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Hydrology, Biogeochemistry and Metabolism in a Semi-Arid Mediterranean Coastal Wetland Ecosystem

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Abstract

Experimental and numerical approaches were used to assess the functioning of a flagship coastal wetland ecosystem for improved water management. Very pronounced seasonal contrast in Salinity and Chlorophyll *a* were found, with high correlation between Chl*a* and Phosphorus during winter and Chl*a* and Nitrogen during summer. Water and Dissolved Inorganic Phosphorus (DIP) and Dissolved Inorganic Nitrogen (DIN) fluxes exhibited seasonal variation, where the lake is a source of DIN and DIP during the wet season. A considerable anthropogenic-driven amount of nitrogen is transferred into N₂/N₂O to the atmosphere during the dry season with predominance of denitrification-anammox processes. The primary production is impacted by forcing the respiration of the ecosystem to reduce the Net Ecosystem Metabolism so that the system is functioning as heterotrophic. Climate change and anthropogenic pressures explain the deterioration of water quality and possibly the decrease in populations of Palearctic birds, warranting depollution and effective National Wetland Management Strategies through improved water resources management.

Key words: Biosphere Reserve, UNESCO World Heritage, Wetlands, Water budget, Nutrient budget, Net Ecosystem Metabolism

1. Introduction

Wetlands are important wildlife ecosystems that play distinctive and unique roles on a planetary scale in climate regulation, biodiversity, food security, energy, blue carbon, water management, disaster risk reduction, human health, sustainable livelihood, and urban future (Gibbs 2000; Turner et al. 2000; Zedler and Kercher 2005; Euliss et al. 2008; Costanza et al. 2014; Macreadie et al. 2019). They are attractive to many primary and secondary trophic consumers due to their abundant habitats and their high productivity (Basset et al. 2013; Newton et al. 2018, 2020). However, wetlands remain one of the most threatened habitats because of their vulnerability and attractiveness for human development (RAMSAR 2010). Despite recent sustainable management attempts, most wetlands have undergone major disruptions, and the areas of well-conserved aquatic habitats are still declining (Kingsford et al. 2016). In addition to habitat loss and degradation, the main pressures are exerted by reduced watershed inputs due to the damming of rivers and the excess of nutrient inputs and organic matter from urbanization, agriculture and pollution (Newton et al. 2014).

Indeed, the pressures of effluents from urban sewage, industry, agriculture, urban development, fishing and aquaculture adversely impact wetland ecosystem ecology and aesthetics as well as public health through a deterioration of water quality (Mitsch and Gosselink 2015; Goudling et al. 2019; Newton et al. 2020). Urbanization, the increase of human population, the intensification of agriculture, tourism, land reclamation, the construction of dams, and the overexploitation of biotic and abiotic resources caused a change of the hydrology and the sedimentology cycles of wetland ecosystems as well as the loss of wetland habitat and coastal vegetation (salt marshes, seagrass meadows, and algae beds) that provide nurseries for waterfowls and other species (Beck et al. 2001; Newton et al. 2020). In addition, pressures from invasive species have been

threatening the ecological status, the biodiversity, and the socio-economic services of wetlands (Ayache et al. 2009; Newton et al. 2020). Regardless of their spatial extent, the watershed size and human population, coastal wetland ecosystems provide goods and benefits for human life and welfare. These goods, with their economical, societal, heritage, and scientific values have a positive impact on human well-being (Newton et al. 2014, 2018). The components of the latter include the basic materials for good life, security, health, and social relations. To evaluate their ecological status and to assess their sensitivity to anthropogenic pressures and climate change, numerical and statistical models (Kitsiou and Karydis 2011), and biogeochemical models (Hu 2016) have often been used to assess the characteristics as well as the eutrophication mechanisms and water quality of coastal wetlands (Ganju et al. 2016).

Globally, up to 70% of wetlands have been lost since 1900 AD, including coastal wetlands which provide higher estimated values of services (Newton et al. 2018). The latter, considered unique ecosystems between the continent and the sea, are characterized by high spatial and temporal variability, and provide the highest ecosystem services along with coral reefs, seagrass meadows, and algae beds (Costanza et al. 2014, Newton et al. 2014, Béjaoui et al. 2016). The extents of the different kind of pressures on wetlands of North Africa are particularly exacerbated as their spatial range has been contracting and their ecological condition deteriorating (Ramdani et al. 2011, Junk 2013). Among the coastal ecosystems of North Africa that are exposed to climatic and human pressures is the Tunisian wetland ecosystem - the Ichkeul Lake; this unique Lake is endowed with great national and international importance (Ouni et al. 2020). The Ichkeul Lake is geolocated at the interface between a Mediterranean climate and a semi-arid climate of North Africa. It has long been recognized as one of the most important preserved wetlands in the Mediterranean region and as an important overwintering site of Palearctic waterfowls, with peak winter records of up to 100.000–200.000 birds (Hollis et al. 1986, Casagrande and Boudouresque

