



Periphytic algae from rice fields: taxonomic and functional analysis in a harsh environment (NW Italy)

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Abstract

Rice fields are one of the most important agricultural environments in Northern Italy. These agroecosystems are characterized by high variations in water temperature, shading by rice plants, and sporadic droughts that affect the life of aquatic organisms. In the present study, we carried out an analysis within the limits of two rice fields and their water supply canal in the Lomellina (Lombardy; NW Italy). The aims of this study were (1) to quantify the main benthic primary producers colonizing the two rice fields and their feeding canal, focusing on diatoms, green algae, and cyanobacteria; and (2) to shed light on the taxonomic and functional composition of diatom communities living in these three environments. The study was conducted during the spring and summer 2023, corresponding to the growth phases of rice plants and the peak of diatom primary productivity. A total of 54 samples were collected from these three environments, by using artificial substrates. Diatoms dominated the canal channeling water to the rice fields, while diatoms and cyanobacteria were co-present in the two rice fields. Among the diatoms, low-profile and motile guilds were dominant in the water canal while, to the contrary, we observed a higher percentage of motile tolerant species in the rice fields, such as *Navicula veneta*, *Nitzschia amphibia* and *Planothidium incuriatum*, a recently described species. The analysis of the microalgae communities can be useful to define the proper management of wetland-like environments and the conservation of their biodiversity.

Keywords Diatoms · Rice fields · Farmland · Shading · Rice growth stages · Drought

Introduction

Rice paddy fields cover about 218,000 ha across the whole Italian peninsula (NRI 2023a), especially in Northern Italy (ISTAT 2019), and in particular in Piedmont and Lombardy. The submersion dynamics of rice-growing environments require water supply from nearby streams and rivers, achieved through a dense net of artificial channels that deliver water to the rice fields. In this context, several European and/or national regulations and directives provide with strict rules, highlighting the importance of agricultural sites in terms of water exploitation and flow modification, as well as chemical treatments (European Union Nitrate Directive

91/676/CEE (1991); Common Agricultural Policy [CAP] 2023–2027). While the Water Frame Directive (2000/60/CE; European Union [2000]) highlights the needs for the re-naturalization of all water bodies, the CAP defines among its objectives the need of an “efficient management of natural resources,” including water resources. Moreover, water use in the agricultural context is normed especially concerning chemical concentrations by the Nitrate Directive 91/676/CEE and the European Agenda 2030, with its 17 objectives of sustainable development. Furthermore, European regulations require the control of water released in the environment also after its use for human activities.

The submergence dynamics, water derivation and environmental characteristics of rice-growing environments places them at the center of distinct types of aquatic systems (i.e. riverine, lacustrine or extreme locations), thereby creating a unique environment (Bona and Fenoglio 2021). The management of water flowing over paddy fields depends on the growing area. Good water management ensures proper plant growth phases (Balasubramanian and Hill 2002; Hill et al. 1991) by providing optimal conditions for the correct

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rooting of plants and thermal regulation (Angelini et al. 2008; Balasubramanian and Hill 2002; Lim et al. 1991; MED 2003); by reducing weed species (Angelini et al. 2008; Balasubramanian and Hill 2002; MED 2003) and costs in the use of herbicide during crop establishment (Tuong et al. 2000); and by ensuring better plant tolerance to abiotic stresses (Fukai 2002) by allowing chemical treatments to be carried out during the drying phase (Angelini et al. 2008; MED 2003; Romani et al. 2023). On the other hand, hydrological stress derived from different drought events has an impact on the communities of aquatic phototrophic organisms (Falasco et al. 2016, 2018; Piano et al. 2017; Romani et al. 2013), and is capable of modifying the survival, presence and distribution of these organisms through direct and indirect impacts, such as changing detrital input and decomposition (Cooper 2013; Lake 2003). In general, green algae and cyanobacteria are more tolerant to drought events in aquatic environments than diatoms, as highlighted in recent studies (Barthés et al. 2015; Klamt et al. 2020; Lengyel et al. 2023; Piano et al. 2017).

The physical impacts of drought events mostly result from exposure to high temperatures. Within rivers, temperature can change the specific composition, structure, distribution and movement of organisms (Chen et al. 2022; Cohn et al. 2003; Fenoglio et al. 2005, 2008; Lengyel et al. 2023; Virta and Hedberg 2024). Also, changes in temperature affect the growth, proliferation and colonial organization of diatoms (Lengyel et al. 2023), ultimately affecting their adhesion capacity and movement speed (Cohn et al. 2003). Temperature also affects species traits, with small, pedunculate and high-profile species preferring low temperature, in contrast to large, adnate and low-profile species (Virta and Hedberg 2024). Temperature and thermal stratification also influence the taxonomic composition and size of organisms in the lacustrine environment (Bramburger et al. 2017; Crossetti et al. 2013; Klamt et al. 2020), as observed in recent years in many Michigan lakes (Bramburger et al. 2017). A further aspect impairing the growth of primary producers in rice fields is the shading resulting from the growth of the cultivated plants (*Oryza sativa* L.), which result in changes in light radiation (De Nicola et al. 1992; Lu et al. 2020). The growth of rice plants develops in different phases: (1) horizontal swelling, (2) vertical growth, (3) booting stage, (4) sexual maturation and the subsequent fruit ripening (reproductive phase), followed by (5) the rice harvest (Angelini et al. 2008; Romani et al. 2023). Changes in bright radiation influences temporal succession and assemblage composition of diatoms (Lin et al. 2013), and also affect soil and water temperatures (DeNicola et al. 1992; Lin et al. 2013; Lu et al. 2020; Taylor 2004).

