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To cite this article: Yvon J.M. Verstijnen, Valentini Maliaka, Giorgos Catsadorakis, Miquel Lüring & Alfons J.P. Smolders (2021): Colonial nesting waterbirds as vectors of nutrients to Lake Lesser Prespa (Greece), Inland Waters, DOI: [10.1080/20442041.2020.1869491](https://doi.org/10.1080/20442041.2020.1869491)

To link to this article: <https://doi.org/10.1080/20442041.2020.1869491>



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Published online: 29 Mar 2021.



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Colonial nesting waterbirds as vectors of nutrients to Lake Lesser Prespa (Greece)

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ABSTRACT

The nutrients imported by breeding waterbirds should be considered when identifying the main sources of nutrient input to lakes. Lake Lesser Prespa (Greece), including the adjacent Vromolimni pond, hosts numerous protected waterbirds that nest in densely populated colonies across the reedbeds. The accelerated eutrophication of the lake in recent years has been of increasing concern. In addition to likely large sources of nutrients (i.e., anthropogenic activities, especially agriculture), nutrient input via waterbird excrement may further trigger eutrophication. We estimated the annual phosphorus (P) and nitrogen (N) input by the most abundant colonial-nesting waterbirds (great white pelican, Dalmatian pelican, great cormorant, and pygmy cormorant) into the lake and investigated their influence on water and sediment quality. Near the waterbird colonies, soluble nutrient concentrations in the lake sediments were higher, and chlorophyll measurements indicated higher algal growth near these sites in summer. Stable isotope analysis suggests that near the colonies, waterbirds are responsible for nutrient loadings that affect the lake sediment. The estimated N and P nutrient input into the lake by both pelican and cormorant species is at least 1243 and 1649 kg/yr, respectively. On a landscape scale, this level of loading could be of minor importance for the lake because N and P can reach 32.8 (SD 9.3) and 38.9 (5.8) mg/m² per year, respectively. Locally, however, this level of loading might induce cyanobacterial blooms, illustrated by the analysis of isolated Vromolimni pond near the lake. Our findings emphasize the likely importance of nutrient loading by waterbirds for the lake system.

ARTICLE HISTORY

Received 30 May 2020
Accepted 19 December 2020

KEYWORDS

bird droppings; cormorants; eutrophication; pelicans; sediment nutrients; stable isotopes

Introduction

Waterbirds can play a key role in many freshwater ecosystems and provide important cultural, supportive, and regulatory ecosystem services, especially when maintaining biodiversity locally, regionally, or even on a continental scale (Green and Elmberg 2014). However, their role in the trophic dynamics of the waterbodies they frequently use is often ignored (Rönicke et al. 2008). Waterbirds that form dense flocks at roosting or breeding sites can potentially import enough nutrients, mainly via droppings, to cause major shifts in the trophic status of their aquatic habitats (Gere and Andrikovics 1992, Marion et al. 1994, Mukherjee and Borad 2001, Rönicke et al. 2008, Gwiazda et al. 2010, Gwiazda et al. 2014). Their droppings are rich in phosphorus (P) and nitrogen (N) and may thus stimulate eutrophication

(Leentvaar 1967, Manny et al. 1994, Marion et al. 1994, Chaichana et al. 2010). Eutrophication caused by birds, also known as guanotrophication (Leentvaar 1967), may affect the water quality of both small waterbodies (Manny et al. 1994, Scherer et al. 1995, Post et al. 1998, Chaichana et al. 2010, Klimaszyk et al. 2015) and large lakes (Gere and Andrikovics 1992, Rönicke et al. 2008).

The shallow Lake Lesser Prespa (Greece) area is recognized internationally for its endemic biodiversity and migratory birds (Catsadorakis 1997). In recent decades, conspicuous signs of increasing eutrophication have been observed (Koussouris et al. 1989, Hollis and Stevenson 1997, Tryfon et al. 1997, Petaloti et al. 2004, Maliaka et al. 2018, 2021). Substantial increases in cyanobacterial biomass occur during algal blooms in

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 Supplemental data for this article can be accessed here: <https://doi.org/10.1080/20442041.2020.1869491>.

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summer and autumn (Tryfon et al. 1997, Maliaka et al. 2021). Cyanotoxins produced by cyanobacteria were detected in collected fish tissues (Papadimitriou et al. 2010) and surface algal scums at potentially harmful levels (Gkelis et al. 2005, Christophoridis et al. 2018, Maliaka et al. 2021). Knowing the sources of excessive nutrient input in the lake is crucial to reducing nutrient input and subsequent algal blooms. One possible source of nutrients is agricultural activities, particularly bean farming. These activities have intensified, especially in the eastern part of the lake's catchment, and furrow irrigation practices have contributed to increased nutrient runoff (Koussouris and Diapoulis 1989, Koussouris et al. 1989, Löffler et al. 1998). In addition, domestic effluents and/or resuspended stream sediments may introduce nutrients into the lake water (Petaloti et al. 2004). Fishing activities, which may cause sediment resuspension, also occur in the lake, but the fishing boats are small and the number is low relative to the surface area of the lake (Catsadorakis et al. 2018).

Anthropogenic activities, erosion, or resuspension may not be the only sources of nutrient inputs in Lesser Prespa. In recent decades, not only have signs of eutrophication increased, but also the number of pelicans and cormorants that breed every year on the reedbeds of Lake Lesser Prespa and the adjacent Vromolimni pond (Catsadorakis 1997, Catsadorakis et al. 2015). These waterbirds potentially affect the water quality of the lake by bringing nutrients into the lake via their droppings. Moreover, Maliaka et al. (2020) found that pelican droppings can increase algal biomass, especially that of cyanobacteria, in the lake water of Lesser Prespa.

The objective of this study was to (1) estimate the annual input of nutrients (N, P) introduced via the droppings of the most abundant waterbirds that breed annually in the Lesser Prespa area and (2) detect links between the presence of the bird colonies and sediment and water quality variables measured in the field. The target species were Dalmatian pelican (*Pelecanus crispus*), great white pelican (*Pelecanus onocrotalus*), great cormorant (*Phalacrocorax carbo*), and pygmy cormorant (*Microcarbo pygmeus*). We collected long-term monitoring data and relevant literature concerning the behavior and development of the population sizes of the 2 pelican and 2 cormorant species. Nutrient loads via the bird droppings were estimated using the models in Scherer et al. (1995) and Hahn et al. (2007). We also conducted a field study of the main water and sediment quality variables at different distances from the waterbird colonies in Lake Lesser Prespa. This study is part of a larger research project investigating potential causes of eutrophication of Lake Lesser Prespa. We

hypothesized that nutrient input by birds can, at least locally, strongly affect the water and sediment quality of Lake Lesser Prespa.

Study site

Shallow Lake Lesser Prespa (also known as Mikri, Mikra, or Micro Prespa) in northwest Greece (40°46'N; 21°06'E) is a Wetland of International Importance under the Ramsar Convention as well as a Special Protection Area (Directive 79/409/EEC) and a Site of Community Importance (Habitat Directive 92/43 EEC). It has further received numerous designations as a protected area (Catsadorakis 1997). The lake is connected via an outflow channel with the adjacent Lake Great Prespa (also known as Megali or Macro Prespa). The outflow is controlled by 4 sluice gates. Underground seepage also occurs from Lake Lesser Prespa toward Lake Great Prespa near the outflow channel (Parisopoulos et al. 2009). Both lakes lie on the borders of Greece, Albania, and North Macedonia and form one of the largest transboundary freshwater systems in the Balkan area. Most of Lake Lesser Prespa lies in Greece (90%) while only a small part is Albanian territory (10%). The lake covers an area of 47.4 km² within a catchment of 189 km² (Hollis and Stevenson 1997). The mean and maximum depths were measured as 4.2 and 8.4 m respectively (Koussouris et al. 1989). The water turnover time of the lake is estimated at 4.8 years (Hollis and Stevenson 1997). The mean total lake volume was estimated at 226×10^6 m³ at a mean lake level of 850.4 m a.s.l. based on bathymetry measurements from September 2014 (A. Manolopoulos, pers. comm.).

The avifauna of the Prespa area is internationally important because of its great richness (>275 species, of which at least 160 breed in the area) and the notable populations of rare species (Catsadorakis 1997). The extensive reedbeds around the lake provided vital nesting grounds for almost all of Prespa's waterbird species (Supplemental Fig. S1). The most numerous species that breed in the area are the Dalmatian pelican, the great white pelican, the pygmy cormorant, and the great cormorant (Catsadorakis 1997, Society for the Protection of Prespa 2013, Catsadorakis et al. 2015). Systematic monitoring showed that the breeding pairs of Dalmatian and great white pelicans have increased linearly between 1991 and 2016 by ~600% and 500%, respectively (Society for the Protection of Prespa 2013, Catsadorakis 2017). Notably, the Dalmatian pelican, which is a globally "Near Threatened" species (BirdLife International 2018), formed the largest colony worldwide within the Lesser Prespa area, comprising 20% of the global

population (Catsadorakis et al. 2015). The population of pygmy cormorants has increased from 600 breeding pairs during 1968–2007 to >2000 pairs in 2015, while the breeding pairs of great cormorants doubled between 1991 and 2016 (Society for the Protection of Prespa 2013, Catsadorakis 2017). Both species of pelicans and cormorants breed in large mixed colonies during spring/summer (Catsadorakis 1997). One of the preferred breeding areas at Prespa is the pond of Vromolimni, which lies at the isthmus between Lesser and Great Prespa (Fig. 1). We estimated the surface area of Vromolimni pond at 0.25 km² (Maliaka et al. 2018) with a mean depth of 1 m. The 2 pelican species and the great cormorant mainly feed in Great Prespa and occasionally in other wetlands outside Prespa, whereas the pygmy cormorant feed exclusively in Lesser Prespa early in the season and later (in May and June) feed mainly in Great Prespa (SPP, unpubl. data). The feeding and nesting habits of the Dalmatian and great white pelican have been thoroughly described in various publications (Hatzilacou 1992, Crivelli et al. 1998, Pyrovetsi and Economidis 1998, Catsadorakis and Crivelli 2001).