2009, Hamdi et al. 2012; <http://datazone.birdlife.org/site/factsheet/ichkeul-iba-tunisia/text> last
accessed September 1, 2021)). The lake also presents a rather spectacular hydrological
functioning, with a seasonal reversal of the water exchange with the Bizerte lagoon, which is in
turn connected with the sea. Thanks to its high ecological value and the specificity of its
hydrological functioning, the Ichkeul wetland is one of the few sites listed under three
international conventions namely the Biosphere Reserves of 1977 (UNESCO 2009a), the World
Heritage Convention of 1979 (UNESCO World Heritage Centre 2009b) and the Ramsar
Convention of 1980 (RAMSAR Convention and Wetlands International 2009). It was ratified as
a national park in 1980. However, since the 1980s, this area has been threatened by the
construction of dams on the main rivers (Joumine dam in 1983, Ghezala dam in 1984, and
Sejnane dam in 1994); this drastically reduced the freshwater inputs to the Lake (Hamdi et al.
2012). A sluice was installed in 1993 at the outlet of the lake at the Tinja channel to regulate the
seawater fluxes between the lake and the adjacent lagoon of Bizerte. These locks have caused the
formation of new sedimentary deposits upstream of the channel (Tamisier et al. 2001).
Several studies have been carried out to evaluate the Ichkeul Lake ecological status (Yazidi et al.
2017); however, quantitative studies based on numerical analyses are scarce. The present study
aims at characterizing the seasonal contrasting state of the Ichkeul Lake. This study is rooted in
experimental observations carried out during a 5-month campaign. It quantifies the water, salt
and nutrient budgets by applying a Box Model tool and the Land–Ocean Interactions in the
Coastal Zone (LOICZ). This work is, therefore, the first to use a Box Model approach in the
study of a Southern Mediterranean coastal ecosystem to sustain the management of a RAMSAR
coastal wetland via improved water management strategies

2. Material and methods

2.1 Study area and main features

Ichkeul Lake, located in far Northern Tunisia, is a system of 90 km² surrounded by 30 km² of temporary marshes (Tamisier et al. 2001). The Southern shore of the lake is dominated by a limestone mountain - Jebel Ichkeul (Fig. 1). The Ichkeul Lake receives freshwater from a 2,600 km² catchment area via six main rivers, and it is also linked by the Tinja channel to the coastal Bizerte Lagoon. The channel is about 5 km long and 3 m deep during the flood period (Béjaoui et al. 2017), and it ensures the exchange of water and heat between the Ichkeul Lake and the Bizerte Lagoon.

This Lake is known for the seasonal fluctuations of water levels and salinity concentrations due to the variation of freshwater inputs between winter and summer, and it is characterized by its very shallow water depth, with a maximum depth of only 2-3 meters during the wet seasons (Casagrande and Boudouresque 2009, Ouni et al. 2020). The water budget in the Ichkeul Lake is controlled by contributions from both marine waters from the Bizerte Lagoon and freshwater from direct rainfall and from its watersheds. During the rainy seasons, a large volume of the lake water spills off to the Bizerte lagoon through the Tinja channel (Affouri and Sahraoui 2017). In summer, high evaporation rates lower the water level and allow seawater to enter to the lake. The wetland is, therefore, characterized by a double seasonal alternation of high-water levels (2.0 m <) and low salinity (< 8.0) in the wet season from October to March due to freshwater from run-off, while it shows a low water levels (<1 m) and a high salinity (50 g/l <) in the dry season from April to September due to the inflow of sea water (Tamisier et al. 2001, Shaiek 2016, Affouri and Sahraoui 2017).

The Ichkeul region has a Mediterranean climate with mild rainy winters and hot dry summers. The average annual rainfall is about 575.5 mm/year of which only 4% fall in the summer period. The mean temperature is about 19 °C and the potential evaporation is between 1,300 and 1,400 mm/year (INM 2017).

2.2 Experimental observations and statistical assessment

Water sampling at 7 stations (from S1 to S7, Fig. 1) in the Ichkeul Lake was performed during a 5-month campaign (November 2016, March, April, May, and August 2017). The locations of the sampling stations were selected according to the environmental and ecological conditions of the Lake.

In-situ measurements of water temperature (T), dissolved oxygen (DO), and salinity (S) were carried out by a pre-calibrated multi-parameter Thermo Orion meter. The laboratory analyses of the surface water samples were performed for the ammonium (NH_4^+), nitrates (NO_3^-), nitrites (NO_2^-) and phosphorous (PO_4^{3-}) using a BRAN and LUEBBE Auto-Analyzer-3, and their concentrations were determined calorimetrically using a UV-visible (6400/6405) spectrophotometer (APHA 1992, Jenway Corporation, UK). Total nitrogen (TN) and total phosphorus (TP) were determined after mineralization into ammonia and orthophosphate, respectively (Rodier et al. 1996). The Chlorophyll *a* (Chl *a*) concentrations were measured using the spectrophotometric method of Lorenzen (1967), following the procedure given by Parsons et al. (1984), after 24-hour extractions in 90% acetone at 5 °C in the dark. The dissolved inorganic nitrogen (DIN) and the dissolved inorganic phosphorus (DIP) were computed for further analysis.

2.3 Multivariate statistical tool

A Principal Component Analysis (PCA) using R package Ade4 was performed to relate the sampling stations, Chl*a*, physico-chemical and chemical parameters in the wet and dry seasons.

2.4 Material budgets model

Budget models are used to assess the budgets of physical and biological variables in coastal ecosystems. The Land Ocean Interaction Coastal Zone (LOICZ) model approach was used to assess water, salt, and non-conservative material budgets in the Lake. This tool has been proven to efficiently describe essential features of lagoon systems in the Mediterranean context (Giordani et al. 2005, Strobl et al. 2009). The LOICZ was used to investigate the impact of Climate Change on the coastal ecosystem and also to evaluate the strain of the anthropological effect (Kremer et al., 2005).

The System Ichkeul Lake-Bizerte Lagoon is reproduced by the model as a simple single-layer box, simulating the Ichkeul Lake input-output fluxes on the entry/exit sides of the box, respectively (Fig. 2).

