FISHERIES & AQUATIC LIFE (2022) 30: 112 - 124
Archives of Polish Fisheries
DOI 10.2478/aopf-2022-0011

RESEARCH ARTICLE

The fish community of the ancient Prespa Lake (Southeast Europe): Non-indigenous species take over

Michael Pietrock, David Ritterbusch, Wolf-Christian Lewin, Spase Shumka, Zoran Spirkovski, Dusica Ilik-Boeva, Uwe Brämick, Ralf Peveling

Received – 19 April 2022/Accepted – 31 August 2022. Published online: 30 September 2022; ©Inland Fisheries Institute in Olsztyn, Poland
Citation: Pietrock, M., Ritterbusch, D., Lewin, W. C., Shumka, S., Spirkovski, Z., Ilik-Boeva, D., Brämick, U., Peveling R. (2022). The fish community of the ancient Prespa Lake (Southeast Europe): Non-indigenous species take over. Fisheries & Aquatic Life 30, 112-124.

Abstract. Greater Prespa Lake, located on the Balkan Peninsula, is an ancient freshwater lake inhabited by numerous endemic and endangered species and represents an important part of Europe's natural heritage. Between 2013 and 2015, standardized gillnet fishing was conducted for the first time ever with the aim of obtaining large-scale information on the status of the fish community in terms of the relative abundance, biomass, and spatial distribution of the species occurring in the lake. Although 15 fish species were caught, the catches were numerically dominated by just five – the native Prespa roach (*Leucos basak)*, Prespa bleak (*Alburnus belvica),* and Prespa spirlin (*Alburnoides prespensis*), and the non-indigenous bitterling (*Rhodeus amarus*) and topmouth gudgeon (*Pseudorasbora parva*). Overall, the non-indigenous fishes combined outnumbered the native species, while Prespa bleak, Prespa spirlin, Prespa roach, and bitterling accounted for the highest biomass proportions. The fish assemblages of the northeastern and southwestern basins were more similar to each other than to the fish communities at the other sampling sites. The results indicated that non-indigenous fishes have become well established in the lake within just 20 to 40 years of their initial introduction. Altogether, the current data provide a solid basis for the knowledge-based management of the aquatic resources of this precious freshwater body.

Keywords: Balkan Peninsula, biodiversity, endemism, fish, invasive species, transboundary management

M. Pietrock [✉], D. Ritterbusch, U. Brämick
Institute of Inland Fisheries Potsdam-Sacrow, Im Königswald 2, 14469 Potsdam, Germany
E-mail: michael.pietrock@ifb-potsdam.de, Telephone: +49-(0)33201-406-15, Fax: +49-(0)33201-406-40

W.-C. Lewin
Thünen Institute of Baltic Sea Fisheries (Thünen-OF), Alter Hafen Süd 2, Rostock, Germany

S. Shumka
Agricultural University of Tirana, Faculty of Biotechnology and Food, Kodër Kamëz, SH1, Tirana, 1000, Albania

Z. Spirkovski, D. Ilik-Boeva
Hydrobiological Institute Ohrid, Naum Ohridski 50, 6000 Ohrid, North Macedonia

R. Peveling
Deutsche Gesellschaft für Internationale Zusammenarbeit, Postfach 5180, 65726 Eschborn, Germany
Department of Environmental Sciences, University of Basel, St. Johanns-Vorstadt 10, 4056 Basel, Switzerland

Introduction

Over the past few decades, the introduction of non-indigenous species into new environments, whether intentional or unintentional, has increasingly become a topic of concern to environmental scientists, regulators, and the general public. One reason for this concern is that introduced species can become invasive, thus negatively impacting native flora and fauna, ecosystem services, and human well-being (IUCN 2021). Negative effects on native biota caused by newly-introduced species outside their natural ranges have been recorded across the world and can lead to, inter alia, biodiversity loss and species extinctions (Bellard et al. 2016, Doherty et al. 2016). Conversely, not every unintentional introduction of a species into a novel environment will result in its wider spread (and negative effects) because the invasion process is complex and comprises several stages, such as transport, introduction, establishment and spread, each of which presents hurdles or barriers that must be overcome by non-indigenous species for them to become invasive (Blackburn et al. 2011). Additionally, ecological impacts can vary depending on a variety of factors that might be related to the traits of the introduced species or the ecosystem that is being invaded, the nature, number, and strength of biological interactions among non-indigenous species and native species, their evolutionary background, and other factors (Ricciardi et al. 2013).

Greater Prespa Lake, hereafter referred to as Prespa Lake, is a large, relatively shallow natural freshwater body on the Balkan Peninsula that is shared by the riparian countries of Albania, North Macedonia, and Greece. With an estimated age of two to three million years (Reed et al. 2004), it is considered an ancient lake and, although its exact age is still under debate (Wagner and Wilke 2011, Pashko and Aliaj 2020), it is presumed to be one of the oldest existing lakes in Europe (Wagner et al. 2010). Based on its remarkable age and favorable environmental conditions, Prespa Lake is home to myriad animal and plant species, many of which are endemic to the lake or region (Albrecht et al. 2012, Griffiths et al. 2004). For this reason, the lake and its surrounding area form an important part of Europe's natural heritage that is regarded as a European and, as part of the Balkan Peninsula, a global hotspot of biodiversity (Myers et al. 2000, Griffiths et al. 2004, Darwall et al. 2014, van der Schriek and Giannakopoulos 2017).

The exceptional value of the lake both in terms of biodiversity and species conservation is also reflected by its unique fish community that includes several endemic species (Oikonomou et al. 2014). Among them are fishes with conservation statuses of either vulnerable, endangered, or critically endangered according to the Red List categories of the IUCN (Freyhof and Brooks 2011, Milošević and Talevski, 2015). To date, 26 fish taxa have been identified in Prespa Lake (Ilik-Boeva et al. 2017, Shumka et al. 2020, Trajchevski et al. 2020). With the exception of the catadromous European eel, *Anguilla anguilla* (L.), none of them is a migratory species. At present, the fish community of Prespa Lake faces many stressors such as increasing eutrophication, toxicant pollution, illegal fishing, climate change, and considerable annual water level fluctuations (Popovska and Bonacci 2007, Grazhdani et al. 2010, Markovic et al. 2017, Peveling et al. 2015, van der Schriek and Giannakopoulos 2017). Additionally, at the end of the twentieth century, several non-indigenous species were introduced into the lake, and knowledge about the status of these species in the lake is limited (Piria et al. 2018, Bounas et al. 2021).

Since ancient times, fish and fishery have played an important role in the lives of local people; thus, there is some information from faunistic surveys and catch statistics about the fish of Prespa Lake (Crivelli et al. 1997, Talevski et al. 2009, Grazhdani et al. 2010, Spirkovski et al. 2012 a, Shumka et al. 2015, Catsadorakis et al. 2018, Bounas et al. 2021). However, the available information is largely outdated, and catch statistics are affected by fishing effort (which is unknown) and reflects primarily market demand rather than real species abundance. Consequently, many species are currently exploited haphazardly with little if any knowledge about the status of stocks. The necessity of up-to-date sampling has, therefore, been called for repeatedly (Wagner and Wilke 2011, Shumka et al. 2015, Shumka and Apostolou 2018).