Materials and methods

Field measurements and sampling

Sampling at Lesser Prespa took place on 12 September 2015 along a 8.6 km transect (Sites 1–6; Fig. 1) and on 6 October 2015 along a 4.3 km transect (sites 7–10; Fig. 1), following a gradient from a site near the current largest bird colonies (high bird presence) toward the middle of the lake (low bird presence). This approach was used to examine the possible spatial influence of the birds on the water and sediment quality of the lake. Field measurements of dissolved oxygen (DO, in mg/L) and temperature (°C) were made at each sampling site using a HACH IntelliCAL LDO101 Rugged luminescent/optical dissolved oxygen probe (Hach Lange GmbH, Düsseldorf, Germany), and conductivity (µS/cm) was measured using a HACH IntelliCAL CDC401 Rugged conductivity probe. Total chlorophyll (µg/L), cyano-chlorophyll (µg/L), and turbidity were measured in situ using a portable bbe Moldaenke Algae-Torch10 (Schwentinental, Germany), and water transparency (m) with a Secchi disk. In addition, water samples were collected at each sampling site at the surface (1 m depth) and near the bottom of the lake (0.5 m above the sediment surface) using a Rüttner water sampler. Water pH was measured in the lab directly after sampling using an IntelliCAL PHC101 Standard Gel Filled pH Electrode. Sediment samples were collected in triplicate from sites 1, 10, 6, and 7 and as individual

samples from sites 2–5, 8, and 9 (Fig. 1) using a medium-sized Van Veen grab sampler. Sediment pore water samples were collected anaerobically with soil moisture samplers (Rhizons SMS, Eijkelkamp Agri-search Equipment, Giesbeek, Netherlands) connected with vacuum syringes (60 mL). Field sampling was also conducted at Vromolimni pond, where large bird colonies breed every year. Water was sampled at 3 sites in this pond (Fig. 1), whereas in situ field measurements and sediment sampling were not possible because accessibility of the site was restricted at that time.

Lake water samples were filtered over glass-fibre filters (Whatman GF/C, 47 mm diameter) and HgCl₂ was added directly after sampling to inhibit microbial alteration prior to nutrient analysis. Sediment pore water samples were treated with the same method prior to their analysis. Unfiltered lake water samples were also collected to determine total nutrients and total metal ions. All water samples prepared for nutrient analysis were stored in polyethylene bottles in the freezer (−20 °C) until further analysis. All water samples for metal analysis were acidified with 0.2 mL of 65% HNO₃ per 20 mL directly after sampling and stored together with the sediment samples at 4 °C for 1–1.5 months prior to their analysis.

In spring/summer (Aug 2012 and June–Sep 2013, Aug–Oct 2014 and May 2015) lake water samples and sediment samples (including pore water) were also collected from each site close to the bird colonies (site 6 and 7, *n* = 17–20) and far from the bird colonies (site 1 and 10, *n* = 13–18). During the same sampling campaigns, sediment samples were collected from sites near the lake's shoreline (Supplemental Fig. S2; *n* = 17) and processed following the same sampling techniques and storage method described earlier. Total chlorophyll *a* concentration was also measured in situ by using a portable bbe Moldaenke AlgaeTorch10 at each site.

During field sampling in September 2015, fresh pelican droppings (*n* = 11, dry weight [DW]: 6.2 [SE 1.3] g) were collected from a concrete platform at Lake Great Prespa where several Dalmatian pelicans were resting. Samples for total N (TN) and total P (TP) analysis were preserved separately and stored at −20 °C until transported to the laboratory and freeze-dried.

Additional sampling was conducted to determine potential external sources of N in the sediments of Lesser Prespa via stable isotope analyses using the sediment samples as well as bird droppings from 2015. Furthermore, 2 types of the most frequently used synthetic fertilizers in Prespa were collected from local farmers: YaraMila Complex NPK (12-11-18+20% SO₃) and YaraMila NPK (11-15-15 MOP+15 SO₃; Yara, Tampa, FL,

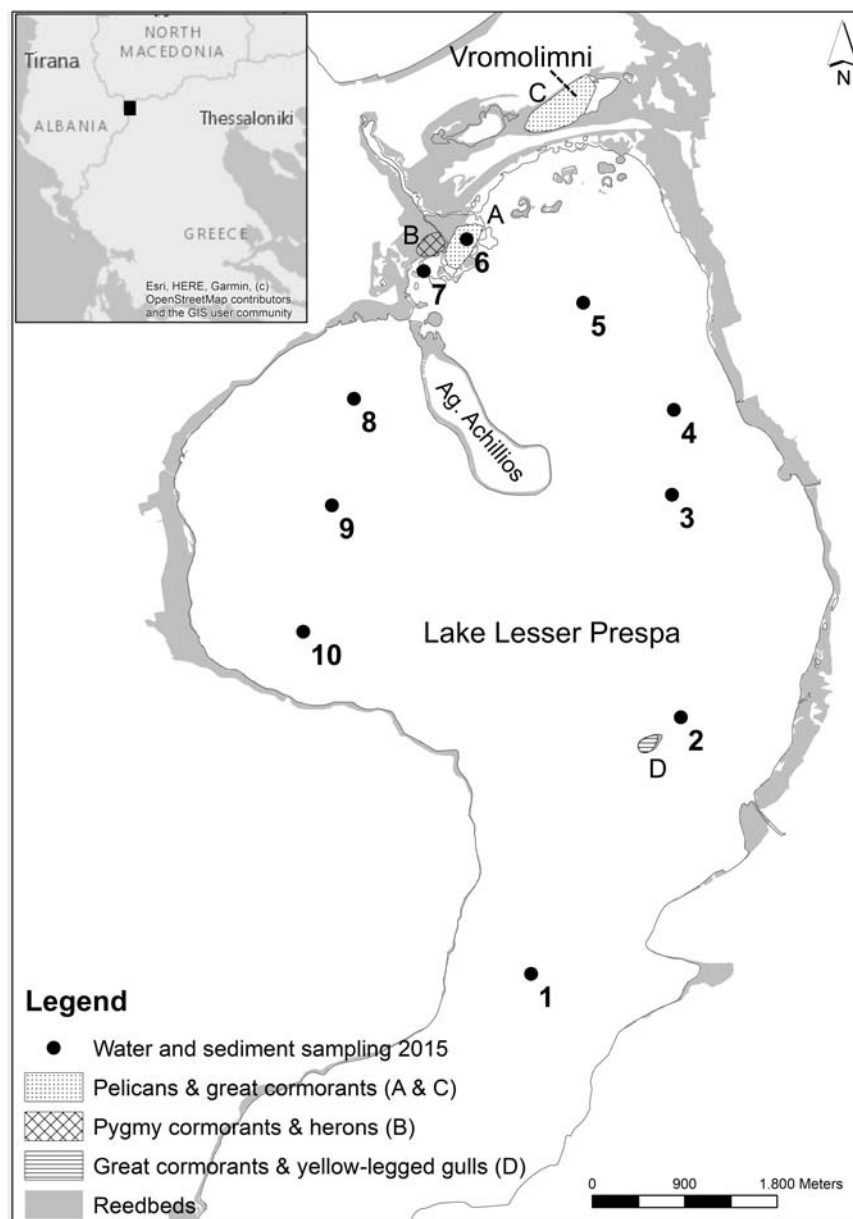


Figure 1. Lake Lesser Prespa and Vromolimni pond with localization of pelican and cormorant nesting sites (A, B, C, and D) and the water and sediment sampling sites in the lake in 2015.

USA). In the northern part of Lesser Prespa, near sites 6 and 7 and the island of Agios Achillios, the most abundant macrophyte/helophyte species (*Phragmites australis*, *Typha angustifolia*, *Myriophyllum spicatum*, *Ceratophyllum demersum*, and *Nymphaea alba*) were collected in September/October 2015. Phytoplankton was collected with a plankton net (55 μ m) at 3 sites in the lake: near the island of Agios Achillios, near the shore west of site 9, and near the shore southeast of site 2. Phytoplankton samples were filtered over pre-combusted GF/F filters. Last, we collected muscle tissue from 3 Prespa barbels (*Barbus prespensis*) and 2 common carp (*Cyprinus carpio*) caught by local fishermen.

Macrophytes, phytoplankton, and fish were stored in the freezer (-20°C) until further analysis.

Chemical analysis

Surface water and sediment pore water samples

The concentrations of PO_4^{3-} (soluble reactive P), NO_3^- (including NO_2^-), and NH_4^+ were measured colorimetrically with an Auto Analyzer 3 system (SEAL Analytical, Norderstedt, Germany) using the methods described in Tomassen et al. (2005). We used inductively coupled plasma (ICP) spectrophotometry (ICP Optical emission spectrometer, iCAP 6300, Thermo Fisher Scientific,

Bremen, Germany) to determine dissolved P and TP (Tomassen et al. 2005).