2.4.1 Water budget

The water volume of the Lake, V_{sys} , is based on the mass balance equation (Equation 1) while dV_{sys}/dt represents the water storage in the lake. In the steady state, the water budget equation allows the computation of the residual flux (V_R) (Equation 3) which represents the amount of freshwater exchanged between the Ichkeul Lake and the Bizerte Lagoon. The theoretical flux (V_R) is foreseen as the flux which restores the equilibrium of the Lake at the steady-state condition and could be either an outflow or inflow. The horizontal water exchange fluxes V_{in} and V_{out} are hydrographically driven by advection entering and leaving the system, respectively. Their difference is the residual flux.

The fluxes to the system are under several forms which are inflows from the rivers (V_Q), direct precipitation (V_P), ground water (V_G) and other sources (V_O) not streaming on the ground such as sewage and industrial waste. The out fluxes with respect to the Ichkeul Lake are under the form of evaporation (V_E). In the LOICZ, budget computation approach is based on the consideration of

steady-state (V_{sys} and V_R are constants). In the present study, the groundwater volume (V_G) and other volumes (V_O) such as industrial and sewage waste are ignored. The difference between the inputs and outputs to and from the lake are called V_{Q*} and is expressed by Equation 2.

$$\frac{dV_{sys}}{dt} = V_{in} - V_{out} + V_{Q*} \quad (1)$$

$$V_{Q*} = V_Q + V_P + V_G + V_O - V_E \quad (2)$$

$$V_R = V_{in} - V_{out} = \frac{dV_{sys}}{dt} - V_{Q*} \quad (3)$$

In the steady state condition:

$$V_R = -V_{Q*} = V_E - (V_P + V_G + V_O + V_Q) \quad (4)$$

2.4.2 Salt budget

The salt budget is estimated based on the amount of seawater exchanged between the system and the ocean due to the influence of currents exchanging materials (*mixing flux* V_X). This flux does not lead to significant changes in volume and is, therefore, not included in the water budget. However, it is very important for nutrient flows as a mass of nutrient-rich system water is replaced by an equal mass of nutrient-poor seawater. To quantify V_X , the salt budget which has a conservative behavior can be used to estimate the mixing flux. Therefore, the salt flux not considered by the salinities used to describe the freshwater, should be balanced by the mixing flux $V_X*(S_{ocn}-S_{sys})$; although in freshwater systems, the mixing flux tends to be null (Swaney et al., 2011).

At steady state, the salt mixing flux (V_X) is equal to the sum of the residual flux which is carrying an amount of salinity (S_R) described as the salinity of the residual flow (Equation 7), and the freshwater inflow flux which is carrying an amount of salinity (S_{Q*}) (Equation 9). The quantity

of water exchanged through the residual and the mixing flux allows for the estimation of the residence time of materials within the system (Equation 10).

$$\frac{d(V_{sys}S_{sys})}{dt} = V_{in}S_{ocn} - V_{out}S_{sys} + V_{Q*}S_{Q*} \quad (5)$$

$$V_R S_R = V_{in} S_{ocn} - V_{out} S_{sys} \quad (6)$$

$$S_R = \frac{(S_{sys} + S_{ocn})}{2} \quad (7)$$

$$\frac{d(V_{sys}S_{sys})}{dt} = V_R S_R + V_{Q*} S_{Q*} \quad (8)$$

In the steady state condition:

Mixing Flux is,

$$V_X (S_{ocn} - S_{sys}) = -(V_R S_R + V_{Q*} S_{Q*}) \quad (9)$$

Water renewal time is,

$$\tau = \frac{V_{sys}}{(V_X + |V_R|)} \quad (10)$$

2.4.3 Non-Conservative variables budget

Non-conservative materials (Y: DIP, DIN) owe their names to their non-conservativeness with respect to water and salt and could be considered as reactive substances. They are called so since their exchange fluxes through the lake are expected to leave an internal residual flux (ΔY), due to the internal processes occurring within the lake. The budgets for non-conservative materials follow a salinity-based approach but consider the internal flux.

In the present work, the Dissolved Inorganic Nitrogen (DIN) is represented by the sum of nitrites NO_2^- , nitrates NO_3^- and ammonia NH_4^+ while the Dissolved Inorganic Phosphorous (DIP) is represented by phosphate PO_4^{3-} . LOICZ estimates the non-conservative materials DIN and DIP

budgets at steady state by determining the residual flux of DIP and DIN namely ΔDIP and ΔDIN , respectively (Equation 12).

$$V * \frac{dY}{dt} + Y * \frac{dV}{dt} = \sum(V_{in} * Y_{in}) - \sum(V_{out} * Y_{out}) + \Delta Y \quad (11)$$

At steady state:

$$\Delta Y = - \left(V_{Q^*} Y_{Q^*} + V_R Y_R + V_X (Y_{sys} - Y_{ocn}) \right) \quad (12)$$

The value of Y_R computed as the average between Y_{sys} and Y_{ocn} is given by Equation 13.

$$Y_R = \frac{(Y_{sys} + Y_{ocn})}{2} \quad (13)$$

2.4.4 Stoichiometric coefficients

Mass-balance budgets are described to stoichiometrically link nutrient budgets through C:N:P Redfield ratios (Redfield 1958). LOICZ principally uses those ratios to determine the expected ΔDIN , *Nfix-Denit* and Net Ecosystem Metabolism (*NEM*). The expected ΔDIN could be well estimated through the observed ΔDIP (Gordon et al., 1996). The difference between the observed and expected ΔDIN (equation 14) is supposed to be equal to the difference of the quantity of N_2 produced through denitrification and that consumed through fixation (Seitzinger 1988). As for the *NEM*, it is supposed to reflect the difference between the *production* and *respiration* (p-r) within the lake, estimated (in Carbon) through the observed ΔDIP , exploring the Redfield ratio. The P:C Redfield ratio is about (106:1) for phytoplankton (Redfield 1958) and (550:1) for sea grass (Atkinson and Smith 1983).

