

Diatom assemblages colonizing floating photovoltaic floaters are distinct from those in benthic and pelagic compartments of gravel pit lakes

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Abstract – The development of novel renewable energy technologies, such as floating photovoltaics (FPVs), is expanding, but their environmental consequences remain understudied. FPVs physically alter freshwater ecosystems by limiting light and wind penetration at the lake surface, while providing new substrates for biofilm development, including diatoms. Diatoms are essential to primary production and carbon cycling in aquatic systems, however, the composition of diatom assemblages on FPV structures remains unexplored. This study aimed to characterise the diatom assemblages colonising FPV floaters and compare them with those in the pelagic and benthic compartments of gravel pit lakes. Results showed significantly lower taxonomic richness and diversity on FPV floaters, followed by pelagic assemblages, with the highest values observed in benthic habitats. Community composition also differed significantly between the three compartments. *Community composition also differed significantly* across all habitats, but its dominance was particularly pronounced on FPV floaters (72%), compared to 54% and 32% in the benthic and pelagic compartments, respectively. As a low-profile, disturbance-tolerant taxon, *Achnanthes* may thrive in low-light conditions created by FPV shading. It can also serve as a good water quality indicator, while baseline studies are needed to assess whether its dominance on FPVs reflects positive conditions for gravel pit lakes. By creating novel artificial habitats in the pelagic zone, FPVs can modify the patterns of primary production and pelagic-benthic coupling that remain to be investigated.

Keywords: Gravel pit lakes / renewable energy / artificial substrates / biofilm / community structure

1 Introduction

In response to the global climate crisis, governments worldwide are shifting towards renewable energy sources to decarbonise their energy production (Spillias *et al.*, 2020; Olabi and Abdelkareem, 2022). Floating photovoltaic (FPV) systems, a recent innovation in the solar energy sector that consists of photovoltaic panels mounted on floating structures made from high-density polyethylene and anchored on water bodies such as seas, reservoirs, gravel pit lakes, and ponds, have recently emerged as a novel technology for producing decarbonised energy (Sahu *et al.*, 2016; Gorjian *et al.*, 2021). These systems have been reported to offer advantages over land-based installations, including enhanced efficiency, land preservation, and evaporation reduction (Sahu *et al.*, 2016; Farrar *et al.*, 2022). FPV deployment is increasing globally at an exponential rate

(Gorjian *et al.*, 2021), outpacing the scientific research needed to understand their environmental impacts. Recent syntheses have highlighted the scarcity of empirical studies on the ecological and environmental effects of FPV on freshwater ecosystems (Nobre *et al.*, 2023), particularly their potential impacts on aquatic organisms (Oliveira *et al.*, 2024). Consequently, FPVs are currently recognised as an growing concern for global biodiversity conservation (Sutherland *et al.*, 2022).

In freshwater environments, FPV systems are typically installed as one or multiple floating pontoons, covering significant portions of the lakes with an average global coverage of 34.2% (± 22.0 SD) (Nobre *et al.*, 2024). These installations can significantly alter wind intensity and light arrival, directly and indirectly affecting multiple environmental parameters such as water temperature, water column stability, nutrients resuspension and concentration of dissolved oxygen (Exley *et al.*, 2021; Wang *et al.*, 2022; Nobre *et al.*, 2023). Additionally, FPV floaters represent novel artificial structures in the aquatic ecosystem providing submerged

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surfaces that have the potential to support biofilm development and create habitat for sessile species within the pelagic zone (de Lima *et al.*, 2021). Diatoms (Bacillariophyceae), a diverse group of eukaryotic, siliceous algae, are especially responsive to these environmental changes due to their short life cycles and narrow tolerance ranges in many species (Weckstrom *et al.*, 1997; Soininen, 2007; Soininen and Teittinen, 2019). This sensitivity has made diatoms as valuable bioindicators of water quality and ecosystem health (Winter and Duthie, 2000; Stenger-Kovács *et al.*, 2007). In particular, diatom assemblages are used throughout the world by the application of diatom indices (Kelly and Whitton, 1995; Pan *et al.*, 1996; Potapova and Charles, 2007), and trait-based multimetric diatom indices (Riatio *et al.*, 2022).

Diatom assemblages have traditionally been considered cosmopolitan organisms, aligning with the concept that “everything is everywhere, but the environment selects” (Soininen, 2007; Becking and Canfield, 2015; Soininen and Teittinen, 2019). This suggests that their spatial distribution patterns are primarily shaped by local environmental conditions, including light and nutrient availability as well as substratum quality and quantity (Soininen, 2007; Yang and Flower, 2012; Cantonati and Lowe, 2014; Nemes-Kókai *et al.*, 2024). Diatoms’ life strategies are typically related to their growth habitat, including planktonic, and periphytic functional groups (Rühland *et al.*, 2015). For instance, planktonic algae have cell shapes and sizes that are adapted to floatation, while periphytic algae usually have traits such as the development of mucilaginous stalks that allow them to attach to substrates like rocks, plants, or sediments (Dunck *et al.*, 2013). Diatoms often dominate planktonic and benthic microalgal assemblages, contributing significantly to ecosystem services related to photosynthesis, such as oxygen production, while also driving primary production, supporting carbon cycling, and serving as a basal resource for higher trophic levels, thereby sustaining freshwater food webs (Rühland *et al.*, 2015; B-Béres *et al.*, 2023). Given their sensitivity to environmental changes and their crucial role in ecosystem functioning and health, it is essential to determine which diatom assemblages colonise FPV floaters, as these could substantially impact ecosystem functioning and carbon dynamics in lakes with FPV installations.

