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Temporal trends and determinants of fish biomass in two contrasting natural lake systems: insights from a spring long-term monitoring scheme

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Abstract – Freshwater fish declines are triggered by a suite of anthropogenic threats, including habitat degradation, climate and land use change, biological invasions, pollution and overfishing. Robust monitoring schemes are needed to understand and detect any effects of different factors on freshwater fish abundance and to be able to predict and respond to potential stressors. Here, we used standardized biomass-per-unit-effort (BPUE) data deriving from gillnet sampling over a 34-year period in the two Prespa Lakes and determined species trends using general additive models coupled with structural change models. Furthermore, the influence of seven environmental variables was assessed for each fish species using an analytical approach based on random forests. We showed that the total annual BPUE is increasing in Lake Mikri Prespa whereas it is stable in Megali Prespa and that the relative BPUE of introduced species in the former is increasing through the years. Differences in the lakes' trophic status were reflected in species trend patterns. Random forests showed that air temperature, the introduction of the invasive *Lepomis gibbosus*, predation and water management played a role in shaping species biomass in Mikri Prespa whereas abiotic factors are the main drivers of biomass changes in Megali Prespa. Our results provide empirical evidence on the importance of long-term monitoring in distinguishing between direct and indirect effects of large-scale stressors on fish abundance as well as insights towards sustaining the integrity of fish communities.

Keywords: Gillnet / invasive species / Prespa wetland / random forests / water management

Résumé – Tendances et facteurs déterminants des variations temporelles des biomasses de poissons dans deux systèmes lacustres naturels contrastés : éléments issus d'un programme de surveillance à long terme réalisé au printemps. Le déclin des espèces de poissons d'eau douce résulte d'une multitude de menaces anthropogéniques, dont la dégradation des habitats, les changements du climat et l'utilisation des sols, les invasions biologiques et la surpêche. Des systèmes de surveillance robustes sont nécessaires pour comprendre les variations d'abondance de poissons et pour détecter, prévoire et faire face aux éventuels facteurs de stress identifiés. À partir de données de biomasse standardisées par unité d'effort (BPUE), provenant d'un échantillonnage réalisé au filet maillant sur une période de 34 ans dans les deux lacs de Prespa, ont été analysées les évolutions temporelles des espèces piscicoles en appliquant des modèles additifs généraux couplés à des modèles de changement structurel. De plus, l'influence de sept variables environnementales a été évaluée par espèce et par lac en utilisant une approche analytique basée sur des forêts d'arbres décisionnels. La BPUE annuelle totale augmente dans le lac Mikri de Prespa alors qu'elle est stable dans le lac Megali de Prespa. Au fil des ans, la BPUE relative des espèces introduites augmente dans le lac Mikri. Les différences de statut trophique entre les deux lacs se retrouvent dans les tendances observées par espèce. Les forêts d'arbres décisionnels ont montré que la température de l'air, l'introduction de l'espèce invasive *Lepomis gibbosus*, la prédation aviaire et la gestion de l'eau ont joué un rôle dans l'évolution de la biomasse des espèces à Mikri Prespa, tandis que les facteurs abiotiques sont les principaux moteurs des changements de biomasse à Megali Prespa. Ces résultats constituent des preuves empiriques de

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l'importance d'un suivi à long terme pour distinguer les effets directs et indirects des facteurs de stress à grande échelle sur l'abondance des poissons, et permettent de préconiser quelques suggestions pour maintenir l'intégrité des communautés de poissons.

Mots-clés : Filet maillant / espèces invasives / zone humide de Prespa / forêts d'arbres décisionnels / gestion de l'eau

1 Introduction

Freshwater ecosystems cover less than 9% of the global land area, yet they contribute approximately 40% of global annual renewable ecosystem services and are considered hotspots of biodiversity (Zedler and Kercher, 2005; Collen *et al.*, 2014). Furthermore, inland waters are of outmost conservation importance as they hold almost half of all fish species (Arthington *et al.*, 2016). Despite their value, these ecosystems are becoming heavily degraded, with freshwater biodiversity declining at a much faster rate than marine or terrestrial biodiversity (Collen *et al.*, 2014), thus rendering inland waters one of the most imperiled habitats at a global scale (Dudgeon *et al.*, 2006).

Freshwater fish declines are triggered mainly by anthropogenic impacts, including habitat degradation, climate and land use change, biological invasions, pollution and overfishing (Stendera *et al.*, 2012; Reid *et al.*, 2019). Habitat degradation encompasses a variety of interacting factors, with direct effects such as stream diversion for agricultural use, excavations and channel morphology alterations. However, indirect impacts as a result of intensive land-use practices can incur changes within the drainage basin; increased sediment and nutrient loads, and subsequent decreased water quality and reduction of habitat suitability, have been linked to declines in fish populations and alteration of freshwater communities (Pusey and Arthington, 2003; Darwall and Freyhof, 2016; Reid *et al.*, 2019). Furthermore, human disturbances may increase the likelihood of invasion by non-native species (Dudgeon *et al.*, 2006; Lee *et al.*, 2017) and such synergy, therefore, makes potential effects of non-native species difficult to pinpoint and predict. Although past research suggests that most introductions of non-native fishes could be quite harmless (Gozlan, 2008), there are many examples of large-scale impacts on native species through predation, competition, habitat alteration, hybridization and the transfer of parasites (Dudgeon *et al.*, 2006; Arthington *et al.*, 2016; Gallardo *et al.*, 2016). Lastly, overfishing is regarded as a persistent freshwater threat. Although the magnitude of bycatch might be greater in marine systems, it also affects a wide range of freshwater taxa (Allan *et al.*, 2005).

This diverse array of threats combined with the declining rates of freshwater fish highlight the need of robust monitoring schemes (Radinger *et al.*, 2019). Analyses of temporal changes and trends in fish populations can be extremely useful in understanding the relationships between different biotic and abiotic factors and freshwater fish abundance as well as to detect the effects of these stressors. Such task, however, can be rather challenging due to the lack of long-term datasets (White, 2018). Ultimately, the examination of long-term trends in fish abundance can improve understanding of population fluctuations caused by either natural variation or anthropogenic influence and further augment the ability to diagnose, predict and respond to potential stressors (Radinger *et al.*, 2019).