In this context, the changes in diatom communities observed in previous studies performed in river and lake

environments should be informative for rice-growing sites, which could be considered as heavily managed wetlands for rice cultivation (Su Jing et al. 2017), which are in additional drained at the horizontal swell stage to allow for the chemical treatments (Angelini et al. 2008; MED 2003; Romani et al. 2023). These treatments are usually carried out early, during the cropping season, and include a pre-seeding application (gaminicides), pre-emergency treatments to reduce the development of weed species and post-emergency treatments with halosulfuron-methyl, tritosulfuron and other chemicals (Angelini et al. 2008; GIRE 2021; MED 2003; NRI 2023b). Thus, these conditions define paddy fields as a harsh environment due to the concomitance of many of the previous biotic (competitive stress), abiotic (physical, hydrological and chemical conditions) and anthropic (human invasion of environment and subsequent siltation and pollution) impacts. Periphyton has been studied over time within rice fields to understand the formation pattern (Lu et al. 2017; Su Jing et al. 2017) and influence of these assemblages on rice cultivation (Li et al. 2020; Lu et al. 2020). Periphyton has been shown to alter phosphorus cycling (Li et al. 2020) and cadmium sequestration (Lu et al. 2020) in a rice-growing environment, thus altering various nutrient cycles. Diatoms have also been studied taxonomically and functionally within rice fields (Fujita and Ohtsuka 2005; Lin et al. 2013; Vijayan and Ray 2016) and were found to be influenced by plant growth in that location (Lu et al. 2020).

Based on these considerations, rice-growing environments can be considered to be a surrogate for various lotic and semi-lentic aquatic ecosystems. In this context, the monitoring of rice fields might be useful as a strategy to keep chemical, physical and biological features under control (Water Frame Direction 2000/60; European Union [2000]), as required by the European and Italian directives or policies that have been drafted in recent years. The main aims of this study were: (1) to quantify the main benthic primary producers colonizing two rice field sites and the channel feeding water to the rice fields that are located in the Lomellina are (Lombardy, NW Italy), focusing on diatoms, green algae and cyanobacteria; (2) to shed light on the taxonomic and functional composition of the diatom communities living in these harsh environments. Our hypotheses were: (1) according to previous studies, cyanobacteria and green algae should be favored by the environmental conditions characterizing rice paddy fields, while the diatoms should be limited by rice plant growth and field management; moreover (2) in the rice-growing environments, the most tolerant and resistant benthic diatom species (i.e. motile species) dominate in terms of relative abundance. The research presented here is the first analysis to be carried out in rice field sites in the European

Union. We have analyzing diatom communities in relation to physical and hydrological disturbance and offer a functional perspective for the development of biological indices to define the ecological status of these heavily modified, but still relevant ecosystems.

Methods

Site description and organization of rice fields

The study was conducted in two rice fields located in Castello d'Agogna (Pavia Province [PV]), Lomellina, Lombardy Region, NW Italy; Fig. 1). Water to the sites was fed through an artificial canal connected to a first rice field (R1) during the submergence periods. In turn, the R1 was connected with a second rice field (R2) through a small canal. Submergence times were estimated by the field manager to be approximately 12 h, with slight temporal differences between the two environments due to their different hydraulic organization. These two rice-growing environments were considered to be valid sites to assess the colonization pattern of primary producers based on their logistic and organization features (i.e. a single water derivation channel, the accessibility of the sites and the fact that the standard fertilization and chemical treatments procedures were followed; Fig. 2).

Water derivation upstream of the canal feeding water to R1 and R2 canal are part of the "Drainage and Irrigation Consortia of Est-Sesia". The study was carried out between

14 June 2023 (horizontal swelling plant stage) and 21 September 2023 (rice harvest). Samplings were performed every 14 days, for a total of six sampling times (T1–T6). The sites differed in their management of submergence during the cultivation period: R1 was affected by a higher hydrological stability (lower number of verified drought events: 3 out of 6 surveys) compared to the nearby R2 (4 drought events out of 6 surveys).

Both the fungicide and herbicide treatments were applied under dry conditions. Specifically, these treatments consisted of halosulfuron-methyl, tritosulfuron and rapeseed oil (herbicides and additive) applied altogether on 11 July 2023 and of azoxystrobin (fungicide) applied on 25 July and 7 August 2023 (Table 1).

Experimental design

For this study, we used a total of 90 artificial substrates (i.e. glazed clay tiles, 20 × 10 cm) placed at the different sampling sites (i.e. water supply canal and the two rice fields). In detail, artificial substrates were placed in a horizontal position in the rice fields to maintain the correct submergence level over the whole study period (Electronic Supplementary Material [ESM] Fig. S1a). In the major water supply canal, the tiles were placed in a vertical position in order to support biofilm formation and avoid burial by sediments on the riverbed. The canal tiles were fastened to a metal frame and submerged in the water column, with the frame fastened at the banks (ESM Fig. S1b). During each sampling event (T1–T6),

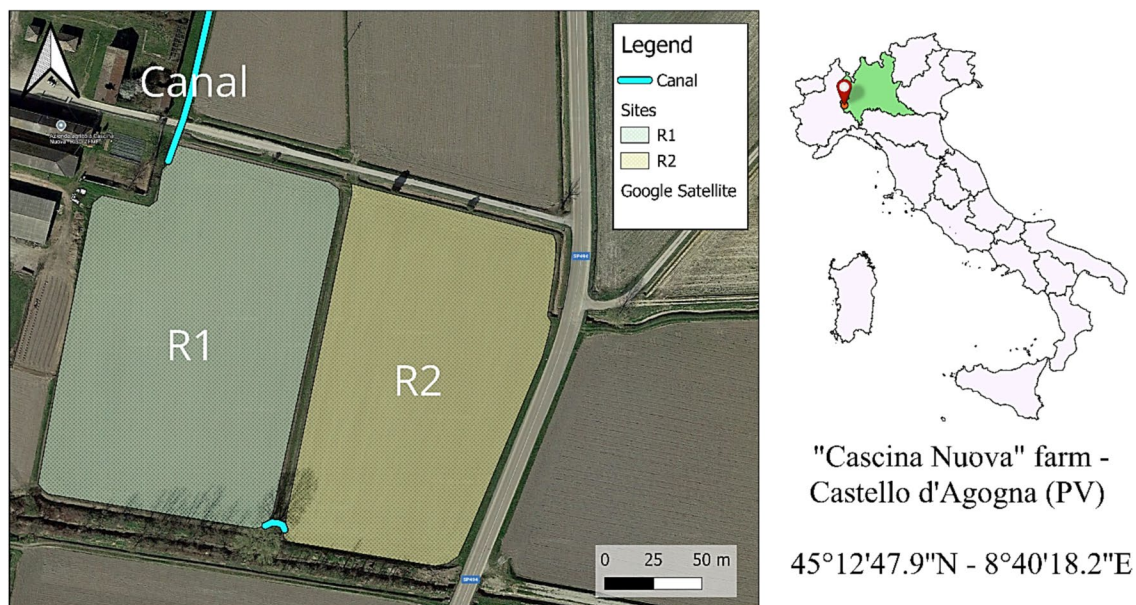


Fig. 1 Geographical representation of the location of the two rice fields included in the study (Lomellina-Lombardy Region, NW Italy). Photograph was made using QGIS3.30.0 software. *R1* first rice field,

irrigated directly with water from the canal, *R2* second rice field, irrigated through a small canal connecting the two fields

