Spatio-temporal Surface Variations and Freshwater Fish Diversity in a Complex of Small-sized Lentic Ecosystems in NW Greece

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Abstract: Studies targeting to explore fish species diversity and seasonal surface variations at small-sized, lentic ecosystems are extremely limited in the Mediterranean region. These ecosystems are often ignored by scientists under the erroneous assumption that they play an insignificant socio-economical role or they are of low ecological importance. This study aimed to explore the seasonal surface variations using GPS readings (March 2013 to March 2014), in a complex of nine small freshwater ecosystems in NW Greece. Precipitation and temperature data were also obtained from two local meteorological stations. Additionally, electrofishing was conducted in all lakes on two occasions (March and July 2013), in order to provide a preliminary fish species list based on field surveys. Overall, water surface variations in all lentic ecosystems exhibited extreme recessions during the summer period, with two lakes drying completely, and expansions during winter-spring periods. Lakes shallower in depth, with an initial smaller surface and depending solely on precipitation inputs were the first to dry out. The endemic fish diversity was extremely low in the entire study area, since only one native fish was caught (Pelagius thesproticus). On the contrary, alien species (Carassius gibelio, Gambusia holbrooki and Silurus aristotelis) have intruded into new localities and expanded their distributional range. This study conforms, that habitat loss and the introduction of non-native species are the two major threats for biodiversity in these small-sized Mediterranean lentic ecosystems.

Key words: fish fauna, non-native species, shore mapping, small lakes, surface variation, NW Greece

Introduction

Studies of small-sized lentic ecosystems have been considerably limited in comparison to the overgrowing scientific research of larger lakes (Downing 2010, Boix et al. 2012). This trend could be attributed mainly to the incorrect assumption that small-sized ecosystems have an insignificant socio-economical role or they are of low ecological importance in contrast to larger lakes. Therefore, it is was not uncommon for many temporary ponds, small lakes, marshes and wetlands to be often poorly surveyed by nature scientists and even ignored by nearby citizens. However, during the last decade, this negative trend has started to improve with several studies establishing the high value of small-sized lentic ecosystems and urging the need for conservation actions (see references in Boix et al. 2012).

Small lakes, ponds, wetlands and transitional waters are highly vulnerable ecosystems, especially in Southern Europe and around the peri-Mediterranean region, mainly due to their high natural seasonal environmental variability, combined with increasing anthropogenic pressures (Zalidis et al. 2002). Many
small-sized lentic ecosystems are projected to completely dry out, become temporary or severely recessed due to shorter precipitation seasons and higher incidence of droughts, with severe consequences to water quality and habitat availability (Coops et al. 2003, Beklioglu et al. 2007, Dimitriou & Moussoulis 2010). Although, surface topography is not so drastically affected in deep lakes, small-sized, shallow lakes and wetlands are particularly vulnerable to extreme surface variations, affecting nutrient cycling, trophic complexes and structural and functional aspects of aquatic flora and fauna (Coops et al. 2003, Beklioglu et al. 2006, Stefanidis & Papastergiadou 2013).

From a water management perspective, the Water Framework Directive (2000/60/EC) required all aquatic systems larger than 0.5 km² to fulfil the criteria of good ecological and chemical status until 2015. Therefore, morphology, surface variation and biotic elements are basic structural elements that have to be incorporated in the ecological quality assessments (Stefanidis & Papastergiadou 2012). Despite this, small lentic ecosystems in the Mediterranean region are usually omitted or ignored from water management plans which are mainly focused on lotic systems or larger lakes.

In Greece, there are approximately 400 lentic ecosystems (i.e. lakes, marshes and periodically flooded wetlands) over 200,000 hectares (Gerakis & Koutrakis 1996). However, 70% of small wetlands have been lost over the past 80 years (Gerakis 1992). The causes of these losses are usually poorly documented and most assuredly are multi-faceted and additive. Many are clearly associated with landscape alteration via deforestation, urbanisation and agricultural expansion. In addition, the demand for groundwater and surface water for irrigation is increased nowadays, making it difficult to disentangle the human induced effects from regional changes due to climate change and tectonic activity (Hollis & Stevenson 1997, Karakhanian et al. 2001).