The Prespa wetland, formed by two natural lakes Mikri Prespa and Megali Prespa (Crivelli and Catsadorakis, 1997), is situated in south-eastern Europe between Albania, North Macedonia and Greece (40.8N, 20.9E). The lakes are of Tertiary origin and among the oldest ones in Europe. They are located at 850 metres above sea level (m a.s.l.) enclosed by mountains rising to over 2500 m a.s.l. (Crivelli *et al.*, 1997a). Mikri Prespa covers an area of 47.4 km^2 and is a shallow (maximum depth of 8 m) eutrophic lake with no permanent streams. The lake has limited outflow into Lake Megali Prespa through a narrow semi-artificial channel at its north-western side; additionally, a channel was dug in the southern part of the lake for irrigation purposes and operated for almost three decades (*ca* 1976- early 2000; Crivelli, 1990; Hollis and Stevenson, 1997). On the other hand, Megali Prespa is a much larger (253.6 km^2) and deeper (maximum depth of 55 m) mesotrophic lake with several permanent tributaries. The only natural outlet is an underground karstic connection with Ohrid lake (Matzinger *et al.*, 2006). The region is internationally recognized as one of Europe's most ecologically important areas or biodiversity "hotspots" and its fish fauna is characterized by high endemism (Crivelli, 1997a; Wagner and Wilke, 2011). Human action has affected the lakes throughout the years, especially Mikri Prespa, with main impacts on its hydrological system through water irrigation and regulation: until the mid '60s the two lakes' water levels were equal and jointly fluctuated but over the course of years a sluice was placed in the semi-artificial channel permitting Lake Mikri Prespa to stand above Lake Megali Prespa with water outflowing to the latter when necessary. The channel was eventually reconstructed into a concrete deep and narrow channel and a sluice gate was installed and operated since 2005 to regulate water level aiming to sustain both local economy and the lake's good ecological status (Hollis and Stevenson, 1997; Parisopoulos *et al.*, 2009). Furthermore, the area used to support an important fishery but eventually fishing intensity has dropped, reflecting overall patterns of inland fisheries in Europe (Cowx, 2015). Active traditional fishing methods, such as the "pelaizia", have been abandoned since the early 2000s (Crivelli *et al.*, 1997a; Catsadorakis *et al.*, 2018). Finally, several non-native species were introduced through the years (Shumka and Apostolou, 2018) but only two invasive ones are currently established; the Topmouth gudgeon (*Pseudorasbora parva*), appeared in the 1970s and its abundance had increased significantly by the 1990s (Crivelli, 1990; Rosecchi *et al.*, 1993) and the Pumpkinseed (*Lepomis gibbosus*) that was first observed in the lakes in 1996.

The aim of this study is to summarize long-term patterns in fish biomass data of Prespa Lakes, collected over a period of 34 years, to identify the factors that play a role in shaping species-

Table 1. Average values and standard deviations (sd) of the environmental variables for both lakes.

Variable	Abbreviation	Mikri Prespa		Megali Prespa	
		Mean	SD	Mean	SD
Monthly average temperature (°C)	t.air	15	4.2	15.2	4.3
Monthly total precipitation (mm)	precipitation.mm	41.4	27.5	40.6	29.8
Monthly average water level (m a.s.l.)	water.level	854.1	0.4	844.6	0.7
Monthly average secchi disk (m)	secchi	1.7	0.6	3.23	1
Number of piscivorus birds (breeding pairs)	predation	663.5	482.5	1709.4	343.4
Water management (before/after 2005)[†]	water.management				
Introduction of Lepomis gibbosus (before/after 1996)	lepomis.intro				

[†]Only applicable for Mikri Prespa.

specific biomass trends and to disentangle the direct and indirect effects of various large-scale ecological stressors in the two different (ecologically and human-impacted) natural lake systems. Besides serving as a case study for quantifying the relative effects of different anthropogenic impacts at important areas for conservation, the results of the present study can be used to assist the development of effective management strategies.

2 Material and methods

2.1 Sampling

Data were collected for 26 monitoring years from 1984 to 2017 (1984–1985, 1990–1994, 1996–1998, 2000, 2002–2013, 2015–2017) in Lake Mikri Prespa and for 13 monitoring years from 1996 to 2017 (1996–1998, 2007–2013, 2015–2017) in Lake Megali Prespa. Gillnet monitoring was carried out three times per year (April, May, June) in both lakes to cover the whole spawning season. Sampling stations in each lake were located in the littoral zone; a shallower area (0.5–5 m) with a gravelly substrate and scattered vegetation in Mikri Prespa and a station close to the shore (0.9–2.2 m) with a sandy substrate near a stream outlet in Megali Prespa. Due to increase in macrophyte cover that interfered with gillnet setting, from 2015 onwards the sampling station in Mikri Prespa was relocated 150 m away. Two sets of 50 m monofilament gill-nets with 10 mesh sizes (10, 14, 18, 23, 27, 32, 38, 45, 52 and 60 mm) were deployed perpendicularly to the coast in both lakes. Nets were set for two consecutive days and were visited daily. All fish were measured (fork length in mm), weighed (g) and sexed. For each sampling event, catches were standardized as biomass-per-unit-effort (BPUE) calculated as the aggregated weight of fish captured in each mesh size (g) per mesh surface area (m^2) and fishing duration (in hours). Before the statistical analyses BPUE values were transformed as: $\log_{10}(\text{BPUE}+1)$ to reduce the influence of exceptionally high biomass values.

2.2. Environmental variables

To investigate which environmental factor(s) may affect each species BPUE, we identified and collected data on 7 predictor variables characterizing abiotic, biotic and human-induced processes (Tab. 1). Monthly average air temperature and monthly total precipitation from 1984 to 2017 were retrieved from the meteorological stations located between the two lakes, and run by the Power Public Corporation S.A. Hellas, the Society for the Protection of Prespa (SPP) and the Ministry of Environment, Energy and Climate Change (https://kyy.hydroscope.gr/stations/d/200166/). Monthly data of the average water level for both lakes were collected throughout all years by the SPP as part of their long-term monitoring scheme. To quantify any predation pressure on fish abundance, we used the number of piscivorous birds (in breeding pairs) as a proxy (SPP, unpublished data): for Mikri Prespa we included numbers of Pygmy Cormorant (*Microcarbo pygmaeus*) whereas for Megali Prespa we included pairs of both Dalmatian Pelican (*Pelecanus crispus*) and Great Cormorant (*Phalacrocorax carbo*), since these species differentially forage in each lake (Hatzilacou, 1993; Willems and de Vries, 1998). For each fishing month, Secchi disk transparency measurements were also recorded (20 cm diameter disc, ten replicates each time). The introduction of *Lepomis gibbosus* that took place in 1996 was included as a categorical variable with two levels (before/after 1996). Finally, a categorical variable for water management was included (before/after 2005) only for Mikri Prespa, where a reconstructed sluice gate regulating the flood of the littoral zone operates since January 2005.

