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Disentangling determinants of nearshore fish and crayfish assemblages in a canyon-shaped Mediterranean reservoir

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Abstract The distinct origin and hydrological characteristics of reservoirs, shaped by fluctuating water levels and seasonal variations, play a crucial role in determining aquatic species assemblages across diverse limnological zones. This study aimed to analyze fish and crayfish assemblages in the nearshore area of a canyon-shaped Mediterranean reservoir, seeking to identify seasonal and spatial convergent patterns and infer the factors influencing them. Samplings were conducted at five stations along the longitudinal profile of the reservoir at depths around 7 m using gillnets and hoops nets. A seasonal pattern emerged regarding species abundance and biomass, with higher values recorded during the warmer period. Additionally, a spatial trend was observed, indicating higher species abundance in the middle part of the reservoir and lower abundance near the dam, particularly during the colder period. Water transparency, temperature, and the distance from the dam were identified as the most significant factors affecting species assemblages in terms of abundance and biomass. This research provides valuable insights into the intricate interplay between environmental factors, seasonal changes, and the assemblages of aquatic species in a Mediterranean reservoir, contributing to our understanding of its ecological dynamics.

Keywords Freshwater fish · Assemblages · Nearshore areas · Mediterranean reservoirs

Introduction

The unique origin and hydrological characteristics of reservoirs, which share similarities with both rivers and lakes (Gido et al. 2009), can have a significant impact on aquatic organism assemblages. The act of damming disrupts river continuity, creating physical barriers that constrain the movement of fish both upstream and downstream. This disruption particularly affects the migration routes of long-distance migratory species, such as those belonging to the genus *Anguilla* and *Salmo*, leading to population isolation and extirpation (Hughes et al. 2005; Araújo et al. 2008).

Furthermore, damming alters the hydrological conditions in the river valley, leading to shorter retention times, higher water level fluctuation, and increased organic loads. These alterations favor the dominance of lentic species over lotic ones (Kubečka 1993; Irz et al. 2002; Hughes et al. 2005). Consequently, the

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fish assemblage that originally inhabited the river undergoes substantial modifications. Additionally, reservoirs with a canyon-shaped structure, featuring steep banks that result in restricted littoral areas and a limited diversity of habitats (Veselý et al. 2020), also impact the prevailing fish fauna.

However, even years after the reservoir construction, which initially led to the described significant changes, species assemblages continue to differ spatially and temporally. In general, fish are not randomly distributed within a water body. Instead, their assemblages result from a complex interplay of environmental factors, including physical and chemical conditions (such as water depth, temperature, oxygen levels, proximity to inlets/outlets) (Godinho et al. 1998; Vašek et al. 2004; Prchalová et al. 2008), biotic interactions (such as competition, predation, human activities) (Prchalová et al. 2008), preferences for specific microhabitats, spawning seasons, food availability, and the presence of cover and structure (such as submerged rocks, vegetation, artificial structures) (Choi and Kim 2020). Water quality also plays a crucial role in shaping their communities (Dustin and Vondracek 2017; Hatcher et al. 2019). Similarly, crayfish distribution in reservoirs is influenced by factors such as predation, resource, and shelter availability, as well as physicochemical parameters and their intricate interactions (Veselý et al. 2020).

In reservoirs, fish distribution can vary spatially along the longitudinal profile of the reservoir (i.e., among the present limnological zones: dam zone, middle zone, and upstream zone), vertically (along the water column), or among the littoral, profundal, and pelagic zones (Prchalová et al. 2008, 2009; Yang et al. 2012; Becker et al. 2016). The dam zone (or lacustrine zone), characterized by greater depth, exhibits more lake-like features, the upstream zone displays mainly riverine characteristics, and the middle zone is marked by intermediate environmental conditions, thus supporting differences in fish assemblages. Vertical distribution is influenced by thermal stratification, with fish favoring surface depths with adequate dissolved oxygen concentrations while avoiding layers with lower temperatures and hypoxia beneath the thermocline (Vašek et al. 2004; Järvalt et al. 2005; Prchalová et al. 2008). Concerning the littoral and profundal zones, while conditions vary, a common pattern is the movement of fish to shallower shoreline areas for spawning in spring, as well as for nesting and feeding (García-Berthou 2001; Winfield 2004; Penne and Pierce 2008; Vander Zanden et al. 2011). Conversely, species favoring warmer waters, such as catfish, may become more active in warmer, shallower areas as temperature rises (Alp et al. 2004; Ferreira 2019; Santos 2021). In autumn, fish may exhibit increased feeding activity in preparation for winter, with predatory species like pike or pikeperch becoming more active (Vehanen and Lahti 2003; Říha et al. 2022). During winter, most fish species are likely found in deeper areas where temperatures are more stable (Vehanen and Lahti 2003; Penne and Pierce 2008). Concerning crayfish, their habitat utilization extends across both littoral areas and the deepest zones. The selection of these habitats is influenced by environmental suitability and the fulfillment of their ecological needs (Reynolds et al. 2013; Veselý et al. 2020).

The research explores the composition of fish and crayfish species in the nearshore zone of a canyon-shaped Mediterranean reservoir, seeking spatiotemporal patterns and trends and investigating the primary environmental factors influencing them. This knowledge is crucial for understanding ecological dynamics of these reservoirs, providing valuable insights for environmental management and design. Such understanding is instrumental in guiding spatial planning for conservation or protection areas, aligning with the overarching goals of environmental sustainability and preservation (Hughes et al. 2005; Wang et al. 2006).

Materials and methods

Study area

The Polyphytos Reservoir is located in the municipality of Kozani, in the northwest of Greece. Established in 1975 by the Public Power Corporation, it was created by damming the Aliakmon River to facilitate electrification through hydroelectric power. Multiple reservoirs (Ilariona, Polyphytos, Sfikias, Asomaton, and Ag. Varvaras) have been installed along the main course of the Aliakmon River, disrupting its continuity and modifying hydrological conditions over extensive sections (Fig. 1).