From an ecological point of view, lakes and wetlands in Greece are of great importance, since they could host unique species of high conservation value assigned to a threatened category. However, the ichthyofauna of small-sized lentic ecosystems in Greece has been poorly investigated (Economou et al. 2007, Kottelat & Freyhof 2007, Koutsikos et al. 2012), particularly in the north-western continental part of the country (Region of Epirus). This region, which belongs to the wider Ionian ichthyogeographic region, hosts a unique fish fauna, characterised by a high degree of endemism (75%), with a large proportion (39%) of the species being assigned to the IUCN Red List of Threatened species (Oikonomou et al. 2014).

We studied the spatio-temporal variation of surfaces/shorelines and fish fauna diversity in a complex of nine small-sized lentic ecosystems located in NW Greece. Given that these lakes are particularly vulnerable to extreme climatic conditions (i.e. summer droughts) and available data on fish diversity are extremely scarce, the aim of the current study was: a) to record their surface variation (spatial contraction and retraction) and b) to provide a fish faunistic list based on field surveys.

**Materials and Methods**

**Study area**

This study was conducted in nine small-sized lentic ecosystems located in NW Greece – Regional Unit of Thesprotia, Region of Epirus (Fig. 1). Hydrogeologically, the study area is divided in two sub-catchments. The first is located in the north-eastern part of the area belonging to the sub-catchment of the Kokytos River (major tributary of the Acheron River; catchment area of 705 km²). It includes the lakes Limnopoula, Prontani, Mesovouni, Kyra Panagia and Kalosykes. The second is located in the south-western part of the area belonging to the omonymous south-western sub-catchment (catchment area of 69 km²) and it includes the Kalodiki Marsh and the wetlands of Margariti, Palaiokastro and Kaneta. This karstic sub-catchment discharges to the sea through the Parga anticline. The systems of Kalodiki and Limnopoula are protected under the NATURA 2000 framework as Sites of Community Importance (SCI) (92/43/EC Directive), while Kalodiki, Margariti, Palaiokastro and Prontani as Special Protection Areas (SPAs) for avifauna (79/408/EC Directive). Finally, the Kalodiki Marsh is included in the Common Database on Designated Areas (CDDA) as Wildlife Refuge under the CORINE program. In the former sub-catchment, the Limnopoula Lake is a permanently flooded wetland fed primarily by karstic springs. It dries out partially during the summer and then it is used for grazing and agriculture. A dam was constructed in 2007 in the deepest part (23 ha) of the system, which sustains a minimum level during the summer season. The Prontani Lake is a permanently flooded area mainly fed by rainfall inputs with a maximum depth of 4 m. The lake dried out in August 1990 and 1992. The Mesovouni Lake is fed exclusively by rainfall with a mean winter depth of 1.5 m, while it completely dries out during the summer. The Kyra Panagia Lake is a seasonally flooded area, mainly used for grazing.
and it is fed by precipitation and small ephemeral streams. Finally, the Kalosykies Lake is a permanent formation, exclusively fed by in-bottom springs. In the latter sub-catchment, the Kalodiki Marsh is a unique peat wetland (fen) in western Greece at its final evolutionary stage. Its depth varies from 0.5-4.5 m and its aquifer is fed by karstic waters, derived from springs at the south-western and north-eastern edges of the marsh, as well as by irregular run-off from the surrounding drainage area (KAGALOU et al. 2010). The marsh experiences high water-level fluctuations between the dry and the wet season (SARIKA-HATZINKOLAOU 1994) and during autumn 1992, the marsh completely dried out (BOTIS et al. 1993). In addition, based on personal observations, a new drying episode has occurred recently (summer 2017) in the Kalodiki Marsh, when the marsh was confined in shallow, scattered pools with many dead

Fig. 1. Location of lakes complex in the Regional Unit of Thesprotia (NW Greece). Seasonal surface variations recorded during the present work are indicated by different lines. The triangle and the rombus indicate the positions of Paramythia and Parga meteorological stations, respectively.
fish floating. Based on chlorophyll-a measurements (Kagalou et al. 2010), the system was characterised as eutrophic. The Margariti Wetland is a seasonally flooded area, which is mainly fed by the overflow of the Kalodiki Marsh and, in one spring, also by precipitation. During the summer, the entire area is partially dried through sinks and used for cultivation of alfalfa, corn and barley. During the past, this wetland was unsuccessfully subjected to hydraulic and excavation works, aiming to transform it to agricultural land. The Palaiokastro Lake is a permanently flooded area. It is physically connected to the Margariti Wetland and fed mainly by precipitation. During the summer, when the maximum depth is about 0.5 m, it is used for cattle grazing. Finally, the Kaneta Lake is a seasonally flooded area fed exclusively by precipitation. It dries out during the summer and then it is used for agriculture (olive trees, alfalfa and barley).