Multi-annual fishing campaigns have been conducted in Prespa Lake as part of the Technical Assistance program implemented by the Deutsche Gesellschaft für Internationale Zusammenarbeit (GIZ) in the EU-candidate countries of Albania and North Macedonia. For the first time ever, these were performed across national borders and employed a standardized method. The primary objective of the investigations was to provide information on the state of the fish community in terms of abundance and biomass, including threatened endemic and non-indigenous species. Additionally, as transboundary fishing resulted in the most comprehensive overview ever generated for this lake, it was of particular interest whether there are specific spatial patterns of fish species distribution in the lake.

Material and Methods

The hydrological and physicochemical conditions of Prespa Lake are given in detail in Peveling et al. (2015). Briefly, the Prespa Lakes Basin is a high altitude system with a catchment area of over 2,500 km^2. It comprises the Greater Prespa and the Lesser Prespa lakes, which are connected by a narrow artificial channel. Greater Prespa Lake, herein called Prespa Lake, is a subtropical dimictic waterbody situated at an altitude of 849 m a.s.l. It has a surface area of about 254 km^2 with maximum and mean water depths of 48 m and 14 m, respectively (Matzinger et al. 2006). Because of excessive nutrient inputs and subsequent eutrophication, its water chemistry reflects conditions typical of eutrophic lakes. Anoxic conditions below depths of 15 m as well as areas with limited oxygen content are currently regular phenomena during the summer season (Spirkovski 2004, Skarbřvik et al. 2010). Annual water temperatures fluctuate between about 1°C in winter and 27°C in summer (Peveling et al. 2015). The flora and fauna of the region is legally protected by national laws and the establishment of national parks in the respective riparian states.

Fish collection followed the recommendations in European standard EN 14757 (CEN 2015). As this standard was developed for lakes up to a size of about 5,000 ha, for sampling, Prespa Lake was divided into five sub-basins (SB) with SB 1 and SB 2 located in Albanian territory and SB 3–5 in North Macedonian territory (Fig. 1). Fish collection was conducted in lake areas belonging to these two countries since the GIZ Technical Assistance program targeted EU candidate countries but not EU member states. When deployed, the multi-mesh gillnets (MMG) covered lake areas of approximately 250–1,000 ha. The SBs sampled differed in part in physical and/or ecological conditions, such as bathymetry, wind exposure, and plant coverage (Blinkov et al. 2017). Briefly, the sampling sites were characterized as follows:

- SB 1 Liq (locality of Liqenas, AL): The bottom consisted of rocks and gravel along the entire shoreline up to depths of 5–6 m, and the littoral zone has scattered patches of reed (*Phragmites* sp.) belts.
- SB 2 Kal (Kallamas, AL): Physical conditions on the lake bottom were similar to those at SB 1. At the shoreline, however, there were extensive areas of reed belts growing into the lake up to about 40 m from shore.
- SB 3 Kon (Konjsko, MK): From the lakeshore to a depth of about 4 m, the substrate consisted of rocks and gravel, which became increasingly sandy as depth increased (up to 12 m). The aquatic flora in this area was composed primarily of *Phragmites* sp. and *Myriophyllum* sp.
- SB 4 Ote (Otesevo, MK): From the lake shoreline up to a depth of about 6 m the bottom was muddy substrate, and the entire area displayed extensive reed belts. In front of the reeds there were large

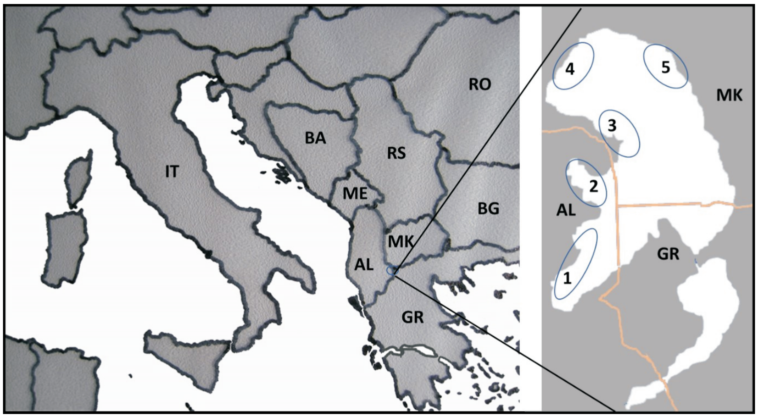

Figure 1. Geographic location (left) of Prespa Lake (North Macedonia/Albania/Greece) and the sub-basins sampled (1- Liqenas, 2 - Kallamas, 3 - Konjsko, 4 - Otesevo, 5 - Asamati, right).

fields of underwater vegetation (*Potamogeton* sp., *Myriophyllum* sp.)

- SB 5 Asa (Asamati, MK): This site was under the direct influence of the tributary of the Golema Reka River, which was the main source of nutrient loads from agricultural areas in the watershed (Matevski et al. 2013). The structure of the lake bottom as well as the extent and composition of the aquatic flora was similar to conditions at SB 4.

Fish sampling was done in fall (October and November, respectively) in 2013, 2014, and 2015 (Ilik-Boeva et al. 2017). Benthic MMG composed of 12 panels each 30 m long and 1.5 m deep were employed. Mesh sizes ranged from 5 to 55 mm knot to knot in a defined geometric series (CEN 2015). All nets were set before dusk, were in position overnight, and were collected after dawn (12 h of sampling) to cover both of the highest circadian activity peaks. The number of nets set per sampling site and year are shown in Table 1. At each SB fish were sampled in different directions relative to the shoreline at different depth strata between 0 and 12 m below the water surface. More details about the sampling methods (including GPS coordinates of the individual nets each year) are in Ilik-Boeva et al. (2017).

Table 1

Number of benthic multi-mesh gillnet set per sub-basin (SB) and year

Sub-basin	2013	2014	2015	Total
SB 1, Liqenas	32	32	32	96
SB 2, Kallamas	32	32	32	96
SB 3, Konjsko	12	40	40	92
SB 4, Otesevo	12	40	40	92
SB 5, Asamati	15	40	40	95

All fish caught were identified to the species, counted, weighed (to the nearest 0.1 g) and measured (total length to the nearest mm) with a portable balance and fish measuring board, respectively. If fewer than 50 specimens of each species were caught per panel, all the fish were measured individually. In cases when, for example, several hundred fish of a species were caught per panel, the length and weight of 50 specimens each were measured, and the total weight of all fish of that species was then determined and divided by the mean weight of a fish from the subsample to subsequently calculate the total number of individuals of that species.

Data analysis

Catch per unit effort expressed as number of individuals of species per net surface area (NPUE, ind. m^{-2}) and biomass of species per net surface area (BPUE, g m^{-2}) was calculated separately for each SB and year. The normality of distribution and homogeneity of variances were verified with the Kolmogorov-Smirnov and Levene's tests, respectively. Spatial comparisons in fish abundance (number of fish per net) were made using the nonparametric Kruskal-Wallis test followed by Bonferroni-corrected pairwise Mann-Whitney U-test (since the data did not meet normality and homogeneity of variance requirements for ANOVA).