Sediment samples and waterbird droppings

The moisture content of each sediment sample was determined by drying ~50 g for 48 h at 60 °C in duplicate. Then 200 mg of homogenized dried sediment of 1 replicate was digested with 4 mL HNO₃ (65%) and 1 mL H₂O₂ (30%) using a microwave oven (MLS 1200Mega, Milestone Inc., Italy). Digestates were diluted to 100 mL with Milli-Q water and analyzed by ICP as described previously. One replicate of dried sediment was incinerated for 4 h at 550 °C to determine the loss of ignition (LOI, approximating organic matter content). The soluble (or exchangeable) and labile P and N content of the sediments was determined via water extraction (mixing 17.5 g of fresh sediment sample with 50 mL Milli-Q water) and 0.2 M NaCl (salt)-extraction (mixing 17.5 g of fresh sediment sample with 50 mL NaCl solution) method, respectively. The supernatant was collected via soil moisture samplers and analyzed colorimetrically with an Auto Analyzer 3 system (SEAL Analytical, Norderstedt, Germany).

Homogenized portions of 200 mg of each freeze-dried dropping ($n = 11$) were digested with 4 mL HNO₃ (65%) and 1 mL H₂O₂ (30%), and digestates were diluted with 100 mL Milli-Q water and analyzed by ICP as described previously.

Isotope analysis

For isotope analysis of carbon (c) and N, all samples were freeze-dried and ground to dust-sized particles. A small homogenized portion of dried sample was weighed with an analytical balance and put into ultra-pure tin cups. Weights depended on the type of sample (0.2–6.5 mg). The cups were rolled into pellets with a pair of tweezers and subsequently analyzed for C and N stable isotope composition with a Flash 2000 elemental analyzer coupled online with a Delta V Advantage isotope ratio mass spectrometer (IRMS,

Thermo Scientific, Bremen, Germany). The reference gases used were calibrated using the International Atomic Energy Agency reference standards (IAEA-N-2 and IAEA-CH-6), with a maximum deviation of 0.15‰. The ¹³C/¹²C and ¹⁵N/¹⁴N were determined (R in permil; ‰) for every sample. Caffeine was used as an internal standard control. Isotope ratios were expressed in the δ notation (δ¹³C and δ¹⁵N) relative to Vienna Pee Dee Belemnite (PDB) and atmospheric N₂ using:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000(1).$$

Data collection on waterbirds

Monitoring data

The most prominent breeding colonies of waterbirds at Lake Lesser Prespa are spread across 4 sites (Fig. 1): A, in the northern part of Lesser Prespa (40°47'56"N; 21°04'55"E), where large mixed colonies of Dalmatian and great white pelicans and great cormorants breed; B, in the northern part of Lesser Prespa (40°47'56"N; 21°04'41"E), where the colony consists mainly of pygmy cormorants and heron species; C, at Vromolimni pond (40°48'40"N; 21°05'35"E), where the colony consists of Dalmatian pelicans and great white pelicans and great cormorants; and D, on a small island in Lesser Prespa called Vidronisi (40°45'18"N; 21°06'11"E), where a mixed colony of great cormorant and yellow-legged gulls (*Larus michahellis*) is present. We estimated the cumulative surface area of all nesting islands of both pelican species at 3487 m² and the surface area covered by the nests of pygmy cormorants at 2434 m². The entire area these breeding islands occupy in Lesser Prespa (including surrounding water) was estimated at ~78 203 m². The total surface area of the nesting colonies of pelicans within Vromolimni pond was estimated at 678 m². The number of breeding pairs and the breeding success of both pelican and cormorant species in each colony have been monitored annually for >35 years by the Greek environmental organization Society for the Protection of Prespa (SPP; Table 1).

The presence of waterbirds in the Lake Lesser Prespa area

Early in the breeding season, the piscivorous waterbirds return to the nesting grounds from their wintering grounds. We consider that Dalmatian pelicans, great white pelicans, and great cormorants can act as vectors for external nutrients input into Lesser Prespa and Vromolimni because they mostly feed in other

Table 1. Average number of breeding pairs in the Prespa area during 2003–2014 (SPP, unpubl. data) and breeding success (fledglings per nest, per year) of great white pelican (GW), Dalmatian pelican (DAL), great cormorant (GCOR), and pygmy cormorant (PYGC).

Species	Breeding success (SE)	Site A and B breeding pairs (SE)	Site C breeding pairs (SE)	Site D breeding pairs (SE)
GW	0.83 (0.12) ^{a,b,c}	39 (15)	388 (40)	
DAL	1.03 (0.17) ^{a,d}	673 (69)	526 (36)	
GCOR	2.1–2.7 ^e	219 (28)	230 (46)	255 (27)
PYGC	2.86 (0.07) ^f	877 (214)		

^aCrivelli et al. (1991), ^bHatzilacou (1992), ^cSPP unpubl. data, ^dCrivelli et al. (1998), ^eLiordos and Goutner (2008b), ^fNazirides and Papageorgiou (1996).

lakes and wetlands. Great white pelicans feed partly on Lake Great Prespa but also outside the Prespa basin, such as in Lake Chimaditis, Axios River Delta, and Lake Kerkini (Pyrovetsi 1989, Hatzilacou 1992). Almost all Dalmatian pelicans and great cormorants of the Lesser Prespa and Vromolimni colonies feed in Great Prespa and only a few in the surrounding shallows (Pyrovetsi and Crivelli 1988, Pyrovetsi and Economidis 1998). Dalmatian pelicans regularly use other lakes as well, such as Lakes Kastoria and Kerkini (Crivelli 1987, Efrat et al. 2019). Pygmy cormorants make a partial contribution to external loading to Lesser Prespa by feeding partly in Great Prespa and partly in Lesser Prespa. We assumed that they feed ~1.7 times more in Great Prespa than in Lesser Prespa based on arrival-departure counts (Willems and de Vries 1998; SPP, unpubl. data). Because the diet of piscivorous waterbirds has high protein levels (and therefore high N content), which are associated with high P levels, the N and P input can be relatively large compared with the input from herbivorous birds of similar size (Marion et al. 1994, Hahn et al. 2007). To calculate nutrient loading by pelicans and cormorants, the number of bird-use days (number of days [24 h] that birds are actually present in the colony) was estimated after gathering information on the time budgets of the birds (Table 2). The great cormorant colony at Vidronisi (site D) as well as the colonies in the northern part of the lake (sites A and B) were taken into account when assessing the nutrient input to Lesser Prespa.

Table 2. Average day of arrival (over last 10 years for both pelicans and estimated for both cormorants), days between arrival and the laying of the first egg, incubation period, fledging period, and rearing period.

Presence at Lesser Prespa (in days)	GW	DAL	GCOR	PYGC
Average day of arrival	24 March ^c	31 January ^c	1 April ^f	16 May ^f
Time between arrival and laying first egg	6 ^a	9 ^d	7	7
Incubation period	32 ^b	32 ^e	29 ^f	28 ^f
Fledging period	80 ^b	80 ^e	50 ^f	42 ^g
Rearing/brooding period	26 ^b	25 ^e	14 ^f	12
Post-fledging period, chicks	21 ^b	28 ^e	34 ^f	30 ^g
Post-rearing period (fledging period minus rearing period), adults	54	55	36	30
Minimum presence of breeders in the colony	37.3	39.8	30	28.3
Minimum presence of chicks/juveniles in the colony	101	87	67	57

Minimum presence of chicks and adults in the Prespa area and in the colony was calculated (days). Great white pelican = GW, Dalmatian pelican = DAL, great cormorant = GCOR, and pygmy cormorant = PYGC.

^aHatzilacou (1992), ^bCrivelli et al. (1997b), ^cSPP unpubl. data, ^dCrivelli (1987), ^eCrivelli et al. (1997a), ^fNelson (2006), ^gWillems and de Vries (1998).

Time budget – assumptions

To estimate the minimum presence of adults and chicks in the colony, the following assumptions were made, based on regular bird monitoring observations: (1) during incubation, one parent is present on the nest while the other parent is not in the colony (for each species; Hatzilacou 1992); (2) during the rearing period, we assumed that for each species both parents visit the colony equally to feed the chick for ~1 h/d (Hatzilacou 1992); (3) Dalmatian pelican chicks are present in the colony for only 25% of the post-fledging period; (4) the pre-laying period for both cormorant species is in the same range as for pelicans, set at 7 d; (5) chicks of both cormorant species spend at least 50% of the post-fledging time in the colony; and (6) the post-fledging period of pygmy cormorants is proportionally the same as the post-fledging period of great cormorants (12 d; Cramp and Simmons 1977).

Defecation rates per species – assumptions

The defecation rates for the waterbirds were estimated per species. The average daily food intake for piscivorous waterbirds is ~10% of their body mass (Table 3; Guillet and Furness 1985, Shmueli et al. 2000). The fresh weight to dry weight (FW/DW) ratio for food and the food intake/excrement ratio were obtained from the literature (Marion et al. 1994, Hahn et al. 2007; Table 3).