Environmental data

Data on precipitation and air temperature from January 2011 to April 2014 were obtained from two meteorological stations in the study area (Paramythia station, close to the first sub-catchment and Parga station, close to the second sub-catchment) through the National Observatory of Athens. Seasonal changes in surfaces were recorded by several GPS readings along the perimeter of each ecosystem during March, June, September and December 2013 and March 2014. The coordinates of the shoreline limits were imported in the ArcGis 10.1 GIS program (ESRI) to produce the relevant layers along with Natura 2000 areas and other basic features (channels, sinks, dams, industrial areas and nearby villages).

Fish sampling

Qualitative samplings by a 30 min sampling effort in random locations in all systems were performed on two occasions (March and July 2013), in order to record presence of fish species. Electrofishing was carried out using a back-pack electrofishing device (Hans Grassl IG200/2, 250 W, Hans Grassl GmbH). Each area was fished once by two waders, one using the anode and an assistant collecting the stunned fish with a dipnet. Fish were identified to species level according to Kottelat & Freyhof (2007), measured, photographed and released alive in the capture location.

Results

Climatic data

The highest air temperature (27.2°C) was recorded in July 2012 (Parga station) and the lower value (2.5°C) was recorded in January 2012 (Paramythia station). Annual mean air temperature for the period 2011-2013 were higher in the Parga station (17.8°C) compared to the Paramythia station (14.0°C) and the mean temperature of July 2012 was about 2-3°C higher in both stations, compared to the rest of the years (Fig. 2).

Precipitation levels at the Paramythia station were higher for all years compared to the Parga station, with 2012 being the rainiest year. On the other hand, precipitation levels were almost two times higher at the Parga station in 2012 and 2013, compared to the ones in 2011 (Fig. 2), with the maximum value being recorded in November 2013 (588.4 mm, Paramythia station).

![Fig. 2. Precipitation and air temperature at (a) Paramythia and (b) Parga meteorological stations (based on data from the National Observatory of Athens).](image-url)
Table 1. Surface variation of nine small lakes in NW Greece (in hectares). Numbers in the parentheses represent the surface as a percentage compared to the March 2013 maxima.

<table>
<thead>
<tr>
<th></th>
<th>Kalodiki</th>
<th>Margariti</th>
<th>Palaiokastro</th>
<th>Kaneta</th>
<th>Mesovouni</th>
<th>Prontani</th>
<th>Limnopoula</th>
<th>Kyra Panagia</th>
<th>Kalosykies</th>
</tr>
</thead>
<tbody>
<tr>
<td>March 2013</td>
<td>70.6 (100)</td>
<td>81.0 (100)</td>
<td>46.7 (100)</td>
<td>0.69 (100)</td>
<td>2.9 (100)</td>
<td>20.1 (100)</td>
<td>42.2 (100)</td>
<td>5.83 (100)</td>
<td>1.12 (100)</td>
</tr>
<tr>
<td>June 2013</td>
<td>56.9 (80.6)</td>
<td>0.63 (0.78)</td>
<td>27.9 (59.7)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>13.0 (64.7)</td>
<td>7.2 (17.1)</td>
<td>2.90 (49.7)</td>
<td>0.45 (40.2)</td>
</tr>
<tr>
<td>September 2013</td>
<td>47.2 (66.8)</td>
<td>0.58 (0.72)</td>
<td>18.8 (40.2)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>8.67 (43.1)</td>
<td>5.8 (13.7)</td>
<td>0.39 (6.7)</td>
<td>0.28 (25.0)</td>
</tr>
<tr>
<td>December 2013</td>
<td>55.7 (78.9)</td>
<td>1.62 (2.0)</td>
<td>12.1 (25.9)</td>
<td>0.46 (66.6)</td>
<td>0.0 (0.0)</td>
<td>7.91 (39.3)</td>
<td>7.58 (17.9)</td>
<td>4.45 (76.3)</td>
<td>0.14 (12.5)</td>
</tr>
<tr>
<td>March 2014</td>
<td>60.8 (86.1)</td>
<td>2.83 (3.5)</td>
<td>26.0 (55.7)</td>
<td>0.22 (31.9)</td>
<td>1.12 (38.6)</td>
<td>11.0 (54.7)</td>
<td>15.9 (37.7)</td>
<td>4.02 (68.9)</td>
<td>0.41 (36.6)</td>
</tr>
</tbody>
</table>