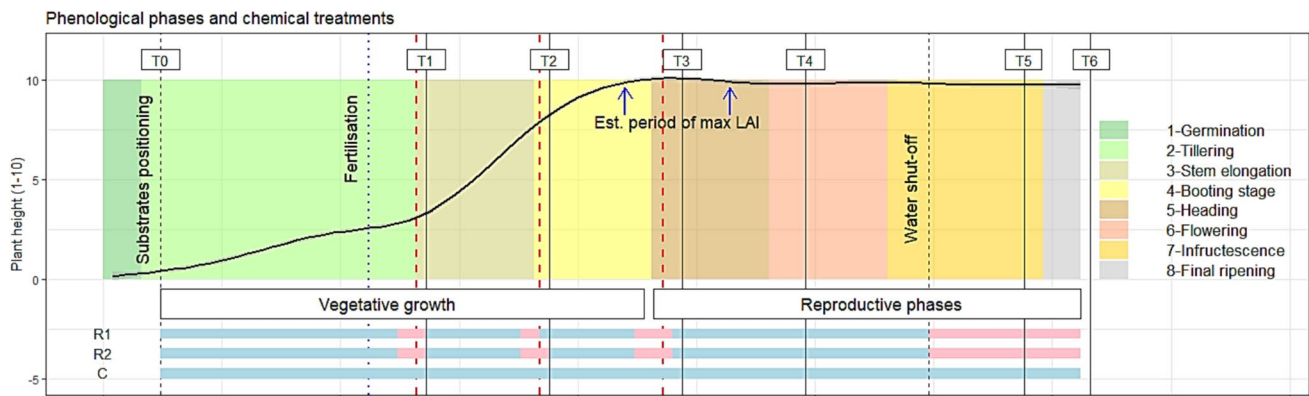


Fig. 2 Graphic reconstruction of the phenological phases characterizing the study periods. The black line is the rated height level of rice plants, and the dashed red lines represent the chemical treatments performed. Bars at bottom of figure show the drought events that occurred during the study, with the light-blue bars indicating the

presence of water and the pink bars indicating the absence of water. *C* Water-feeding canal, *LAI* leaf area index, *R1* first rice field, *R2* second rice field, *T1–T6* sampling times, *T0* day of substrate placement

Table 1 Summary table of the chemicals applied during study period, with the substances and length of dry period

Study periods and sampling times	Application date	Treatments ^a	Chemicals	Dry condition		Estimated length of dry period
				R1	R2	
T0 ^b	14 June	–	–	–	–	–
	6 July	Fertilization	Urea	–	–	–
	11 July	Herbicide + additive	Halosulfuron-methyl tritosulfuron + rapeseed oil	X	X	From 9 to 12 July
T1	12 July	–	–	X	X	From 9 to 12 July
T2	25 July	Fungicide	Azoxystrobin	–	X	Undefinable
	7 August	Fungicide	Azoxystrobin	X	X	Undefinable
T3	9 August	–	–	–	–	–
T4	22 August	–	–	–	–	–
T5	13 September	–	–	X	X	6 days
T6	21 September	–	–	X	X	14 days

R1 First rice field (receiving water directly from irrigation canal), *R2* second rice field (receiving water through a small canal linking *R1* and *R2*), “X” dry period, “–” presence of water

^aOnly the post-emergency treatments were considered (from the calendar of the field manager; Fig. 2)

^bDate of placement of substrates on site

we randomly collected three tiles from each sampling site (i.e. canal, *R1* and *R2*) to enhance the robustness of the data. In total, nine substrates were removed during each sampling occasion for a total of 54 biological samples collected over the whole study period (9 samples × 6 sampling occasions).

Biological analyses, collection and counting

Upon collection of the tiles, we first visually assessed the thickness of the biofilm colonizing the surface of each tile and assigned the thickness to one of three categories: 0 = bare, 1 = colonized or 2 = highly colonized. On each tile, we then evaluated the benthic chlorophyll-*a* (Chl-*a*) of the

three main autotrophic groups colonizing the periphyton (i.e. diatoms, cyanobacteria and green algae) using a portable fluorimetric probe (BenthoTorch; BBE Moldaenke GmbH, Schwentental, Germany), performing three measurements on each substrate along the diagonal line of the major axis.

Secondly, periphyton was collected from each substrate for analysis of the diatom community, by brushing the upper surface of each tile with a toothbrush. Samples from each substrate were kept separated and fixed with ethanol (70% final concentration). In the laboratory, samples were treated following the standard procedure (UNIEN 13946:2014) by removing organic compounds with H₂O₂ (hydrogen peroxide: 110 volume) placed on a hot plate. The cleaned diatom suspension was diluted, and slides were mounted

with Naphrax resin on a light microscope (Leica model DM2500; Leica Microsystems, Wetzlar, Germany) for examination at 1000 \times , following UNIEN:14407 (2014) standards. Taxonomic identification at the species level was performed by using the following monographs and recent taxonomic papers: Bey and Ector 2013; Blanco et al. 2010; Ector et al. 2015; Falasco et al. 2013; Krammer 1997a, 1997b, 2002, 2003; Krammer and Lange-Bertalot 1986, 1988, 1991a, 1991b; Lange-Bertalot 2001, 2017; Lange-Bertalot and Metzeltin 1996; Levkov 2009; Mora et al. 2015; Reichardt 1999; Werum and Lange-Bertalot 2004; Wetzel et al. 2015. A minimum of 400 valves were identified in each sample. Inventories were inserted in OMNIDIA 6.1.7. software (with the database updated in October 2023; Lecointe et al. 1993) to calculate the Shannon–Wiener diversity index, the Evenness, the relative abundance of ecological guilds (namely low profile, high profile, motile and planktonic) according to Passy (2007) and Rimet and Bouchez (2012). In detail, low profile species are likely to be resource-stressed but disturbance-free—i.e. this guild has an advantage in resource-poor environments and is resistant to physical disturbance. A high-profile guild is prevalent in resource-rich environments, but is sensitive to physical disturbance. The motile guild comprises mostly eutrophic and pollution-tolerant species that are not particularly resistant to physical disturbance: however, due to its mobility, this guild has the physical capability of selecting the most suitable habitat.