The spatial distribution of the demersal fish assemblages was visualized with nonmetric multidimensional scaling (NMDS). Ordination was calculated from distance matrices based on square rooted numbers of the fish species caught per gillnet using the Bray-Curtis distance. The maximum number of iterations was set to 200. NMDS was performed using R software (version 3.4.2, R Development Core Team 2017) and the additional R picante package (Kembel et al. 2010). Two-way PERMANOVA was used to test for the influence of year and sub-basin on the demersal fish assemblage. PERMANOVA analysis was based on Bray-Curtis distance measure and 3,000 permutations. Prior to PERMANOVA, permutation tests were conducted to test for the homogeneity of multivariate dispersions. NMDS and PERMANOVA were performed using R software (version 3.4.2, R Development Core Team 2017) and the additional R picante (Kembel et al. 2010) and vegan (Oksanen et al. 2019) packages. To prevent the influence of different sample sizes on NMDS and PERMANOVA (Anderson and Walsh 2013), the number of nets per SB was narrowed down to 15 randomly chosen nets per sampled SB and year.

Results

During the three years of sampling, almost 62,000 fish were collected and analyzed. Using benthic MMG, 15 fish species were caught during the sampling campaigns (Fig. 2). Generally, the fish community of Prespa Lake is composed predominantly of five species (Table 2): Prespa bleak (*Alburnus belvica* (Karaman)); Prespa roach (*Leucos basak* (Heckel)); Prespa spirlin (*Alburnoides prespensis* (Karaman)); bitterling (*Rhodeus amarus* (Bloch)); topmouth gudgeon (*Pseudorasbora parva* (Temminck & Schlegel)).

Other species contributed only slightly numerically to the whole fish community (Fig. 2). In terms of absolute fish numbers, introduced species (especially topmouth gudgeon and bitterling) dominated the catches and clearly outnumbered native fishes. Roughly speaking, three out of five fishes were non-indigenous.

NPUE values (whole lake) varied among years and ranged from 233.98 to 431.93 ind. 100 m^{-2} net. Over time, site-specific NPUEs fluctuated between 107.94 and 569.23 ind. 100 m^{-2} net (Fig. 2). Prespa bleak, Prespa spirlin, bitterling, and Prespa roach contributed the most to the fish biomass in the samples (Fig. 2). Annual BPUE values for Prespa Lake as

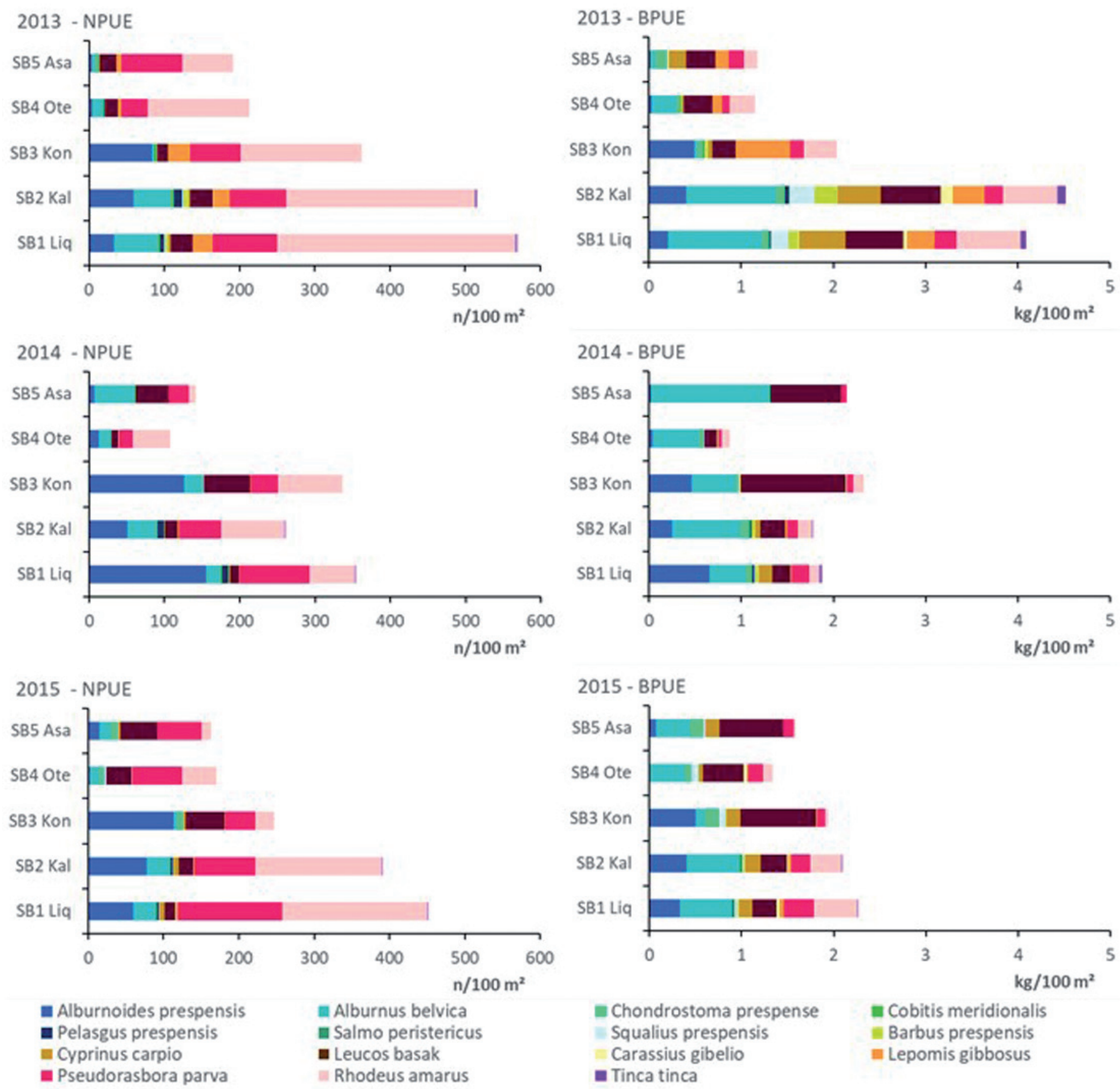

Figure 2. Standardized catches with benthic multimesh-gillnets in Prespa Lake in the three sampling years differentiated by lake basin. Left: catches by number, right: catches by biomass.

