. PeerJ 8, e8825. https://doi.org/10.7717/peerj.8825.
Boix, D., Kneitel, J., Robson, B.J., Duchet, C., Zúñiga, L., Day, J., et al., 2016. Invertebrates of freshwater temporary ponds in mediterranean climates. Invertebrates in freshwater wetlands: an international perspective on their ecology 141–189. https://doi.org/10.1007/978-3-319-24978-0_5.
Cantonati, M., Casoria, C., Gerecke, R., Bilous, O.P., Maisto, G., Segadelli, S., et al., 2023. Diatom indicators of fluctuating/intermittent discharge from springs in two Bavarian nature conservation areas. Diversity 15 (8), 915. https://doi.org/10.3390/d15080915.
Cantonati, M., Hofmann, G., Spitale, D., Werum, M., Lange-Bertalot, H., 2022. Diatom red lists: important tools to assess and preserve biodiversity and habitats in the face of direct impacts and environmental change. Biodivers. Conserv. 31 (2), 453–477. https://doi.org/10.1007/s10531-021-02339-9.
Cantonati, M., Angeli, N., Bertuzzi, E., Spitale, D., Lange-Bertalot, H., 2012. Diatoms in springs of the alps: spring types, environmental determinants, and substratum. Freshw. Sci. 31 (2), 499–524. https://doi.org/10.1899/11-065.1.
Celewicz, S., Gołdyn, B., 2021. Phytoplankton communities in temporary ponds under different climate scenarios. Sci. Rep. 11 (1), 17969. https://doi.org/10.1038/s41598-021-97516-9.
Coccia, C., Almeida, B.A., Green, A.J., Gutiérrez, A.B., Carbonell, J.A., 2021. Functional diversity of macroinvertebrates as a tool to evaluate wetland restoration. J. Appl. Ecol. 58 (12), 2999–3011. https://doi.org/10.1111/1365-2664.14038.
Cui, Z., Gao, W., Li, Y., Wang, W., Wang, H., Liu, H., et al., 2023. Dissolved oxygen and water temperature drive vertical spatiotemporal variation of phytoplankton community: evidence from the largest diversion water source area. Int. J. Environ. Res. Publ. Health 20 (5), 4307. https://doi.org/10.3390/ijerph20054307.
Dalu, T., Cuthbert, R.N., Weyl, O.L., Wasserman, R.J., 2022. Community structure and environmental factors affecting diatom abundance and diversity in a mediterranean climate river system. Sci. Total Environ. 810, 152366. https://doi.org/10.1016/j.scitotenv.2021.152366.
de Necker, L., Brendonck, L., Vanschoenwinkel, B., Florencio, M., Rhazi, L., Gołdyn, B., 2025. Lessons from pond creation and restoration projects in Europe. Restor. Ecol. 33 (3), e14342. https://doi.org/10.1111/rec.14342.
Della Bella, V., Puccinelli, C., Marcheggiani, S., Mancini, L., 2007. Benthic diatom communities and their relationship to waterchemistry in wetlands of central Italy. In: Annales De Limnologie-International Journal of Limnology, 43. EDP Sciences, pp. 89–99. https://doi.org/10.1051/limn/2007021, 2.
Diana, J.S., Szyper, J.P., Batterson, T.R., Boyd, C.E., Piedrahita, R.H., 2017. Water quality in ponds. Dynam. Pond Aqua. 53–71.
Dimitriou, E., Moussoulis, E., Stamati, F., Nikolaidis, N., 2009. Modelling hydrological characteristics of mediterranean temporary ponds and potential impacts from climate change. In: Oertli, B., Céréghino, R., Biggs, J., Declerck, S., Hull, A., Miracle, M.R. (Eds.), Pond Conservation in Europe. Developments in Hydrobiology 210, 210. Springer, Dordrecht. https://doi.org/10.1007/978-90-481-9088-1_29.
Dimitriou, E., Karaouzas, I., Skoulikidis, N., Zacharias, I., 2006. Assessing the environmental status of mediterranean temporary ponds in Greece. In: Annales De Limnologie-International Journal of Limnology, 42. EDP Sciences, pp. 33–41. https://doi.org/10.1051/limn/2006004, 1.
Domis, D.S., Lisette, N., Elser, J.J., Gsell, A.S., Huszar, V.L., Ibelings, B., et al., 2013. Plankton dynamics under different climatic conditions in space and time. Freshw. Biol. 58 (3), 463–482. https://doi.org/10.1111/fwb.12053.
DREAL Languedoc Roussillon, 2021. Atlas Des Diatomées De L'Ex Partie Languedoc-Roussillon.