$$Nfix-Denit = \Delta(DIN) - \Delta(DIN)_{exp} \quad (14)$$

$$NEM = p - r = -\Delta(DIP) * (C : P) \quad (15)$$

3. Results

3.1 Physico-Chemical parameters

In the Ichkeul Lake, due to its shallow depth, the temperature is tightly linked to that of the atmosphere. In the wet season, the water temperature was between 16.7 °C in S1 and 19.3 °C in S7 (Fig. 3A) where the water depth was relatively high. In the dry season, the Western and Southern sectors were characterized by higher water temperatures of about 25 °C due to water confinement and shallow depth (Fig. 3A').

Salinity of the Ichkeul Lake was high throughout the study period between 2016 and 2017. The lowest value was about 30.7 recorded in winter then reaches 40.0 in the late summer (August). In winter and summer, the salinity was likely to be homogeneously distributed with an average of 31.17 ± 0.3 (Fig. 3B) and 39.91 ± 0.2 (Fig. 3B'), respectively. In winter, lower values were noticed at the outlet of the rivers carrying out freshwater. Meanwhile, in summer, they were recorded by the side of the Tinja channel where the lagoon salinity was about 38.6, lower than the other compartments of the lake.

Similar to salinity, the DO was almost homogenous during the year with average values of $10 \text{ mg.l}^{-1} \pm 0.3$ in winter (Fig. 3C) and $6.8 \text{ mg.l}^{-1} \pm 0.5$ in summer (Fig. 3C'). In winter, the highest concentrations were in the South (S4 and S5) and Eastern side (S1) of the lake, whereas, in summer, the highest concentrations were recorded in the Western side characterized by blooming of *Phanerogams*.

Based on the overall field observations, the waters were turbid throughout the year essentially due to the effect of meteorological conditions and also due to the morphology of the lake which is characterized by very shallow water depth. Seasonally, the waters were more turbid in winter during northwestern winds which force the sediment to re-suspend in the water column.

However, in summer, the turbidity was relatively low in comparison to that observed in winter due to the calm meteorological conditions. Spatially, the western sector was often characterized by low turbidity due to the presence of phanerogams and water confinement.

3.2 Chemical parameters

3.2.1 Dissolved Phosphorus

Overall, the Ichkeul Lake is characterized by low phosphorus levels during the sampling period. The distribution of the Total Phosphorus (TP) in the lake was almost homogeneous during the year with a high concentration observed in the north sector of the lake and a lower value in the southern sector. In winter (Table 1), the total phosphorus varied between 3.6 μM in the southern sector where the Joumine River discharges and 8.1 μM in the Northern sector where the Douimis River discharges (Fig. 4A). In summer, we observed a similar distribution of the phosphorus in the lake as in winter (Fig. 4A'), with an increase in values (Table 2) especially in the northern sector where the TP reached 10.9 μM .

The Dissolved Inorganic Phosphorus (DIP) varied between 0.2 μM and 1.3 μM in winter (Table 1), while it varied between 0.1 μM and 1.6 μM in summer (Table 2). The highest concentration is observed in the northern sector close to the Douimis River discharge in both winter (Fig. 4B) and summer (Fig. 4B'), and the lowest values were observed in the southern sector of the lake.

3.2.2 Dissolved Nitrogen

The distribution of the Total Nitrogen (TN) in the lake is characterized by a non-uniform spatial distribution during the year. In winter (Table 1), a high concentration of about 27.5 μM was observed in the center of the lake and in the Tinja channel while the lowest value of 23.0 μM was observed in the western and in the North-eastern side (Fig. 4C). In summer (Table 2), a high concentration of about 23.8 μM was observed in the southern sector (Fig. 4C') where discharges

of the Joumine River take place, whereas the lowest value of $14.3 \mu\text{M}$ was observed in the western sector and in the North-eastern side of the lake.

For the Dissolved Inorganic Nitrogen (DIN) (Fig. 4D) the level of concentrations is obviously higher in winter than in summer (Fig. 4D'). In winter, the Eastern sector recorded the highest concentration ($15.4 \mu\text{M}$) while in summer the highest level was detected in the West-southern side ($6.2 \mu\text{M}$) where the discharges of the Joumine River take place.

3.2.3 Chlorophyll *a*

The Chl*a* concentration showed a clear contrast and variation between seasons. In winter, the average concentration reached $8.5 \pm 3.3 \mu\text{g.l}^{-1}$ (Table 1), with the highest concentrations observed at S2 (Fig. 4E). In summer, the average concentration was relatively low at about $3.1 \pm 0.6 \mu\text{g.l}^{-1}$ (Table 2) in the Western sector (S3, S4) (Fig. 4E').

3.3 Multivariate statistical analysis

The PCA was performed for winter and summer separately to comprehend the correlation between the sampling area, Chl*a*, and chemical and physico-chemical parameters for each season, and also to highlight the seasonal functioning (Fig. 5).

In winter (Fig. 5A), the two first components described 68% of the total variance. The first component (41,4%) tracked a combination of trophic related variables, phosphorus and Chlorophyll *a*, opposed to dissolved oxygen, and discriminated the area close to the inlet (S1) and the coastal area localized close to the mouth of the Douimis River (S2). The second component (26,6%) mainly discriminated the nitrogen and the temperature between the area close to the inlet (S1) and the inner sector (S5) from one side and the southeast coast area (S3 and S4) which captured the effect of Sejnene and Melah Rivers.