Table 2
Annual and total abundances of species (all sub-basins combined, in %)

Species	Endemism and IUCN Red List status[1]	Year 2013	2014	2015	Years (and sub-basins) combined
Alburnoides prespensis	e, VU	8.85	27.98	18.82	18.46
Alburnus belvica	e, VU	9.52	14.66	8.03	10.60
Barbus prespensis	n, LC	0.67	0.12	0.11	0.29
Carassius gibelio	i, NE	0.13	0.02	0.18	0.11
Chondrostoma prespense	e, VU	0.70	0.38	1.69	0.95
Cyprinus carpio	n, VU	0.58	0.13	1.37	0.72
Leucos basak	n, LC	6.78	13.33	12.86	11.03
Pelasgus prespensis	e, EN	1.24	1.27	0.38	0.94
Pseudorasbora parva	i, LC	16.44	17.99	26.42	20.53
Rhodeus amarus	i, LC	49.55	23.41	29.14	33.97
Squalius prespensis	e, LC	0.24	0.04	0.37	0.22
Tinca tinca	i, LC	0.28	0.05	0.04	0.12
Lepomis gibbosus	i, LC	4.79	0.30	0.43	1.80
Cobitis meridionalis	e, VU	0.24	0.328	0.15	0.22
Salmo peristericus	e, EN	0.005	0	0.01	0.005

[1]According to iucnredlist.org; e: endemic (to the lake or basin), i: introduced, n: native; VU: vulnerable, LC: least concern, NE: not evaluated, EN: endangered

Table 3
PERMANOVA results comparing the species composition of the net catches from different sub-basins of Prespa Lake in the 2013–2015 period (D.f.: degree of freedom, Sums of sqs.: sums of squares, Mean sqs.: mean squares)

Factor	D.f.	Sums of sqs.	Mean sqs.	F Model	r^2	p
Year	2	2.76	1.38	9.59	0.06	0.0003
SB	4	9.08	2.27	15.78	0.20	0.0003
Year:SB	8	4.80	0.60	4.17	0.10	0.0003
Residuals	204	29.35	0.14	-	0.64	-
Total	218	46.00	-	-	1.0	-

a whole fluctuated between 1.79 and 3.21 kg 100 m^{-2} net with introduced species contributing about one third of the overall biomass. Among sites, BPUE varied between 0.87 and 4.51 kg 100 m^{-2} net (Fig. 2).

In terms of species occurrence, locality (SB), and year (and their interactions), all three had a statistically significant effect on standardized species abundance (NPUE) but, as indicated by the low r^2 value, the influence of sub-basin was small and that of year was negligible (Table 3).

Global Multidimensional Scaling indicated that the fish assemblages of SBs 1 and 2, and SBs 4 and 5 were more similar to each other than to the fish assemblages in the other SBs (Fig. 3). With regard to species occurrence and abundance, SB 3 (Konjsko) was midway between SBs 1 and 2, and SBs 4 and 5, respectively (Fig. 3). The stress value of 0.28 indicated, however, that the data were not very well represented in the two-dimensional display of the data variation.

Even though the fish assemblages were similar at all SBs, there were, overall, both more individual fishes and species in the southwestern parts of the lake (SBs 1 and 2) than in the north/northeastern

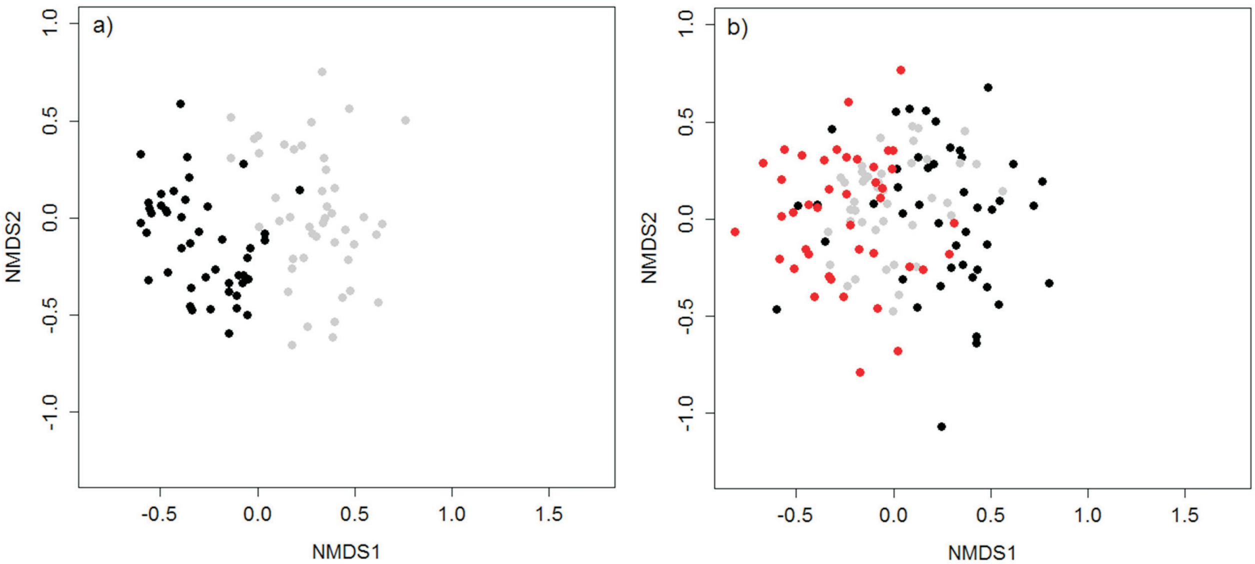

Figure 3. NMDS plot of the square root transformed CPUE (fish/net) for demersal fish assemblages in the five sub-basins. To improve readability, the NMDS plot is divided into plots (a) and (b). a) SB 1 (gray), SB 5 (black); b) SB 2 (black), SB 4 (red), and SB 3 (gray). The final stress value of 0.28 for the two-dimensional solution was reached after 20 iterations.