In this study, we aimed to analyse the structure and composition of diatom assemblages on FPV floaters and to compare them with pelagic and benthic compartments of artificial freshwater lakes, exploring the potential influence of compartment type and seasonal variation on diatom community patterns. We predicted that the diatom community on FPV floaters are likely to represent a hybrid assemblage of pelagic and benthic diatoms, shaped by both their spatial position in the water column and their ability to colonise and persist on substrates. Indeed, diatom community composition is often influenced by spatial autocorrelation (Passy, 2007), meaning that proximity to the pelagic zone should result in similarities to open-water, free-floating diatom assemblages. In addition, due to functional traits such as the ability to attach to surfaces, these FPV-associated diatom assemblages may also resemble benthic or periphytic assemblages typically found on natural substrates like pebbles.

2 Methods

2.1 Study area

The study was conducted in three gravel pit lakes equipped with FPVs located in the Garonne River floodplain (43°18'11"N, 1°11'14"E), southwestern France (Fig. 1). These lakes have similar general hydromorphological and environmental characteristics, including similar surface areas (0.12 km², 0.13 km² and 0.15 km², mean surface area 0.13 km², ±0.02 SD, Table 1), and experience similar climatic conditions due to their geographical proximity. These lakes are hydrologically disconnected from each other and from the hydrological network (Zhao *et al.*, 2016). In the studied gravel pit lakes, FPV plants were installed between November 2021 and March 2022, covering 40.3%, 51.5%, and 55.5% (mean 49.1% ± 7.9 SD) of the lake area, respectively.

2.2 Sampling of diatom assemblages

Diatoms were sampled every three months (March, June, September and December) from June 2022 (summer) to March 2024 (spring) in the three studied sites. Specifically, in each lake, diatoms were sampled in the benthic and pelagic compartments and on the FPV floaters (FPV compartment). The sampling methodology was designed to obtain semi-quantitative data (relative abundance) to assess the composition of diatom assemblages in each compartment. Pelagic diatoms were sampled in the deepest part of each lake, which also corresponds approximately to the center of the FPV plant. Sampling consisted of filtering water with a 10 µm mesh plankton net, a mesh size capable of collecting the smallest known diatom taxa. The net was submerged a few meters below the surface and gently raised to collect diatoms throughout the water column. The filtration of a large volume of water with a smaller mesh size (e.g. 5 µm) would have been impractical due to the rapid clogging of the net by planktonic organisms, particularly Cyanophyceae during their growth periods. Filtration continued until the net became clogged and could no longer effectively filter water. Benthic diatoms were sampled on pebbles collected along the lake shoreline (depth of approximately 20-50 cm) that were brushed with a toothbrush to gather the biofilm. To obtain a representative sample of the benthic community, including organisms sensitive to sunlight and water mixing, three pebbles were sampled from three different points in the littoral zone. All the collected biofilms were pooled into an integrative sample. Regarding FPV floaters, diatoms were collected on a floater (identical to those used in the FPV plants) that was installed in the central part of the FPV platform using ropes. The sampling protocol involved removing the floater, flipping it upside down, brushing off the biofilm with a toothbrush in distinct areas of the floater, and collecting the biofilm into a plastic container. All sampled surfaces had been installed in the lakes for at least three months prior to the first sampling to allow time for biofilm development. In total, eight samples per compartment and lake were collected. For each sample, the resulting material was subsequently concentrated and stored in a 40ml flask, and fixed with 90% ethanol.



Fig. 1. Map of the study area situated in the Garonne floodplain, southwest France. A, B, and C are the three studied gravel pit lakes equipped with FPVs. FPV power plants were developed by Urbasolar.

Table 1. Characterization of the studied lakes. Physico-chemical parameter values represent averages based on eight quarterly samples collected from June 2022 (summer) to March 2024 (spring) across the three study lakes.

Parameter	Mean \pm SD (n)
Surface area (km ²)	0.13 \pm 0.02 (3)
Maximal depth (m)	5.27 \pm 0.83 (3)
Perimeter (m)	2115 \pm 494.74 (3)
Altitude (m)	211.45 \pm 4.73 (3)
Secchi (cm)	261.12 \pm 102.5 (24)
pH	8.13 \pm 0.33 (24)
Conductivity (μ S/cm ²)	390.39 \pm 98.00 (24)
Turbidity (NTU)	1.95 \pm 1.08 (21)
Total Phosphorus (mg/L)	0.015 \pm 0.008 (20)
Total Nitrogen (mg/L)	1.93 \pm 1.24 (23)

2.3 Diatom preparation and observation

In the laboratory, samples were prepared according to the BDI NF T90-354 standard used for river assessment in France (AFNOR, 2016). For each sample, a subsample (2ml, approximately) was oxidised in boiling hydrogen peroxide 30% and hydrochloric acid. All traces of hydrochloric acid were removed through successive rinse cycles with deionised water. To obtain permanent slides, aliquots of the oxidised samples were dried onto cover slips and fixed on microscope slides using a high-refractive index resin (Naphrax[®],