Earl, B.C., McIntosh, A.R., O'Regan, R.P., Brown, S.K., Warburton, H.J., 2023. Invasion of a non-native anuran likely disrupts pond ecosystems. Freshw. Biol. 68 (7), 1194–1210. https://doi.org/10.1111/fwb.14097.
Ector, L., Hlúbiková, D., 2010. Atlas Des Diatomées des Alpes-Maritimes et de la Région Provence-Alpes-Côte d'Azur.
Falasco, E., Piano, E., Doretto, A., Fenoglio, S., Bona, F., 2018. Resilience of benthic diatom communities in mediterranean streams: role of endangered species. Mar. Freshw. Res. 70 (2), 212–224. https://doi.org/10.1071/MF17282.
Falasco, E., Ector, L., Ciaccio, E., Hoffmann, L., Bona, F., 2012. Alpine freshwater ecosystems in a protected area: a source of diatom diversity. Hydrobiologia 695, 233–251. https://doi.org/10.1007/s10750-012-1114-0.
Fehlinger, L., Misteli, B., Morant, D., Juvigny-Khenafou, N., Cunillera-Montcusi, D., Chaguaceda, F., et al., 2023. The ecological role of permanent ponds in Europe: a review of dietary linkages to terrestrial ecosystems via emerging insects. Inland Waters 13 (1), 30–46. https://doi.org/10.1080/20442041.2022.2111180.
Ferdoushi, Z., Hassan, K.T., Alam, M.S., Azad, M.A.K., Ara, Y., Khatun, M.M., 2023. Diatom assemblages and their interrelationships between different water quality parameters in gorveshwari river of Bangladesh. Trends Sci. 20 (9), 6697. https://doi.org/10.48048/tis.2023.6697, 6697.
Fernández-Zamudio, R., García-Murillo, P., Díaz-Paniagua, C., 2016. Aquatic plant distribution is driven by physical and chemical variables and hydroperiod in a mediterranean temporary pond network. Hydrobiologia 774, 123–135. https://doi.org/10.1007/s10750-016-2701-2, 2016.
Gelis, M.M.N., Cochero, J., Donadelli, J., Gómez, N., 2020. Exploring the use of nuclear alterations, motility and ecological guilds in epipelic diatoms as biomonitoring tools for water quality improvement in urban impacted lowland streams. Ecol. Indic. 110, 105951. https://doi.org/10.1016/j.ecolind.2019.105951.
Häder, D.P., Gao, K., 2017. The impacts of climate change on marine phytoplankton. Climate Change Impacts on Fisheries and Aquaculture: A Global Analysis 2, 897–924. https://doi.org/10.1002/9781119154051.ch27.
Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4, 9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.
Hays, G.C., Richardson, A.J., Robinson, C., 2005. Climate change and marine plankton. Trends Ecol. Evol. 20 (6), 337–344. https://doi.org/10.1016/j.tree.2005.03.004.
Hill, M.J., Heino, J., Thornhill, I., Ryves, D.B., Wood, P.J., 2017. Effects of dispersal mode on the environmental and spatial correlates of nestedness and species turnover in pond communities. Oikos 126 (11), 1575–1585. https://doi.org/10.1111/oik.04266.
Hofmann, G., Lange-Bertalot, H., Werum, M., Klee, R., 2018. Rote Liste und Gesamtartenliste der limnischen Kieselalgen (Bacillariophyta) Deutschlands. In: Metzing, D., Hofbauer, N., Ludwig, G., Matzke-Hajek, G. (Eds.), (Red.): Rote Liste Gefährdeter Tiere, Pflanzen und Pilze Deutschlands, Band 7: Pflanzen. – Münster (Landwirtschaftsverlag), 70. Naturschutz und Biologische Vielfalt, pp. 601–708, 7.
ISPRA, 2014. Protocollo di campionamento e Analisi Delle Diatomee Bentoniche dei Corsi D'Acqua.
Kooistra, W.H., Gersonde, R., Medlin, L.K., Mann, D.G., 2007. The origin and evolution of the diatoms: their adaptation to a planktic existence. Evol. Primary Prod. Sea 207–249. https://doi.org/10.1016/B978-012370518-1/50012-6.
Koren, A.Š., Neduk, A., Šarić, K.K., Šalamon, D., Sisan, P., 2023. Guidelines for Restoring and Managing Mediterranean Ponds and Canals.
Krammer, K., 2002. Diatoms of the European inland waters and comparable habitats. In: Lange-Bertalot, 3. Cymbella. ISBN 978-3-904144-84-1.
Krammer, K., Lange-bertalot, H., 1991a. Bacillariophyceae, 3.Teil : Centrales, Fragilariaceae, Eunotiaceaeceae, Band 2/3, Subwasserflora Von Mitteleuropa. Veb Gustav Fischer Verlag, p. 576.