The drainage basin of the reservoir encompasses an area of 5630 km^2. The reservoir has a narrow and

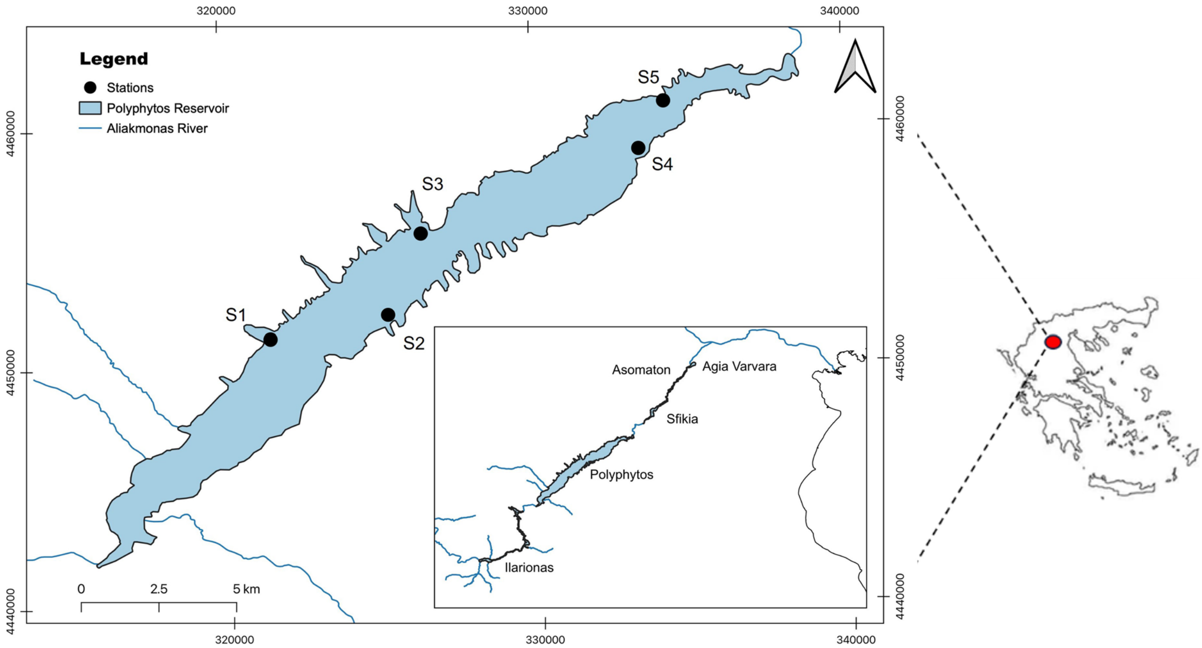

Fig. 1 Sampling stations in Polyphytos Reservoir during the sampling campaign in 2022. The five reservoirs (Ilarionas, Polyphytos, Sfikia, Asomanton, and Agia Varvara) comprise the complex of Aliakmonas River

elongated shape (canyon-shaped), with a maximum width of 2.5 km, and its length varies between 22 and 31 km, depending on the balance of inflows and outflows. Its useful capacity is 1220×10^6 m^3, its maximum operational level is at + 291 m a.s.l., its surface area is 74.1 km^2, and its length is 4.5 km (Ministry of Environment and Energy, 2017b). Seasonally, the water level fluctuates by approximately 15 m. The average depth is approximately 26.2 m, with a maximum depth of 91 m. The water renewal time is estimated at 1.5 times per year. It is a warm monomictic reservoir. During the summer period, it displays thermal stratification, with the oxygen concentration in the thermocline lower than in the hypolimnion. The epilimnion extends up to a depth of 10 m, while the thermocline zone has a width of 7 m. It is characterized as mesotrophic with tendencies toward eutrophication. The richness and abundance of aquatic macrophytes in its littoral zone are low due to high water level fluctuations.

Samplings

A series of four seasonal samplings (spring to winter 2022) was carried out at Polyphytos Reservoir across five stations along its longitudinal axis (Fig. 1). These sampling points were strategically positioned in depths around 7 m, in close proximity to the reservoir's littoral zone, owing to its abrupt bathymetric features. Specifically, stations positions were moved a few meters each season, so that water depths remained approximately constant.

Water temperature (WT, °C), dissolved oxygen concentrations (DO, mg/l) in the surface and the reservoir's bottom, pH, electrical conductivity (EC, μS/cm), salinity (Sal, ppt), and total dissolved solids (TDS, mg/l) were measured in the surface water, at each sampling station, using a YSI ProDSS (digital sampling system) multiparameter probe. Additionally, water transparency (m) was determined using a Secchi disk.

Samplings of fish and crayfish were conducted using benthic gill nets and hoop nets (traps). The gill nets were 25 m long and 6 m high, made of yellow thread, consisting of ten different segments with mesh sizes ranging from 6.5 to 60 mm. The hoop nets were 8 m long, with dimensions of 40 cm × 22 cm and a net mesh size of 9 mm. No bait was used in the traps to attract aquatic organisms. One fishing tool of each type (i.e., one gillnet and one trap) was placed at each station. The fishing gear was retrieved the next morning (i.e., the fishing duration was approximately 20 h).

Catches were identified at the species level. The total length (mm) and weight (g) of each fish were measured, while only weight was recorded for the crayfish.

Data analysis

Comparisons of environmental variables and catch abundances (specimens' number and biomass) among seasons were performed. After checking for homoscedastic and normality's parametric statistical test requirements, the non-parametric Kruskal–Wallis test was used to check for differences in parameters' values (estimated from five sampling stations) among seasons.

In addition, a Spearman correlation analysis was conducted using values of the physicochemical parameters, distance from the dam (measured as the straight distance of each station from the dam using Google earth, imagery date: 15/7/2023), species number, and total catches (fish and crayfish) in terms of abundance and biomass to detect multicollinearity among parameters.