2.3. Data analysis

Previous investigation on net selectivity (Boy and Crivelli, 1988; Crivelli *et al.*, 1997a) showed that some fish taxa are incorrectly sampled using the above method, since only the largest individuals can be caught in the 10 mm mesh size. Therefore, we limited our data analysis to a total of 10 species, seven of them native: Prespa spirlin (*Alburnoides prespensis*), Prespa bleak (*Alburnus belvica*), Prespa barbel (*Barbus prespensis*), Prespa nase (*Chondrostoma prespense*), European carp (*Cyprinus carpio*), Prespa roach (*Rutilus prespensis*), Prespa chub (*Squalius prespensis*), and three introduced: Prussian carp (*Carassius gibelio*), Pumpkinseed (*Lepomis gibbosus*) and the Tench (*Tinca tinca*). Although not an indigenous species, we considered *Cyprinus carpio* as native in the area as it was first introduced since Greco-Roman times (Barbieri *et al.*, 2015). Furthermore, *Tinca tinca* was not considered in the analyses for Lake Megali Prespa as it was rarely caught.

BPUE data can show periodic signals and non-linear patterns of temporal change, thus a General Additive Model

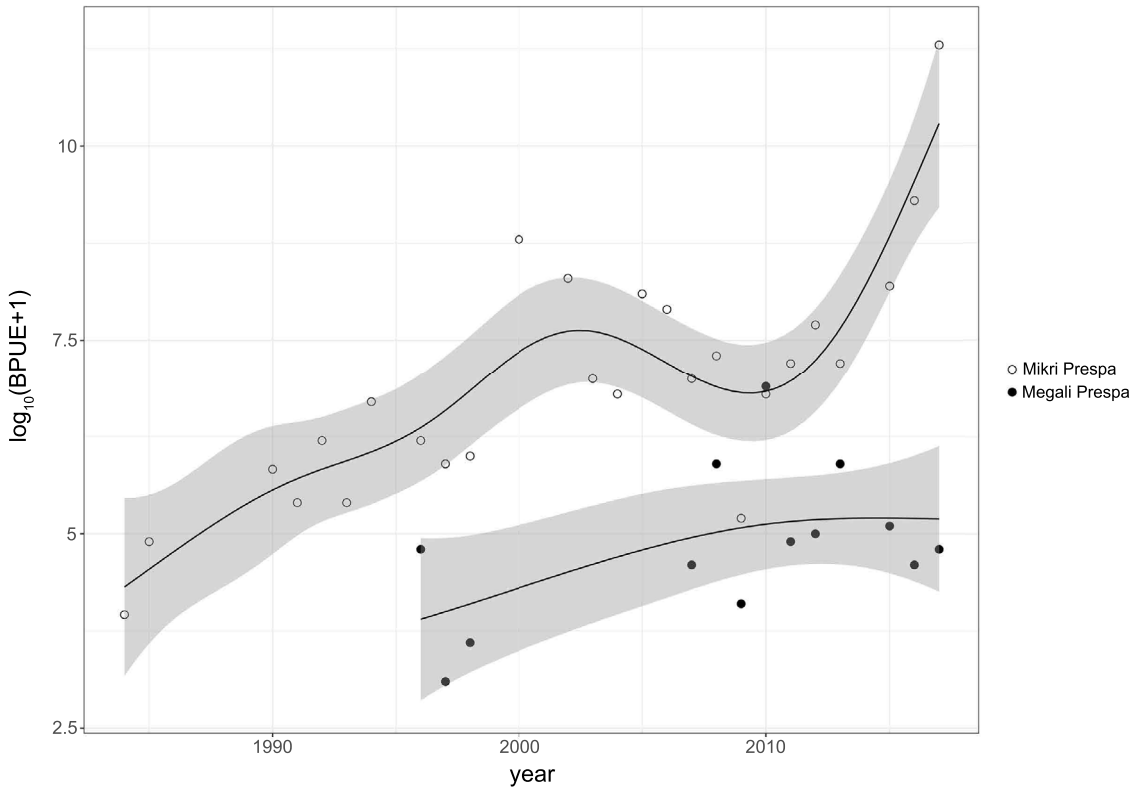

Fig. 1. Time series of mean annual catches expressed as biomass per unit effort (BPUE), for Mikri Prespa (open dots) and Megali Prespa (filled dots). Black line shows the smoothed trend and shaded areas show the 95% confidence limits.

approach (GAM) was used to model the overall and species-level temporal BPUE trends as a smooth nonlinear function of time. GAMs were built in the "mgcv" package (Wood, 2018) in R 3.6.2 (R Core Team, 2019) using the Restricted Maximum Likelihood (REML) estimation method. Since the relocation of the sampling station in Mikri Prespa after 2015 could have influenced BPUE trends, we tested for such effect by examining any structural changes in the mean of the monthly BPUE changes over time. The analysis was performed using the "strucchange" R package (Zeileis *et al.*, 2002). Tests against changes were conducted using the Ordinary Least Squares (OLS)-based cumulative sum (CUSUM) process and the corresponding significance test. When significant results were obtained, changes were dated by applying the function 'breakpoints' which allows for the simultaneous estimation of multiple breakpoints along with their respective 95% confidence intervals (Zeileis *et al.*, 2003). The optimum number of breakpoints in each species trend was evaluated using the Bayesian Information Criterion (BIC). When a breakpoint (along with its confidence intervals) included 2013 for any species (no fishing occurred in 2014), BPUE data for years 2015–2017 were not included in subsequent analyses.

The influence of environmental variables was assessed for all fish species in both lakes using an analytical approach based on random forests. A random forest is a powerful machine-learning algorithm based on regression/classification tree ensembles that does not require assumptions such as linear or nonlinear relationships between predictors and response factors (Breiman, 2001; Cutler *et al.*, 2007). Models were fitted using the R package 'randomForest' (Liaw and Wiener, 2002) using 500 trees and two random variables at each split. Model performance was assessed based on its respective Mean of Squared Residuals (MSR) and pseudo R^2. Furthermore, we used the R package "rfUtilities" (Evans and Murphy, 2015) to perform significance tests on the built models. The importance of the predictors was tested for statistical significance ($p < 0.05$) using a permutation approach (Altmann *et al.*, 2010) as implemented in the R package "pRF" (Chakravarthy, 2016). The number of permutations was set to 1000. The permuted importance values of environmental factors influencing the biomass of fish species were then rescaled from 0 to 100.The variable regarding predation (number of breeding pairs), that showed high variation was square-root transformed before the data analysis. Finally, the direction and magnitude of the effect of the most important variables on BPUE was evaluated through partial dependence plots (Elith *et al.*, 2008).