Environmental analyses

In each sampling site, we measured the water temperature once per hour by using data-loggers (HOBO Pendant Temperature Data Logger UA-001–64; Onset, LI-COR, Lincoln, NB, USA), during the entire study period. During each sampling occasion, temperature, conductivity (Cond), pH and dissolved oxygen (DO; in percentage and mg/L) were measured with a multi-parameter probe. Nitrate nitrogen (N-NO₃⁻) and ammonia nitrogen (N-NH₄⁺) concentrations in the water column of the fields were provided by the Department of Agricultural, Forestry and Food Sciences of Turin, within the framework of the project supported by the Agritech National Research Center PNRR.

Statistical analyses

To compare the Chl-*a* values of benthic diatoms, we conducted a generalized linear mixed models (GLMM) analysis in R-Studio, using the *lme4* package, with the *glmer* function and a Gamma distribution (Bates et al. 2015; R Core Team 2022); we used fixed effects for the sites and times, and random effects for the pseudo-replicates conducted on each substrate. We then conducted

a post-hoc test with the *emmeans* function on R-Studio (*emmeans* package; Lenth 2024; R Core Team 2022). On the community data, we performed a multiple comparison test between the three Shannon–Wiener indices (*gls* function with the *nlme* package; R Core Team 2022) and Evenness values (*gls* test with *nlme* package; R Core Team 2022), with correlation parameter (*corAR1*; R core team 2022), after checking the distribution of data and the homogeneity of variances. To visually inspect for possible differences between the three sampling sites in terms of diatom community composition, we performed a principal coordinates analysis (PCoA), by using both the Bray–Curtis and Jaccard as similarity distance. Statistically significant differences detected with the PCoA were assessed by performing a PERMANOVA test with a multiple comparison by using the *RVAideMemoire* package on R-Studio (Herve 2023; R Core Team 2022). The indicator species analysis (ISA; De Caceres and Legendre 2009; R Core Team 2022) was performed to highlight the presence of statistically significant species within the two rice fields and water supply canal. On the functional analyses, we conducted a GLMM analysis to compare the guilds between the sites, as provided by OMNIDIA software (version 6.1.7). The analysis was conducted with the *glmmTMB* function (*glmmTMB* package; Brooks et al. 2017; R Core Team 2022), in R-Studio with fixed effects on sites and random effects for the times and beta distribution of the values. The post-hoc test was performed by using *emmeans* function (*emmeans* package; Lenth 2024; R Core Team 2022).

Results

Environmental characterization

The environmental parameters measured in the sampling sites, over the whole study period, are reported in Table 2; ESM Table S2 summarizes the temperature data. In the rice fields, the average daily water temperatures readings showed a decreasing trend during the study period, from 28.8 °C in R1 and 27.5 °C in R2 in June, to 21.3 °C in R1 and 20.8 °C in R2 in September. Similarly, the values of maximum temperature were achieved in June in the rice-growing environments (38 °C in R1 and 37.2 °C in R2; ESM Table S2), with a clear decrease in September (27.7 °C in R1 and 25.2 °C in R2; ESM Table S2). These trends were observed only in the rice fields and not in the water supply canal where the temperature was more constant during the study. The range of conductivity ($\mu\text{S}/\text{cm}$) values was almost completely overlapping between the two rice fields, while it was wider in the channel during the

Table 2 Summary table for pH, conductivity, dissolved oxygen, ammonia nitrogen and nitrate nitrogen values over the study period in the three sites

Environmental parameters ^a	Site ^b	Sampling occasions ^c									Mean ^d
		T1	20 July	T2	2 August	T3	T4	31 August	T5	T6	
pH	R1	NA	–	7.15	–	7.57	7.05	–	NA	NA	7.25
	R2	NA	–	NA	–	7.07	7.25	–	NA	NA	7.16
	C	7.79	–	7.95	–	7.94	7.00	–	8.05	7.59	7.72
DO (%)	R1	NA	–	37.9	–	75	9.2	–	NA	NA	40.7
	R2	NA	–	NA	–	17.5	36.8	–	NA	NA	27.2
	C	81	–	83	–	68.9	80.9	–	83.8	43.3	73.5
DO (mg/L)	R1	NA	–	3.3	–	7.08	0.9	–	NA	NA	3.76
	R2	NA	–	NA	–	1.37	2.96	–	NA	NA	2.16
	C	6.91	–	7.13	–	9.41	6.65	–	7.5	4.93	7.08
Conductivity (µS/cm)	R1	NA	–	271	–	330	318	–	NA	NA	306
	R2	NA	–	NA	–	291	337	–	NA	NA	314
	C	360	–	297	–	356	337	–	276	244	312
N–NH ₄ ⁺ (mg N/L)	R1	0.131	0.076	0.177	0.159	0.058	–	0.076	0.032	–	0.10
	R2	0.047	0.356	0.066	0.030	0.049	–	NA	0.039	–	0.10
N–NO ₃ ⁻ (mg N/L)	R1	0.059	0.023	0.030	0.026	0.217	–	0.039	0.115	–	0.07
	R2	0.043	0.045	0.020	0.219	0.019	–	0.015	0.015	–	0.05

NA Not available

^aDO, Dissolved oxygen; N–NH₄, ammonia nitrogen ; N–NO₃, nitrate nitrogen

^bR1, rice field 1; R2, rice field 2; C, canal

^cDates falling within a range of ± 1 days around times T were considered to correspond to T sampling occasions

^dMean values are based on the average of values at each site for the entire study period

study period. Average pH was 7.25 in R1 and 7.16 in R2 (Table 2). DO in the water column was markedly lower in the rice fields than in the water supply canal (average %DO R1 = 40.7%; average %DO R2 = 27.2%; average %DO canal = 73.5%). On the other hand, conductivity (with average values of 306 and 314 µS/cm in the rice fields and 312 µS/cm in the canal) and pH values (average values of 7.25 and 7.16 in the rice fields and 7.72 in the channel) did not show strong differences between the sites.