R.I. = 1.7). Slide observations were performed using an Olympus BX51 microscope equipped with Differential Interference Contrast optics (Nomarski) at 1000X magnification, where a minimum of 400 diatom valves were counted on each slide. The identification of diatoms at the species level followed the Freshwater flora of Central Europe handbooks (Süßwasserflora von Mitteleuropa (Krammer and Lange-Bertalot, 1991), the collection Diatoms of Europe 2000-2020 Lange-Bertalot *et al.* (2017)). In this study, genus-level taxonomic resolution was used as it allows capturing relevant ecological information, such as life forms and functional traits, (Tudesque *et al.*, 2012, 2019; Marcel *et al.*, 2017), which are essential for understanding community patterns, providing sufficient information for analyzing the structure and composition of diatom assemblages between compartments. Relative abundances were calculated for each taxon. Genera richness (hereafter referred to as taxonomic richness), Shannon diversity index (H') and Pielou's evenness (J') were calculated in R (R Core Team, 2023) using the *vegan* package (Oksanen *et al.*, 2001). Diatom analysis related to community composition was performed on the taxa with $\geq 5\%$ relative abundances on at least one sampling occasion. The codes for Diatoms genera were assigned according to the Omnidia software (Lecointe *et al.*, 1993).

2.4 Statistical analysis

First, linear mixed-effects models (LMMs) were used to test differences in diatom community structure (taxonomic richness, Shannon index, and Pielou's evenness) between pelagic, benthic, and FPV compartments, accounting for

Table 2. Codes and denomination of the main genera diatom observed in the studied lakes in the three habitats (>5% of relative abundance).

Code	Genus
ACHD	<i>Achnanthydium</i> F,T, Kützing
AMPH	<i>Amphora</i> C,G, Ehrenberg Ex F,T, Kützing
ASTE	<i>Asterionella</i> A,H, Hassall
BRAC	<i>Brachysira</i> F,T, Kützing
COCO	<i>Cocconeis</i> C,G, Ehrenberg
DISC	<i>Discostella</i> Houk Et Klee
ENCP	<i>Encyonopsis</i> Krammer
FRAG	<i>Fragilaria</i> H,C, Lyngbye
NAVI	<i>Navicula</i> J,B,M, Bory De St, Vincent
NITZ	<i>Nitzschia</i> A,H, Hassall
PANT	<i>Pantocsekiella</i> K,T, Kiss Et Ács
PSST	<i>Pseudostaurosira</i> (Grunow) D,M, Williams & F,E, Round
AULA	<i>Aulacoseira</i> G,H,K, Thwaites
CYMB	<i>Cymbella</i> C,Agardh
GOMP	<i>Gomphonema</i> C,G, Ehrenberg
LIND	<i>Lindavia</i> (Schütt) De Toni & Forti
PUNC	<i>Punctastriata</i> D,M, Williams & F,E, Round
STRS	<i>Staurosira</i> (C,G, Ehrenberg) D,M, Williams & F,E, Round
ENCY	<i>Encyonema</i> F,T, Kützing
GPNL	<i>Gomphonella</i> Rabenhorst
ULNA	<i>Ulnaria</i> Compère
CBPL	<i>Cymbopleura</i> (Krammer) Krammer
EUNO	<i>Eunotia</i> C,G, Ehrenberg

seasonal variation across different periods. Periods were defined as cold season (samples from December and March) and warm season (samples from June and September). This grouping was chosen to simplify the interaction between habitat and season, which could increase the risk of model overfitting, while ensuring a meaningful ecological interpretation of key drivers of seasonal variation in diatom community dynamics, such as light and temperature. Compartment, period and their interaction were used as a fixed effect, while lake identity and sampling year were used as random effects. Lake identity was included as a random effect to account for natural variability among sites, while the random effect of year was used to account for interannual fluctuations in environmental conditions that may influence diatom community patterns. The significance of the fixed effects and their interaction was tested using the Anova function from the *car* R package (Fox and Weisberg, 2019). Post hoc pairwise comparisons were performed to assess statistical differences across compartments and periods.

Differences in community composition between habitat types and their interaction with periods were assessed using a permutational analysis of variance (PERMANOVA) based on Bray-Curtis distances. Pairwise comparisons were further conducted to evaluate which combinations significantly differed from each other. To determine which taxa most contributed to the observed differences between compartments

and their interaction with periods, a similarity percentage (SIMPER) analysis was performed (Clarke, 1993). Additionally, non-metric multidimensional scaling (NMDS) was conducted based on Bray-Curtis dissimilarity to visualise diatom community composition in each habitat type and period combination. Prior to these analyses, abundance data were Hellinger transformed to limit the influence of dominant species. Community composition analyses were carried out in R version 4.3.1 (R Core Team, 2023) using the *adonis2*, *simper*, and *metaMDS* functions from the *vegan* package (Oksanen *et al.*, 2001).