3 Results

Total annual BPUE in Lake Mikri Prespa showed an increasing trend through the years ($R^2_{adj.} = 0.75$, $p < 0.001$) whereas total annual BPUE was found to be rather stable in Megali Prespa ($R^2_{adj.} = 0.23$, $p = 0.15$; Fig. 1). Mean annual BPUE values were constantly higher in Mikri Prespa compared to those of Megali Prespa ($t = 5.28$, df = 12, $p < 0.001$). The highest overall mean BPUE in Mikri Prespa took place in June, with a value of 177.7 g h^{-1} m^{-2}, although May was also a prolific fishing month with a mean BPUE value of 165.1 g h^{-1} m^{-2}. On the other hand, May held the highest

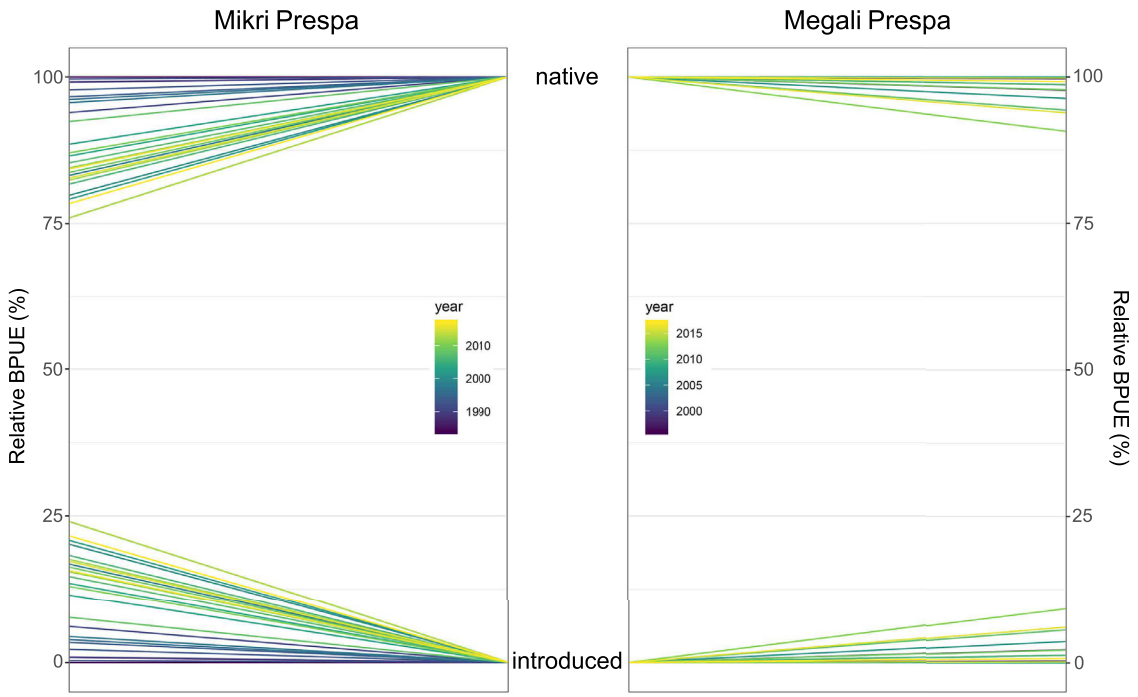

Fig. 2. Parallel coordinates plots of relative BPUE (expressed as a percentage of the total annual BPUE) for each fishing year and lake.

BPUE in Megali Prespa with a mean value of 171.3 g h^{-1} m^{-2} (Tab. S1). At the species-level, *Alburnus belvica* was the most prominent species in Mikri Prespa with an overall mean annual BPUE of 73.9 g h^{-1} m^{-2}, comprising 65.8% of the total annual BPUE. In Lake Megali Prespa, *Rutilus prespensis* was the species with the highest mean annual BPUE (48.9 g h^{-1} m^{-2}, 49.9% of total annual BPUE; Tab. S1). When examining BPUE from a species provenance perspective (native/introduced), it seems that the relative BPUE of introduced species is increasing through the years in Mikri Prespa where they were found to comprise more than 20% of the total BPUE in 2017, in contrast to less than 1% until 1990 (Fig. 2). However, no such process was evidenced in Megali Prespa.

There was high species-specific variation in BPUE trends during the monitoring scheme (Fig. 3). In Lake Mikri Prespa, only two out of 10 species were found to have stable trends, *Chondrostoma prespense* ($R^2_{adj.} = 0.03$, $p = 0.29$) and *Rutilus prespensis* ($R^2_{adj.} = 0.03$, $p = 0.07$). The BPUE of both *Alburnoides prespensis* and *Barbus prespensis* showed an overall decreasing trend ($R^2_{adj.} = 0.57$, $p < 0.001$; $R^2_{adj.} = 0.31$, $p < 0.001$ respectively). Although *Alburnus belvica* BPUE showed a high variation within years, overall it presented an increasing trend ($R^2_{adj.} = 0.04$, $p < 0.05$). The BPUE of *Carassius gibelio* showed a slight increase until 2005 (95% CIs = 2004-2013), followed by a decline ($R^2_{adj.} = 0.15$, $p < 0.05$). *Lepomis gibbosus* BPUE increased abruptly since its introduction in 1996, reaching a mean annual BPUE value of 18.4 g h^{-1} m^{-2} in 2002. After that, BPUE fluctuated irregularly with high variation between years ($R^2_{adj.} = 0.43$, $p < 0.001$). *Squalius prespensis* and *Cyprinus carpio* also showed fluctuations in BPUE through time; although for *Squalius prespensis* an overall slight increase was identified ($R^2_{adj.} = 0.27$, $p < 0.001$), this was not the case for *Cyprinus carpio*. Its BPUE first increased in the early '90s, then slightly declined before increasing again reaching its maximum observed BPUE in May 2008 with 34.7 g h^{-1} m^{-2}. Despite these fluctuations the species overall BPUE showed an increasing trend ($R^2_{adj.} = 0.51$, $p < 0.001$). Finally, *Tinca tinca* showed a slight increase through the years ($R^2_{adj.} = 0.55$, $p < 0.001$). It should be noted that for three species (*Alburnoides prespensis*, *Barbus prespensis* and *Tinca tinca*) a common breakpoint was identified around 2012–2013, which is consistent with the change in the sampling station as stated in the methods section. In Lake Megali Prespa, trends in BPUE were more straightforward (Fig. 3b). Four out of nine species examined showed stable trends in BPUE (*Alburnus belvica*, $R^2_{adj.} = 0.01$, $p = 0.26$; *Barbus prespensis*, $R^2_{adj.} = 0.02$, $p = 0.93$; *Chondrostoma prespense*, $R^2_{adj.} = 0.02$, $p = 0.56$; *Lepomis gibbosus*, $R^2_{adj.} = 0.04$, $p = 0.13$). Another four species showed increasing BPUE trends (*Carassius gibelio*, $R^2_{adj.} = 0.22$, $p < 0.05$; *Cyprinus carpio*, $R^2_{adj.} = 0.17$, $p < 0.05$; *Rutilus prespensis*, $R^2_{adj.} = 0.13$, $p < 0.05$; *Squalius prespensis*, $R^2_{adj.} = 0.27$, $p < 0.05$), whereas *Alburnoides prespensis* was the sole species found to be in slight decrease ($R^2_{adj.} = 0.12$, $p < 0.05$).