Chlorophyll analyses

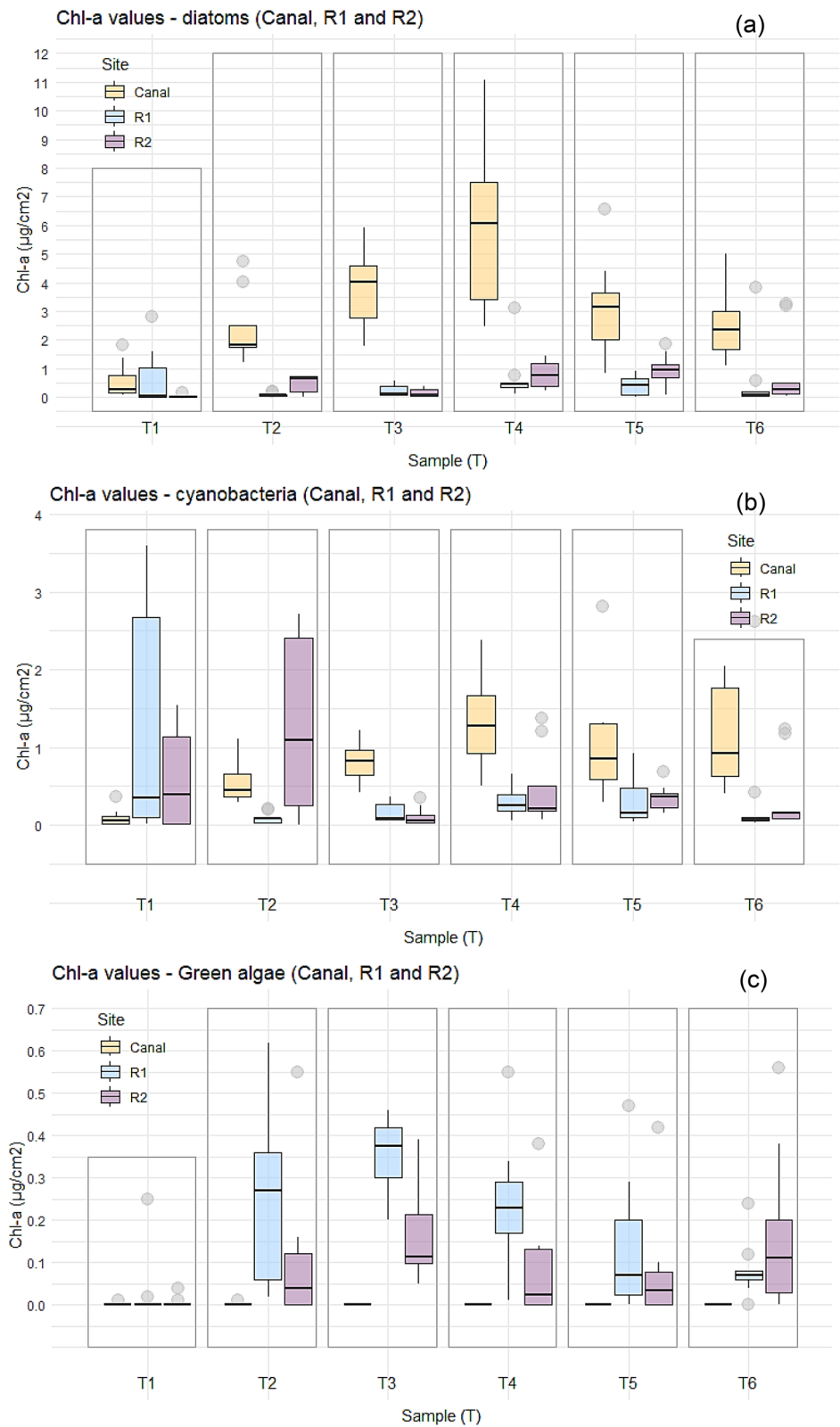
The Chl-*a* values of benthic diatoms differed significantly between the sites (ESM Table S3). Chl-*a* values were significantly different between R2 and the canal for the entire study period (emmeans test: estimate = 2.008; standard error [SE] = 0.229; *z*-ratio = 8.773; *p*-value < 0.001) and between R1 and the canal for the entire study period (emmeans test: estimate = 1.950; SE = 0.229; *z*-ratio = 8.519; *p*-value < 0.001). To the contrary, Chl-*a* values between the two rice fields did not differ significantly (emmeans test: estimate = 0.058; SE = 0.229; *z*-ratio = 0.254; *p*-value = 0.965). Specifically, the two rice fields showed significant differences only in four samplings (T1, T2, T4 and T6), out of the six conducted. In the water supply canal, benthic diatom

Chl-*a* values ranged from 0.07 to 11.07 µg/cm², with significant differences between the samples; the maximum peak was reached at T3, T4 and T5. In the water supply canal, a trend of growth, plateau and decrease in diatom Chl-*a* is evident, while this trend is less clear in the rice fields due to both lower Chl-*a* values and the drought events, which altered the community structure. Cyanobacteria (Fig. 3b) showed a bloom in the first two sampling occasions in R1 and R2, but not in the water supply canal. Lastly, green algae (Fig. 3c) maintained low values in all the three sampling sites, especially in the water supply canal, with values never exceeding the threshold of 0.01 µg/cm²; sporadic peaks were recorded in R1 at T2, T3 and T5, and in R2 at T3 and T6.