3 Results

A total of 220 species belonging to 62 genera were identified in benthic, pelagic and FPV compartments. Among these genera, 23 exhibited relative abundances $\geq 5\%$ in at least one sampling occasion (Fig. 2, Tab. 2), collectively accounting for 98.71% of the total observed abundance of diatoms. The three compartments shared 21 genera. While *Asterionella* was found exclusively in benthic and pelagic compartments, *Gomphonella* was restricted to the benthic compartment. Overall, taxonomic richness, Shannon diversity, and evenness were significantly affected by the compartment type, but no significant effects were observed for the period or the interaction between compartment and period. Taxonomic richness differed significantly between the three compartments ($\chi^2 = 65.86$, $df = 2$, $p < 0.001$, Fig. 3a). Fixed effects explained 37% of the variance (LMM, marginal $R^2 = 0.37$), while random effects (season and site) contributed an additional 26% (LMM, conditional $R^2 = 0.63$). Taxonomic richness was highest in the benthic compartment (mean 35.30 ± 11.03 SD), followed by the pelagic habitat (mean 26.50 ± 10.10 SD), with the lowest richness observed on the FPV floaters (mean 17.12 ± 5.01 SD) (post-hoc pairwise comparisons, $p < 0.001$, Table S1, Fig. 3a). Shannon diversity also significantly differed between compartments ($\chi^2 = 50.80$, $df = 2$, $p < 0.001$, LMM, marginal $R^2 = 0.40$, conditional $R^2 = 0.48$), with the highest diversity observed in the benthic compartment (mean 3.24 ± 0.74 SD), followed by pelagic compartment (mean 2.24 ± 0.91 SD) and the FPV floaters (mean 1.68 ± 0.71 SD) (post-hoc pairwise comparisons, $p < 0.001$, Table S2, Fig. 3b). Finally, equitability was significantly affected by compartment ($\chi^2 = 27.86$, $df = 2$, $p < 0.001$, LMM, marginal $R^2 = 0.30$), being higher in the benthic compartment (mean 0.63 ± 0.11 SD) compared to the other two compartments (mean 0.47 ± 0.15 SD and mean 0.41 ± 0.17 SD for pelagic and FPV assemblages, respectively, Fig. 3c). There was no significant difference in equitability between FPV and pelagic compartments (post-hoc pairwise comparisons, $p = 0.33$, Table S3).

Community composition was significantly affected by period (PERMANOVA, $F = 2.38$, $R^2 = 0.02$, $df = 1$, $p = 0.03$), habitat (PERMANOVA, $F = 21.03$, $R^2 = 0.37$, $df = 2$, $p < 0.001$), and their interaction (PERMANOVA, $F = 2.15$, $R^2 = 0.04$, $df = 2$, $p = 0.02$). Pairwise PERMANOVA revealed that within the same compartment, only pelagic assemblages differed between warm and cold periods ($R^2 = 0.17$, $p = 0.02$), while within the same period, all compartments were different from each other (Table S4), as observed in the NMDS plot (Fig. 4). Over the study period, *Achnanthydium* presented the highest