Random forest model performance differed considerably across species. In Mikri Prespa, models performed poorly for three out of ten species, *Carassius gibelio* (MSE = 0.03, $R^2 = 0.01$, $p = 0.07$), *Rutilus prespensis* (MSE = 0.07, $R^2 = -0.05$, $p = 0.18$) and *Squalius prespensis* (MSE = 0.07, $R^2 = 0.03$, $p = 0.06$). In Megali Prespa models explained none of the variation for five out of nine species: *Alburnoides prespensis* (MSE = 0.09, $R^2 = -0.07$, $p = 0.12$), *Barbus prespensis* (MSE = 0.03, $R^2 = -0.25$, $p = 0.67$), *Carassius gibelio* (MSE = 0.08, $R^2 = -0.12$, $p = 0.32$), *Rutilus prespensis* (MSE = 0.29, $R^2 = 0.001$, $p = 0.06$) and *Squalius prespensis* (MSE = 0.1, $R^2 = 0.001$, $p = 0.06$). Five environmental variables showed an influence on seven species' BPUE in Mikri Prespa

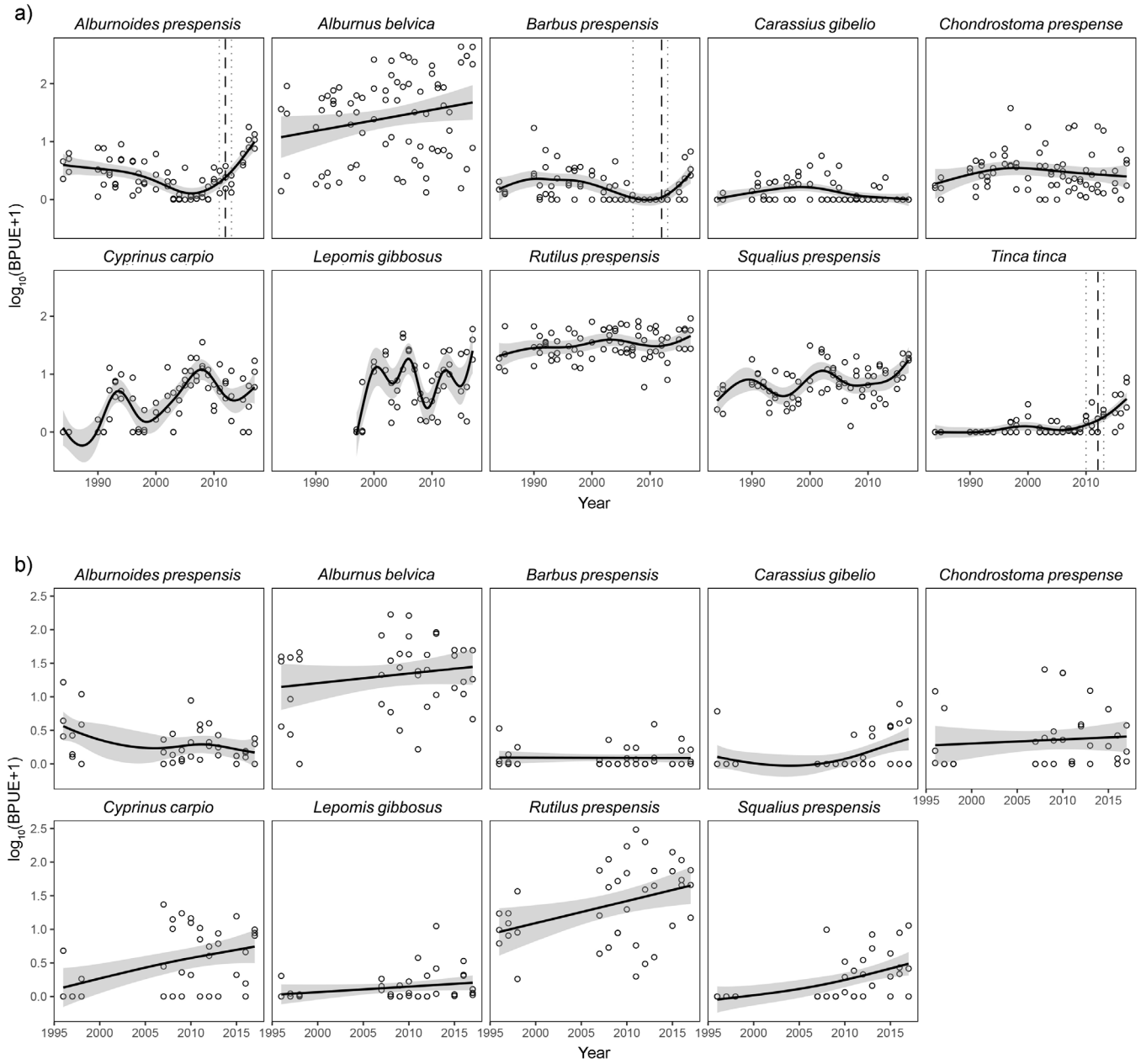

Fig. 3. Smoothed BPUE trends (black lines) along with 95% confidence limits (shaded areas) for all species examined in a) Mikri Prespa and b) Megali Prespa. Vertical dashed lines correspond to structural change points (along with 95% CIs in vertical dotted lines) attributed to the station relocation.