Given that we observed pelicans defecate during flying, roosting, and resting and that they can be active at night (SPP unpubl. data), we assumed that both pelican species and both cormorant species have a regular defecation rate during a natural day. Bird excrement deposited on the colony substrate was assumed to end up in the lake because events such as rainfall and

Table 3. Body mass (g) and food intake (g) DW per species.

Species	Adult body mass (g)	Food intake (g DW)	References	FW/ DW ratio	Intake/ excrement ratio (DW)*
GW	8400	203.3	Guillet and Furness 1985	0.242 ^a	0.395 ^{a,b}
DAL	9000	205.7	Dentressangle et al. 2008; SPP unpubl. data		
GCOR	3300	79.9	Marion et al. 1994		
PYGC	700	36.3	Willems and de Vries 1998, Vizi and Vizi 2010		

Fresh weight to dry weight ratio (FW/DW) and food intake/excrement ratio were estimated. Great white pelican = GW, Dalmatian pelican = DAL, great cormorant = GCOR, and pygmy cormorant = PYGC.

^aMarion et al. (1994), M. Shmueli, personal comm.; ^bHahn et al. (2007)

*In Shmueli et al. (2000) the fecal excretion and food intake were measured for (temporarily) captive held great white pelicans. A comparable intake/excrement ratio of 0.401 (SE 0.016) was found.

waves cause nutrient run-off (Tatur and Myrcha 1983, Bosman et al. 1986, Klimaszyk et al. 2015), and the soft reed substrates presumably enable fast percolation to the lake water.

Estimations of nutrient input

Two methods were used to calculate the TN and TP load delivered into Lake Lesser Prespa and Vromolimni pond by great white pelican, Dalmatian pelican, great cormorant, and pygmy cormorant. The first method was based on the equation used by Scherer et al. (1995):

$$\text{Input} = B \times D \times C_d \times p. \quad (2)$$

The bird-use days (B) were calculated per species (Manny et al. 1994) by multiplying the average number of adult birds present and the number of fledged chicks, both during the breeding period, with their estimated minimum presence (days) in the colony (Table 2). Further, the mass of droppings produced (D , in mg DW/d) was calculated by determining the food intake per species (based on DW) and an intake/excrement ratio of 0.395 (Table 3). The nutrient contents (TN and TP in mg/g DW) of droppings (C_d) measured in collected Dalmatian pelican droppings were used for pelican calculations. For great cormorants, the N and P nutrient content of droppings of 32.8 and 143.2 mg/g, respectively, was used as described in Marion et al. (1994). We used the same values for pygmy cormorants and great cormorants because their diets are similar (Cramp and Simmons 1977). The probability of droppings entering the water (p) for pelicans was estimated from bird observations during the field study in Prespa ($p = 0.9$). For cormorants, the probability was set to 0.95 because cormorants are mainly found on the water or shore when they are near the colony (YJMV, personal field observations from 2015).

The second method was based on calculations in Hahn et al. (2007), in which 2 equations were used to separate adult load (equation 3) from chick load (equation 4):

$$\text{Input}_{\text{ad}} = p \times \alpha \times (\text{DER}/[E \times \text{AM}]) \times C_d. \quad (3)$$

The nutrient input created by adults (Input_{ad} , in mg/d) was calculated with the probability fraction (p), the ratio between food intake and excretion ($\alpha = 0.395$), daily energy requirement (DER, in kJ/d), the gross energy of the food ($E = 23.9$ [0.46] kJ/g), apparent metabolizable energy coefficient (AM: 0.76 [0.013]). DER is calculated by: $10^{1.0195} \times M^{0.6808}$, in which M is adult body

mass (g) (Hahn et al. 2007). The chick load was given by:

$$\text{Input}_{\text{ch}} = \text{BS} \times (\alpha \times (\text{TER}/[E \times \text{AM}]) \times C_d - C_{\text{syn}}). \quad (4)$$

The nutrient loading (mg) by a clutch of one breeding pair over the rearing period (Input_{ch} , equation 4), was calculated from the breeding success of the species (BS; Table 1), the total energy requirement during the entire chick rearing period (TER, in kJ), the fixed nutrient content of synthesized mass during chick growth (C_{syn} , in mg), and the previously mentioned parameters. TER was calculated as: $28.43 \times M^{1.062}$, in which M is adult body mass (g), and C_{syn} was calculated using the assumed average nutrient contents of N and P in a bird's body (Hahn et al. 2007). The increase in body mass was calculated as the difference between adult body mass and 72% of fresh egg mass. The egg mass was estimated at 177 g for both pelican species (Cramp and Simmons 1977, Guillet and Furness 1985), 58 g for great cormorants (Hahn et al. 2007), and 20 g for pygmy cormorants (Barati et al. 2008). To calculate the loads over the entire breeding season, the results of equation 3 were multiplied with the adult bird-use days, whereas the results of equation 4 were multiplied with the number of breeding pairs of each species in the Lesser Prespa and Vromolimni colonies. In both calculation methods the input by pellets produced by cormorants was not taken into account, although it may contribute to the total nutrient input as well. The 2 studied pelican species never produce pellets.

Statistical analyses

Field data and analytical data on nutrient concentrations in the water and the sediments of the lake, as well as stable isotope data ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$), were analyzed statistically using an independent T test. When data failed the normality test ($p < 0.050$; Shapiro-Wilk), the data were either log transformed or, if the normality requirement was still not met, they were analyzed using a non-parametric Mann-Whitney rank sum test in SigmaPlot 12.3.

Results

Water and sediment quality

Field measurements were taken along 2 transects at Lake Lesser Prespa (Fig. 1). In the sediment pore water along the transects (2015), the highest levels of total inorganic N (TIN: on average 1.6 [SD 0.7] mmol/L) and dissolved P (on average 41.0 [39] $\mu\text{mol/L}$) were detected close to the bird colonies (sites 6 and 7). Pore water TIN

concentration at the sites away from bird colonies was on average 0.5 (0.2) mmol/L while pore water dissolved P concentration was 9.3 (4.1) $\mu\text{mol/L}$. Sediment TIN (NaCl extracted) in the lake sediments likewise strongly increased at sites close to bird colonies by up to 22 (5) mmol/kg DW at site 7 (Fig. 2). The elevated sediment TIN concentration was associated with higher organic matter content (up to 31% [1.6%]) near the bird colonies (Fig. 2).

If all available nutrient measurements in sediment samples collected from sites similar to 6 and 7 (near bird colonies) and to 1 and 10 (away from the bird colonies) are compared, a significant accumulation of dissolved P ($p = 0.002$) and TIN ($p < 0.001$) is found in sediment pore water of the sediments near the bird colonies (Fig. 3). Similarly, organic matter content, sediment TP, and particularly sediment TIN concentration were found to be significantly higher ($p < 0.001$) in the sediments near the bird colonies (Fig. 3). Additional data analysis on the nutrient measurements in sediment samples collected from shallow sites near the shoreline of Lesser Prespa and away from waterbird colonies (Supplemental Fig. S2) show that pore water dissolved P and pore water TIN concentrations were significantly lower than at sites near waterbird colonies ($p = 0.006$ and $p \leq 0.001$, respectively; Supplemental Fig. S3). Similarly, sediment TP, TIN (NaCl extracted), and organic matter content were also significantly lower at these sites than at sites near waterbirds ($p = 0.009$, $p = 0.005$, and $p = 0.016$, respectively; Supplemental Fig. S3).

Mean total chlorophyll levels of 13.7 (3.7) $\mu\text{g/L}$ near the largest bird colonies (sites 6 and 7) did not exceed the mean total chlorophyll levels at the sites away from colonies (15.6 [4.9] $\mu\text{g/L}$; sites 1–5 and sites 8–10). Similar results were found for the mean cyano-chlorophyll values, which were 7.8 (1.5) and 9.6 (3) $\mu\text{g/L}$, respectively. DO concentrations decreased with depth at all sites, reaching a minimum of 5.0 mg/L (site 5, depth 4.5 m; Fig. 1), but spatial variation was low among the sites (DO = 8.7 [0.8] mg/L close to bird colonies and DO = 8.2 [1.5] mg/L away from the colonies). No thermal stratification was observed in the water column during sampling ($T = 20.6$ [1.7] $^{\circ}\text{C}$). Average TP and dissolved P concentrations in the lake water were between 0.8–1.3 and 0.2–0.8 $\mu\text{mol/L}$, respectively. The concentrations were mostly uniform along both transects, and no significant variance was observed in water TP ($p = 0.410$) or dissolved P ($p = 0.648$) near waterbird colonies versus far. Measurements of average TIN in the lake water revealed no clear difference between the sampling sites and varied irregularly between 1.7 and 6.7 $\mu\text{mol/L}$ for sites 1–6 and between 2 and 4.1 $\mu\text{mol/L}$ for sites 7–10.

In Vromolimni pond, which also hosts a mixed colony of pelicans and cormorants, the concentrations of TP and dissolved P in the surface water were on average 10.3 (2.2) and 2.0 (1.6) $\mu\text{mol/L}$, respectively, while the average dissolved TIN concentration was 10.9 (2.3) $\mu\text{mol/L}$ in 2015.