Diatom community

A total of 72 diatom species were recorded, 52 species in the water supply canal, 52 species in R1 and 51 species in R2. Specifically, we observed no notable differences in the average number of species colonizing the two rice fields (average number of species in R1 and R2 was 19 and 18, respectively) while there was a slightly higher number of species in the water supply canal but the average number of species was not significantly different in the samples C = 22).

Fig. 3 Boxplot of benthic chlorophyll-*a* (*Chl-a*) values for diatoms (a), cyanobacteria (b) and green algae (c) over the duration of the study at sampling times T1–T6. Extreme outliers for green algae were removed for better graphic resolution and with threshold factor=3. Data analyzed according to Wickham et al. 2019 and R Core Team 2022. *R1* Rice field 1, *R2* rice field 2



In terms of diversity, there was no significant difference between the three sites for the Shannon–Wiener C vs. $R1$: $SE=0.291$; t -value = 0.347; p -value = 0.730; C vs. $R2$: $SE=0.291$; t -value = -0.630; p -value = 0.531 and Evenness C vs. $R1$: $SE=0.028$; t -value = 1.044; p -value = 0.301; C vs. $R2$: $SE=0.028$; t -value = -0.416; p -value = 0.679) indices, although diversity was slightly lower in $R2$ when compared to $R1$ and the water supply channel (Shannon–Wiener average values: $R1=3.23$; $R2=2.93$; $C=3.15$; Evenness average values: $R1=0.76$; $R2=0.70$; $C=0.72$).

Taxonomical composition

Visual inspection of the PCoA ordination (Fig. 4a, b) depicted a clear difference in terms of taxonomic composition between the sampling sites, which was confirmed by the PERMANOVA. In detail, we observed a significant difference between the composition of the diatom community of the water supply canal when compared with that of the two rice fields (Bray–Curtis index: sum of squares = 4.226; $R^2=0.385$; $F=15.957$; $p=0.001$; Jaccard index: sum of squares = 3.004; $R^2=0.267$, $F=9.301$; $p=0.001$) using both the Bray–Curtis and Jaccard indices as similarity distance (Bray–Curtis: C vs. $R1$: $F=18.278$; $p=0.001$; $R^2=0.350$; C vs. $R2$: $F=25.024$; $p=0.001$; $R^2=0.424$; Jaccard: C vs. $R1$: $F=12.453$; $p=0.001$; $R^2=0.268$; C vs. $R2$: $F=13.806$; $p=0.001$; $R^2=0.289$). We also observed a significant difference between the two rice paddy communities when using

the Bray–Curtis distance ($p=0.004$), but not when using the Jaccard distance ($p=0.066$).

We identified a total of 32 indicator species within the three sites (ESM Table S4). Among the species characterizing the canal, *Karayevia clevei* (Grunow) Round e I. Bukhtiyarova, *Caloneis lancettula* (Schulz) Lange-Bertalot et Witkowski, *Planothidium frequentissimum* (Lange-Bertalot) Lange-Bertalot, *Amphora pediculus* (Kützing) Grunow and *Platessa hustedtii* (Krasske) Lange-Bertalot were predominant in terms of frequency and mean abundance. The most frequent and abundant characteristic species in the two rice fields were *Navicula veneta* Kutzing, *Nitzschia amphibia* Grunow, *Navicula trivialis* Lange-Bertalot, *Navicula rostellata* Kutzing and *Planothidium incuriatum* C.E. Wetzel, Van der Vijver and Ector.

Functional composition

In the canal, a low-profile and motile guild was dominant guild, being more frequent than high-profile and planktonic ones. In the rice-growing environments, a significant difference in species belonging to the motile guild occurred when compared with the water supply canal @ vs. $R1$: estimate = 1.233; $SE=0.266$; z -value = 4.635; $Pr(>|z|) < 0.001$; C vs. $R2$: estimate = 1.733; $SE=0.279$; z -value = 6.208; $Pr(>|z|) < 0.001$), with a median value of 69.9% in $R1$ (Emmeans test: estimate = -1.233; $SE=0.266$; z -ratio = -4.635; p -value < 0.001) and 90.7%

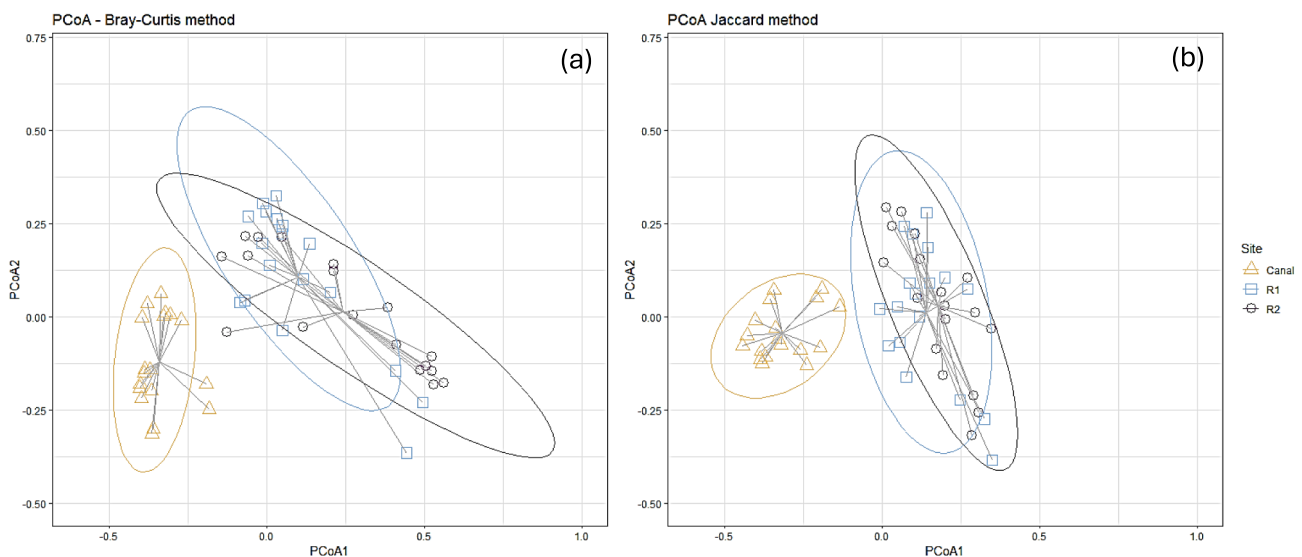


Fig. 4 Comparison of the distribution of communities when using the Bray–Curtis method (a) and using Jaccard's comparison method (b) in the canal (triangle), the first rice field ($R1$, square) and second rice