In summer (Fig. 5A'), when the lake received waters from the lagoon, the first two components accounted for 60.9 % of the total variability. The first component (37.3%) - dominated by the combination of nitrogen, Chlorophyll *a*, and, with the opposite sign, phosphorous - discriminated the inner and western coastal regions close to the Douimis River (S3, high Chl*a*, high N, and low P) from the eastern stations close to Joumine and Tine Rivers (S5, high P, low N, and Chl*a*) and the inlet (S1, high P, low N, and Chl*a*). The second component (23,6 %), however, described mainly gradients in temperature and dissolved oxygen between areas south and close to the Melah River (S4, high T, low DO) or Tine-Joumine system (S5) and northern stations close to the inlet of Tinja Channel (S1, low T, and high DO).

3.4 LOICZ Results

3.4.1 Water and salt budget

During the winter season (Fig. 6A), the Ichkeul Lake received a quantity of freshwater from the six rivers ($V_Q = 390.6 \cdot 10^3 \text{ m}^3 \cdot \text{d}^{-1}$) and a flux of direct precipitations ($V_P = 381.7 \cdot 10^3 \text{ m}^3 \cdot \text{d}^{-1}$). Meanwhile, evaporation was about $-234.0 \cdot 10^3 \text{ m}^3 \cdot \text{d}^{-1}$. The water residual flow given as a result from the LOICZ model was equal to $-538.2 \cdot 10^3 \text{ m}^3 \cdot \text{d}^{-1}$. Its negative value indicates that water leaves the Ichkeul Lake towards the Bizerte Lagoon. At steady state, the V_R freshwater outflow carried salt by advection outside of the lake with the boundary salinity S_R being almost equal to 34.2. The advective salt delivery to the lagoon is given by the flux $V_R \cdot S_R$ which was about $-18,406.4 \cdot 10^3 \text{ m}^3 \cdot \text{d}^{-1}$, thus explaining the lower salinity in the lake (31.7) than the lagoon (37.2). To remove the excess of salt in the latter, the water mixing flux V_X was computed so that $V_X (S_{\text{ocn}} - S_{\text{sys}})$ was equal to $-(V_R S_R + V_Q \cdot S_Q^*)$. In this case, at steady-state, the mixing flux entering the lake from the lagoon was about $2,589.5 \cdot 10^3 \text{ m}^3 \cdot \text{d}^{-1}$. The residence time in winter was about 31 days.

In summer (Fig. 6A'), the amount of freshwater flowing to the lake from precipitation ($V_P = 15.1 \cdot 10^3 \text{ m}^3 \cdot \text{d}^{-1}$) and rivers ($V_Q = 15.4 \cdot 10^3 \text{ m}^3 \cdot \text{d}^{-1}$) remained low compared to the losses by evaporation ($V_E = -131.9 \cdot 10^3 \text{ m}^3 \cdot \text{d}^{-1}$) inducing lagoon waters to enter the lake ($V_R = 101.4 \cdot 10^3 \text{ m}^3 \cdot \text{d}^{-1}$) thereby carrying salt to the lake which its salinity increased to 40.0 while that of the lagoon was about 38.6. To equilibrate the slight salt difference between the two systems $V_R S_R + V_Q S_Q^*$ and $V_x (S_{\text{ocn}} - S_{\text{sys}})$ fluxes must be equal in opposite signs, V_x had to be equal to $3,097.2 \cdot 10^3 \text{ m}^3 \cdot \text{d}^{-1}$. In this situation, the residence time in the system was about 10 days.

3.4.2 Non-conservative materials budgets

DIP budget

During winter, the observed ΔDIP value was about 618 mol P d^{-1} (Fig. 7A) while in summer it was about $1,106 \text{ mol P d}^{-1}$ (Fig. 7A'). For winter and summer, the Ichkeul Lake acted as a source of DIP.

DIN budget

LOICZ gives observed ΔDIN from the processes involving nitrogen inside the Lake. In winter, the ΔDIN was positive at about $14,644.0 \text{ mol N d}^{-1}$ (Fig. 7B), indicating that the lake acts as a source of DIN. The expected DIN (based on the Redfield ratio) was about $9,888.0 \text{ mol N d}^{-1}$ for phytoplankton and $18,540.0 \text{ mol N d}^{-1}$ for seagrass. Therefore, the difference between N-fixation and denitrification was $4,756.0 \text{ mol N d}^{-1}$ and $-3,896.0 \text{ mol N d}^{-1}$ for phytoplankton and seagrass, respectively.

In summer, the ΔDIN was negative at about $-2,355.0 \text{ mol N d}^{-1}$ (Fig. 7B'), indicating that the lake is a sink of DIN. The expected DIN was $33,180.0 \text{ mol N d}^{-1}$ for seagrass and $17,696.0 \text{ mol N d}^{-1}$ for phytoplankton. Therefore, the difference between N-fixation and denitrification was $-35,535.0 \text{ mol N d}^{-1}$ and $-20,051.0 \text{ mol N d}^{-1}$ for seagrass and phytoplankton, respectively.

Net Ecosystem Metabolism (NEM)

NEM is an indicator of the trophic metabolism within the Ichkeul Lake, being the difference between the primary production and respiration. In winter, the NEM was about -65,508.0 and -339,900.0 mol N d⁻¹ for phytoplankton and seagrass, respectively, whereas in summer the NEM was about -117,236.0 and -608,300.0 mol N d⁻¹ for phytoplankton and seagrass, respectively (Table 3).