A subset of independent variables that were not highly correlated to each other was selected to be included in further analysis. Specifically, those were water temperature, Secchi disc depth (transparency), conductivity, and the distance of the sampling station from the dam. All the above analyses were conducted using IBM SPSS Statistics (version 27). The direct gradient canonical correspondence analysis (CCA) was then used for the evaluation of the variability in assemblage structure in relation to the selected environmental factors. Both abundance and biomass species data were used, specifically catches per season and sampling station. The significance of the CCA result was assessed through an analysis of variance (ANOVA) designed for CCA using "vegan" package of R-studio (Oksanen et al. 2007). All data used for the above analyses were $\log(x+1)$ transformed.

Results

Water's physicochemical parameters

Descriptive statistics of the physicochemical parameters measured in the water per season are presented in Table 1. The highest mean water temperature was recorded during the summer sampling, while the lowest in winter. Dissolved oxygen concentrations remained consistently high throughout the year exceeding 8 mg/l, at both the surface and bottom of the reservoir. Conductivity and pH values did not show significant variations among seasons. In autumn, the highest salinity (Sal) and total dissolved solid (TDS) values were recorded, reaching up to two- to threefold compared to other seasons. Secchi disk depth values ranged from 2 to 5 m, with the highest mean transparency values recorded in spring (4.2 ± 0.374 m) and the lowest in autumn

Table 1 Seasonal water measurements [mean of five sampling stations ± standard deviation (SD), (minimum–maximum values)] of the physicochemical parameters in Polyphytos Reservoir during sampling campaign in 2022. *WT* water temperature, *DO* dissolved oxygen, *EC* electrical conductivity, *Sal* salinity, *TDS* total dissolved solids

Season	Water parameters Mean ± SD (Min–Max)							
	WT (°C)	DO (mg/l) surface	DO (mg/l) bottom	EC (μS/cm)	pH	Sal (ppt)	TDS (mg/l)	Secchi (m)
Spring	23.14 ± 0.455 (21.8–24.4)	9.15 ± 0.147 (8.64–9.56)	8.52 ± 0.138 (8.04–8.85))	420.4 ± 20.651 (352–476)	8.32 ± 0.182 (7.86–8.71)	0.14 ± 0.006 (0.12–0.15)	217.8 ± 12.607 (181–255)	4.20 ± 0.374 (3–5)
Summer	27.34 ± 0.508 (25.8–28.4)	10.42 ± 0.047 (10.36–10.61)	9.55 ± 0.357 (8.16–10.20)	391.6 ± 2.462 (382–395)	8.63 ± 0.096 (8.27–8.82)	0.13 ± 0.014 (0.12–0.19)	187.2 ± 1.715 (185–194)	3.14 ± 0.098 (3–3.5)
Autumn	21.58 ± 0.240 (21.0–22.3)	8.72 ± 0.103 (8.39–8.98)	8.55 ± 0.096 (8.19–8.76)	389.0 ± 0.949 (387–392)	8.48 ± 0.020 (8.42–8.53)	0.33 ± 0.052 (0.12–0.4)	402.8 ± 53.617 (190–479)	2.82 ± 0.220 (2–3.3)
Winter	13.72 ± 0.037 (13.6–13.8)	8.74 ± 0.051 (8.60–8.90)	8.98 ± 0.058 (8.80–9.10)	395.7 ± 1.577 (393–400)	8.36 ± 0.028 (8.28–8.41)	0.19 ± 0.000 (0.19–0.19)	257.4 ± 0.872 (256–260)	3.74 ± 0.218 (3–4.2)

(2.82 ± 0.220 m). Specifically, statistically significant differences ($p < 0.001$) were detected among seasons for temperature, DO, Sal, TDS, and Secchi depth, but not for EC and pH.

Species assemblages

In total, 5102 individuals of fish and crayfish were caught using gillnets and hoop nets, with a total weight of 127.17 Kg. The presence of nine fish species belonging to six families and one species of crayfish, *Pontastacus leptodactylus* (Family Astacidae), was recorded (Fig. 2). The most abundant species based on the number of individuals was *Rutilus rutilus*, followed by *Perca fluviatilis* (Fig. 2a). Based on biomass, the most abundant species was *Rutilus rutilus*, followed by *Alburnus thessalicus* (Fig. 2b). Species such as *Cyprinus carpio*, *Esox lucius*, *Silurus glanis*, *Squalius vardarensis*, and *Vimba melanops* had relatively low specimen counts (≥ 10). A total of 153 crayfish were captured using both gillnets and hoop nets, with approximately 95% of this species caught by hoop nets. In contrast, gillnet fishing contributed more substantially to the overall fish catch.

The highest number of species was recorded in the catches during summer (nine species), while the lowest was observed in winter (six species) (Fig. 3). The highest total catch in terms of numerical abundance and biomass occurred in summer, followed by spring, with the lowest catches observed in winter (Fig. 3). Species abundance and number did not differ significantly ($p > 0.05$) across seasons. The opposite, however, was observed for biomass ($p < 0.05$).

The highest number of species was recorded at sampling station S3, while the highest catches and biomass were observed at sampling station S2, indicating that both parameters were higher in the middle section of the reservoir. In contrast, the smallest values were estimated from the catches in the "lower" section of the reservoir concerning its longitudinal profile, specifically at stations S4 and S5, which were closer to the dam (Fig. 3).

In general, all species exhibited lower abundance and biomass catches during winter (Fig. 4), except for *E. lucius*, which showed its highest catch during that period, and *R. rutilus*, whose catches during winter remained at the same level as in autumn. *C. carpio*, *A. thessalicus*, and *R. rutilus* had their highest catches during spring. *P. fluviatilis* recorded the highest catch during summer as crayfish *P. leptodactylus*, while *S. glanis* was not recorded in winter catches and exhibited the highest catch in summer.

Factors affecting species assemblages

Spearman correlation revealed significant correlations between water temperature and DO, pH, Sal, TDS as long as abundance, biomass, and species number, proving that the seasonal shift is a major factor affecting the species assemblages of this nearshore zone (Table 2). However, the distance of the sampling station from the dam (distance from dam) was not correlated with either species number nor abundance or biomass data.