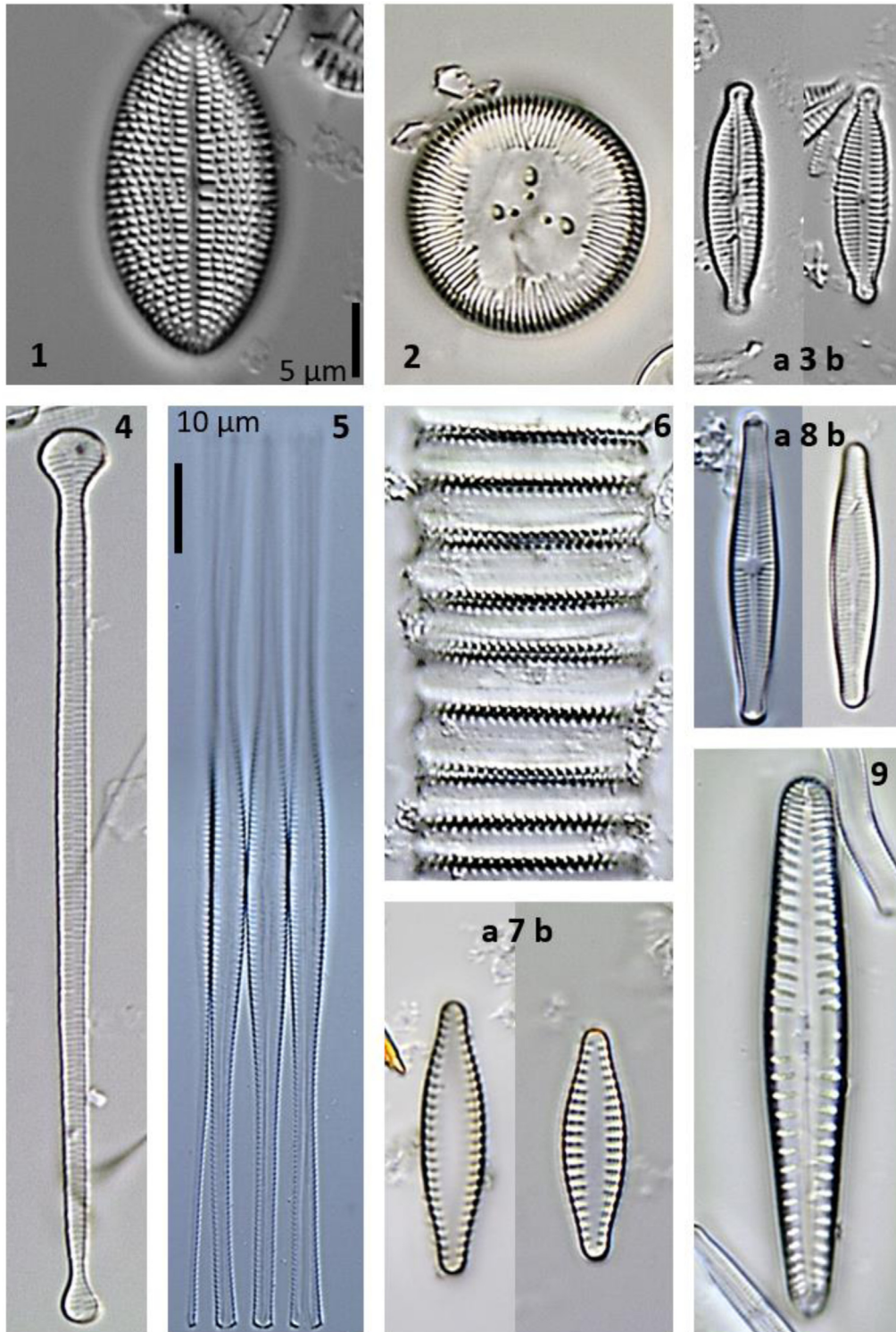


Fig. 2. Main genera of diatoms found in the benthic, pelagic, and FPV habitats observed using light microscopy (Tab. 2). 1. *Cocconeis* Ehrenberg; 2. *Pantocsekiella* K.T. Kiss & Ács; 3a & b. *Encyonopsis* Krammer; 4. *Asterionella* Hassall; 5. *Fragilaria* Lyngbye; 6. *Pseudostaurosira* Williams & Round. Colony in girdle view; 7a & b. *Pseudostaurosira* Williams et Round. Girdle view; 8a & b. *Achnanthyidium* Kützing, raphe valve and rapheless valve; 9. *Gomphonema* Ehrenberg. All photos were from FPV installations in the studied lakes.

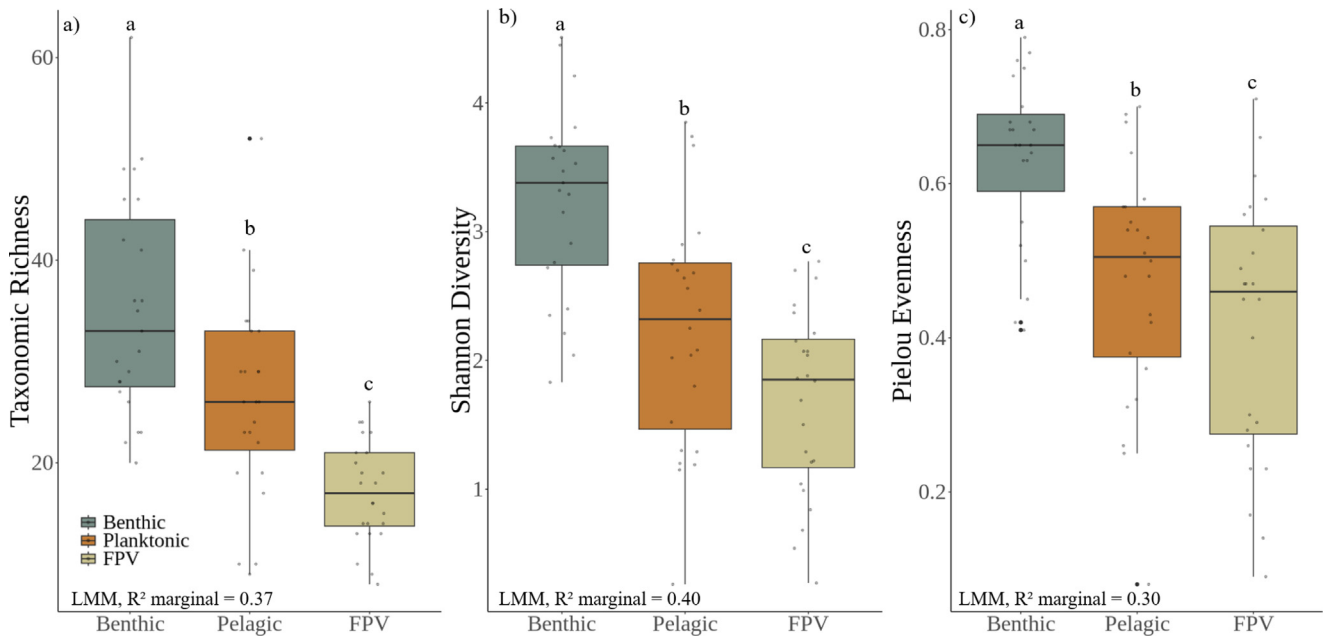


Fig. 3. (a) Taxonomic richness, (b) Shannon diversity and (c) Pielou's evenness index in the benthic, pelagic and FPV habitats. Different letters indicate significant differences ($p < 0.05$) based on post hoc pairwise comparisons.

relative abundance on FPVs ($72\% \pm 24$ SD), followed by *Gomphonema* ($12\% \pm 14$ SD) and *Encyonopsis* ($6\% \pm 14$ SD). Together, these genera accounted for 90% of the total diatom abundance on the FPV floaters. *Achnanthydium* was also dominant in benthic compartments ($54\% \pm 16$ SD), followed by *Encyonopsis* ($12\% \pm 9$ SD) and *Pseudostaurosira* ($8\% \pm 8$ SD) (Table S5). In the pelagic compartment, during the cold season, *Pantocsekiella* ($27\% \pm 28$ SD), *Asterionella* ($24\% \pm 34$ SD), *Achnanthydium* ($19\% \pm 20$ SD) and *Fragilaria* ($16\% \pm 28$ SD), together, represented 86% of genera relative abundance, while the warm season was mainly composed by *Achnanthydium* ($45\% \pm 27$ SD), *Pantocsekiella* ($21\% \pm 26$ SD) and *Asterionella* ($10\% \pm 23$ SD) (Fig. 5).

The SIMPER analysis showed that the taxa that were highly abundant exclusively in one of the compartments contributed the most to the differences in community composition between the different compartments. Overall, dissimilarities between pelagic and benthic assemblages were driven by *Pantocsekiella*, *Achnanthydium*, *Asterionella*, and *Encyonopsis*. *Achnanthydium*, *Pantocsekiella*, *Asterionella*, and *Gomphonema* were responsible for the main differences between pelagic and FPV compartments. *Encyonopsis*, *Pseudostaurosira*, *Gomphonema*, and *Achnanthydium* drove the difference between FPV and benthic compartments (Tab. 3). The observed seasonal differences within the pelagic compartment were driven by *Asterionella*, *Achnanthydium*, *Pantocsekiella*, and *Fragilaria*.