whereas only two variables showed a significant importance for four species in Megali Prespa (Fig. 4). Air temperature was the factor that affected most species in both lakes (Fig. 5). In Mikri Prespa both *Alburnus belvica* and *Lepomis gibbosus* BPUE showed a positive relationship with increasing temperature while *Chondrostoma prespense* showed the opposite pattern. The exact same relationships between BPUE of these three species and temperature were also obtained for Megali Prespa, with the addition of *Cyprinus carpio*, which showed the highest BPUE values in temperatures above 20 °C. The introduction of *Lepomis gibbosus* in 1996, seems to have a negative impact on *Alburnoides prespensis* BPUE (Wilcoxon rank sum test: $p < 0.001$; Fig. 5a). *Tinca tinca* showed an increase after *Lepomis* introduction but based on the trend analysis this is a correlation rather than causal relationship. Water management in Mikri Prespa seems to be beneficial for *Cyprinus carpio* but quite detrimental for *Barbus prespensis*, with the species' mean BPUE in the period 2005–2017 being 95% lower than that from 1984 to 2004 (Wilcoxon rank sum test: $p < 0.001$; Fig. 5a). Predation by piscivorous birds (*Microcarbo pygmaeus*) in Mikri Prespa was found to be important for *Cyprinus carpio* and *Tinca tinca* BPUE, showing

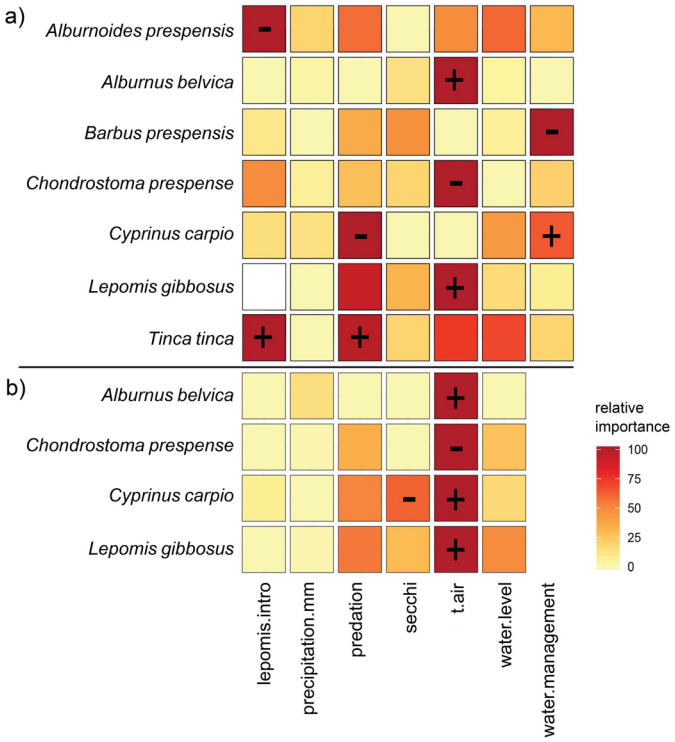

Fig. 4. Relative importance of environmental variables in the BPUE of species for a) Mikri Prespa and b) Megali Prespa, based on the Random Forest models. Descriptions of environmental factors are presented in Table 1. Plus (+) and minus (−) symbols show the direction of the effect (positive and negative respectively) only for variables with statistically significant importance after 1000 permutations.

a negative relationship with the former and a positive one with the latter, which most probably is another correlation rather than causation. Finally, *Cyprinus carpio* BPUE in Mikri Prespa was found to be negatively affected by water level, whereas the species BPUE displayed high values when Secchi disk transparency was low in Megali Prespa.

4 Discussion

Considering that Prespa Lakes host a fish community dominated by cyprinids, results are in accordance with the different trophic status of the lakes. Research has shown that cyprinids dominate highly productive lakes (Persson *et al.*, 1991) due to their omnivory and efficiency in zooplankton predation as well as their ability to adapt to turbid waters (Persson *et al.*, 1991; Schiemer and Wieser, 1992). On the other hand, in the temperate lakes of Europe usually percids are expected to be the most abundant species in mesotrophic waters but they are not common in Greece (Crivelli, 1992). However, *Rutilus rutilus*, a cyprinid species, has also been found to strongly dominate mesotrophic lakes (Olin *et al.*, 2002), as is the case in Lake Megali Prespa where *Rutilus prespensis* shows the greatest increase in BPUE over time (Fig. 3). In fact, our results suggest that lower values of Secchi disk transparency in Megali Prespa, are associated with increased biomass of *Cyprinus carpio* (Fig. 5). Since eutrophication can induce changes in biotic and abiotic environmental factors it is expected that eutrophic lakes would show less stability than mesotrophic ones and this could be reflected in species trend patterns: in Mikri Prespa only two species showed stable trends, two were found to be decreasing whereas the rest six species showed an increase albeit with several fluctuations. Contrastingly, in Megali Prespa four species were found to be stable in terms of BPUE and only one showed a significant decline (Fig. 3). A significant increase in the biomass of introduced species was observed in Mikri Prespa (Fig. 2), that is mainly driven by *Lepomis gibbosus*. Though the species first appeared in 1996, it showed the greatest increase over time in Lake Mikri Prespa and by 2002 its population had become well-established. In 2017 the species BPUE had more than doubled, making it the third most abundant species in the lake. It should be noted, especially since we used biomass-based estimates (BPUE) from gillnet sampling, that some underestimation may have taken place regarding both the smaller individuals (as mentioned in the methods section; Olin *et al.*, 2009) and the larger individuals of some fish species (*i.e. Cyprinus carpio*, *Tinca tinca*; Šmejkal *et al.*, 2015). However, since gillnet sampling was constantly used throughout the study period, data are sufficient to calculate species trends and provide an informative assessment of factors that shape them.