4. Discussion

It is evident from the literature and from recent studies that the hydraulic constructions that started in the 90's have caused significant hydrological and salinity imbalance of the Ichkeul Lake ecosystem. The Constructions of the six dams on the main rivers flowing into the lake, the high evaporation rates, and the scarcity of precipitation have reduced the water level in the lake. However, under the strain of climate change, the latter has been drastically reduced, resulting in very high salinity and lower water depth. The campaign carried out in the frame of the present study (2016–2017) has shown that the water depth varied between 0.37 m in August and 1.3 m in March (annual mean = 0.71 m), whereas the salinity ranged from 27.7 in March to 40.0 in August (annual mean = 33.8). Other issues which impacted the water level in the lake were the deposit of fine sediment on the Northeast sector and the locks installed in the Tinja channel. During this year, the lack of freshwater inputs from precipitation and from the rivers coupled with high evaporation rates has dropped the lake water levels to acute depths (Affouri and Sahraoui 2017). The calculation performed by the LOICZ model showed the seasonal residual flux to be $-0.25 \cdot 10^6$ m³. Consequently, the net water budget is about $68.45 \cdot 10^6$ m³ (average of 2016–2017), which is obviously low compared to the average volume of about $90.00 \cdot 10^6$ m³ for the lake. This situation has strongly affected the salinity which reached 40.0 in the summer season.

398 Many of the world largest lakes, including Lake Victoria (Vanderkelen et al. 2018) and lake Chad
399 (Coe and Foley 2001, Gao et al. 2011) in sub-Saharan Africa, the Caspian Sea at the Europe-Asia
400 boundary (Prange et al. 2020), the Dead Sea in the Middle-East (Glausiusz, 2010), the Great
401 Lakes in USA (Gronewold and Stow 2014), and Poyang Lake in China (Mei et al. 2015) have
402 seen a significant decrease in their water levels. Shrinkage or even a complete disappearance of
403 lakes such as the Aral Sea in Central Asia (Micklin 2007) may be attributed to damming and
404 irrigation canals as well as to the mismanagement of their associated wetland ecosystems (Feng
405 et al. 2016). In spite of their reduced cover, lakes are globally important ecosystems that have for
406 too long been ignored in the estimations of global ecosystem processes, notably the material
407 processing in small lakes (Downing et al. 2006). In addition to the anthropogenic constructions
408 and mismanagement, climate change has been shown to affect the water level and/or water
409 hydrology in several large to small lakes, from the highest latitudes to the tropics including
410 coastal lakes and wetlands (Awange et al. 2008, Carroll et al. 2011). The Ichkeul Lake, at the
411 heart of the coastal wetland ecosystem and as a small freshwater body, has been shown in our
412 study to also be dramatically impacted by the damming upstream and the control of water
413 exchange with the adjacent lagoon and sea via the construction of locks which led to decreased
414 water levels, fluxes, and high salinity. Such mismanagement of water input and sediment deposits
415 compounded by climate change would add further multiple stressors to the lake and associated
416 ecosystem in the future. Indeed, it has been recently reported that climate change may increase
417 the vulnerability of wetlands in the Mediterranean. The cumulative evaporation in the region far
418 exceeds the cumulative precipitation leading to negative water balances that are enhanced by
419 mismanagement of water resources and thereby lead to further water scarcity in one of the most
420 impacted Ecoregions. Under climate projections scenarios RCP 4.5 and RCP 8.5, more than 70%

of the wetlands in North Africa will be affected by hydrological stress, unless proper strategies at the regional, national and local scales are adopted (Lefebvre et al. 2019).

The global climatic conditions as well as human activities have affected not only the hydrological conditions, but also the water quality of the lake. As an example, the dissolved oxygen measurements have shown that waters are usually close to being saturated in dissolved oxygen (11.3 mg l⁻¹). These high values could be linked to phytoplankton and seagrass photosynthetic activities (Casagrande and Boudoureaques 2009). However, the very low concentrations, observed in the southwest sector may be due to the presence of organic waste from the Joumine River that receives wastewater discharges from the Mateur town (Touaylia et al. 2016). As for water quality, calculations performed using TRIX index (Béjaoui et al. 2016, 2018) have revealed very poor water quality ($5.61 < \text{TRIX} < 8.46$). The residence time reaching 1 month (31 days in winter) may contribute to the development of phytoplankton and macroalgae blooms, therefore reducing water quality and generating episodes of eutrophication in the lake. The Ichkeul Lake being a Biosphere Reserve and a RAMSAR Site, does not permit the use of biomanipulation measures to control eutrophication, and, therefore, the best procedures to control localized anoxia and eutrophication would be an improved management of the water fluxes and the organic waste from towns and cities bordering the Lake (Chislock et al. 2013). Indeed, several lakes and water bodies that have seen increased eutrophication and anoxia have witnessed a drastic rise and increase in phytoplankton and macroalgal blooms with the recent increase in climate change effects. In many cases, the blooming species were toxic to food webs and humans and could pose a real threat to the large diversity of the waterfowls of the Lake Ichkeul under the projected climate change scenarios for the Mediterranean region (Paerl and Hisman 2009; Paerl et al. 2009; O'Neil et al. 2012).

444 The nutrient budgets in the lake are also the direct consequence of the terrigenous waters from
445 rivers which are enriched by chemical components coming from the agricultural activities and
446 urban waste of the Mateur town.