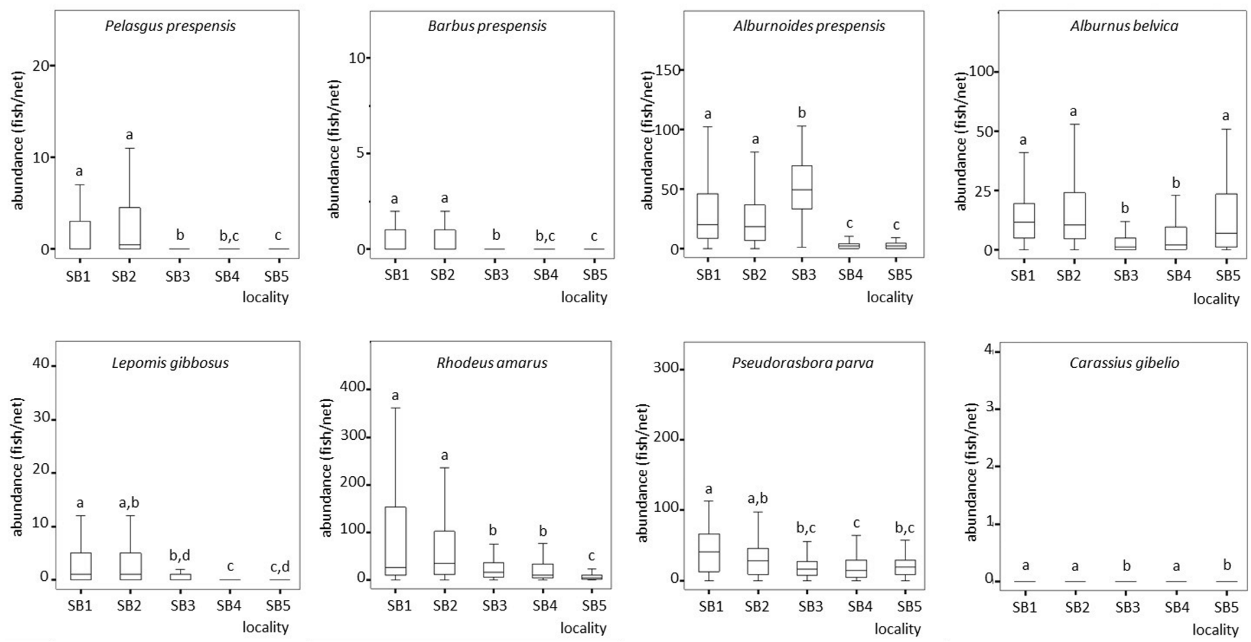

Figure 4. Abundance (fish per net, all years combined) of endemic Prespa minnow, Prespa barbel, Prespa spirlin, and Prespa bleak (top, left to right) and introduced pumpkinseed, bitterling, topmouth gudgeon, and Prussian carp (down, left to right) in different sub-basins (SB) of Prespa Lake. Boxplots reflect numbers (medians, 1^{st} and 3^{rd} quartiles) of fish per net for the different sub-basins. Significant differences among sampling sites are marked by different letters. Please note the different scaling of the y-axes.

areas. Furthermore, spatial comparisons at the species level revealed that, combined over all years, the abundances of Prespa minnow (*Pelasgus prespensis* (Karaman)) and Prespa barbel (*Barbus prespensis* (Karaman)) were both significantly higher at each SB 1 and SB 2 compared to the more northern sampling locations SB 3 to SB 5 (Fig. 4). Differences in the abundances of endemic species were also noted in Prespa spirlin and Prespa bleak (Fig. 4). Conversely, the abundance of Prespa nase (*Chondrostoma prespense* (Karaman)) was not significantly different among all five SBs (data not shown).

The introduced pumpkinseed (*Lepomis gibbosus* (L.)), bitterling, and topmouth gudgeon were, in overall, significantly more abundant at SB 1 and SB 2 (Fig. 4). Prussian carp (*Carassius gibelio* (Bloch)) numbers per net were statistically lower at SB 3 and SB 5 compared to the other sites. These differences, however, were marginal.

Discussion

Of the 26 fish species that have ever been recorded in Prespa Lake, 15 were sampled in the current study using MMG. Given the fact that several species, such as grass carp (*Ctenopharyngodon idella* (Valenciennes)), bream (*Parabramis pekinensis* (Basilewsky)), and rainbow trout (*Oncorhynchus mykiss* (Walbaum)) have not been caught over the past few decades and might be locally extinct by now, using MMG to sample fishes is a good method to obtain an overview of the fish inventory of Prespa Lake. Some fishes that could not have been caught included the Eastern mosquitofish (*Gambusia holbrooki* (Girard)) and the European eel, which was not surprising since, because of their small size or elongated shape, these species are underrepresented in gillnet catches or typically not caught with gillnets at all (Olin and Malinen 2003, Ravn et al. 2019). According to previous research, MMG fishing generally underestimates the relative abundance of individuals and species of fishes that are small (body lengths < 4–5 cm) and large (body lengths > 30 cm) (Olin and Malinen 2003, Šmejkal et al. 2015, Ravn et al. 2019). On the other hand, it overestimates the relative abundance of active species compared to passive and/or territorial species (Prchalová et al. 2010).

By standardizing the method applied and conducting transboundary sampling, the current study is the first ever to permit quantitative insights into the fish community on a larger spatial scale. The large portion of non-indigenous fishes in terms of both the number of individuals and biomass of the present fish stock was striking. The introduced species topmouth gudgeon and bitterling, in particular, appear to have exceptionally good conditions for survival, reproduction, and dispersal, and they seem to be able to withstand anthropogenic and natural stressors (such as eutrophication, water level fluctuations, interspecific competition) better than their native competitors. When assuming a similar catchability, the higher numbers of bitterling individuals (as reflected by higher NPUE values) relative to topmouth gudgeon were surprising since the reproduction of this fish is bound to the existence of bivalves (*Unio* spp. and *Anodonta* spp., respectively), and changes in bivalve population dynamics, therefore, should affect the bitterling population. Furthermore, considering that bitterling first appeared in the lake in the 1990s (topmouth gudgeon was introduced in the 1970s), this lake seems to offer ideal conditions for this species (Spirkovski et al. 2012a). Therefore, the available data show that, despite the considerable size of the water body and the specifics of this species' reproduction, a period of only 20 years was sufficient for bitterling to spread throughout the lake and to develop into one of the most abundant fish species. Furthermore, in view of the fact that MMG fishing results can be affected by fish size (see above), presumably the high numerical abundances of small non-indigenous species, such as bitterling and topmouth gudgeon, were significantly underestimated despite their high numerical presence in the catches. Conversely, the abundance of active perch was presumably overestimated in the catches made with benthic multi-mesh gillnets (Olin et al. 2016, Linløkken and Haugen 2006).

Other fishes that were highly abundant in the lake were Prespa roach, Prespa bleak, and Prespa spirlin, which underlined the cyprinid character of this waterbody. Prespa roach and Prespa bleak are omnivorous species that are comparatively undemanding in terms of their habitat conditions and, therefore, they were previously noted in large numbers in Prespa Lake (Crivelli et al. 1997, Spirkovski et al. 2012 b, Bounas et al. 2021). In contrast, Prespa spirlin is a rheophilous fish that normally inhabits lotic waters. Because of competition with introduced species, its numbers were assumed to be declining in Prespa Lake (Spirkovski et al. 2012a, b); however, the current data showed that Prespa spirlin is still very abundant in the lake although there were spatial differences in occurrence (see below). Regarding the abundance of the other fishes combined over all years and sites, pumpkinseed contributed almost 2% in numbers to the fishes sampled while the relative abundances of all other species was less than 1%. As shown in Table 2, the pattern of the five numerically dominating species being highly abundant and all other fishes being very rare was stable throughout the sampling period, which suggests that, under the current environmental conditions, this situation is typical of this lake.

In terms of biomass, the abundant occurrence of rather small-bodied fishes (such as Prespa spirlin, topmouth gudgeon, Prespa roach, and bitterling) in the samples meant that these species also had a significant share of the biomass of the total catch. Moreover, since high numbers of individuals of non-indigenous species were caught, their proportionate biomass values were also high. On some occasions carp (*Cyprinus carpio* (L.)) reached noteworthy shares of total biomass; however, this was because of its higher body mass relative to other species so that a few (comparatively large) individuals distinctly increased their share of the BPUE, which differed from the mean BPUE of 171.3 g h^{-1} m^{-2} net that Bounas et al. (2021) calculated. The discrepancies between these two studies are likely because of sampling differences. For example, the authors mentioned above collected fish only at a single sampling site, conducted the field work in early summer (April to June), and also used different mesh sizes than in the present study. Compared to other large lakes in the Balkan region, the annual BPUE of about 1.7–3.2 kg 100 m^{-2} net determined in the current investigation is somewhat lower than that of the highly productive, eutrophic Shkodra/Skadar Lake, where the BPUE fluctuates between 2.5–3.5 kg 100 m^{-2} net (Mrdak et al. 2017), but it is higher than that of the oligotrophic Ohrid Lake with a BPUE that varied between 1.1 and 1.9 kg 100 m^{-2} net (Spirkovski et al. 2017).