Surface variation

A surface recession was evident in the majority of the studied lakes from March to June-September 2013, while two were completely dry (Kaneta and Mesovouni) already at the initial phase of the summer period (Fig. 1, Table 1). The most profound recession was observed in the Margariti Lake followed by Kyra Panagia, compared to primarily spring-fed (Limnopoula, Kalosykies) or deeper systems (Kalodiki, Prontani) that retained a critical water surface. Nevertheless, the overall pattern was not reversed in most systems even until December 2013 and the ecosystems restored their surface partly during the following spring (March 2014). However, March 2013 was an exceptionally rainy month (Fig. 2a,b).

Fish fauna

Collectively, the presence of five species and one variety (koi carp) was documented during the current study from the lakes complex (Table 2). Three systems were fishless (Kaneta, Mesovouni and Kyra Panagia), with two of them being dried out from June to December 2013. Two systems (Prontani and Palaiokastro) were characterised by the presence of non-native species—Carassius gibelio (Bloch, 1782) and Gambusia holbrooki (Girard, 1859). Three systems (Margariti, Limnopoula and Kalosykies) had two species—Pelagus thesproticus (Stephanidis, 1939) and G. holbrooki. The remaining Kalodiki Marsh presented the highest species diversity, with five species and one variety—C. gibelio, Cyprinus carpio (L.), koi carp, G. holbrooki, P. thesproticus, Silurus aristotelis (Agassiz, 1856). Based on the current survey and literature data (Table 2), the overall percentage of non-native species in the lakes-complex reached 62.5%, which is further increased if we exclude older recordings of the native Anguilla anguilla (L.) and Economidichthys pygmaeus (Holy, 1929).

Carassius gibelio, S. aristotelis and koi carp were caught for the first time in these systems, while the range of the most widely distributed G. holbrooki and P. thesproticus was extended to five and four ecosystems, respectively (Table 2).

Discussion

Most of the lakes in the study area (Mesovouni, Kaneta, Palaiokastro, Kyra Panagia) are typical Mediterranean ecosystems, greatly affected by seasonal climatic oscillations (Gasith & Resh 1999). They rely particularly on precipitation inputs, which ultimately determine, along with temperature, their spatial dimensions, due to their low depth. In fact, our climatic data indicated that the outer limits of the lakes recorded during March 2013, mainly reflected the precipitation values during the dry period from September 2012 to March 2013, which were two times higher compared to the relevant period of 2011-2012.

According to the European Water Framework Directive (Directive 2000/60/EC), lakes with depth below 3 m are considered very shallow but lake surface of 50 ha is regarded as a possible cut-off for categorising lakes under monitoring and conservation actions. In our study, only two systems (Kalodiki and Margariti) were above this cut-off value and seven lakes (Limnopoula, Kyra Panagia, Mesovouni, Kaneta, Palaiokastro, Margariti and Kalosykies) were found to be very shallow. This in turn explains the extreme surface retraction during the summer. Reversely, the Prontani Lake and the Kalodiki Marsh, with depths exceeding 3 m, were able to better resist to extreme water-level declines.
Table 2. Diversity of fish fauna in nine small lakes of NW Greece based on electrofishing (March and July 2013). Previous documentation of species presence is indicated by relevant citations. Conservation status according to the IUCN Red List of threatened species (DD: deficient data, LC: least concern, NT: nearly threatened, VU: vulnerable, EN: endangered). PS: Present study, P: Protected.