447 The multivariate analysis suggests that the trophic status in the lake is phosphorous-dependent in
448 winter and nitrogen-dependent in summer. In winter, the gradients between the areas close to the
449 inlet and the coastal area near the mouth of the Douimis River, captured by the first two principal
450 components of the PCA, suggest that the hydrodynamic pattern driven by the influence of the
451 lagoon from one side and the effect of Douimis River from the other side has a major influence in
452 shaping the lagoon biogeochemical functioning. Indeed, the observed values of the dissolved
453 oxygen in the area around the inlet were high (10 mg/l), likely a hydrodynamic effect between the
454 Lake and the Lagoon. Similar results were observed for the phosphorous (1.3 μ M) and
455 Chlorophyll *a* (15 μ g/l) which showed the highest values around the mouth of the Douimis River.

456 In general, in this season, the ordination of the station indicates a high heterogeneity among all
457 stations and variables, with a less clear *a posteriori* geographical interpretation of results, in
458 respect to summer. Salinity has a more important ordination role in summer, possibly as a result
459 of the rivers-lagoon gradients, and the pattern of nitrogen and phosphorus shows some
460 dissimilarity, possibly related to the presence of different sources. The temperature gradient also
461 differed from the summer one. In summer, the lake functioning was characterized by the
462 superposition of a major gradient between the inlet and the Douimis River tracked by the trophic
463 status variables Chlorophyll *a* and phosphorous and by the dissolved oxygen and also possibly
464 explained by the hydrodynamic functioning. In the summer season, the lake functioning is driven
465 by the influence of the inlets and the Melah, Joumine and Tine Rivers.

466 The application of the LOICZ model allowed for more detailed nutrient budgets in the lake.

467 During the wet season, the value of Dissolved Inorganic Phosphorus (Δ DIP) calculated by the

468 model is positively close to zero, suggesting that the Ichkeul Lake acts as a source of DIP. Based
469 on the Redfield approximation, the expected DIN for phytoplankton and seagrass was about
470 9,888.0 and 18,540.0 mol N d⁻¹, respectively, indicating that the Ichkeul Lake is a source of DIN
471 in the wet season. The accumulation of nitrogen may be due to the decomposition of
472 phanerogams and the release of organic matter from sediments (Casagrande and Boudoureaques
473 2009). The difference between the DIN measured in the lake and the DIN expected by the model
474 is assumed to be the gaseous form of nitrogen in the lake as N₂ gas. The Di-Nitrogen is supposed
475 to be equal to the difference between the N-fixation and Denitrification. The Nitrogen fixation
476 and denitrification are likely to be important pathways for non-conservative nitrogen flux, in
477 warm coastal ecosystems (Saunders and Kaffl 2001, Swaney et al. 2011); the nitrogen being
478 balanced by the denitrification and fixation processes. In the winter season, the Nfix-Denit is
479 about 4,756.0 and -3,896.0 mol N d⁻¹ for phytoplankton and seagrass, respectively, suggesting
480 that the N₂ fixation is more important than the denitrification for phytoplankton; however, for
481 seagrass the Nfix-Denit is negative suggesting that the nitrogen fixation is relatively hard and the
482 denitrification is a very dominant process due to several environmental factors. This situation
483 also demonstrates that the ecosystem is suffering from pollution and deoxygenation. The Net
484 Ecosystem Metabolism (NEM = production-respiration) determined through the Redfield molar
485 ratio between the phosphorus and the Carbon in the ecosystem is about -65508.0 and -339,900.0
486 mol N d⁻¹ for phytoplankton and seagrass, respectively. These negative values suggest that
487 respiration is prevailing in comparison to production, and is attributed to the environmental
488 conditions within the ecosystem. In this situation, the ecosystem is qualified as a confined
489 ecosystem, whereas the metabolism of the Lake is considered as heterotrophic.

490 Unlike the wet season, in the summer, the lake has shown different characteristics. The ΔDIP is
491 1,106.0 mol N d⁻¹, also positive close to zero, suggesting that the lake acts as a source of DIP.

The corresponding expected ΔDIN is about 17,696.0 and 33,180.0 mol N d⁻¹ for phytoplankton and seagrass, respectively, indicating that the lake is a source of DIN. The difference between the observed and the expected ΔDIN , based on the LOICZ model, could be attributed to the N₂ amount generated by the denitrification and/or anammox, the process of ammonium and nitrite conversion into N₂ gas by chemoautotrophic bacteria in anoxic conditions (Davidson and Seitzinger 2006). For Ichkeul Lake the flux of Nfix-Denit is usually negative at about -20,051.0 for phytoplankton and -35,535.0 mol N d⁻¹ for seagrass, respectively, indicating that the denitrification/anammox processes are dominant in the Lake.

On the other hand, the NEM fluxes are about -117,236.0 and -608,300.0 mol N d⁻¹ for phytoplankton and seagrass, respectively, indicating that respiration exceeds production and also suggesting that an important amount of nitrogen gases diffuses to the atmosphere through the interface atmosphere-Lake, either as N₂ or as N₂O. Although the amount of gaseous N that escapes to the atmosphere from the lake was not quantified in the present study, a recent study examining nitrogen processing and patterns in 34 lakes of the Midwest of the USA found that all lakes had a net loss of N₂ (Loeks-Johnson and Cotner 2020). Comparable seasonal differences reported in our study have also been found in the Midwest lakes, with higher gaseous nitrogen escape advanced by denitrification associated with anoxic conditions (Reddy et al. 1989). In addition, increased temperature from climate change, as it is the case for North-Africa, increases the production of N₂ via the enhancement of the denitrification and/or anammox processes (Adrian et al. 2009). Most studies on the supersaturation of lakes in N₂ have shown that nitrogen escapes to the atmosphere as N₂, yet eutrophication likely increases its escape to the atmosphere in its N₂O form, thereby contributing to the greenhouse gas loading of the atmosphere; this is critical since, N₂O is 300 times more potent than CO₂ (Seo and De Laune 2010, Montzka et al. 2011). The recent development of climate change and increased human activities, notably the

excessive use of agricultural fertilizers, warrant further research into the transfer of nitrogen to the atmosphere from wetlands and coastal wetland ecosystems.