The species composition and abundance of the fish assemblages at SB 1 and SB 2 were more similar to each other than those of the fish assemblages in the other SBs. The same applied to the fishes at SB 4 and SB 5. This pattern most probably stemmed from the geographical distance and associated structural dissimilarity of the sampling locations. Sub-basins 1 and 2 were situated on the southwestern shore of the lake and are, therefore, relatively far away from SB 4 and SB 5, which were both located in the northeastern part of Prespa Lake. The lake bottom at SBs 1 and 2, for example, were rocky and consisted of gravel and stones, whereas the bottoms at SBs 4 and 5 were largely muddy, presumably as a result of the heavy nutrient loads from the nearby Golema Reka River (Matevski et al. 2013, Vasilevska et al. 2019). Moreover, there were also slight differences in the macrophyte communities between the southwestern and northern sites with rigid hornwort (*Ceratophyllum demersum*) and Eurasian water milfoil (*Myriophyllum spicatum*) dominating at the former, and fan-leaved water-crowfoot (*Ranunculus circinatus*) and pondweed species (*Potamogeton* spp.) prevailing at the latter (Peveling et al. 2015). In conclusion, differences in habitat conditions between the northern and southwestern shores, even if small, led to variations in local fish assemblages. Nonetheless, it must be stated that, in general, these differences were minor as indicated by the high stress value of the NMDS.

Knowledge about the spatial distribution of species is important for, among other things, transboundary fisheries management and conservation. In the current study, the majority of species occurred at all sampling sites although it again was the southwestern SBs where the highest numbers of both species and individuals were noted. At present, it is unclear whether the higher numbers of fishes at SBs 1 and 2 relative to the other SBs is a permanent or merely a seasonal phenomenon since fish sampling was restricted to the fall. Conversely, it must be taken into account that some fishes, such as tench (*Tinca tinca* (L.)) and Prespa trout (*Salmo peristericus* (Karaman)), were only caught in very small numbers or as single individuals, and their occurrence in the lake is probably generally very low. Consequently, their collection at SBs 1 and 2 might have been accidental rather than a reflection of the particular habitat conditions at these locations. Similarly, Prespa barbel and Prespa minnow were statistically significantly more abundant in SBs 1 and 2 than in the other SBs, but their numbers were generally low so these sites cannot truly be regarded as preferred habitats of these two species or sites where these fishes gather for certain purposes. Prespa spirlin numbers have occasionally been mentioned as declining as a result of the introduction of non-indigenous competitors, especially topmouth gudgeon and pumpkinseed (Spirkovski et al. 2012a, b, Bounas et al. 2021). The current results indicated, however, that this species is still very common in the lake although less so in the north (SBs 4 and 5). Whether Prespa spirlin abundance had declined at the northern sites and whether this is related to the presence of the two competitors is hard to determine especially since topmouth gudgeon was widespread and highly abundant everywhere in the lake and pumpkinseed abundance was statistically significantly higher in southern SBs 4 and 5 compared with SBs 1 and 2. These facts did not result in low Prespa spirlin numbers at the former sites (although a reduction at SBs 4 and 5 can still not completely be ruled out either as earlier data for comparative purposes are unavailable). Therefore, the current findings suggested that if Prespa spirlin numbers in the north did indeed decrease, this observation might not be solely because of the concurrent presence of topmouth gudgeon and/or pumpkinseed.

To sum up, after a period of only 20–40 years, introduced species are currently widely distributed and well established in Prespa Lake. By numbers, they dominated the native fish community and also formed a significant share of the overall fish biomass of this ancient lake. Of course, it also would have been valuable if comparable data from the Greek (i.e., southeastern) part of Prespa Lake had been available which, unfortunately, was impossible this time. Nonetheless, recent data from both fish monitoring and catch statistics of Greek fishers indicate that, consistently with the present results, Prespa bleak, Prespa roach, and pumpkinseed are also highly abundant in the southeastern lake basins (Leonardos 2016, Catsadorakis et al. 2018, Bounas et al. 2021). Unfortunately, small-sized fishes such as topmouth gudgeon were not included or targeted in these studies, so direct comparisons cannot be made. Whether introduced fishes have impaired the native fish community is conceivable, given that the former might use resources (such as food or habitats) which are otherwise available to the latter. It is, however, not clear whether this also translates into effects at the population level. Fishery data from the past show that carp, Prespa bleak, and Prespa nase have historically had high shares in the catches (Crivelli et al. 1997, Spirkovski et al. 2012b), but, as already indicated, fisheries most often target species that are in high market demand, therefore, catches do not reflect the composition or abundance of species in lakes. Thus, the comparatively low numbers of carp and Prespa nase caught in the present study could be related to methodological differences between scientific fish sampling and artisanal fishing. Global meta-analysis has shown that, in general, invaders at the same trophic level tend to cause linear declines in native local populations (Bradley et al. 2019). In Lesser Prespa, the sister lake of Prespa Lake, there are indications that the introduction of pumpkinseed caused a reduction in Prespa spirlin biomass (Bounas et al. 2021); however, a similar negative impact on native fishes at the population level has thus far not been shown in Prespa Lake.

In conclusion, the present investigation provided the first large-scale data about the relative abundance, biomass, and spatial distribution of Prespa Lake fish species. The results showed that non-indigenous fishes have become well established in the lake and outnumber native species. We propose implementing a regular fish monitoring program, which ideally also includes the Greek part of the lake, to facilitate the proper management of this lake's precious aquatic resources. Moreover, in order to obtain a more precise picture of the fish community and to avoid misinterpretations stemming from the size selectivity of fishing gears, fish sampling according to European standard EN 14757 should be accompanied by other methods, such as trawling, electrofishing, and the additional use of large mesh gillnets (Olin and Malinen 2003, Šmejkal et al. 2015).

Acknowledgments. We wish to thank Blagoja Trajchevski, Trajce Talevski, and Kosta Trajce for their help during fish sampling. The study at Prespa Lake was conducted with support from the TA program "Conservation and sustainable use of biodiversity at Lakes Prespa, Ohrid and Shkodra/Skadar" implemented by the Deutsche Gesellschaft für Internationale Zusammenarbeit (GIZ) GmbH on behalf of the German Federal Ministry of Economic Cooperation and Development.

Author contributions. S.S., Z.S., D.I.-B., U.B., R.P. designed the study. S.S., Z.S., D.I.-B. conducted the field investigations and provided environmental data. D.R. managed the database and did some of the analyses. W.-C.L. conducted specific statistical analyses. M.P. did some of the data analyses and drafted the manuscript. All authors contributed to writing the manuscript and approved the submitted final version of it.