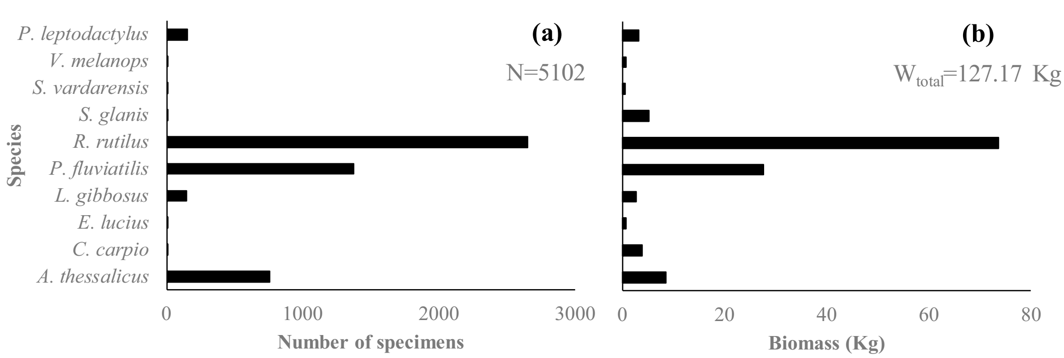

Fig. 2 **a** Numerical abundance (number of specimens) and **b** biomass (Kg) of crayfish and fish caught per fishing tool (nets and traps) in Polyphytos Reservoir during the sampling campaign in 2022. The total abundance and biomass of the total catches (crayfish and fish) is also provided

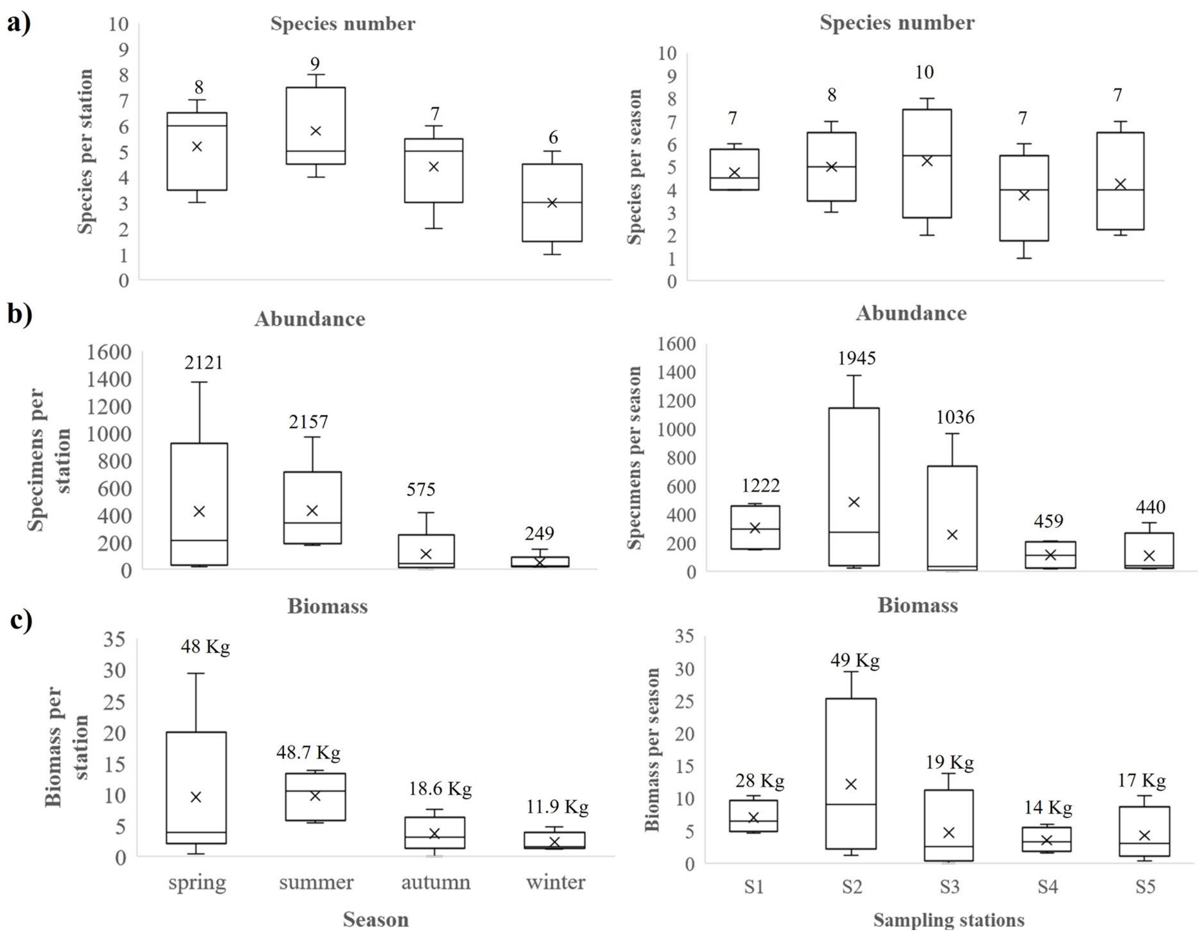

Fig. 3 Seasonal (left) and spatial (right) distribution of catches estimated in terms of **a** species, **b** numerical abundance, and **c** biomass in Polyphytos Reservoir during the sampling campaign in 2022. Mean values (x), median values (represented by horizontal lines), 50% of the values (box), and the highest and lowest values (outer lines) are provided. The numbers above the boxes indicate the total number of species, numerical abundance, and biomass catch per season or sampling station

The first two CCA dimensions (CCA1 and CCA2) indicated that environmental variables accounted for approximately 26.6% of the total variation in species assemblages concerning abundance data and 24.8% concerning biomass data (Table 3). In addition, ANOVA revealed a statistically significant relationship between species assemblages and the environmental variables used, considering both numerical abundances and biomass data (Fig. 5). Specifically, the CCA models showed that the variables most significantly affecting species abundance were the Secchi disc (indicating water transparency) in the first axis (CCA1) and the distance from the dam in CCA2 axis (Table 3, Fig. 5a). On the other hand, for species biomass, Secchi depth (CCA1) and temperature (CCA2) had the most pronounced impact (Table 3, Fig. 5b).