4 Discussion

Our results showed that FPV floaters supported diatom assemblages with lower taxonomic richness and diversity compared to the assemblages observed in the benthic and pelagic compartments of the lakes. Although nearly all diatom genera were observed across the three compartments,

community composition assessed as the relative abundance of the dominant groups ($>5\%$) significantly differs between the benthic, pelagic, and FPV compartments.

The observed pattern of lower diversity in FPVs was mainly driven by the dominance of the genus *Achnanthydium*, which accounted for 72% of the total diatom abundance on FPV floaters across the study period. Similarly, a study using submerged artificial substrata found that, after one month of exposition, the substrate was composed mainly of benthic diatoms belonging to *Achnanthydium* and *Gomphonema* genera, although some planktonic organisms were also present (Jöbgen *et al.*, 2004). Changes in substrate properties and availability, as well as changes in environmental parameters such as light, nutrients, and temperature, which can be influenced by the introduction of artificial structures like the FPVs (Exley *et al.*, 2021; Nobre *et al.*, 2025), are known to shape the structure and composition of pelagic and benthic primary producers assemblages in freshwater ecosystems (Nemes-Kókai *et al.*, 2024). The successful establishment of diatom assemblages in any given habitat depends on factors such as colonization ability, morphological traits, and ecological adaptations, including tolerance to disturbances and low resource availability (Passy, 2007; Rimet and Bouchez, 2012; B-Béres *et al.*, 2016). Light limitation due to floater and panels' shading, for example, can act as an environmental filter favoring species with particular functional traits optimised for low-light conditions (Reynolds, 1998; Finkel *et al.*, 2009; Exley *et al.*, 2022). The genus *Achnanthydium* includes pioneer species that can colonise substrates more rapidly than other taxa and are small in size (Oemke and Burton, 1986; Peszek *et al.*, 2021). They are typically associated with benthic habitats, having the ability to adhere to substrates via mucilaginous stalks or pads (Rimet and Bouchez, 2012). This taxon belongs within the low-profile guild, characterised by tolerance to low resources, including

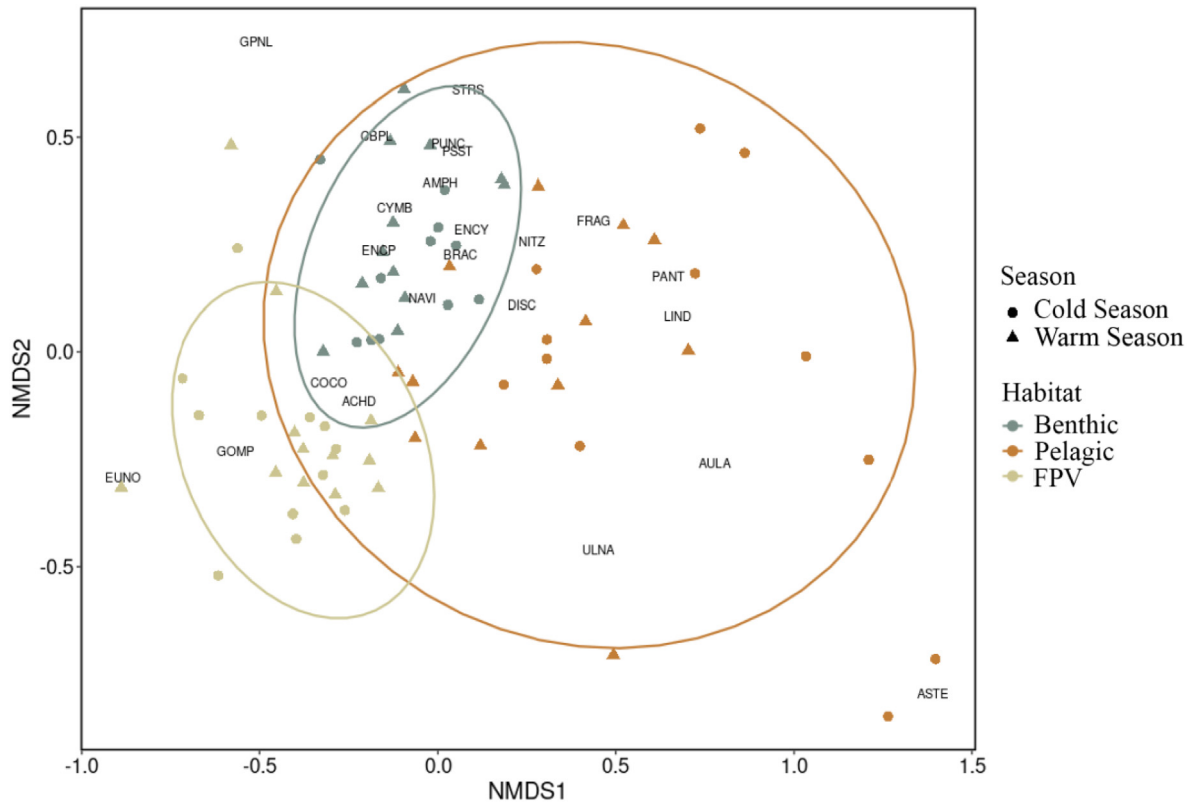


Fig. 4. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity of the diatom assemblages (stress = 0.15). Point shapes indicate different periods (warm and cold seasons). Compartments (benthic, pelagic, and FPV) are distinguished by different colors. Ellipses represent 95% confidence intervals (CI) around the centroids for each compartment.