In samples collected during previous sampling campaigns, mean total chlorophyll concentration collected from site 6 and 7 (near waterbird colonies; 20.8 [16.8] $\mu\text{g/L}$, $n = 51$; Fig. 1) was similar ($p = 0.208$) to the chlorophyll concentrations (16.6 [8.6] $\mu\text{g/L}$, $n = 77$; Fig. 4a) at site 1 and 10 (away from waterbird colonies; Fig. 1). The range of the cyano-chlorophyll levels was similar ($p = 0.494$) both near and far from the bird colonies: 11.2 (8.4) $\mu\text{g/L}$ ($n = 51$) and 10.0 (6.1) $\mu\text{g/L}$ ($n = 77$), respectively (Fig. 4a). Within Vromolimni pond, total chlorophyll and cyano-chlorophyll concentrations measured in September 2013 ($n = 9$) were much higher: 208.6 (63.4) and 171.5 (64.3) $\mu\text{g/L}$ (both $p < 0.001$), respectively, than the concentrations in Lesser Prespa (Fig. 4b).

Measurements of lake water nutrients at the sites both near and far from bird colonies between 2012 and 2015 (Mar and Aug 2012; Apr–Oct 2013; Apr–Oct 2014; and May, July, and Sept 2015) revealed no significant difference (Fig. 5a; $p = 0.689$ for TP; $p = 0.689$ for TIN). Overall, the concentration of TP was much higher in Vromolimni than in Lesser Prespa (Fig. 5b).

Estimates of waterbird-nutrient loadings

Pelican droppings had an average DW of 6.2 (1.3) g ($n = 11$); the TN fraction of the DW droppings was 110.1 (7.7) mg/g and the TP fraction was 72.8 (3.1) mg/g (N:P ratio 1.5). These TN and TP values were used to calculate the nutrient input of both pelican species. For cormorant species, we used the N and P values found in the literature (Marion et al. 1994). The calculated defecation rate (as DW) for each waterbird species was 80.3 g/d for great white pelicans, 86.0 g/d for the Dalmatian pelicans, 31.5 g/d for great cormorants, and 14.3 g/d for pygmy cormorants (based on Table 3). The N and P input by the 4 species into Lake Lesser Prespa was estimated based on their minimum presence in the colonies, using calculation methods 1 and 2 (Table 4). Internal loading (nutrients originating from inside Lesser Prespa) and external loading (nutrients originating from outside Lesser Prespa) were distinguished.

Calculation 1 indicated lower TN and TP input loadings (in $\text{mg/m}^2/\text{yr}$ or $\mu\text{g/L}/\text{yr}$) than calculation 2, but they both were of the same order of magnitude (Table 4). On average, the TN input was 32.8 $\text{mg/m}^2/\text{yr}$

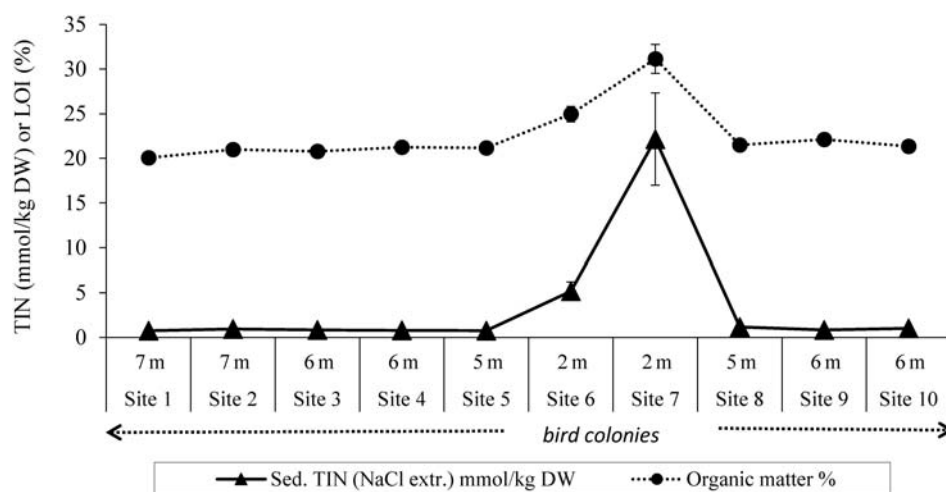


Figure 2. Total inorganic nitrogen (TIN) concentration and organic matter content measured in sediments of each sampling site in Lesser Prespa (Sep–Oct 2015). The depth at each site is noted in meters below the surface. $n = 3$ for sites 1, 6, 7, and 10.

(or $8.0 \mu\text{g/L/yr}$; 1243 kg/yr) and the TP input was $38.9 \text{ mg/m}^2\text{/yr}$ (or $9.5 \mu\text{g/L/yr}$; 1649 kg/yr). The internal loading of TN and TP by pygmy cormorants was only a small fraction of the total nutrient input in both calculations. Vromolimni pond had no pygmy cormorants, so no internal loading was calculated for this species. The range of estimated total external loading into Vromolimni was $5180\text{--}6343 \text{ mg/m}^2\text{/yr}$ for TN and $4171\text{--}5924 \text{ mg/m}^2\text{/yr}$ for TP (Table 4). In Lesser Prespa TP loading exceeded the TN loading and vice versa in Vromolimni pond. When only taking into account the surface area of the surrounding water with breeding sites in Lesser Prespa ($\sim 0.8 \text{ km}^2$), the local TN and TP input was $15\,539\text{--}23\,330$ and $20\,314\text{--}25\,486 \text{ mg/m}^2\text{/yr}$, respectively.

An overview of the relative contribution of TN and TP input according to calculation 1, which represents the minimum nutrient input by each of the species studied, shows that the main contributor for TN input (78%) as well as for TP input (39%) in Lesser Prespa was the Dalmatian pelican (Fig. 6a and b). The low number of great white pelicans in Lesser Prespa led to a lower contribution to TN (4%) and TP inputs (2%; Fig. 6a and b). Pygmy cormorants and great cormorants seem to be significant contributors to TP inputs (32% and 27%, respectively) to the lake, but both species contribute much less to the TN input (10% and 8%, respectively; Fig. 6a and b).

As in Lesser Prespa, Dalmatian pelicans were the largest contributors to TN (58%) and TP input (48%; Fig. 6c and d) into Vromolimni. Great white pelicans also contributed substantially to TN (38%) and TP (31%) input. By contrast, great cormorants made a much lower contribution to TN (4%) and TP (21%) input in Vromolimni (Fig. 6c and d) than the pelicans.

Based on calculation method 2, great cormorants made a relatively large contribution to TN (Lesser Prespa 19%, Vromolimni 15%) and TP (Lesser Prespa 38%, Vromolimni 25%) input in both aquatic systems compared to calculation 1 (Fig. 7a–d). Conversely, pygmy cormorants contributed less TN (6%) and TP (17%) in Lesser Prespa (Fig. 7a and b).

Main external and internal nitrogen sources for Lesser Prespa – isotope analysis

All pelican droppings had a comparable $\delta^{13}\text{C}$ of around -22.8‰ (0.3‰) while $\delta^{15}\text{N}$ varied between $\sim 5.8\text{‰}$ and 9.0‰ (mean 7.3‰ [1.2‰]; Fig. 8). For lake sediments near the bird colonies (site 6 and 7), the $\delta^{13}\text{C}$ values were between -20.3‰ and -16.4‰ for $\delta^{13}\text{C}$ (mean -18.2‰ [1.7‰]) and $\delta^{15}\text{N}$ values were between 3.8‰ and 5.3‰ (mean 4.6‰ [1.2‰]), whereas the values of lake sediments away from the bird colonies (sites 1–5 and 8–10) were scattered between -17.5‰ and -15.6‰ for $\delta^{13}\text{C}$ (mean -16.5‰ [0.6‰]) and $2.6\text{--}3.4\text{‰}$ for $\delta^{15}\text{N}$ (mean 2.9‰ [0.3‰]). Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the sediments varied significantly ($p = 0.022$ and $p < 0.001$, respectively) between the sites near and away from the bird colonies and correlated with organic matter (Supplemental Fig. S4). The stable isotope signature of synthetic fertilizers differed from the other samples, with a mean $\delta^{15}\text{N}$ of 0.8‰ (0.6‰) and a mean $\delta^{13}\text{C}$ of -25.0‰ (1.4‰) (Fig. 8). Internal sources of nutrients such as fish, dominant macrophytes/helophytes, and phytoplankton from Lesser Prespa were also analyzed. All plant species and phytoplankton had lower $\delta^{15}\text{N}$ values than bird droppings, whereas fish were more enriched in ^{15}N . With exception of Eurasian