field ($R2$, circle). Data are analyzed according to Wickham et al. 2019 and R Core Team 2022. PCoA Principal coordinates analysis

in R2 (emmeans test: estimate = - 1.733; SE = 0.279; z -ratio = -6.208; $p < 0.001$). At the same time, there was a significant decrease in the low-profile guild of up to 22.4% in R1 (emmeans test: estimate = 1.388; SE = 0.288; z -ratio = 4.810; $p < 0.001$) and 7.8% in R2 (emmeans test: estimate = 1.869; SE = 0.302; z -ratio = 6.199; $p < 0.001$), compared to the water supply canal. In the canal, the motile and low-profile guilds achieved median percentage values slightly below 50%. Conversely, the high-profile and planktonic guilds showed low values over the whole study period, with an isolated peak of 9.5% for high-profile species in R1 (see ESM Fig. S5). These results confirm our previous hypothesis.

Discussion

Agriculture is responsible for severe chemical and hydro-morphological impacts on water environments, mainly due to chemical treatments, nutrients runoff, increases in suspended solids as well as changes in the water canal morphology and water flow discharge (Mateo-Sagasta et al. 2018). Moreover, in rice fields, a chemical-based strategy is considered to be the most effective solution for weed management and control, despite the high potential for risks and adverse effects on the environment and human health (Mateo-Sagasta 2018; Voccia et al. 2024). Despite the important role of diatoms in the ecosystems and their use as biological indicators in the assessment of the water resources, diatoms living in rice fields have been analyzed in only a few studies, mainly those conducted in Asia and, in particular, in Kuttunadu area (South India; Vijayan and Ray 2016), in mid-Taiwan (Lin et al. 2013) and in Northern Laos (between Thailand and Vietnam; Fujita and Ohtsuka 2005). To our knowledge, our study is the first to analyze diatom communities living in a harsh environment, such as that represented by rice fields, in Europe.

From a quantitative point of view, the analyses conducted on Chl-*a* showed a higher presence of diatoms in the water supply canal, compared to the rice fields. This result, as previously pointed out by authors of recent studies in rivers (Piano et al. 2017, 2019), could be explained by the affinity of diatoms to relatively stable environments without hydrological stress and water scarcity. During the present study, a decrease in diatom concentration was recorded at the second drought event occurring in the rice fields and mainly in R2, where the drought was more severe than in the nearby R1 site. It has already been observed that during the “lentification” process, diatoms can be replaced by cyanobacteria and green algae, facilitated by an increase in water temperature (Lengyel et al. 2023; Piano et al. 2017). A high water temperature could also be responsible for a reduction in DO level (Bona and Fenoglio 2021) and a

decrease in the optimal conditions for diatom survival. In the rice fields, the decrease in diatoms and the subsequent increase in green algae confirm our original hypothesis. Indeed, in the two rice paddy fields, green algae developed as a response to shallow water and high, bright radiation (Okada and Watanabe 2002; Piano et al. 2019). Solar radiation in these sites was limited by the rice plants, which reached a maximum vegetative peak of growth between the booting and heading stages (Angelini et al. 2008; Romani et al. 2023). The leaf area index (LAI) of the rice plants decreases in the last developmental stages (Maqueira-López et al. 2019; Prabhakar et al. 2024; Ribeiro et al. 2019), probably due to the translocation of nutrients from the leaf to the reproductive structure of the same plants (Maqueira-López et al. 2019). However, during the present study, this reduction was not visible on the shading effect of plants.

At the same time, the cyanobacteria showed a bloom that corresponded with an increase in dissolved nutrient levels in the site (nitrogen-containing urea; Chorus and Welker 2021; Martins et al. 2011; Post and Bullerjahn 2015). The decrease in cyanobacteria occurred at the first and second water removal/reintroduction dynamics from the rice fields (in R1 and R2, respectively), in a process of “self-purification” (Vagnetti et al. 2003; Vaideliene and Michailov 2008). It is likely that R1 was subject to a decrease in nutrient load as a consequence of water removal followed by submergence, which diluted nutrients. In comparison, in R2, the nutrient concentrations remained stable due to the hydraulic management of the fields. Indeed, the water mass flowing from R1 to R2 also transported the nutrients dissolved in it. For this reason, in R2 the purification process occurred during the second water removal/reintroduction dynamics (T2; Vagnetti et al. 2003; Vaideliene and Michailov 2008), with a consequent reduction in cyanobacteria (Chorus and Welker 2021; Martins et al. 2011; Post and Bullerjahn 2015).

Regarding species richness and biodiversity, we found no significant differences among the studied sites; however, we did find that R1 had slightly higher Evenness and Shannon–Wiener values than the water supply canal and R2. Environmental conditions were indirectly related to the increased disturbance affecting the sites and could be ascribable to the intermediate disturbance theory, especially in R1 (Catford et al. 2012; Grime 1973).

On the other hand, in terms of taxonomic and functional composition, the differences between diatom communities colonizing the water supply canal and the two rice paddy fields were significant, as revealed by the statistical analysis (PERMANOVA). Species found in rice fields usually show a higher tolerance to high levels of dissolved organic compounds in the water, to high levels of trophic substances and to strong anthropogenic pollution, as well as to physical impacts (Bey and Ector 2013) in comparison to species found in water supply canals. Even though R1 and R2

mainly sheltered the same species, significant differences in the relative proportions of taxa were observed (see results obtained by the PCoA performed with the Jaccard distance and Bray–Curtis' method, respectively). These results could result from the hydrological impact, which mainly affected R2, as evidenced by the greater number of drought events. Therefore, in the present study, species colonizing rice fields were not limited by dispersal, and the environment played a pivotal role in shaping community composition in terms of relative abundance.