5. Conclusion

The most significant aspects of the functioning of the Lake Ichkeul ecosystem revealed through the numerical and experimental approach used in this study concern the hydrological, the biogeochemical and the metabolic functioning of the Lake (Supporting Information Fig. S1). Concerning the hydrological functioning, in winter the waters leave the Lake towards the Bizerte Lagoon; however, the lake gets filled from the Lagoon in summer, significantly increasing its salinity. This situation is becoming critical for the biotope with the decrease of the freshwater inputs from rivers and the bad management of locks installed on the Tinja Channel. Concerning the biogeochemical functioning, the lake acts as a source of phosphorus and nitrogen during the wet season; however, it acts as a sink of nitrogen and as a source of phosphorus during the dry season. The internal processes of the trophic web seem to be marked by the high denitrification and/or anammox and low production; this suggests that a considerable amount of N_2 , and potentially some amount of N_2O , escapes toward the atmosphere. The study also indicates that the denitrification/anammox processes are strongly linked to environmental conditions. Pollution is among the main inhibiting factors for not only water quality, but also for the net ecosystem metabolism which is marked by respiration. For the management of the Ichkeul Lake wetland, the key to success resides in improved water management and depollution.

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773

774 **Figure Caption**

775 **Figure 1.** Geographic location of Ichkeul Lake and localization of sampling stations

776 **Figure 2.** Land-Ocean Interaction in the Coastal Zone (LOICZ) budgeting procedure for the

777 Ichkeul Lake. V_P : Precipitation volume (m^3d^{-1}), V_Q : runoff flow volume (m^3d^{-1}), V_0 : Other flow

778 volume (m^3d^{-1}), V_E : evaporation volume (m^3d^{-1}), V_G : Groundwater flow volume (m^3d^{-1}), V_R :

779 residual flow (m^3d^{-1}), V_X : Exchange flow (m^3d^{-1}).

780 **Figure 3.** Spatial distribution of physico-chemical parameters in winter (*capital letter*) and

781 summer (*apostrophic capital letter*) including Temperature (A, A'), Salinity (B, B') and

782 Dissolved Oxygen (C, C')

783 **Figure 4.** Spatial distribution of Chlorophyll a, phosphorous and nitrogen components in winter

784 (*capital letter*) and summer (*apostrophic capital letter*), including Total Phosphorous TP (A, A'),

785 Dissolved Inorganic Phosphorus DIP (B, B'), Total Nitrogen TN (C, C'), Dissolved Inorganic

786 Nitrogen DIN (D', D') and Chlorophyll a *Chla* (E, E')

787 **Figure 5.** Principal Component Analysis (PCA). Plots of the PCA performed for Chlorophyll *a*,

788 physical and chemical parameters according to the winter (A) and summer (A') with sampling

789 stations

790 **Figure 6.** Generalized box diagrams for seasonal changes in hydrology and biogeochemistry.

791 **Figure 7.** Generalized box diagrams illustrating DIP and DIN budgets in the winter (A, B) and

792 summer (A', B') respectively

793 **Supplementary material**

794 **Figure SM1.** Summary of the seasonal hydrological, biogeochemical and metabolic functioning

795 of the Ichkeul Lake wetland ecosystem

Figures

Figure 1

Geographic location of Ichkeul Lake and localization of sampling stations

V_P – Precipitation volume (m^3d^{-1}), V_Q – Runoff flow volume (m^3d^{-1}), V_O – Other flow volume (m^3d^{-1}), V_E – Evaporation volume (m^3d^{-1}), V_G – Ground water flow volume (m^3d^{-1}), V_R – Residual flow (m^3d^{-1}), V_X – Exchange flow (m^3d^{-1}).

Figure 2

Land-Ocean Interaction in the Coastal Zone (LOICZ) budgeting procedure for the Ichkeul Lake. V_P : Precipitation volume (m^3d^{-1}), V_Q : runoff flow volume (m^3d^{-1}), V_O : Other flow volume (m^3d^{-1}), V_E : evaporation volume (m^3d^{-1}), V_G : Groundwater flow volume (m^3d^{-1}), V_R : residual flow (m^3d^{-1}), V_X : Exchange flow (m^3d^{-1}).

Figure 3

Spatial distribution of physico-chemical parameters in winter (*capital letter*) and summer (*apostrophic capital letter*) including Temperature (A, A'), Salinity (B, B') and Dissolved Oxygen (C, C')

Figure 4

Spatial distribution of Chlorophyll a, phosphorous and nitrogen components in winter (*capital letter*) and summer (*apostrophic capital letter*), including Total Phosphorous TP (A, A'), Dissolved Inorganic Phosphorus DIP (B, B'), Total Nitrogen TN (C, C'), Dissolved Inorganic Nitrogen DIN (D', D') and Chlorophyll a *Chla* (E, E')

Figure 5

Principal Component Analysis (PCA). Plots of the PCA performed for Chlorophyll a, physical and chemical parameters according to the winter (A) and summer (A') with sampling stations

Winter

Summer

Figure 6

Generalized box diagrams for seasonal changes in hydrology and biogeochemistry.