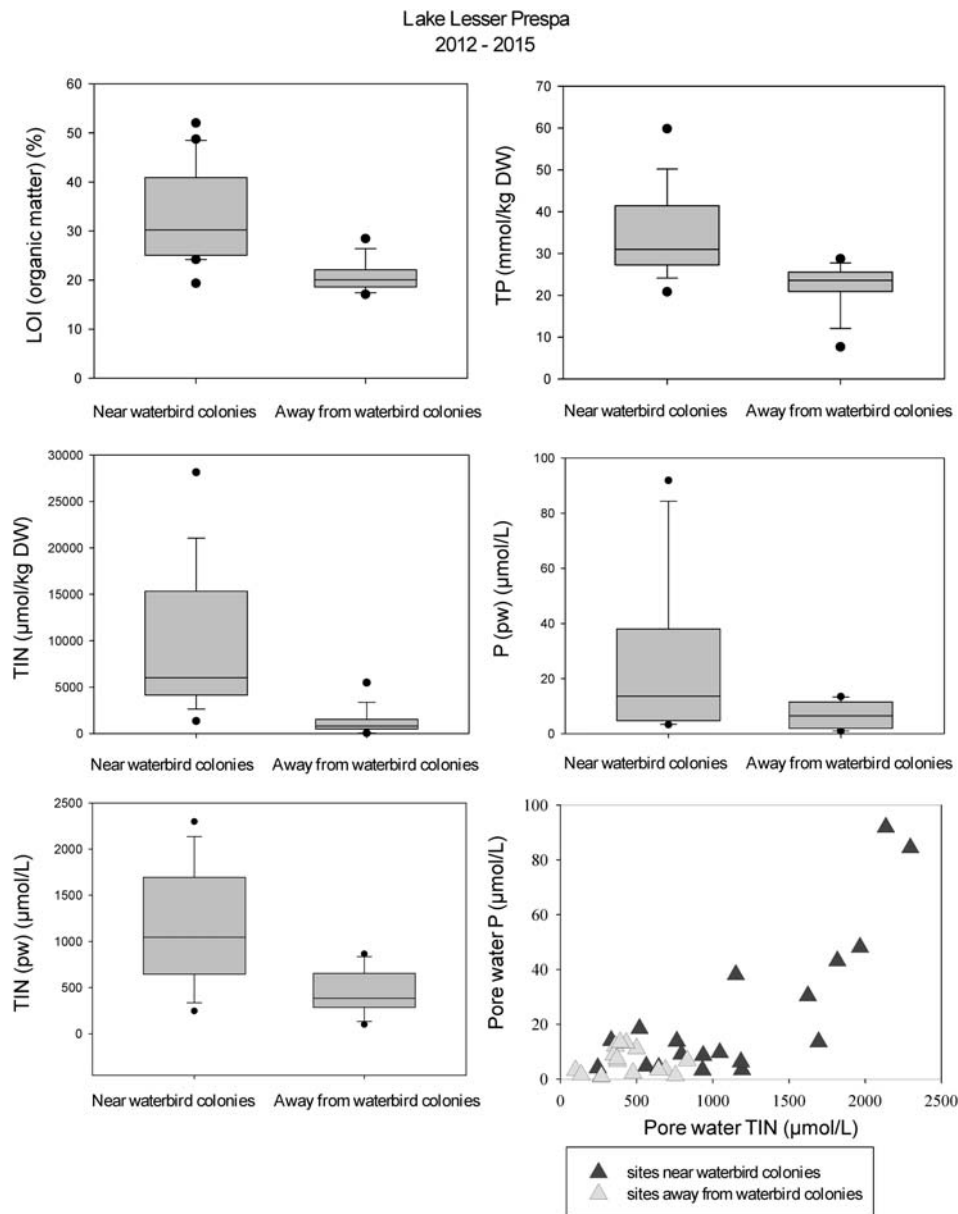


Figure 3. Organic matter content, total phosphorus (TP), and total inorganic nitrogen (TIN: NaCl-extracted), pore water (pw) P, and pw TIN measured at the sediments near waterbird colonies ($n = 17\text{--}20$; sites 6 and 7) and far from waterbird ($n = 13\text{--}18$; sites 1 and 10) at Lesser Prespa during 2012–2015.

watermilfoil (*M. spicatum*) and hornwort (*C. demersum*), $\delta^{13}\text{C}$ was low in aquatic plants and fish compared to bird droppings.

Discussion

Nutrient input by waterbirds in Lake Lesser Prespa and Vromolimni pond

The average total N and P nutrient loading into Lake Lesser Prespa attributed to populations of great white pelican, Dalmatian pelican, great cormorant, and pygmy cormorant between 2003 and 2014 was 26.2

and 34.8 mg/m²/yr, respectively, according to method 1 (Scherer et al. 1995), and 39.4 and 43.0 mg/m²/yr, respectively, according to method 2 (Hahn et al. 2007). For Vromolimni pond, which is much smaller than Lake Lesser Prespa, the N and P inputs per square meter and per liter by these waterbirds were much higher than the estimates for Lesser Prespa (Table 4). Method 1 is based on the daily defecation of waterbirds according to their assumed daily food intake, based on body mass, whereas method 2 is based on the daily defecation of waterbirds according to the estimated energy requirement of the bird. Further, method 2 distinguishes between adult and chick nutrient input because

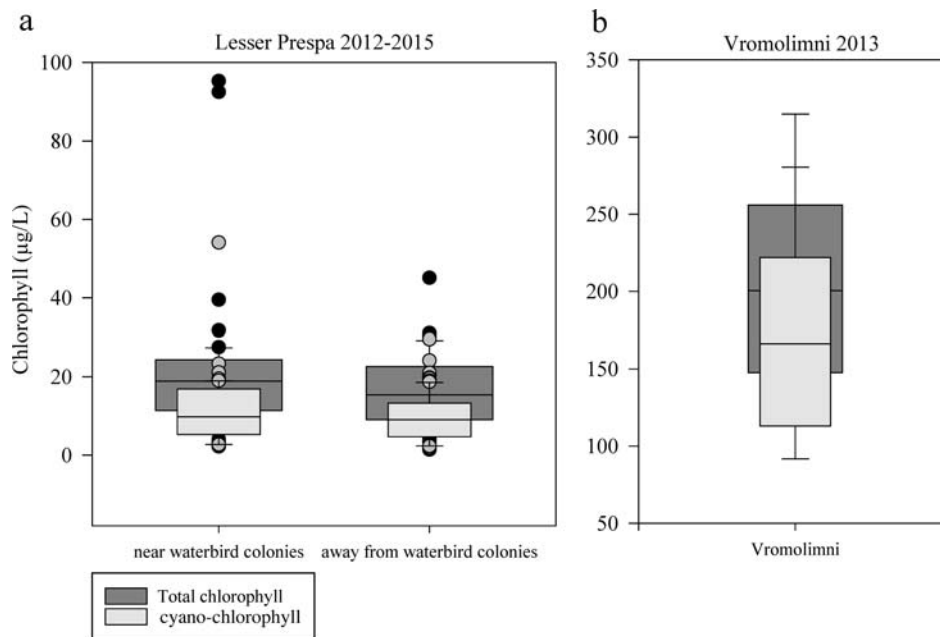


Figure 4. (a) Average in situ chlorophyll *a* measured in sites near bird colonies ($n = 51$; sites 6 and 7) and away from bird colonies ($n = 77$; sites 1 and 10) during Aug 2012 and June–Sep 2013, Aug–Oct 2014, and May and Aug 2015 at Lesser Prespa. (b) Average in situ total and cyano-chlorophyll ($n = 9$; µg/L) measured at Vromolimni pond in Sep 2013.

chicks need energy for growth and therefore absorb extra nutrients (Gere and Andrikovics 1992, Hahn et al. 2007). More specifically, Hahn et al. (2007) considered that chick growth reduces N input by up to 28% and P input by up to 10% compared to adult waterbirds, information not taken into account in method 1 by Scherer et al. (1995). The results from both methods are in the same order of magnitude, although method 1 indicates lower nutrient inputs than method 2. Apparently the assumed energy requirements used in method 2 result in higher food intake and corresponding defecation. Although the outcomes of the calculations strongly depend on the assumptions required, they provide valuable insight into the order of magnitude of the nutrient input by waterbirds in Lesser Prespa and Vromolimni.

Dalmatian and great white pelicans made the highest contribution to the nutrient inputs in both waterbodies according to both calculations because of their high abundance, presence in the colony, and the amount they excrete. Remarkably, a difference in mass fractions of N and P was found between Dalmatian pelicans and great cormorants, although they both feed on fish. Dalmatian pelicans had a higher N fraction and a lower P fraction, but vice versa for great cormorants, possibly because metabolic processes or rates can differ among species and body masses (Bennett and Harvey 1987). The higher N relative to P concentrations in pelican droppings we found in the Prespa area are in accordance with the findings of Hutchinson (table 4 in Hahn et al. 2007) for Peruvian pelicans (*Pelecanus thagus*). Because

great white pelicans are related to Dalmatian pelicans, and pygmy cormorants to great cormorants (they live in the same area and have similar diets), the nutrient content of the droppings is assumed similar. Although the composition and amount of the diets can be highly variable, they are also highly overlapping (Crivelli 1987, Hatzilacou 1992, Liordos and Goutner 2008a).

The calculated values of waterbird use days are based on the minimum presence of the birds in the Prespa area and in the colony as well as on assumptions made for these parameters. Also, the counts of breeding pairs refer to minimum numbers because seasonal counts might not cover every nest as nests are repeatedly abandoned and reoccupied. Although highly accurate numbers for the waterbird populations of the colonies are difficult to provide, our estimates are the best available by any means. The bird colonies in the Prespa area are among the most monitored in Europe. Nonbreeding Dalmatian pelicans were also present in the breeding season, suggesting extra nutrient input from these birds. An estimated 2–5% of adult waterbirds might be nonbreeders. Additionally, cormorants do not all migrate after the breeding period, and breeding biology parameters per species may vary over time and area (Peja et al. 1996, Kazantzidis et al. 1997, Crivelli et al. 1998, Liordos and Goutner 2008a). Because our calculations are mostly based on average or minimum numbers of waterbirds and breeding variables, the estimated nutrient inputs are probably an underestimation of the actual nutrient input.