The analyses of the possible impact of environmental factors on fish biomass further reflect the differences between the two lake systems; more factors seem to be implicated in explaining species trends in the smaller, shallower and more variable Mikri Prespa than in the larger, more stable Megali Prespa (Fig. 4). Additionally, the high variation in BPUE that was predominantly higher for the rarer species has probably incurred difficulties in isolating any significant factor for them. It should be further noticed that despite the large number of monitoring years encompassed in this study, the strength of the detected environmental effects should generally be interpreted in relation to the seasonal sampling duration that only covers the spawning period. Air temperature was the most prominent environmental factor shaping the biomass patterns of species in both lakes. In general, our results on the effect of temperature in BPUE should firstly be interpreted as reflecting the activity patterns of species rather than a long-term effect. Our sampling scheme using gill-nets is a passive method and therefore catches are intertwined with spawning timing that is temperature-driven. *Chondrostoma prespense* was the only species that showed high values of BPUE in lower temperatures, a result further reflected in the species monthly BPUE patterns with the highest values occurring always in April in both lakes. This is congruent with the species' ecology, as *Chondrostoma prespense* does spawn in late March to May with optimal temperatures ranging between 10 and 15 °C for embryo and larvae development respectively (Crivelli *et al.*, 1997b; Souchon and Tissot, 2012). Although stability of the species' trend in both lakes indicates that increasing temperature has not affected population biomass over the years, the species could face severe difficulties coping with future climate warming scenarios due to increased mortality of eggs and larvae (Kamler *et al.*, 1998). Like other Cyprinids, *Alburnus belvica* and *Cyprinus carpio* BPUE proved to be enhanced by warmer temperatures, as was the BPUE of *Lepomis gibbosus*. Warmer temperatures have been found to

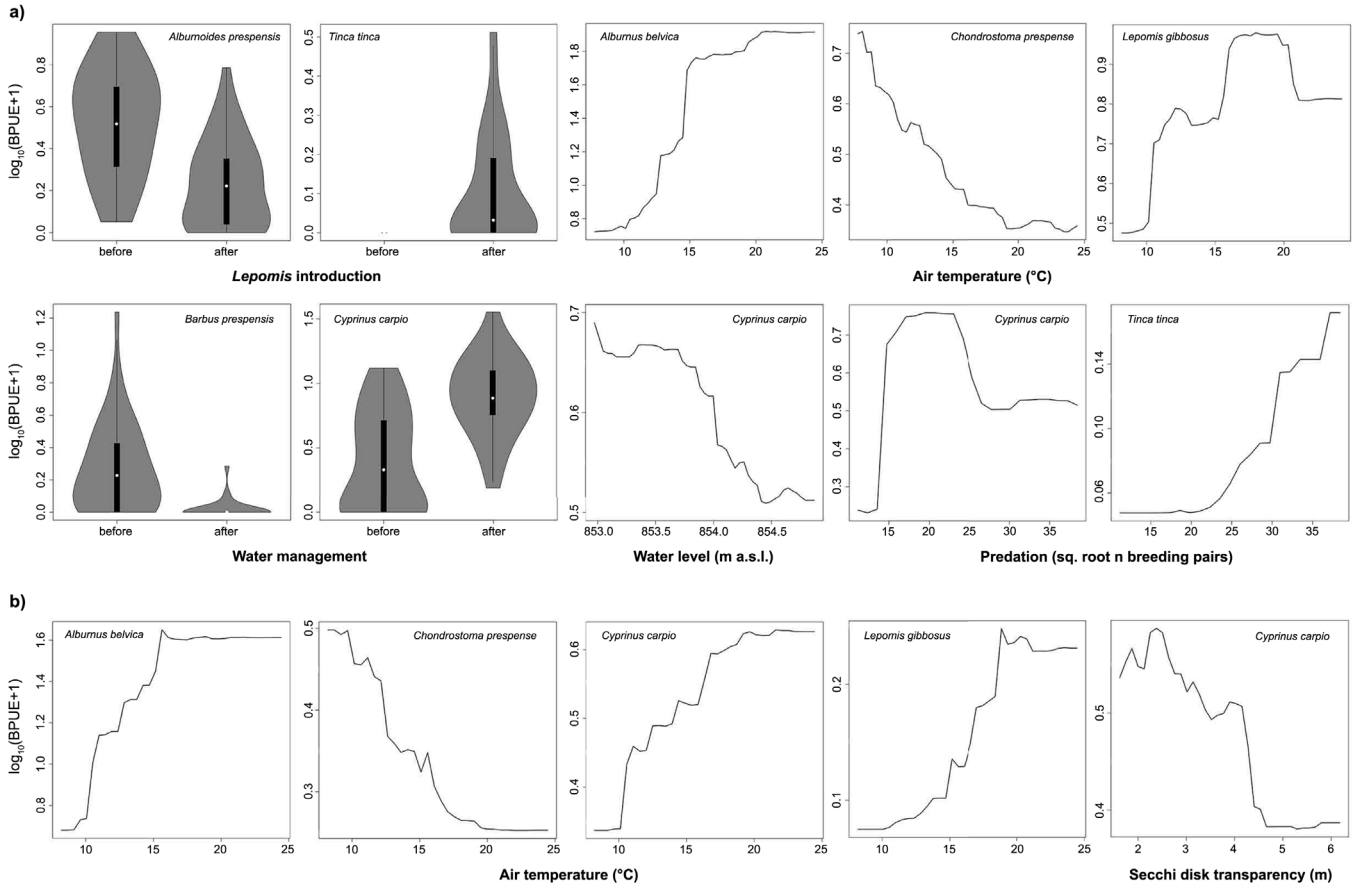

Fig. 5. Partial dependence plots showing the relationship between biomass per unit effort (BPUE) and significant environmental variables for a) Mikri Prespa and b) Megali Prespa.

favour a longer breeding season and earlier maturity for *Lepomis gibbosus* (Fox and Crivelli, 2001), while warmer climate is predicted to benefit the species recruitment thus increasing interactions with native fish species in the future (Zięba *et al.*, 2015; Copp *et al.*, 2017).

However, some effects of the introduction of *Lepomis gibbosus* may already be apparent since the long-term monitoring of the lakes made it possible to pinpoint the exact year when the introduction of the species took place. Our results suggest that the species' introduction constitutes an important stressor affecting the endemic *Alburnoides prespensis* BPUE with the beginning of its decline coinciding with the period of *Lepomis* establishment in Mikri Prespa. Disentangling causes of change in native fish communities can be very challenging since freshwater ecosystems are subject to both anthropogenic habitat modifications and non-native species invasions, often at the same time. An interesting approach to non-native species effects on native ecosystems is the driver versus passenger models proposed by MacDougall and Turkington (2005). According to these models, non-native species may act either as direct drivers of change or as "passengers", successfully establishing populations but having low or no effects on ecosystems already affected by other non-interactive factors. In the case of Mikri Prespa, *Pseudorasbora parva* that was introduced in the 1970s may have played the "passenger" role, as despite the fact that its diet overlaps with that of *Alburnoides prespensis*, no population declines had been observed until the 1990s (Rosecchi *et al.*, 1993). The subsequent introduction of *Lepomis* therefore, could work in synergy and thus represent an additional pressure through food resource competition (van Kleef *et al.*, 2008; Almeida *et al.*, 2014; Copp *et al.*, 2017). Although the species has been introduced and adapted successfully in several freshwater ecosystems in Greece (Economidis *et al.*, 2000), its potential impacts are largely unknown (Perdikaris *et al.*, 2016). However, declines in the abundance of native fish species after *Lepomis gibbosus* introduction has been recently reported from another lake in Greece (Bobori *et al.*, 2019), where it was found to compete with most native cyprinids.