Stations located in the middle section of the reservoir, farther from the dam, consistently exhibit higher abundances of *A. thessalicus* throughout the year (Fig. 5a). The peak in water transparency occurred during spring, correlated with increased numerical catches of *C. carpio*, especially in the lower part (S3_s, S4_s, and S5_s) of the reservoir where the deepest areas are located (Fig. 5a). Conversely, lower water transparency values recorded during summer and autumn samplings in stations S4 and S1 were associated with higher numerical catches of species *S. vardarensis*, *L. gibbosus*, and *V. melanops.*

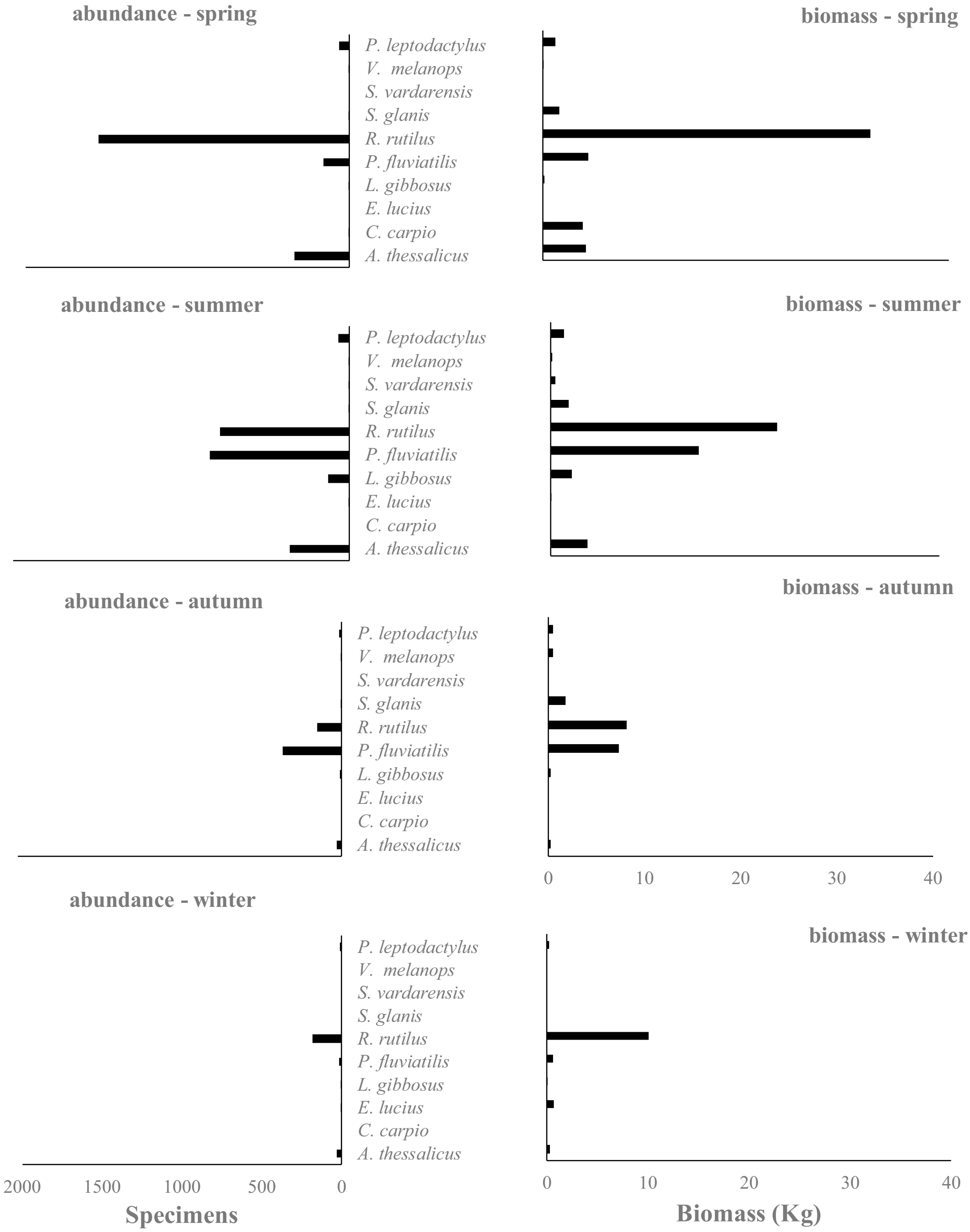

Fig. 4 Species abundance (number of specimens) and biomass (Kg) estimated in seasonal catches in Polyphytos Reservoir during the sampling campaign in 2022

Since abundance serves as a proxy for biomass, most of the observations noted in the CCA abundance model were corroborated by the CCA biomass model (Fig. 5b). However, the CCA model using biomass data showcased a correlation of higher catches of species *L. gibbosus*, *S. glanis*, and *S. vardarensis* with the warmer temperatures of the summer period, while higher biomass catches of species *E. lucius* were

Table 2 Spearman's rank correlation coefficients among water's physicochemical parameters, species abundance, biomass, and species number. *WT* temperature (°C), *DO* dissolved oxygen (mg/l), *EC* conductivity (μS/cm), *Sal* salinity (ppt), *TDS* total dissolved solids (mg/l)

Parameters	WT	DO	EC	pH	Sal	TDS	Secchi depth	Distance from dam	Abundance	Biomass	Species number
WT	1.000	0.809**	0.025	0.504*	−0.537*	−0.662**	−0.172	0.172	0.669**	0.687**	0.517*
DO		1.000	−0.032	0.356	−0.509*	−0.613**	0.017	0.304	0.763**	0.787**	0.679**
EC			1.000	0.038	−0.127	−0.064	0.230	−0.154	0.133	0.047	−0.044
pH				1.000	0.027	−0.148	−0.404	0.242	0.382	0.372	0.362
Sal					1.000	0.905**	−0.121	0.284	−0.488*	−0.494*	−0.439
TDS						1.000	−0.130	0.037	−0.485*	−0.502*	−0.470*
Secchi depth							1.000	0.126	−0.156	−0.200	−0.119
Distance from dam								1.000	0.402	0.368	0.162
Abundance									1.000	0.968**	0.724**
Biomass										1.000	0.707**
Species number											1.000

*Correlation is significant at the 0.05 level (2-tailed). **Correlation is significant at the 0.01 level (2-tailed)

evident during the winter period marked by lower temperatures, particularly in the upper part of the reservoir (S1_w and S1_s) (Fig. 5b).