<table>
<thead>
<tr>
<th>Species/varieties</th>
<th>Kalodiki</th>
<th>Margariti</th>
<th>Palaiokastro</th>
<th>Kaneta</th>
<th>Mesovouni</th>
<th>Proutani</th>
<th>Limnopoula</th>
<th>Kypria Panagia</th>
<th>Kalosykies</th>
<th>Protection frameworks/legislation and conservation status</th>
<th>Introduction pathway</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Anguilla anguilla</em> (Linnaeus, 1758)</td>
<td>Economou et al. (2007)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>II</td>
<td>CR</td>
<td>-</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Carassius gibelio</em> (Bloch, 1782)</td>
<td>PS</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>LC</td>
<td>Unknown</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cyprinus carpio</em> (Linnaeus, 1758)</td>
<td>PS, Economou et al. (2007)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>VU</td>
<td>LC</td>
<td>Aquaculture</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cyprinus carpio</em> (Koi carp)</td>
<td>PS</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Release by hobbyist?</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Economidichthys pygmaeus</em> (Holy, 1929)</td>
<td>Kagalou et al. (2010)</td>
<td>-</td>
<td>P</td>
<td>-</td>
<td>-</td>
<td>LC</td>
<td>LC</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Gambusia holbrooki</em> (Girard, 1859)</td>
<td>PS, Kagalou et al. (2010)</td>
<td>PS</td>
<td>PS</td>
<td>PS</td>
<td>PS</td>
<td>-</td>
<td>-</td>
<td>LC</td>
<td>Biocontrol</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pelagius thesproticus</em> (Stephanidis, 1939)</td>
<td>PS, Koutsikos et al. (2012)</td>
<td>PS</td>
<td>PS, Economou et al. (2007)</td>
<td>PS</td>
<td>P</td>
<td>-</td>
<td>-</td>
<td>NT</td>
<td>NT</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td><em>Silurus aristotelis</em> (Agassiz, 1856)</td>
<td>PS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of species/varieties</td>
<td>6(8)</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
</tbody>
</table>

1 It refers only to the natural form.
2 The number of species in parenthesis include current findings and older presence records from the literature.
Another interesting finding that arose from our spatio-temporal survey was that in three of the lakes (Margariti, Palaiokastro and Limnopoula) – the outer limits recorded have not been included in the Natura 2000 area limits. Moreover, the Kaneta, Mesovouni, Kyra Panagia and Kalosykkies Lakes are currently excluded from any protective framework. This finding urges for revision of the relevant country-wide lake and Natura 2000 lists.

Concerning the fish fauna of our study area, the existing published literature was extremely scarce, fragmented and related only to the Kalodiki Marsh and the Limnopoula Lake (see Table 2 and references therein). For the majority of the studied lakes, no information was available in the literature and obviously most of the lakes had never been surveyed for fish diversity before. Excluding fishless systems, in which we assume the presence of some fish species during the past but they have been extirpated possibly due to a past drought event, the current study documented for the first time the presence of C. gibelio, koi carp and S. aristotelis in the area and in addition presented new distributional data for species with known presence. The presence of previously documented populations was confirmed in many occasions, though excluding A. anguilla and E. pygmaeus that were not captured during our survey. In the case of A. anguilla, the species has been possibly locally extirpated from the Kalodiki Marsh according to locals, since individuals have not been caught during the last decade. This is in accordance with the severe decline of A. anguilla stocks in the river estuaries located near the study area as well as with the lack of A. anguilla stocking activity (Fisheries Department of Regional Unit of Thesprotia, unpublished data). For the E. pygmaeus, there are two possible explanations for its absence from our catches. Either our sampling method (i.e. electrofishing) was inappropriate to capture this species given its cryptic behaviour (often hiding at the bottom of dense macrophyte mats) or its abundance and distributional range have been extremely reduced.

The overall state suggests that non-native species (i.e. G. holbrooki, C. gibelio) have established thriving populations. Yet, the introduction of non-native species in the Hellenic freshwaters has a long history with increasingly documented risks for local biota (Economidis et al. 2000, Perdikaris et al. 2010a, 2012, 2016). Greece represents a biodiversity hot spot attributed to the high number of unique and often range-restricted endemic fish species. However, the study of the successive fish checklists (Stephanidis 1939, Economidis 1973, 1991, Economidis et al. 2000, Bobori & Economidis 2006, Economou et al. 2007, Koutsikos et al. 2012, Barbiere et al. 2015) suggests that the number of non-native fish species increases with time. The results of this study confirm this trend as only one native species was caught (P. thesporoticus), while the rest were non-natives. Interestingly, in the most invaded ecosystem of our study area (i.e. the Kalodiki Marsh with 75% non-native fish species), we captured one ornamental species (koi carp) that was probably released by hobbyists during the 2000s and one silurid species (S. aristotelis, originating from the Acheloos River basin and the surrounding lakes). The latter possibly represents either a direct translocation from its native locality 20 years ago or according to the locals, a secondary translocation from the Pamvotis Lake. Its total length (48 cm) represents the largest specimen in length registered up-to-date, compared to the 36.7 cm from the Pamvotis Lake (Leonardos et al. 2009) and the 46 cm reported in Fishbase (Froese & Pauly 2014). Therefore, in the case of S. aristotelis, the population might be well adapted, being self-sustained practically representing the only top predatory fish in the entire lake complex. Moreover, the presence of C. carpio in the Kalodiki Marsh confirmed an earlier report by Economou et al. (2007). This population is obviously the outcome of stocking efforts during the 2000s. Although data on propagule pressure are not available, the risk for such geographically isolated ecosystems from stockings and releases of non-native species cannot be ignored.