Our results suggest that *Barbus prespensis* experienced a severe reduction in BPUE through the years with water management being the main driver behind this decline. This result should be interpreted with caution; the fact that after the relocation of the sampling station in 2013 in a less macrophyte-infested area the species BPUE showed an increase, suggests that the species abundance might not be depleted yet. However, these facts provide evidence of an indirect effect of water management. *Barbus* species are lithophilus, spawning in littoral areas with gravelly and sandy substrate (Catsadorakis *et al.*, 1996). Increased vegetation in the littoral zone could have been triggered before the beginning of water management as a result of increased eutrophic conditions.

Then, the sluice gate has been regulating water level since 2005, leading to less extreme fluctuations in the flooding of the littoral zone (Fig. S1) and subsequently to increased vegetation (Evtimova and Donohue, 2016), thus restricting species' access to inundated bare substrates needed for successful reproduction (Probst *et al.*, 2009; Britton and Pegg, 2011). Therefore, suitable spawning habitats may disappear under the present water management, rendering *Barbus prespensis* of future conservation concern. Revisiting the indicators developed for the evaluation of lake level control (Parisopoulos *et al.*, 2009), should also be prioritized. On the other hand, water management seems to be quite positive for *Cyprinus carpio*. This seems to be a rather contradictory result, since the species' successful reproduction largely depends on the existence of well-flooded wet meadows in the area (Kazoglou *et al.*, 2004). In fact, a remarkably successful breeding in 1991 coincided with a high spring water level of almost 855 m a.s.l., much higher than a water level value of 854.6 m a.s.l. which is considered as the minimum for highly successful spawning (Crivelli *et al.*, 1997a; Fig. S2). Our random forest models, however, suggest that species biomass is higher at lower water levels, indicating that satisfactory *Cyprinus* recruitment is possible under the current management regime (Fig. S2). It should be noted that water management is probably not the sole reason responsible for the species' increased BPUE. By the beginning of water management the species had already started to recover probably due to the exceptional breeding year mentioned above coupled with lower fishing pressure and reduced poaching events (Crivelli *et al.*, 1997a). Therefore, large individuals (that were formerly caught by fishermen) showed increased survival and thus contributed to the breeding pool. That may also be true for other increasing species in Mikri Prespa (*e.g. Squalius prespensis*), although the lack of reliable fishery statistics make that hypothesis difficult to test. Future collection of such information could further elucidate any relationship with fish abundance.

Considering that Prespa lakes are well known for harboring an abundant community of piscivorous birds, we also tested for any effect of predation on fish species BPUE. Birds can impose substantial mortality on fish (Steinmetz *et al.*, 2003), and Prespa lakes host a diverse avifauna with hundreds of *Phalacrocorax carbo* breeding pairs, the largest breeding colony of *Pelecanus crispus* in the world, currently numbering around 1300 breeding pairs as well as several hundred breeding pairs of *Pelecanus onocrotalus* (Catsadorakis *et al.*, 2015). Both pelicans and cormorants have been found to primarily prey on *Alburnus belvica* (Pyrovetsi and Economidis, 1998; Grémillet *et al.*, 2012), therefore our hypothesis was that predation could have affected the species BPUE. However, our results did not show any clear effect of predation. *Alburnus belvica* showed a stable trend in Megali Prespa and seems that thanks to its life history strategy it can cope with both high predation and fishing pressure, as it is also a target species for fishermen (Crivelli, 1992). The only negative effect of predation was shown for *Cyprinus carpio* in Mikri Prespa led by *Microcarbo pygmaeus* numbers. Pygmy Cormorants have indeed been found to prey upon *Cyprinus carpio* in Mikri Prespa (Willems and de Vries, 1998), however, the level on which predation could seriously affect *Cyprinus carpio* on the population level, remains unclear. Asymmetric predation on different age classes (Beckmann *et al.*, 2006) along with the vulnerability of fish that have been stocked in numerous occasions (Kortan and Adámek, 2011) could play some role but further research is needed to determine if this result is something more than a coincidental relationship, especially since *Cyprinus carpio* population shows an increasing overall trend.

Overall, the data collected in this study provide a significant contribution to the exploration of the ecology and dynamics of fish community in an ecologically important region. The analysis showed the importance of long-term monitoring in distinguishing between natural variation and direct versus indirect effects of large-scale stressors on fish biomass as well as the improvement in our understanding of freshwater ecosystems, contributing to the preservation and management of freshwater fish populations. Future monitoring efforts should take into account the different species' life histories as they can be differentially impacted by different stressors (long-lived species could need much more time to recover from a decline than short-lived ones; Crivelli, 1992). Intensified efforts to further assess and mitigate the impact of invasive alien species, improve the compatibility of current water management scheme with preservation of littoral habitats, and preparatory actions to help cope with future changes due to climate warming should be undertaken in order to sustain the integrity of fish communities and promote the conservation of natural resources.

Conflict of Interest

The authors declare no conflict of interest.

Data Availability Statement

A summary of the data used in this paper is available as Supporting Information. Raw monitoring data are available from the corresponding author (A.J.C) upon reasonable request.

Supplementary Material

Table S1. Mean biomass per unit effort (BPUE) along with standard error (SE) and range (min-max), for each sampling month and for the annual mean for each lake.
Figure S1. Violin plots depicting the distribution of water level values before and after the beginning of water management in 2005.
Figure S2. Time series of mean annual catches expressed as biomass per unit effort (BPUE), for Cyprinus carpio in Mikri Prespa along with mean spring water level (April–June).

The Supplementary Material is available at https://www.kmae-journal.org/10.1051/kmae/2021027/olm.

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Author Contributions

AJC and GC conceptualised the study. AB, GC, DN and AJC designed the study. GC, IK, HN, MM and AJC collected the data. AB analysed the data. AB drafted the manuscript with input from all other authors.

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