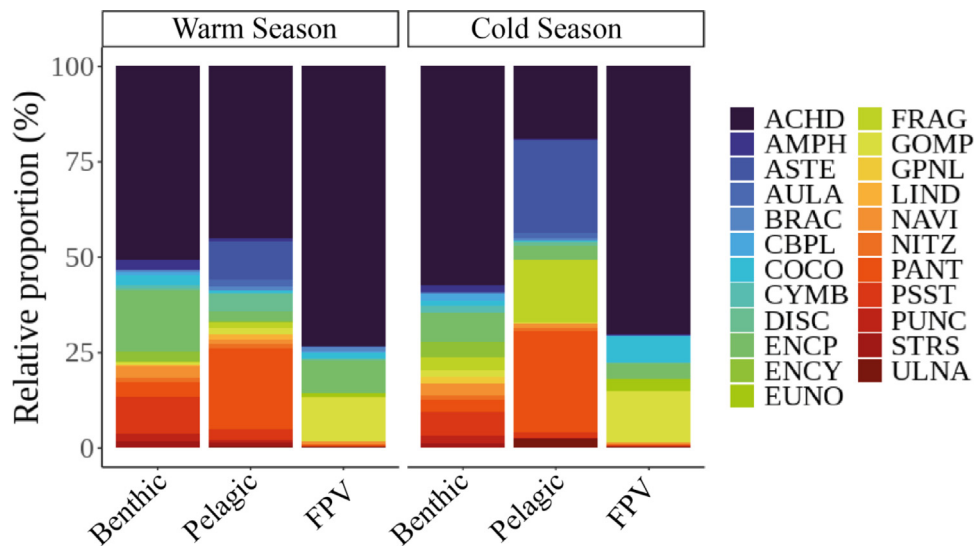


Fig. 5. Relative abundance (%) of each diatom genus in the benthic, pelagic, and FPV habitats across cold and warm periods.

low light and high tolerance to physical disturbances (Passy, 2007; B-Béres *et al.*, 2016; Cibils-Martina *et al.*, 2017). Additionally, the abundance of *Achnantheidium* is often negatively correlated with dissolved oxygen concentrations (B-Béres *et al.*, 2016). FPVs are expected to reduce light penetration and decrease dissolved oxygen concentrations in the water column due to a combination of factors, including

reduced primary production and lower gas exchange at the air-water interface (Exley *et al.*, 2021; Wang *et al.*, 2022; Nobre *et al.*, 2023). These environmental conditions likely favored the establishment of a biofilm dominated by these diatoms.

Lower diversity indices on FPV floaters can also be related to the physical characteristics of the FPV floaters. Although floaters act as artificial substrates that can provide a new

Table 3. Genera making greater contribution to compositional differences between habitats identified using SIMPER analysis.

Compartment	Genus	Cumulative contribution (%)
Pelagic warm vs. Benthic warm	PANT	12.9
	ENCP	23.1
	ACHD	31.5
	PSST	39.8
Pelagic cold vs. Benthic cold	ACHD	14.1
	ASTE	27.3
	PANT	38.6
	FRAG	46.8
FPV warm vs. Benthic warm	ENCP	12.4
	PSST	23.8
	GOMP	34.2
	ACHD	43.6
FPV cold vs. Benthic cold	PSST	9.5
	ENCP	18.8
	GOMP	27.7
	ACHD	34.8
Pelagic cold vs. FPV cold	ACHD	17.3
	ASTE	31.3
	PANT	44.9
	GOMP	54.3
Pelagic warm vs. FPV warm	PANT	13.7
	ACHD	25.6
	GOMP	34.6
	ASTE	42.3
Pelagic cold vs. Pelagic warm	ASTE	15.0
	ACHD	29.60
	PANT	42.2
	FRAG	51.8

surface for colonisation (Lacerda *et al.*, 2019; Taurozzi *et al.*, 2022), the substrate quality may not be optimal for supporting highly diverse diatom assemblages. Floaters are composed of high-density polyethylene presenting relatively uniform and homogeneous surfaces, and thus, comparably lacking the structural complexity of natural substrates such as macrophytes, rocks, and sediments (Yang and Flower, 2012). Indeed, we found in this study that the benthic compartment exhibited higher diatom richness, diversity, and evenness compared to pelagic and FPV compartments. This result aligns with findings that show higher richness of epiphytic diatoms in the littoral zone compared to the pelagic zone of shallow lakes (Riati and Leira, 2020). The littoral zone is more intensely influenced by multiple physical factors, such as wind exposure and fluctuations in water level (Cantonati and Lowe, 2014; Riati and Leira, 2020). This, combined with greater habitat heterogeneity, can contribute to the development of more diverse benthic diatom assemblages.