Discussion

Physicochemical parameters

The study revealed significant seasonal variations in water physicochemical parameters that align with the prevailing climatic conditions of the Mediterranean region, explicitly the distinct shifts between wet winter and dry summer periods (Lionello et al. 2006). The DO concentrations were found to be high throughout the year, both at the surface and at the bottom of the lake. However, the occurrence of anoxic conditions in the deeper layers of the lake during the summer period cannot be ruled out, a phenomenon common in eutrophic Mediterranean systems. Conductivity values were within the range commonly recorded in Greek lakes (200–600 μS/cm) (Kagalou and Leonardos 2009). Also, the measured pH values were within the range typical for most lakes ($6 < pH < 9$) and in the alkaline zone. They were also within the range considered optimal for most aquatic organisms ($6.5 < pH < 8.2$) and within the limits of Directive 44/2006/EC (pH 6–9 for both salmonids and cyprinids). The highest estimated salinity value (0.4 psu) was close to the upper limit characterizing low salinity inland waters (0.5 psu). Total dissolved solid (TDS) concentrations were within the range commonly found in inland waters (20–1000 mg/L), particularly close to the values encountered in calcareous regions (200–400 mg/L) (Boyd and Boyd 2015). TDS concentrations in inland waters typically depend on geological and climatic factors, including the composition of the region's rocks, inflows from streams, precipitation, and even human-made sources (Sherrard et al. 1987). Higher salinity and TDS concentrations were recorded during the autumn sampling, a phenomenon that cannot be attributed to a specific factor. The Secchi disk values, indicative of water transparency were relatively high compared to measurements in Mediterranean systems. In fact, these values were similar to those observed in natural deep Greek lakes, such as Trichonis and the transboundary Great Prespa (Kagalou and Leonardos 2009). The lower water transparency values recorded during the

Table 3 Summary statistics for canonical correspondence analysis (CCA) based on species abundance and biomass data matrices in Polyphytos Reservoir

Parameters	Fish	abundance	Fish	biomass
	CCA1	CCA2	CCA1	CCA2
Eigenvalue	0.08417	0.05406	0.1557	0.07522
Cumulative proportion	26.6%		24.8%	
Environmental variables				
Temperature	0.3162	−0.13903	0.29994	0.79807
EC	−0.3502	0.06858	−0.14078	0.07136
Secchi disc	−0.7615	0.62549	−0.98479	−0.04993
Distance from Dam	−0.5844	−0.68747	0.04814	−0.53740
Summary of ANOVA				
Df	4		4	
F	1.8778		1.6177	
ChiSquare	0.17333		0.28018	
p	0.005		0.04	

autumn may be attributed to higher phytoplankton concentrations during this period. It is noteworthy that, based on the observed phytoplankton succession pattern in Mediterranean systems (Moustaka-Gouni et al. 2014), the phytoplankton community experiences a minimum during spring and continuous growth from summer to autumn and reaches maximum biomass levels in the autumn.

Species composition

Among the fish species recorded in this study, *A. thessalicus*, *S. vardarensis*, and *V. melanops* are endemic to the Balkans. The remaining species, except *L. gibbosus*, are native to Europe and parts of Asia, having a relatively wide distribution. Notably, *E. lucius*, *S. glanis*, *C. carpio*, *P. fluviatilis*, and *R. rutilus* hold commercial significance and are actively targeted for fishing. In contrast, *L. gibbosus* is an introduced species of American origin that has established populations in various European systems (Cucherousset et al. 2009). Additionally, *P. leptodactylus* is an introduced crustacean (Perdikaris et al. 2017) with high economic importance in local fisheries.

Noteworthy is the absence of certain confirmed species in the reservoir, such as *Carassius gibelio*, intentionally targeted by local fishermen in recent years for export to Romania and Turkey. Except overfishing, other factors, such as regular desiccation or sudden water level fluctuations, often associated with fish harvesting or drainage, could significantly influence the abundance of this species (Ferincz et al. 2016). Additionally, *Barbus macedonicus*, due to its rheophilic nature, might have sporadic presence in Polyphytos Reservoir. The absence of some small-bodied fish species like *Gambusia holbrooki* and *Rhodeus amarus*, preferring the littoral zone, could be attributed to the limitations of the capturing method. Their small size might require a more suitable technique, such as electrofishing gear to sweep sections of the littoral zone (Petriki 2015).

Dam constructions have been identified as significant factors in altering riverine environments through inundation, hydrologic alteration, and fragmentation. These alterations lead to shifts in species assemblages (Kubečka 1993). Particularly, following dam construction, fish species assemblages typically show dominance by limnophilic species that prefer stagnant waters. Rheophilic species may coexist but usually in smaller populations, particularly in the transitional zone (the upper section along the longitudinal axis), where the hydrological regime resembles that of a river, or in adjacent tributaries flowing into the lake (Prchalová et al. 2008, 2009). This adaptation is evident in catches from Polyphytos Reservoir where the dominant species were *R. rutilus*, *P. fluviatilis*, and *A. thessalicus*. This observed pattern aligns with findings in many Greek lakes, where species of the genus *Rutilus* or *Leucos* tend to dominate, accompanied by a significant presence of *P. fluviatilis* and *Alburnus* species (Petriki 2015). In addition, it aligns with the eutrophic status of the reservoir that favors the dominance of cyprinids (Olin et al. 2002).