Gambusia holbrooki was first imported in Greece as a biocontrol agent for mosquito and malaria control (Economidis et al. 2000, Zenetos et al. 2009). Its spread and establishment in many ecosystems resulted in it currently being the most invasive species in Greece, with an establishment rate of 49.5% in terms of catchments (Economou et al. 2007). The species is locally present from the estuaries around the mouth of the Kalamas River and in one spring in the catchment of the same river (Perdikaris et al. 2010b). Its wide distributional range in the harsh environmental conditions of the shallow lakes of the study area is fully justified by its hardiness. Invasiveness success is related to its ability to withstand extreme physicochemical conditions and to produce at least three generations of progeny per year at temperatures above 18°C (Kottelat & Freyhoff 2007). Its thermal limits have been reported to 3-38°C (Cherry et al. 1976, Glover 1979). In addition, it is able to survive almost anoxic conditions by gasping air from the water surface (Homske et al. 1994).

Carassius gibelio was introduced in Greece probably during the 1950s (Leonardos et al. 2008). It is the 3rd most widespread invasive species in the
Hellenic freshwaters (Economou et al. 2007) after *G. holbrooki* and *Oncorhynchus mykiss* (Walbaum, 1792). Its dominance is attributed to the presence of sperm-dependent triploid asexuals using sperm from other cyprinid species (Paschos et al. 2004), its omnivorous feeding habits and its ability to thrive in degraded ecosystems (Perdikaris et al. 2012). According to the literature, first maturity in Greece is observed during the second year (Leonardos et al. 2001). However, during the current survey, puberty was evident in 0+ specimens at 5.9 cm in Lake Prontani and at 7.8 cm in the Kalodiki Marsh, suggesting that early maturity is an important factor for establishment and invasion success. In fact, the species dominates both invaded ecosystems, with Lake Prontani being monospecific.

Finally, *P. thesproticus* was the most widespread native species in the lake complex. It is an indicator species of the Region of Epirus and particularly of the Acheron River basin (Kottelat & Barbiere, 2004, Economou et al. 2007). The thriving populations in the Limnopoula and Kalosykes Lakes indicate that the species is mainly related to spring-fed ecosystems. However, its fragmented distribution in small systems indicates possible genetically structured populations. Accordingly, its scattered populations necessitate continuous monitoring and strict protection.

Despite the fact that the presence of invasive species poses risks to trophic complexes and to the native fish fauna of the receiving ecosystems (Perdikaris et al. 2016), they are part of the trophic chain of the diverse piscivorous avifauna in the area. This is particularly true for the vulnerable white stork (*Ciconia ciconia* (L.)) which is forming its breeding populations in the study area (Syntichaki 2016). However, the impact of avifauna on fish populations during the summer period is unknown and, therefore, biodiversity of macroinvertebrates, fish, reptiles and avifauna; the detailed structure and function of food webs and the energy flow in such dynamic ecosystems should be thoroughly investigated. Research efforts should also focus on assessing the combined effects of seasonal variations and the occurrence of non-indigenous species on the native fish populations. In addition, efforts are needed to assess the recovery processes of fish populations after the extreme recessions of the lake surface. Moreover, in the context of global warming, it is crucial to reveal the underlying mechanisms relating seasonal variations to the environmental variables (e.g. high water temperature, high macrophyte cover, low dissolved oxygen during night-early morning) and ultimately to the survival of fish populations. The small-sized ecosystems we have studied are an integral part of the natural heritage of the area and efforts should be focused not only to reveal any remaining cryptic biodiversity elements, but also to wider our protection actions involving scientists and local communities. These ecosystems provide the set for natural experiments as natural laboratories. Finally, they present ecotouristic, environmental education and recreation potential (e.g. ecopaths, school visits and recreational fisheries based on *C. carpio* populations), since they are located near small cities.

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