Diatom community composition varied significantly across compartments (FPV, benthic, and pelagic), highlighting the strong influence of habitat type. However, within the same compartment, seasonal shifts in species composition were observed only in pelagic assemblages. This difference was primarily driven by an increase in *Asterionella* and *Fragilaria* during the cold season. *Asterionella* and *Fragilaria* are colonial, araphid diatoms, typically associated with

planktonic life forms having adaptations for floating (Passy, 2007). More specifically, these two genera are essentially represented by the species *Asterionella formosa* Hassall and *Fragilaria crotonensis* Kitton. They are frequently sampled together and/or in species succession (Sommer, 1988; Negro, 1994). Their population dynamics are driven by physical (water temperature and clarity) and chemical factors (nitrates, phosphates and silica), generally showing higher abundances when water temperatures are low (Kling, 1993). Despite being a benthic life form, *Achnantheidium* was also one of the genera with the highest relative abundance in the pelagic compartment, being the most abundant genus during the warm season (45% relative abundance) and the third most abundant genus in the cold season (19% relative abundance). This finding may suggest that these species are being passively introduced into the plankton from the benthic compartments or the FPV floaters through mechanical actions, such as wind-induced movements of the floaters, generating frequent interactions between the floater and the water surface. This movement could lead to the detachment of *Achnantheidium* from the floaters, resulting in their presence in the plankton. *Achnantheidium* was also the most abundant genera in benthic habitats, probably due to its capacity to rapidly colonise disturbed habitats such as the shallow periphyton in lake shores that are subjected to water level fluctuations (Cantonati and Lowe, 2014), the second most abundant taxon was *Encyonopsis*,

which are typically benthic life forms, with cells adhering horizontally to the substrate (Passy, 2007).

The diatom community on FPVs comprised 21 of the 23 most abundant (>5 %) genera identified across the three studied compartments. Although planktonic forms were present in low proportions, the dominant taxa on FPVs were primarily benthic forms with adaptations for attachment to substrates. Thus, our results suggest that functional traits, such as the ability to thrive in low-light environments and to develop adherent structures, played a more significant role in shaping diatom assemblages on FPVs than spatial proximity to the pelagic zone. This highlights that the unique conditions created by FPV floaters, particularly substrate availability in a shaded zone, were more influential in determining species composition than simple spatial autocorrelation. Additionally, we found no seasonal effects on the FPV compartment the structure and composition of diatom assemblages. This suggests that FPVs may be less influenced by seasonal patterns as the shading effect caused by the FPV floaters likely reduces the seasonal fluctuations in light intensity and water temperature (Liu *et al.*, 2023) that can influence diatom community dynamics, thereby creating a more stable environment for diatom assemblages.

The success of tolerant species under FPVs highlights how these artificial structures can introduce a new habitat for diatom development, particularly in the pelagic zones of lakes, by favoring taxa that can thrive under the physical conditions created by FPV installations. By offering a surface for development of diatom assemblages, FPVs may influence broader ecosystem processes, such as primary production and carbon cycling. Although FPVs reduce light penetration and may limit planktonic photosynthesis, the biofilm formed on the floaters can sustain a certain level of productivity in the pelagic zone. Biofilms that form on artificial surfaces are initially established by exopolysaccharides secreted mainly by bacteria and diatoms (Khan *et al.*, 2020). These biofilms are characterised by complex spatial structures and heterogeneous microorganism distributions that interact in a dynamic way (Barranguet *et al.*, 2004), enhancing the role of the floaters to generate new sources of organic carbon for the pelagic zone. Furthermore, this biofilm can serve as a food source and nesting site for other organisms, such as fish (Rosa-Clot, 2020), potentially linking FPV installations to higher trophic levels. Additionally, as attached diatoms eventually die and sink, they can couple pelagic and benthic habitats as benthic organisms consume or assimilate them (Fitzgerald and Gardner, 1993).

In conclusion, the findings of this study provide the first empirical insights into the influence of FPV systems on diatom assemblages, highlighting the potential of these artificial structures to create novel ecological niches and support different ecological assemblages within freshwater ecosystems. The dominance of *Achnanthydium* suggests both a pioneer community (Passy, 2007) and an indication of good water quality, as this genus is generally sensitive to pollution (CEMAGREF, 1982). While our findings offer valuable insight into diatom assemblages developing under FPV floaters, a broader assessment of FPV impacts on water quality would require baseline data on pre-FPV diatom

assemblages or reference sites. Future studies incorporating such data will be essential to identify the long-term ecological consequences of FPV installations. As the deployment of FPV systems continues to expand globally, further empirical research is needed to better understand their potential ecological impacts on biodiversity and ecosystem functioning.

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Supplementary material

Table S1. Relative abundance (%) of dominant genera in the Benthic, Pelagic and FPV compartments of the three studied lakes. The relative abundances were calculated based on the total abundance of the 23 genera that each had > 5% relative abundance in the initial dataset. Bold values represent the most abundant species in each compartment.

Table S2. Pairwise post hoc comparisons of taxonomic richness between the three compartments analysed in this study (Benthic, Pelagic, and FPV). Estimates represent the magnitude of differences between compartments, with associated standard error and p-values. Significant p-values are shown in bold.

Table S3. Pairwise post-hoc comparisons of Shannon diversity between the three compartments analysed in this study (Benthic, Pelagic, and FPV). Estimates represent the magnitude of differences between compartments, with associated standard error and p-values. Significant p-values are shown in bold.

Table S4. Pairwise post-hoc comparisons of Pielou's evenness between the three compartments analysed in this study (Benthic, Pelagic, and FPV). Estimates represent the magnitude of differences between compartments, with associated standard error and p-values. Significant p-values are shown in bold.

Table S5. Pairwise post-hoc comparisons to assess differences in diatom community composition across different combinations of habitat compartments (benthic, pelagic, and FPV) and seasonal periods (cold and warm seasons). Significant p-values are shown in bold.

The Supplementary Material is available at <https://www.kmae-journal.org/10.1051/kmae/2025006/olm>.

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