Krammer, K., Lange-bertalot, H., 1991b. Bacillariophyceae, 4.Teil : Achnanthaceae, Kritische Ergänzungen Zu *Navicula* (Lineolatae) und *Gomphonema* , Band 2/4, Subwasserflora Von Mitteleuropa. Veb Gustav Fischer Verlag, Jena.
Krammer, K., Lange-bertalot, H., 1988. Bacillariophyceae, 2.Teil : Bacillariophyceae, Epithemiaceae, Surirellaceae, Band 2/2, Subwasserflora Von Mitteleuropa. Veb Gustav Fischer Verlag, p. 595.
Krammer, K., Lange-bertalot, H., 1986. Bacillariophyceae, 1.Teil : Naviculaceae, Band 2/1, Subwasserflora Von Mitteleuropa. Veb Gustav Fischer Verlag, p. 876.
Krivtsov, V., Forbes, H., Birkinshaw, S., Olive, V., Chamberlain, D., Buckman, J., et al., 2022. Ecosystem services provided by urban ponds and green spaces: a detailed study of a semi-natural site with global importance for research. Blue-Green Sys. 4 (1), 1–23. https://doi.org/10.2166/bgs.2022.021.
Kumar, R., Kumari, R., Prasad, C., Tiwari, V., Singh, N., Mohapatra, S., et al., 2020. Phytoplankton diversity in relation to physicochemical attributes and water quality of mandakini river, garhwal himalaya. Environ. Monit. Assess. 192, 1–23. https://doi.org/10.1007/s10661-020-08768-3.
Lavoie, I., Dillon, P.J., Campeau, S., 2009. The effect of excluding diatom taxa and reducing taxonomic resolution on multivariate analyses and stream bioassessment. Ecol. Indic. 9 (2), 213–225. https://doi.org/10.1016/j.ecolind.2008.04.003.
Liu, X., Zhao, Y., Yu, X., Song, Y., Li, Y., Yang, G., et al., 2025. Seasonal changes of species-and guild-based benthic diatom communities in the transitional water zone of the yellow river Delta. Mar. Environ. Res., 106843 https://doi.org/10.1016/j.marenvres.2024.106843.
Lobo, E.A., Heinrich, C.G., Schuch, M., Wetzel, C.E., Ector, L., 2016. Diatoms as bioindicators in Rivers. River Algae 245–271. https://doi.org/10.1007/978-3-319-31984-1_11.
Ma, C., Cui, R., Duan, Y., Zhang, N., Liu, Y., Sui, F., et al., 2023. Differences in biodiversity and assembly mechanisms between planktic and benthic diatom communities in riverine ecosystems: a case study in the ashi river. Ecol. Indic. 157, 111258. https://doi.org/10.1016/j.ecolind.2023.111258.
Maitland, V.C., Robinson, C.V., Porter, T.M., Hajibabaei, M., 2020. Freshwater diatom biomonitoring through benthic kick-net metabarcoding. PLoS One 15 (11), e0242143. https://doi.org/10.1371/journal.pone.0242143.
Mdidimba, N.D., Mlambo, M.C., Motitsoe, S.N., 2021. Trophic interactions and food web structure of aquatic macroinvertebrate communities in afromontane wetlands: the influence of hydroperiod. Aquat. Sci. 83, 1–15. https://doi.org/10.1007/s00027-021-00792-w.
Novak, K., Zelnik, I., 2021. Relations between benthic diatom community and characteristics of karst ponds in the alpine region of Slovenia. Diversity 13 (11), 531. https://doi.org/10.3390/d13110531.
Olmo, C., Gálvez, Á., Bisquert-Ribes, M., Bonilla, F., Vega, C., Castillo-Escrivà, A., et al., 2022. The environmental framework of temporary ponds: a tropical-mediterranean comparison. Catena 210, 105845. https://doi.org/10.1016/j.catena.2021.105845.
Padisak, J., Naselli-Flores, L., 2021. Phytoplankton in extreme environments: importance and consequences of habitat permanency. Hydrobiologia 848 (1), 157–176. https://doi.org/10.1007/s10750-020-04353-4.
Padula, R., Carosi, A., Rossetti, A., Lorenzoni, M., 2021. The diatomic diversity of two mediterranean high-elevation Lakes in the Sibillini Mountains national park (central Italy). Environments 8 (8), 79. https://doi.org/10.3390/environments8080079.
Passy, S.I., 2007. Diatom ecological guilds display distinct and predictable behavior along nutrient and disturbance gradients in running waters. Aquat. Bot. 86 (2), 171–178. https://doi.org/10.1016/j.aquabot.2006.09.018.