Based on the ISA, *A. pediculus*, *P. frequentissimum*, *C. lancettula*, *K. clevei* and *P. hustedtii* (ESM Table S4) were highlighted as species that characterized the water the supply canal. These species are common in environments with a medium to low presence of organic pollution (Bey and Ector 2013), which is consistent with the characteristics found in the water supply canal studied in the present study, as confirmed by the high values of DO and low organic pollution. The characterizing species found in the two rice fields were *N. veneta*, *P. incuriatum*, *N. trivialis*, *N. rostellata* and *N. amphibia*, which have already been reported in rice-growing environments in mid-Taiwan and in Northern Laos (Fujita and Ohtsuka 2005; Lin et al. 2013). More specifically, *Nitzschia* spp., and *Pinnularia* spp. were the most frequent tolerant genera found in previous studies (Fujita and Ohtsuka 2005) together with *Navicula* spp. (Lin et al. 2013; Vijayan and Ray 2016) and along with several species of cyanobacteria and green algae (Lin et al. 2013; Su Jing et al. 2017). All of the requirements of these species are coherent with the environmental characteristics found at the R1 and R2 sites, as well as with the high level of ammonia nitrogen measured according to I to IV level sensu MD 260/2010 (Ministry of the Environment and Protection of the Land and Sea (2010); Bey and Ector 2013). Indeed, *N. veneta*, *N. amphibia*, *N. trivialis* and *N. rostellata* are considered cosmopolitan and tolerant species (Bey and Ector 2013). Furthermore, *N. veneta* has been found in several European sites, such as thermal springs in Italy (Moro et al. 2010), some water bodies in Germany (Bruder and Medlin 2007) and in Sardinia (Italy). In this latter location, *N. veneta* was considered as an alkalophilic, halophilic and α -mesosaprobic species that regularly occurred in moist places (Lai et al. 2016) and which was tolerant to organic compounds and industrial discharges (Bey and Ector 2013). *Planothidium incuriatum* was recently described as a new species, separated from *Planothidium biporumum* by Wetzel et al. (2013), and differs from the latter in having more rows of areole per stria in the raphe valve and slightly smaller, more acutely rounded or rostrate poles (Wetzel et al. 2013). Ecologically, there are still many gaps in knowledge on its spatial distribution and ecological requirements, but it is considered an oligotrophic species, in contrast with the environmental features characterizing the sites analyzed in

the present study. Studies on *P. incuriatum* are still scarce and restricted to South America (Chiossi et al. 2021; da Silva et al. 2017; Mora et al. 2015); this species has been mainly found in the Rio Laja Basin (Brazil), although it was not among the dominant species, in a site characterized by a semi-arid climate, average temperature values (around 17 °C) and altitude between 1850 and 2850 m a.s.l. (Mora et al. 2015). This species was also found in the Rio Itajiai in Brazil (in 16 out of 20 sites) by Chiossi et al. (2021), and in the Arroio Grande Basin (Brazil; in 11 out of 13 samples) by da Silva et al. (2017). Although considered a cosmopolitan species (Mora et al. 2015; Wetzel et al. 2013), nowadays, there are no published records of this species in the Italian watersheds.

The functional analysis highlighted the motile species as the characterizing guild found in both rice fields. On the other hand, in the water supply canal we found a co-dominance of low-profile and motile guilds. The great variability of environmental conditions, as well as the presence of multiple impacts in rice-growing environments (especially in R2), led to an increase in species belonging to the tolerant guild (i.e. the motile guild; Passy 2007). At the same time, the dominance of motile guild can be also related to the thickness of the biofilm during the study and the Chl-*a* values measured on it. Indeed, the thickness and the distribution of the biofilm growing in the two rice fields were strongly variable over time, allowing the formation of patchy refuge zones on the substrate surface, which in turn enables the survival of those species able to move and to reach the most suitable micro-niche available (Sabater et al. 2016). These micro-niches create different conditions in terms of water temperature, bright light intensity, humidity and tolerance to drought events. The ability to move favored some species by providing an ecological advantage to these species while limiting the sensitive species (i.e. low-profile; Passy 2007). Moreover, motile diatoms are generally epipellic, living in association with fine sediments, a condition that characterized the rice-growing environments more than the water supply canal. On the other hand, the high-profile and planktonic guilds showed different ecological needs compared to the characteristics found in the rice-growing sites, and for this reason they were scarce, or completely absent in the rice field samples (Passy 2007), confirming our initial assumption on the dominance of tolerant guilds.

The methods used in the present study highlights the usefulness of studying the diatom community for the assessment and maintenance of correct biological, chemical and physical characteristics of rice field sites. Enhancement of animal and plant conservation in this agricultural environment allows the achievement of the concept of “agroecology” (Benzin 1925); also, the European Union CAP and the 17 UN goals of sustainable development

support the need of an efficient management of natural resources. Furthermore, periphyton and diatoms have been often considered valid tools to detect (Duong et al. 2008, 2010) and to decrease (Lu et al. 2020; Wang et al. 2023) the concentration of cadmium within an aquatic environment, along with other species (Zhao and Huang 2018), and to reduce the potential danger derived from its accumulation in the final cultivation product (Mateo-Sagasta 2018; Zhao et al. 2010). Ultimately, this research represents a first study of diatom communities in a rice field environment, within a limited site. Moreover, linkage between sites is a traditional component of the hydraulic organization of rice fields in Northern Italy. For this reason, this analysis represents a good starting point for more in-depth studies, although it is affected by specific conditions and requirements. However, a more detailed analysis with a longer period of study and a larger number of environmental and ecological variables measured is desirable in future studies to better generalize the results obtained. These will allow an improvement in our understanding of the existing relationships between community composition and environmental characteristics of the rice paddy field sites. Moreover, the potential role of periphyton is clear, although future research is needed to study their importance in rice paddy fields as a promising bio-based solution for reducing nutrients and heavy metal concentrations in water and soil, an issue of great importance for food safety and human health as well as for mitigating the negative effects of eutrophication in these types of agricultural environments.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest No conflicts of interest are present.

Ethical approval The research did not involve human or animal subjects.

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