ORCID iD

Michael Pietrock https://orcid.org/0000-0001-9244-0588
David Ritterbusch https://orcid.org/0000-0001-7180-6819
Wolf-Christian Lewin https://orcid.org/0000-0001-6598-6489
Spase Shumka https://orcid.org/0000-0002-5930-6034
Zoran Spirkovski https://orcid.org/0000-0002-9489-4679
Dusica Ilik-Boeva https://orcid.org/0000-0003-1183-180
Uwe Brämick https://orcid.org/0000-0002-9204-5104

References

Albrecht, C., Hauffe, T., Schreiber, K., Wilke, T. (2012). Mollusc biodiversity in a European ancient lake system: lakes Prespa and Mikri Prespa in the Balkans. Hydrobiologia, 682, 47–59.

Anderson, M. J., Walsh, D. C. I. (2013). PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? Ecological Monographs, 83, 557–574.

Bellard, C., Cassey, P., Blackburn, T. M. (2016). Alien species as a driver of recent extinctions. Biology Letters, 12, 20150623.

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošik, V., Wilson, J. R. U., Richardson, D. M. (2011). A proposed unified framework for biological invasions. Trends in Ecology and Evolution, 26, 333–339.

Blinkov, I., Krstic, S., Kostadinovski, M., Kusterevska, R., Mincev, I., Zaimi, K., Elbasani, O., Peci, D., Simixhiu, V., Zennaro, B. (2017). Shorezone functionality Prespa Lake – Implementing the EU Water Framework Directive in South-Eastern Europe. Deutsche Gesellschaft für Internationale Zusammenarbeit, Bonn, Eschborn.

Bounas, A., Catsadorakis, G., Koutseri, I., Nikolaou, H., Nicolas, D., Malakou, M., Crivelli, A. J. (2021). Temporal trends and determinants of fish biomass in two contrasting natural lakes systems: insights from a spring long-term monitoring scheme. Knowledge and Management of Aquatic Ecosystems, 422, 28.

Bradley, B. A., Laginhas, B. B., Whitlock, R., Allen, J. M., Bates, A. E., Bernatchez, G., Diez, J. M., Early, R., Lenoir, J., Vilà, M., Sorte, C. J. B. (2019). Disentangling the abundance–impact relationship for invasive species. Proceedings of the National Academy of Sciences, 116, 9919–9924.

Catsadorakis, G., Papadopoulou, E., Petrakos, M., Koutseri, I. (2018). Status of fisheries at Megali Prespa Lake and Mikri Prespa Lake, Greece, based on a census of fishermen's opinions. Environment and Ecology Research, 6, 583–592.

CEN (European Committee for Standardization). (2015). Water quality – Sampling of fish with multi-mesh gillnets. EN 14757, ICS 13.060.70; 65.150

Crivelli, A.J., Catsadorakis, G., Malakou, M., Rosecchi, E. (1997). Fish and fisheries of the Prespa lakes. Hydrobiologia, 351, 107–125.

Darwall, W., Carrizo, S., Numa, C., Barrios, V., Freyhof, J., Smith, K. (2014). Freshwater key biodiversity areas in the Mediterranean basin hotspot: informing species conservation and development planning in freshwater ecosystems. IUCN, Cambridge, UK and Malaga, Spain.

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., Dickman, C. R. (2016). Invasive predators and global biodiversity loss. Proceedings of the National Academy of Sciences, 113, 11261–11265.

Freyhof, J., Brooks, E. (2011). European Red List of freshwater fishes. EU Publication Office, Luxembourg.

Grazhdani, D., Grazhdani, S., Shehu, D. (2010). Environment, socio-economic development and sustainability in Albanian part of Prespa Park. Annals of the Valahia University of Targoviste Agriculture, 5, 32–41.

Griffiths, H. I., Kryštufek, B., Reed, J. M. (2004). Balkan biodiversity: pattern and process in the European hotspot. Springer Science+Business Media, Dordrecht.

Ilik-Boeva, D., Shumka, S., Spirkovski, Z., Talevski, T., Trajcevski, B., Shumka, S., Ritterbusch, D., Brämick, U., Pietrock, M., Peveling, R. (2017). Fish and Fisheries Prespa Lake – Implementing the EU Water Framework

Directive in South-Eastern Europe. Deutsche Gesellschaft für Internationale Zusammenarbeit, Bonn, Eschborn.

IUCN (International Union for Conservation of Nature). (2021). Invasive alien species and climate change. Issues brief February 2021. Available at https://www.iucn.org/resources/issues-briefs, accessed 15 February 2022.

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. Bioinformatics, 26, 1463–1464.

Leonardos, I. D. (2016). Fisheries ecology of Greece. In: Freshwater fisheries ecology (Ed.) J. F. Craig, Wiley & Sons, Chichester: 292–303.

Linløkken, A. N., Haugen, T. O. (2006). Density and temperature dependence of gill net catch per unit effort for perch, *Perca fluviatilis*, and roach, *Rutilus rutilus*. Fisheries Management and Ecology, 13, 261–269.

Markovic, D., Carrizo, S. F., Kärcher, O., Walz, A., David, J. N. (2017). Vulnerability of European freshwater catchments to climate change. Global Change Biology, 23, 3567–3580.

Matevski, V., Čarni, A., Ćušterevska, R., Hristovski, S., Levkov, Z., Talevska, M. (2013). Macrophytic vegetation of Ohrid and Prespa Lake (Macedonian part): actual situation, endangerment, protection. Proc. Reg. Int. Conf. „The system Prespa Lakes-Ohrid Lake: The actual state – problems and perspectives", Struga, Podradec, 27.-29.10.2013, North Macedonian Academy of Sciences and Arts: 32–33.

Matzinger, A., Jordanoski, M., Veljanoska-Sarafiloska, E., Sturm, M., Müller, B., Wüest, A. (2006). Is Lake Prespa jeopardizing the ecosystem of ancient Lake Ohrid? Hydrobiologia, 553, 89–109.

Milošević, D., Talevski, T. (2015). Conservation status of native species in natural lakes of Drim system (Prespa, Ohrid and Skadar Lake) and dangers of commercial fishing. Bulgarian Journal of Agricultural Sciences, 21, 61–67.

Mrdak, D., Milošević, D., Despotović, V., Palluqi, A., Flloko, A., Kapedani, E., Kapedani, R., Radovicka, B., Miraku, T., Ritterbusch, D., Brämick, U., Pietrock, M., Peveling, R. (2017). Fish and Fisheries Skadar / Shkodra Lake – Implementing the EU Water Framework Directive in South-Eastern Europe. Deutsche Gesellschaft für Internationale Zusammenarbeit, Bonn, Eschborn.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature, 403, 853–858.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., et al. (2019). Package "vegan" – Community Ecology Package. Available at https://github.com/vegandevs/vegan, accessed 15 February 2022.

Olin, M., Malinen, T. (2003). Comparison of gillnet and trawl in diurnal fish community sampling. Hydrobiologia, 506-509, 443–449.

Olin, M., Tiainen, J., Kurkilahti, M., Rask, M., Lehtonen, H. (2016). An evaluation of gillnet CPUE as an index of perch density in small forest lakes. Fisheries Research, 173, 20–25.