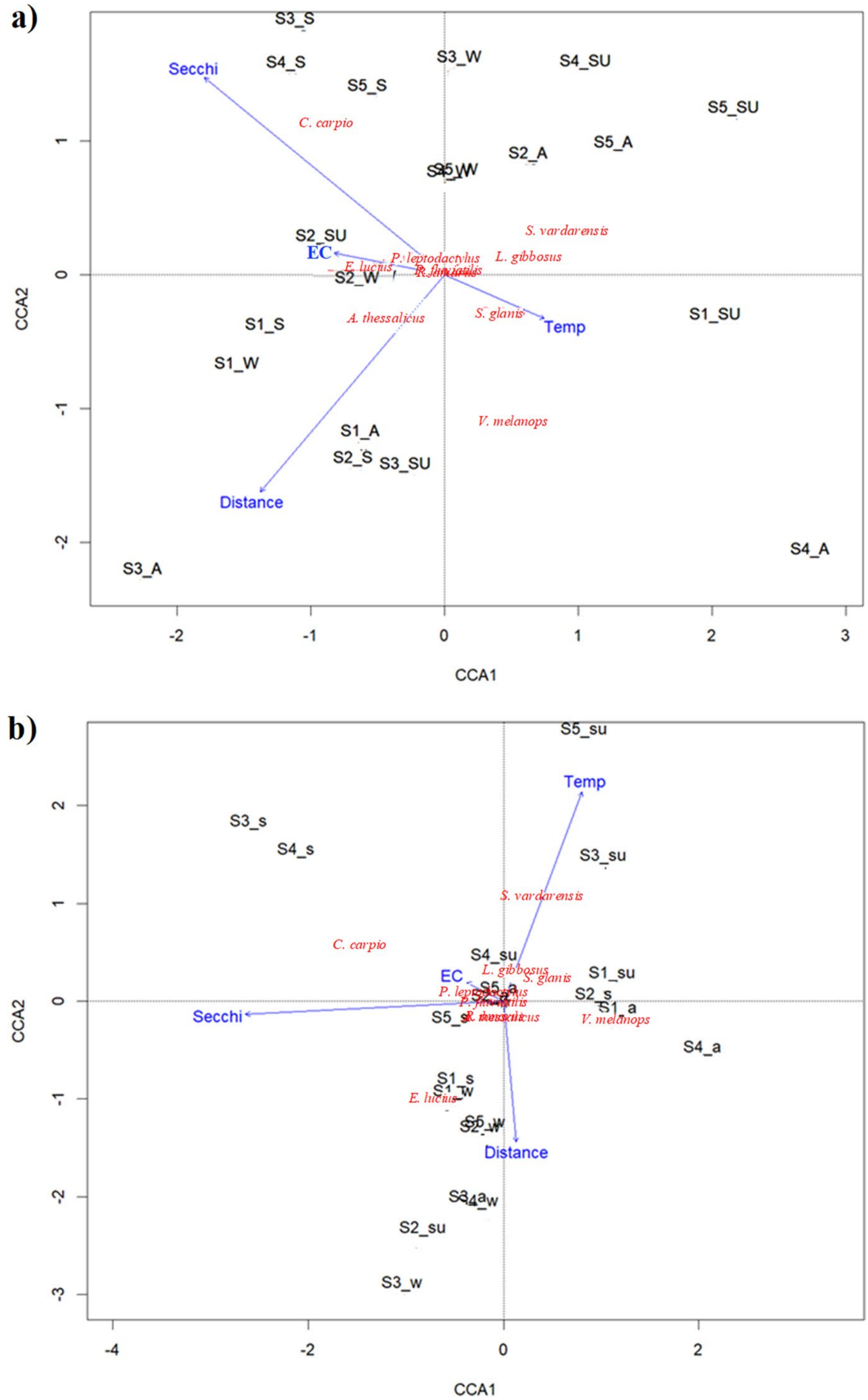

Fig. 5 Plot of CCA analysis showing the correspondence of the main environmental parameters (temperature (temp) and distance from the dam (distance), vectors) with **a** abundance and **b** biomass of species assemblages in Polyphytos Reservoir. S1–S5: the sampling stations, while seasons are represented by s, spring; su, summer; a, autumn; w, winter

In general, native species dominated the catches; thus, the frequently reported pattern of shifting from native-dominated stream fishes to non-native invasive-dominated fish assemblages (Clavero and Hermoso 2010) following the dam construction and driven by intentional and accidental introductions of non-natives to support fisheries was not observed here.

The disparity between the study's catch and professional fishermen (personal observations) is attributed to the latter's use of larger nets with significantly larger dimensions and mesh sizes exceeding 60 mm. These larger mesh sizes are employed by lake fishermen targeting *C. carpio* and *C. gibelio* to capture only commercially sized fish. In contrast, the study utilized nets with mesh sizes ranging from 6.25 to 60 mm to provide a more comprehensive capture of the fish community structure.

Spatiotemporal patterns

Variations in the spatiotemporal distribution of aquatic fauna can be attributed to a range of factors, including abiotic, biotic, and anthropogenic elements. These factors encompass the water body's bathymetric features that generate habitat heterogeneity, water depth, littoral zone structure, substrate composition, and more (Vašek et al. 2004; Prchalová et al. 2008; Miranda 2011). However, water temperature and water transparency, indicative of water productivity, stand out as fundamental factors influencing aquatic assemblages, particularly those of fish (Quirós 1995; Fischer and Eckmann 1997; Gelós et al. 2010; Rosso et al. 2010; Specziár et al. 2013; Bunnell et al. 2021).

The influence of water temperature on fish assemblages primarily manifests through its impact on ecosystem and species metabolism, nutritional requirements, and activity levels, ultimately leading to higher gillnetting efficiency (Linlokken and Haugen 2006; Lall and Tibbetts 2009). Consistent with findings from other studies (Bobori and Salvarina 2010; Gelós et al. 2010), fish species richness and abundance of fish and crayfish were higher during spring and summer and lower during winter. This behavior can be attributed to species' responses to seasonal changes.