Pestryakova, L.A., Herzschuh, U., Gorodnichev, R., Wetterich, S., 2018. The sensitivity of diatom taxa from yakutian Lakes (north-eastern siberia) to electrical conductivity and other environmental variables. Polar Res. 37 (1), 1485625. https://doi.org/10.1080/17518369.2018.1485625.

Pickett, S.T., Pickett, S.T., White, P.S. (Eds.), 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic press.

Pille, F., Pinto, L., Denoël, M., 2023. Functional and temporal facets of predation by marsh frogs across the aquatic–terrestrial ecotone of ponds and implications in the context of biological invasions. Freshw. Biol. 68 (12), 2184–2196. https://doi.org/10.1111/fwb.14186.

Pires, M.M., Bieger, L., Boelter, T., Stenert, C., Maltchik, L., 2021. Spatiotemporal assembly patterns of macroinvertebrate metacommunity structure in subtropical wetlands with different hydroperiods. Int. Rev. Hydrobiol. 106 (5–6), 239–248. https://doi.org/10.1002/iroh.202002072.

Potapova, M.G., Charles, D.F., 2002. Benthic diatoms in USA rivers: distributions along spatial and environmental gradients. J. Biogeogr. 29 (2), 167–187. https://doi.org/10.1046/j.1365-2699.2002.00668.x.

Pulido, M., Alfonso-Torreño, A., Barrena-González, J., Robina-Ramírez, R., Abdennour, M.A., 2020. Identifying problems in watering ponds with different purposes. Environments 7 (9), 63. https://doi.org/10.3390/environments7090063.

R Core Team, 2021. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL. https://www.R-project.org/.

Remmer, C.R., Robichaud, C.D., Polowyk, H., Rooney, R., 2019. The role of ecological drift in structuring periphytic diatom communities. J. Freshw. Ecol. 34 (1), 363–377. https://doi.org/10.1080/02705060.2019.1614104.

Richardson, D.C., Holgerson, M.A., Farragher, M.J., Hoffman, K.K., King, K.B., Alfonso, M.B., et al., 2022. A functional definition to distinguish ponds from Lakes and wetlands. Sci. Rep. 12 (1), 10472. https://doi.org/10.1038/s41598-022-14569-0.

Rimet, F., Bouchez, A., 2012. Life-forms, cell-sizes and ecological guilds of diatoms in european Rivers. Knowl. Manag. Aquat. Ecosyst. 406, 1. https://doi.org/10.1051/kmae/2012018.