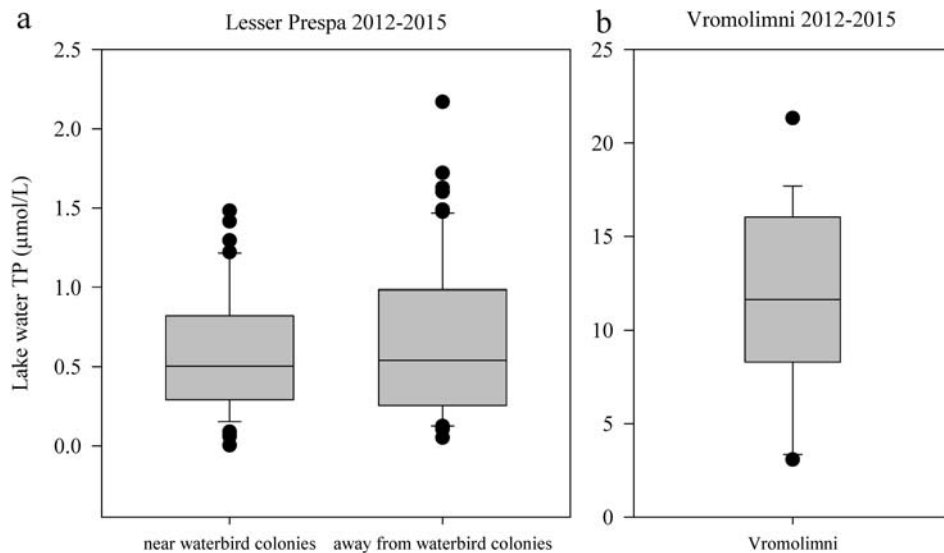


Figure 5. (a) Average total phosphorus (TP) measured in the surface water near bird colonies ($n = 48$; sites 6 and 7) and away from bird colonies ($n = 67$; sites 1 and 10) during Mar and Aug 2012; Apr–Oct 2013 and 2014; and May, July, and Sep 2015 at Lesser Prespa. (b) Average TP ($n = 19$) measured at Vromolimni pond Aug 2012; Sep 2013; July and Oct 2014; and Oct 2015.

Furthermore, because of a growing trend in the numbers of pelican and cormorant breeding pairs (SPP 2013), the N and P inputs by waterbirds are likely increasing (Liordos and Goutner 2008a, 2008b; Supplemental Table S1). Other breeding waterbirds species present around Lesser Prespa are herons, great crested grebes (*Podiceps cristatus*), and yellow-legged gulls (~400, ~80, and ~100 breeding pairs, respectively). However, these species are much less abundant and therefore contribute much less to the bird-derived nutrient load (external or internal) compared to the pelicans and cormorants.

In several lakes the N and/or P inputs derived from waterbirds have been quantified because they possibly increase the lake's productivity. In a Michigan lake, geese and ducks loaded 280 and 88 kg of N and P, respectively, annually, accounting for 27% and 70% of N and P, respectively, entering the lake (0.15 km^2 ; Manny et al. 1994). Scherer et al. (1995) estimated the P loading in Green Lake (Seattle, Washington; 6.0 km^2) to be 162 kg/yr (29% of TP loading), 87% of which was internal loading. Considering the external nutrient inputs in a

small lake in the United Kingdom, bird droppings accounted for 73% of P ($234 \text{ mg/m}^2/\text{yr}$) and 17% of N ($741 \text{ mg/m}^2/\text{yr}$) input (Chaichana et al. 2010), where groundwater was the main source of N input. For the 3 previously mentioned studies, the areal nutrient load is higher than in Lesser Prespa but lower than in Vromolimni pond. Marion et al. (1994) found small N and P inputs by waterbirds to Lake Grand-Lieu (63 km^2) compared to the high nutrient loadings originating from agriculture and human sewage. However, they emphasized the relatively high annual load by birds if anthropogenic contributions were low. In our study we have not yet quantified other nutrient sources, although in a modeling study Coşkun (2017) estimated the P input by waterbirds into the entire lake to be ~27–33% relative to the input via the streams (including drainage ditches) and groundwater (Supplemental Table S2). The importance of N input from birds was minor compared to the input via the streams. However on a local scale, near the breeding colonies, both N and P input by waterbirds is almost 600-fold higher than calculated for the whole lake surface.

Table 4. Estimates of the TP and TN inputs by waterbirds in Lake Lesser Prespa based on calculation method 1 by Scherer et al. (1995) and calculation method 2 by Hahn et al. (2007).

	Calculation 1 (Scherer et al. 1995)				Calculation 2 (Hahn et al. 2007)			
	TN $\text{mg/m}^2/\text{yr}$	TN $\mu\text{g/L/yr}$	TP $\text{mg/m}^2/\text{yr}$	TP $\mu\text{g/L/yr}$	TN $\text{mg/m}^2/\text{yr}$	TN $\mu\text{g/L/yr}$	TP $\text{mg/m}^2/\text{yr}$	TP $\mu\text{g/L/yr}$
Lesser Prespa								
External loading	25.3	6.2	30.7	7.5	38.5	9.4	40.3	9.8
Internal loading	0.9	0.2	4.1	1.0	0.9	0.2	2.7	0.7
Total	26.2	6.4	34.8	8.5	39.4	9.6	43.0	10.5
Vromolimni								
Total	5180	5180	4171	4171	6343	6343	5924	5924

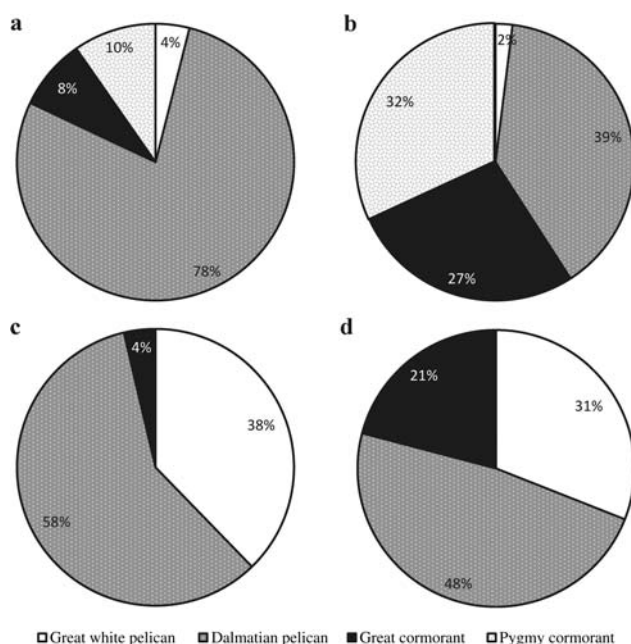


Figure 6. Relative contribution of (a) TN input and (b) TP input in Lesser Prespa as well as (c) TN input and (d) TP input (%) in Vromolimni pond, derived from the 4 waterbird species studied according to calculation method 1 (Scherer et al. 1995).

A modeling approach showed that ~40 000 wintering lesser snow geese and Ross's geese in New Mexico contributed 40% N and 75% P primarily into a wetland area (0.5 km²; Post et al. 1998). Flocks of nesting herons in Texas can include >5000 breeding pairs,

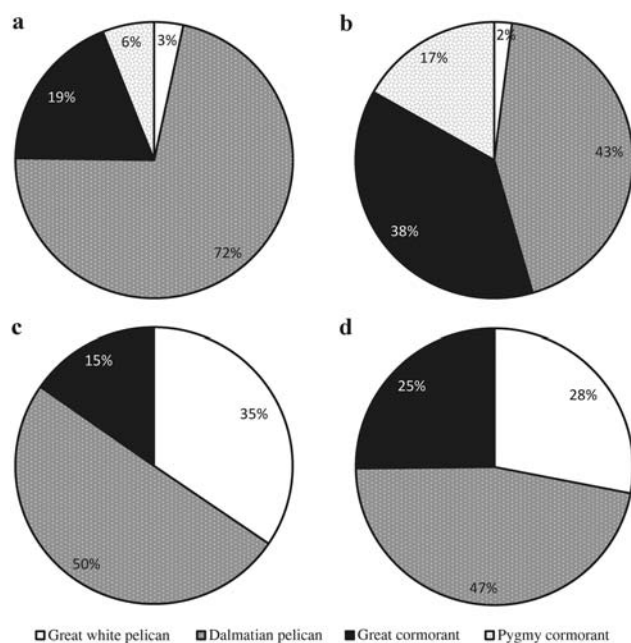


Figure 7. Relative contribution of (a) TN input and (b) TP input in Lesser Prespa as well as (c) TN input and (d) TP input in Vromolimni pond, derived from the 4 waterbird species studied according to calculation method 2 (Hahn et al. 2007).

calculated to deposit 800–2000 kg N per year and 100–200 kg P per year to the colony substrate or directly to the water, mainly through runoff (Telesford-Checkley et al. 2017). Field measurements in Texas lakes showed the relationship between N in feces and N in nearby surface water. In Lesser Prespa, >3000 breeding pairs of pelicans and cormorants excrete >1200 and >1600 kg/yr of N and P, respectively. The notable difference in P load can be partly explained by the high P content in pelican and cormorant droppings compared to the heron droppings measured by Telesford-Checkley et al. (2017). The nutrient content of bird droppings can vary between herbivorous and piscivorous bird species as well as between populations of the same species, depending on their feeding and nesting patterns (Marion et al. 1994, Hahn et al. 2007, 2008). Hahn et al. (2007) models show that carnivorous waterbirds deposit 38.1–91.5 tonnes of external N and 16.7–18.2 tonnes of external P in the Netherlands annually. On a landscape scale these loadings are of minor importance, but breeding colonies can have a large impact on a local scale.