Pashko, P., Aliaj, S. (2020). Stratigraphy and tectonic evolution of Late Miocene – Quaternary Basins in Eastern Albania: A Review. Bulletin of the Geological Society of Greece, 56, 317–351.

Peveling, R., Brämick, U., Densky, H., Parr, B., Pietrock, M., Adhami, E., Bacu, A., Beqiraj, S., Djuranović, Z., Djurašković, P., Gusheska, D., Hadžiablahović, S., Ilik-Boeva, D., Ivanovski, A., Kashta, L., Koçu, E., Kostoski, G., Lokoska, L., Mirta, Y., Mrdak, D., Palluqi, A., Pambuku, A., Patceva, S., Pavićević, A., Peruničić, J., Rakaj, M., Rakočević, J., Saliaga, V., Veljanoska-Sarafiloska, E., Spirkovski, Z., Shumka, S., Talevska, M., Talevski, T., Tasevska, O., Trajanovska, S., Trajanovski, S. (2015). Initial characterization of Lakes Prespa, Ohrid and Shkodra/Skadar. Implementing the EU Water Framework Directive in South-Eastern Europe. Deutsche Gesellschaft für Internationale Zusammenarbeit, Bonn, Eschborn.

Piria, M., Simonović, P., Kalogianni, E., Vardakas, L., Koutsikos, N., Zanella, D., Ristovska, M., Apostolou, A., Adrović, A., Mrdak, D., Tarkan, A. S., Milošević, D., Zanella, L. N., Bakiu, R., Ekmekçi, F. G., Povž, M., Korro, K., Nikolić, V., Škrijelj, R., Kostov, V., Gregori, A., Joy, M. K. (2018). Alien freshwater fish species in the Balkans – vectors and pathways of introduction. Fish and Fisheries, 19, 138–169.

Popovska, C., Bonacci, O. (2007). Basic data on the hydrology of Lakes Ohrid and Prespa. Hydrological Processes, 21, 658–664.

Prchalová, M., Mrkvicka, T., Kubecka, J., Peterka J., Cech, M., Muska, M., Kratochvíl, M., Vasek, M. (2010). Fish activity as determined by gillnet catch: A comparison of two reservoirs of different turbidity. Fisheries Research, 102, 291–296.

R Development Core Team. (2017). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Available at http://www.R-project.org, accessed 20 February 2022

Ravn, H. D., Lauridsen, T. L., Jepsen, N., Jeppesen, E., Hansen, P. G., Hansen, J. G., Berg, S. (2019). A comparative study of three different methods for assessing fish communities in a small eutrophic lake. Ecology of Freshwater Fish, 28, 341–352.

Reed, J. M., Kryštufek, B., Eastwood, W. J. (2004). The physical geography of the Balkans and nomenclature of place names. Chapter 2. In: Balkan biodiversity: pattern and process in the European hotspot (Eds.) H. I. Griffiths, B.

Kryštufek, J. M. Reed, Springer Science+Business Media, Dordrecht: 9–22.

Ricciardi, A., Hoopes, M. F., Marchetti, M. P., Lockwood, J. L. (2013). Progress toward understanding the ecological impacts of nonnative species. Ecological Monographs, 83, 263–282.

Shumka, S., Apostolou, A. (2018). Current knowledge on the status of the most common non-indigenous fish species in the transboundary Greater Prespa Lake (Albanian Side). Acta Zoologica Bulgarica, 70, 203–209.

Shumka, S., Aleksi, P., Mali, S., Trajçe, K. (2015). Implementing standard EU method for sampling freshwater fish with multi-mesh gillnets in lakes sub basins (Prespa Lake, Albania). Sylwan, 159, 326–329.

Shumka, S., Shumka, L., Trajce, K., Ceci, S. (2020). First record of the Western Greece goby – *Economidichthys pygmaeus* (Holly, 1929), in Greater Prespa Lake (Albania). Ecologica Montenegrina, 35, 78–81.

Skarbřvik, E., Shumka, S., Mukaetov, D., Nagothu, U. S. (2010). Harmonised monitoring of Lake Macro Prespa as a basis for Integrated Water Resources Management. Irrigation and Drainage Systems 24, 223–238.

Šmejkal, M., Ricard, D., Prchalová, M., Říha, M., Muška, M., Blabolil, P., Čech, M., Vašek, M., Jůza, T., Herreras, A. M., Encinad, L., Peterka, J., Kubečka, J. (2015). Biomass and abundance biases in European standard gillnet sampling. PLoS ONE 10.

Spirkovski, Z. (2004). The past and present state of the environment of three Balkan transboundary lakes: Dojran, Prespa and Ohrid. Proc. BALWOIS Conf., Ohrid, MK, 25-29 May 2004, Balwois Office Skopje: 1–7.

Spirkovski, Z., Ilik-Boeva, D., Talevski, T., Paluqi, A., Kapedani, E. (2012 a). The fish of Prespa. National and university library "St. Kliment Ohridski", Skopje, MK.

Spirkovski, Z., Kapedani, E., Palluqi, A., Talevski, T., Ilik-Boeva, D., Kostov, V., Talevski, T., Farrow, P., Stojanoski, S., Beli, E., Veljanoska-Sarafiloska, E., Stafilov, T., Baceva, K., Kostoski, K. (2012 b). Transboundary Fish and Fisheries Management Plan for the Prespa Lakes Basin. United Nations Development Programme, Skopje, MK.

Spirkovski, Z., Ilik-Boeva, D., Talevski, T., Trajcevski, B., Palluqi, A. Flloko, A., Miraku, T., Kapedani, E., Ritterbusch, D., Brämick, U., Pietrock, M., Peveling, R. (2017). Fish and Fisheries Lake Ohrid – Implementing the EU Water Framework Directive in South-Eastern Europe. Deutsche Gesellschaft für Internationale Zusammenarbeit, Bonn, Eschborn.

Talevski, T., Milosevic, D., Maric, D., Petrovic, D., Talevska, M., Talevska, A. (2009). Biodiversity of ichthyofauna from Prespa Lake, Lake Ohrid and Lake Skadar. Biotechnology & Biotechnological Equipment, 23, 400–404.

Trajchevski, B., Spirkovski, Z., Ilikj-Boeva, D., Talevski, T. (2020). An alien species or another perspective to the freshwater gobies puzzle: a new finding in Lake Prespa. Turkish Journal of Zoology, 44, 542–547.

van der Schriek, T., Giannakopoulos, C. (2017). Determining the causes for the dramatic recent fall of Lake Prespa (southwest Balkans). Hydrological Sciences Journal, 62, 1131–1148.

Vasilevska, S. P., Veljanoska-Sarafiloska, E. M., Lokoska, L. S. (2019). Water quality of the rivers in the Prespa region in 2014. Acta Zoologica Bulgarica, Supplement 13, 11–18.

Wagner, B., Wilke, T. (2011). Evolutionary and geological history of the Balkan lakes Ohrid and Prespa. Biogeosciences, 8, 995–998.

Wagner, B., Vogel, H., Zanchetta, G., Sulpizio, R. (2010). Environmental change within the Balkan region during the past ca. 50 ka recorded in the sediments from lakes Prespa and Ohrid. Biogeosciences, 7, 3187–3198.