Rousseaux, C.S., Gregg, W.W., 2013. Interannual variation in phytoplankton primary production at a global scale. Remote Sens. 6 (1), 1–19. https://doi.org/10.3390/rs6010001.

Salafsky, N., Salzer, D., Stattersfield, A.J., Hilton-Taylor, C.R.A.I.G., Neugarten, R., Butchart, S.H., et al., 2008. A standard lexicon for biodiversity conservation: unified classifications of threats and actions. Conserv. Biol. 22 (4), 897–911.

Sassenhagen, I., Langenheder, S., Lindström, E.S., 2023. Infection strategies of different chytrids in a diatom spring bloom. Freshw. Biol. 68 (6), 972–986. https://doi.org/10.1111/fwb.14079.

Sbarbati, C., Lacchini, A., Petitta, M., 2022. The role of hydrogeological monitoring in a multidisciplinary context for the preservation of the critical zone in the natural reserve of castelporziano estate. Front. Earth Sci. 10, 935791. https://doi.org/10.3389/feart.2022.935791.

Schriever, T.A., Cadotte, M.W., Williams, D.D., 2014. How hydroperiod and species richness affect the balance of resource flows across aquatic-terrestrial habitats. Aquat. Sci. 76, 131–143. https://doi.org/10.1007/s00027-013-0320-9.

Schuch, M., Oliveira, M.A., Lobo, E.A., 2015. Spatial response of epilithic diatom communities to downstream nutrient increases. Water Environ. Res. 87 (6), 547–558. https://doi.org/10.2175/106143014X14062131178196.

Shibabaw, T., Beyene, A., Awoke, A., Tirfie, M., Azage, M., Triest, L., 2021. Diatom community structure in relation to environmental factors in human influenced Rivers and streams in tropical Africa. PLoS One 16 (2), e0246043. https://doi.org/10.1371/journal.pone.0246043.

Soininen, J., 2007. Environmental and spatial control of freshwater Diatoms—a review. Diatom Res. 22 (2), 473–490. https://doi.org/10.1080/0269249X.2007.9705724.

Sousa, W.P., 1984. The role of disturbance in natural communities. Annu. Rev. Ecol. Systemat. 15, 353–391.

Stenger-Kovács, C., B-Béres, V., 2024. Guilds for diatoms: history and future prospects. Diatom Ecol.: Mol. Metacommun. 233–279. https://doi.org/10.1002/9781394174898.ch8.

Stenger-Kovács, C., Béres, V.B., Buczkó, K., Tapolczai, K., Padisák, J., Selmeczy, G.B., Lengyel, E., 2023. Diatom community response to inland water salinization: a review. Hydrobiologia 850 (20), 4627–4663. https://doi.org/10.1007/s10750-023-05167-w.

Stenger-Kovács, C., Lengyel, E., Crossetti, L.O., Üveges, V., Padisák, J., 2013. Diatom ecological guilds as indicators of temporally changing stressors and disturbances in the small Torna-stream, Hungary. Ecol. Indic. 24, 138–147. https://doi.org/10.1016/j.ecolind.2012.06.003.

Sun, X., Wu, N., Hörmann, G., Faber, C., Messyasz, B., Qu, Y., Fohrer, N., 2022. Using integrated models to analyze and predict the variance of diatom community composition in an agricultural area. Sci. Total Environ. 803, 149894. https://doi.org/10.1016/j.scitotenv.2021.149894.

Taurozzi, D., Scalici, M., 2024a. Assessing the conservation status of mediterranean coastal ponds: checklist, ecological and functional diversity of diatom communities. Cont. Shelf Res., 105359 https://doi.org/10.1016/j.csr.2024.105359.

Taurozzi, D., Scalici, M., 2024b. Mapping Italian high-altitude ponds. Environ. Manag. https://doi.org/10.1007/s00267-024-02061-6, 2024.

Taurozzi, D., Cesarini, G., Scalici, M., 2024a. Diatoms as bioindicators for health assessments of ephemeral freshwater ecosystems: a comprehensive review. Ecol. Indic. 166, 112309. https://doi.org/10.1016/j.ecolind.2024.112309.