As mainly poikilothermic organisms, fish experience body temperature variations associated with the external environment (Lall and Tibbetts 2009). Thus, as water temperature declines along the seasonal shift from autumn to winter, they reduce their metabolism and, consequently, their mobility to lower their energy cost which is depicted in gillnet catches (Linlokken and Haugen 2006). This allows them to endure extended periods without feeding and helps increase their survival rates (Banet et al. 2022). In response, fish may aggregate in deeper areas to overwinter, where water temperature fluctuations are smaller, and temperatures are generally higher than those prevailing in shallower areas. This behavior has been widely observed in cyprinid fish but also salmonids (Vašek et al. 2004; Prchalová et al. 2008). Therefore, the observed decrease in fish catches during these colder seasons can be attributed to the fish's migration to deeper areas. On the contrary, during the warmer periods of the year, such as spring and summer, fish tend to inhabit shallower waters and are often found near the littoral zone, particularly during the spring breeding period.

The highest abundance of species *C. carpio* during spring period may attribute to its reproductive behavior as it prefers to spawn in the littoral zone (Froese and Pauly 2023). Contrastingly, the peak catches of *S. glanis* during summer and *E. lucius* during winter samplings can be attributed to the increased mobility of these species during their respective spawning periods (Alp et al. 2004; Yağcı et al. 2009). In Polyphytos Reservoir, these spawning periods extend from June to August for *S. glanis* and from January to May for *E. lucius*, according to information obtained through personal communication with commercial fishermen.

The higher catches of *L. gibbosus* and *S. vardarensis* during summer also suggest that these species may exhibit increased activity in warmer months, likely due to improved feeding opportunities, favorable reproductive conditions, higher metabolic rates, or a better adaptation or preference for environments with lower water transparency. It is worth noting that lower water transparency values were recorded during summer and autumn samplings.

The influence of turbidity on fish assemblages largely depends on species' visual adaptations and life strategies, particularly their ability to thrive in environments with varying turbidity levels (Michael et al. 2021). Specifically, for species that rely on vision to detect prey, water transparency affects reaction distance, encounter rates, and ultimately, consumption rates (Lehtiniemi et al. 2005; Turesson and Brönmark 2007; Figueiredo et al. 2016). Therefore, water transparency can impose changes in fish assemblages and even fisheries production through a variety of ecological mechanisms, including predator avoidance, reaction distances, and foraging efficiency (Figueiredo et al 2016; Bunnell et al. 2021). Conversely, fish species can act as ecosystem engineers by altering water clarity dynamics through trophic cascade effects conducted by predation or nutrient control, which can significantly influence water clarity (e.g., Quirós 1995; Rowe 2007; Rosso et al. 2010). This truth underscores many biomanipulation techniques where deliberate alteration of fish populations within aquatic ecosystems, typically lakes, is attempted to improve ecological conditions or restore ecosystem balance (Drenner and Hambright 1999).

Moreover, the highest catches of the crayfish *P. leptodactylus* during the summer period were likely due to the approaching mating period in September (Kubec et al. 2019). Generally, during winter, crayfish tend to seek shelter during the day and are primarily active during the night and twilight hours. With higher water temperatures in spring and summer and increased availability of food sources, crayfish exhibit greater activity (Alvanou et al. 2022). Due to this heightened mobility, as observed in commercial catches, the fishing season for many crayfish species is extended from mid-summer to autumn to protect berried females, which may carry eggs or hatchlings until mid-July (Jussila and Mannonen 2004).

The higher number of species, along with higher numerical and biomass catches, in the middle section of Polyphytos Reservoir aligns with findings from relevant studies in canyon-shaped reservoirs, indicating a gradient in species numbers, abundance, and biomass along the reservoir's longitudinal axis (Oliveira et al. 2004; Vašek et al. 2004; Prchalová et al. 2008). This pattern is likely attributed to canyon-shaped reservoirs' gradient in productivity along the same axis, evident through higher nutrient concentrations and phyto- and zooplankton densities (Prchalová et al. 2008). As suspected, fish abundance and biomass align with this gradient, benefiting from the richest resources that occur in more eutrophic environments (Jeppesen et al. 2005; Garcia et al. 2006). Additionally, this gradient could be attributed to the higher heterogeneity of the environment in the riverine and transitional zones that tend to support more native and rare species (Oliveira et al. 2003, 2005; Gao et al. 2010). The suspected preference of the *A. thessalicus* species for the middle part of the reservoir, assuming that this section is indeed more productive compared to the lower part, aligns with the preferences observed in the same genus species, which tend to prey upon zooplankton and spawn in tributaries (Vašek et al. 2004).

The environmental variables explained part of the variability of species distribution. Indeed, more complex mechanisms, such as competition and predation, shape the species assemblages in these nearshore areas. However, given the limited information available on the seasonal and spatial distribution of fishes in Mediterranean reservoirs (Moutopoulos et al. 2023), and even less for canyon-shaped ones (Vašek et al. 2004, 2006; Prchalová et al. 2009), let alone the ongoing lack of knowledge regarding habitat use and the preferences of various aquatic species, the significance of the present study becomes evident.

Understanding the seasonal variations in fish assemblages and the potential mobility patterns of aquatic species provides valuable insights into their ecological strategies and adaptations to changing environmental conditions. Further research and monitoring efforts could help elucidate the underlying mechanisms driving these observed patterns and their implications for the overall dynamics of the reservoir ecosystem. Such understanding is crucial for environmental management and design, as it can guide spatial planning for conservation or protection areas.

Conclusions

In conclusion, fish and crayfish assemblages in Polyphytos Reservoir exhibited spatiotemporal trends, with more pronounced and heterogeneous catches observed during warmer seasons. The highest species numbers and catches were noted in the middle section of the reservoir, contrasting with the deeper areas closer to the dam. Water transparency, temperature, and distance from the dam were identified as the most significant factors influencing species assemblages. These findings provide valuable insights into the dynamics that shape seasonal and spatial patterns in fish assemblages in Mediterranean reservoirs. It is noteworthy that despite reservoirs being common aquatic habitats in Europe, there is limited quantitative information and ecological knowledge on the fish and crustacean assemblages inhabiting them.

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Data availability The data supporting the findings of this study are available within the paper. For additional information, please contact the corresponding author.

Declarations

Ethics approval The research received approval from the relevant committee in Greece for the conducted fish samplings.

Competing interests The authors declare no competing interests.

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