Water and sediment quality

Measurements of total chlorophyll and nutrient concentrations of the water layer did not vary significantly among the sampling sites in Lake Lesser Prespa but were, as expected, notably high in the isolated Vromolimni pond. An experiment by Maliaka et al. (2020) showed that pelican droppings added to Lesser Prespa water stimulated algal growth, particularly cyanobacteria, indicating that bird droppings can profoundly affect lake water quality. The nutrient content of the sediments clearly indicated an accumulation of (soluble) nutrients at the sites near the waterbird colonies, most evident at site 7, compared to other sites away from the colonies (Fig. 2 and 3; Supplemental Fig. S3). The sediments close to the waterbird colonies contained higher pore water N (mainly ammonium) and P concentrations and also higher TIN concentrations. The higher organic matter content of the sediments near the waterbird colonies (33%) also indicates the deposition of bird droppings near these sites (Fig. 2). Although some studies found no effect of bird colonies on sediment nutrient concentrations (Speir and Cowling 1984, Gwiazda et al. 2014), increased N and/or P levels in the sediments below bird colonies or roosting sites were found in various other studies (Speir and Cowling 1984, Baxter and Fairweather 1994, Ligeza and Smal 2003, Tomassen et al. 2005, Klimaszuk et al. 2015).

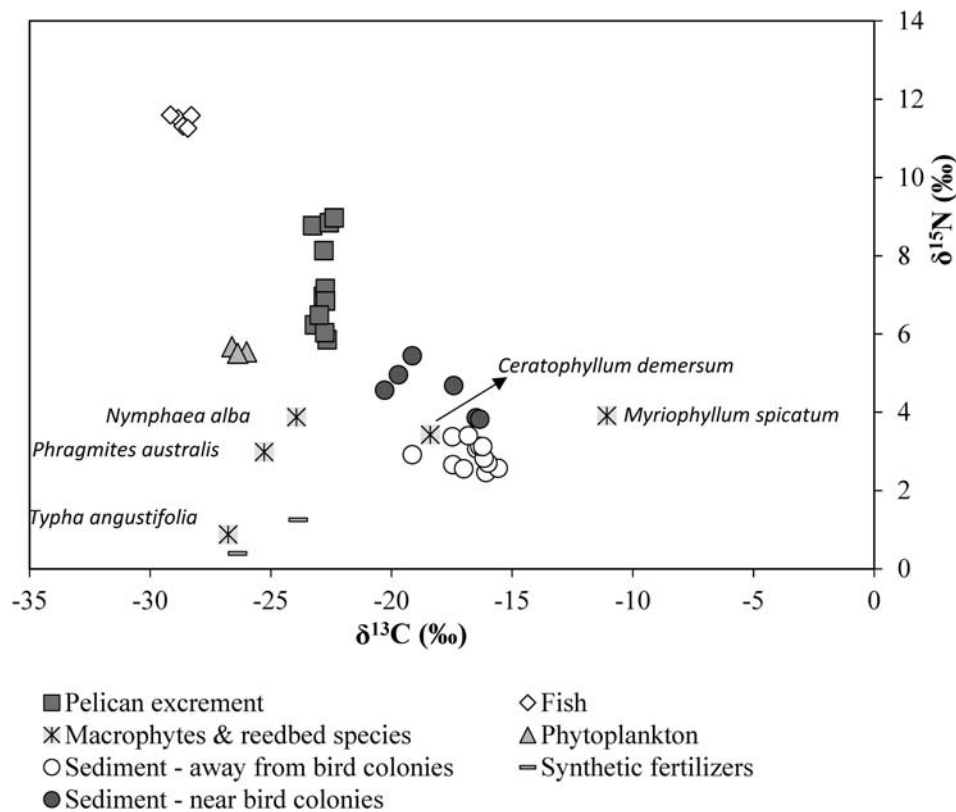


Figure 8. Isotope ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measured in a series of samples collected from the Lake Lesser Prespa area.

Although at least some of the nutrients seem to accumulate in the sediments, these sediments are able to release ammonium and phosphate to the water layer. The high temperatures that occur near the sediment (up to 23 °C) in summer stimulates the decomposition of organic matter, leading to low oxygen concentrations near the sediment and the release of inorganic N and P from these enriched sediments toward the water column (Smolders et al. 2006).

Source of nutrients in lake sediments

In addition to bird droppings, other external nutrient sources may also affect the lake sediments in Prespa, for instance runoff of fertilizer nutrients (synthetic fertilizers; via streams or groundwater flows) from the agricultural fields located mostly along the eastern shore of the lake. Furthermore, human sewage and agricultural runoff can contribute to the nutrient input to the lake. Both sewage outflows and streams (including various drainage ditches) are located at the east part of the lake's watershed (Hollis and Stevenson 1997), but none drain near the breeding colonies. Vromolimni pond is not connected directly with Lesser Prespa or any adjacent stream, and therefore we assumed only

minor additional external nutrient contributors other than the breeding waterbirds.

The stable isotope results for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were significantly different between the sediments far from and close to the bird colonies in Lesser Prespa. The low $\delta^{15}\text{N}$ values of the plants compared to the droppings and sediments close to the birds suggest little effect on the sediment. Phytoplankton, however, had an $\delta^{15}\text{N}$ value similar to the sediment close to the birds. Because sediment organic matter has a $\delta^{13}\text{C}$ ratio close to the source ratio (e.g., Boschker et al. 1995, Cunha et al. 2006), phytoplankton is not a likely source. The phytoplankton samples originated from 3 different locations in the lake and had similar isotope ratios, reflecting the well-mixed water layer. Although seasonal accumulation of phytoplankton near the birds probably affects the sediments locally, sediments away from the birds would be affected by sinking phytoplankton as well.

The analyses clearly suggest, however, that the sediments near the bird colonies at Lesser Prespa are affected by the accumulated waterbird droppings, whereas the most common fertilizers used in the Prespa area (external source) do not seem to have a notable impact on the lake sediment chemistry (Fig. 8). Soils affected by the associated breeding colonies can indeed

be enriched in $\delta^{15}\text{N}$, as found by Mizutani et al. (1986). Sebastian-Gonzalez et al. (2012) also found indications of ^{15}N -enrichment by gull droppings in ponds. Gąsiorowski and Sienkiewicz (2019) reconstructed bird colonization in peaty tundra soils and attributed an increase in $\delta^{15}\text{N}$ to bird colonization and a decrease to the abandonment of a colony. Moreover, these changes in $\delta^{15}\text{N}$ often coincided with an opposite trend in $\delta^{13}\text{C}$. In our analysis, sediments away from birds also had lower $\delta^{13}\text{C}$ values. We conclude that the results of the isotope analysis clearly confirm that waterbird droppings can contribute locally to the sediment C and N pool.

Conclusions

The range of total nutrient input in Lesser Prespa by piscivorous waterbird droppings based on the presence and abundance of Dalmatian pelicans, great white pelicans, great cormorants, and pygmy cormorants was estimated at 1243–1866 and 1649–2038 kg/yr for N and P, respectively. For Vromolimni pond, the range of these estimates is 1295–1586 and 1043–1481 kg/yr for N and P, respectively. The volume of the pond is <0.2% of the volume of Lesser Prespa, resulting in much higher (>100-fold) N and P loadings than in Lesser Prespa: up to 5924 and 6343 mg/m²/yr of N and P, respectively. The waterbody of Vromolimni pond is relatively isolated and therefore assumed to have only minor additional external nutrient contributors other than the breeding waterbirds. The waterbirds thus contribute to eutrophication, leading to increased chlorophyll *a* and dissolved N and P levels in Vromolimni pond.

The waterbird colonies in Lesser Prespa could contribute significantly, although much less than at Vromolimni, to the eutrophication of the lake. The effects on the water quality are less evident, mainly because the nutrient concentration is diluted in a much larger volume of water. Nevertheless, sediment analyses clearly demonstrate a local impact based on enhanced nutrient concentrations linked to birds near their breeding sites. To estimate the relative contribution of birds to the ongoing eutrophication of Lesser Prespa, other external sources of nutrients, such as leakage of fertilizer from surrounding agricultural fields, need to be estimated in future research.

Acknowledgements

Field sampling was conducted with legal permissions from the Greek Management Body of Prespa National Park. No other permits were required. The authors thank the Society for the Protection of Prespa (SPP) for providing long-term monitoring data related to pelicans and cormorants, the staff from SPP, and

especially Lazaros Nikolaou for fieldwork support, and Dr. Olga Alexandrou for assistance with accessing long-term bird monitoring data. Special thanks also to Dr. Marva Shmueli and Dr. Alain Crivelli for providing data for the great white pelican and the time budget. We are grateful to the laboratory staff and the analysts from the General Instrumentation at Radboud University, B-WARE Research Centre, and Wageningen University for supporting the necessary laboratory analyses.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

VM was supported by a grant from SPP. The costs of boat fieldtrips for collecting samples in the Prespa area and all transportation costs were covered by the SPP. The work of the SPP for waterbirds was supported financially by the MAVA Foundation and after 2018 by the Prespa Ohrid Nature Trust (PONT) as well as by the European Commission through projects LIFE2002NAT/GR/8494 and LIFE15NAT/GR/000936.

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