Taurozzi, D., Gallitelli, L., Cesarini, G., Romano, S., Orsini, M., Scalici, M., 2024b. Passive biomonitoring of airborne microplastics using lichens: a comparison between urban, natural and protected environments. Environ. Int. 187, 108707. https://doi.org/10.1016/j.envint.2024.108707.

Taylor, J.C., Harding, W.R., Archibald, C.G.M., 2007a. An illustrated guide to some common diatom species from South Africa. Water Res. Comm.

Taylor, J.C., Harding, W.R., Archibald, C.G.M., 2007b. A Methods Manual for the Collection, Preparation and Analysis of Diatom Samples. Version, 1, 60.

Thompson, C.M., Popescu, V.D., 2021. Complex hydroperiod induced carryover responses for survival, growth, and endurance of a pond-breeding amphibian. Oecologia 195 (4), 1071–1081. https://doi.org/10.1007/s00442-021-04881-3.

Tinelli, A., Folletto, A., Manfredi Frattarelli, F., Maffei, L., Musicanti, A., Recanatesi, F., 2012. Il sistema ambientale della tenuta presidenziale di Castelporziano. Le zone umide. Segretariato Generale Della Presidenza Della Repubblica Italiana. Commissione Tecnico Scientifica Della Tenuta Presidenziale Di Castelporziano. Accademia nazionale delle scienze detta dei quaranta roma 2012.

Van den Broeck, M., Waterkeyn, A., Rhazi, L., Grillas, P., Brendonck, L., 2015. Assessing the ecological integrity of endorheic wetlands, with focus on mediterranean temporary ponds. Ecol. Indic. 54, 1–11. https://doi.org/10.1016/j.ecolind.2015.02.016.

Villa-Alfageme, M., Briggs, N., Ceballos-Romero, E., de Soto, F., Manno, C., Giering, S.L.C., 2024. Seasonal variations of sinking velocities in Austral diatom blooms: lessons learned from COMICS. Deep Sea Res. Part II Top. Stud. Oceanogr. 213, 105353. https://doi.org/10.1016/j.dsr2.2023.105353.

Virta, L., Soininen, J., Norkko, A., 2020. Stable seasonal and annual alpha diversity of benthic diatom communities despite changing community composition. Front. Mar. Sci. 7, 88. https://doi.org/10.3389/fmars.2020.00088.

White, P.S., Harrod, J., Walker, J.L., Jentsch, A., 2000. Disturbance, scale, and boundary in wilderness management. Wilderness science in a time of change conference 2, 27–42.

Widigdo, B., Rifqi, M., Mashar, A., Nazar, F., Wardiatno, Y., 2020. The contribution of phytoplankton in the carbon adsorption and stock during shrimp culture in brackishwater ponds. Biodiv. J. Biol. Div. 21 (11). https://doi.org/10.13057/biodiv/d211123.

Wolin, J.A., Duthie, H.C., 1999. Diatoms as indicators of water level change in freshwater Lakes. The diatoms: Appl. Environ. Earth Sci. 183–202.

Yadav, S., Goyal, V.C., 2022. Current status of ponds in India: a framework for restoration, policies and circular economy. Wetlands 42 (8), 107. https://doi.org/10.1007/s13157-022-01624-9.

Zacharias, I., Zamparas, M., 2010. Mediterranean temporary ponds. A disappearing ecosystem. Biodivers. Conserv. 19, 3827–3834. https://doi.org/10.1007/s10531-010-9933-7.

Zacharias, I., Dimitriou, E., Dekker, A., Dorsman, E., 2007. Overview of temporary ponds in the mediterranean region: threats, management and conservation issues. J. Environ. Biol. 28 (1), 1–9.

Zaharescu, D.G., Hooda, P.S., Burghelea, C.I., Palanca-Soler, A., 2016. A multiscale framework for deconstructing the ecosystem physical template of high-altitude Lakes. Ecosystems 19, 1064–1079. https://doi.org/10.1007/s10021-016-9987-9.