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Temporal and spatial differences in nitrogen and phosphorus biogeochemistry and ecosystem functioning of a hypertrophic lagoon (Curonian Lagoon, SE Baltic Sea) revealed via Ecological Network Analysis

Monia Magri^{a, b, *}, Cristina Bondavalli^a, Marco Bartoli^{a, b, c}, Sara Benelli^a, Mindaugas Žilius^b, Jolita Petkuviene^b, Irma Vybernaite-Lubiene^b, Diana Vaičiūtė^b, Evelina Grinienė^b, Petras Zemlys^b, Rasa Morkūnė^b, Darius Daunys^b, Sabina Solovjova^b, Martynas Bučas^b, Zita Rasuole Gasiūnaitė^b, Artūras Baziukas-Razinkovas^b, Antonio Bodini^a

^a Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, Parco Area delle Scienze 33/A, 43124 Parma, Italy

^b Marine Research Institute, University of Klaipeda, Universiteto al. 17, 92294, Klaipeda, Lithuania

^c Department of Integrative Marine Ecology, Stazione Zoologica Anton Dohrn - National Institute of Marine Biology, Ecology and Biotechnology, Genoa Marine Center, Genoa. Italy

HIGHLIGHTS

- Integrative ecosystem models offer insights on coastal lagoon biogeochemical functioning.
- N and P networks in the Curonian Lagoon were analysed via Ecological Networks Analysis.
- In the transitional area high input and low residence time limit internal recycling.
- In the confined area long water residence boosts recycling exceeding external input.
- P is recycled more than N, contributing to N:P unbalance that favors cyanobacteria.

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G R A P H I C A L A B S T R A C T



ABSTRACT

In coastal lagoons, eutrophication and hydrology are interacting factors that produce distortions in biogeochemical nitrogen (N) and phosphorus (P) cycles. Such distortions affect nutrient relative availability and produce cascade consequences on primary producer's community and ecosystem functioning.

In this study, the seasonal functioning of a coastal lagoon was investigated with a multielement approach, via the construction and analysis of network models. Spring and summer networks, both for N and P flows, have

* Corresponding author at: Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, Parco Area delle Scienze 33/A, 43124 Parma, Italy.

E-mail addresses: monia.magri@unipr.it (M. Magri), marco.bartoli@unipr.it (M. Bartoli), sara.benelli@unipr.it (S. Benelli), mindaugas.zilius@jmtc.ku.lt (M. Žilius), jolita.petkuviene@apc.ku.lt (J. Petkuviene), irma.lubiene@apc.ku.lt (I. Vybernaite-Lubiene), diana.vaiciute@jmtc.ku.lt (D. Vaičiūtė), evelina. griniene@apc.ku.lt (E. Grinienė), petras.zemlys@ku.lt (P. Zemlys), rasa.morkune@apc.ku.lt (R. Morkūnė), darius.daunys@jmtc.ku.lt (D. Daunys), martynas. bucas@jmtc.ku.lt (M. Bučas), zita@apc.ku.lt (Z.R. Gasiūnaitė), Arturas.Razinkovas-Baziukas@ku.lt (A. Baziukas-Razinkovas), antonio.bodini@unipr.it (A. Bodini).

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Phosphorus Trophic flow networks Internal recycling been simultaneously compiled for the northern transitional and southern confined area of the hypertrophic Curonian Lagoon (SE Baltic Sea). Ecological Network Analysis was applied to address the combined effect of hydrology and seasonality on biogeochemical processes.

Results suggest that the ecosystem is more active and presents higher N and P fluxes in summer compared to spring, regardless of the area. Furthermore, larger internal recycling characterizes the confined compared to the transitional area, regardless of the season. The two areas differed in the fate of available nutrients. The transitional area received large riverine inputs that were mainly transferred to the sea without the conversion into primary producers' biomass. The confined area had fewer inputs but proportionally larger conversion into phytoplankton biomass. In summer, particularly in the confined area, primary production was inefficiently consumed by herbivores. Most phytoplanktonic N and P, in the confined area more than in the transitional area, were conveyed to the detritus pathway where P, more than N, was recycled, contributing to the unbalance in N:P stoichiometry and favouring N-fixing cyanobacteria over other phytoplankton groups. The findings of this study provide a comprehensive understanding of N and P circulation patterns in lagoon areas characterized by different hydrology. They also support the importance of a stoichiometric approach to trace relative differences in N and P recycling and abundance, that promote blooms, drive algal communities and whole ecosystem functioning.

1. Introduction

In coastal lagoons large terrestrial nitrogen (N) and phosphorus (P) loads increase primary production and favor the onset of hypertrophic conditions, affecting lagoons biodiversity and functioning (Carpenter et al., 1998; Conley et al., 2009; Smith and Schindler, 2009). The consequences of nutrient excess are often exacerbated by lagoon's hydrology (Lanari and Copertino, 2016). Indeed, in areas with long water residence time primary production undergoes bloom and collapse cycles, resulting in oxygen depletion, biogeochemical short circuits, massive mortality of benthic organisms and large economic losses due to cascading effects over fisheries and tourism (Newton et al., 2014; Rodrigues-Filho et al., 2023). Hypertrophic conditions might also threaten the role of estuaries and lagoons as coastal filters for pollutants, resulting in a large export of phytoplankton or nutrients to the coastal zone (Carstensen et al., 2020).

In Europe, excess nutrient delivery to the coastal zone has been contrasted with policies targeting agricultural practices and wastewater treatment plants, which resulted more effective in reducing P than N, mainly due to the increased use of P-free detergents (Bouraoui and Grizzetti, 2011; Romero et al., 2013; Viaroli et al., 2018; Vybernaite-Lubiene et al., 2018). Conversely, riverine N loads did not show a significant reduction due to large N retention in soil and groundwater and slow release, the so-called nitrogen heredity (Ascott et al., 2017; Bartoli et al., 2012; Van Meter et al., 2018). By significantly reducing generated P loads, the net result of policies targeting the abatement of nutrient external loads was to increase the N to P ratios in rivers (Viaroli et al., 2018). In lagoons characterized by cyanobacterial blooms, the significant reduction in external P loads should have decreased the intensity of blooms, as N2-fixing cyanobacteria are regulated by P rather than N availability (Dolman et al., 2012; Paerl et al., 2011). However, in some cases blooms persisted and lasted longer from summer to late autumn (Vaičiūtė et al., 2021). This raises new questions about a possible phosphorus heredity due to the synergy between internal estuarine loads and local hydrology promoting P recycling (Paerl et al., 2020; Randall et al., 2019; Vahtera et al., 2007). In lagoons that have retained and accumulated nutrients for long periods, during the summer season, and in areas where local hydrology results in long water residence time, oxygen shortage results in short circuits of coupled adsorptionprecipitation or oxidation-reduction processes, which can mobilize from sediments large amounts of N and P and enhance the intensity and duration of algal blooms (Magri et al., 2020; Viktorsson et al., 2013). Such short-circuits can also be favored by heat waves and prolonged drought events, consequences of climate change and hydrological extremes (Magri et al., 2020).

Massive algal blooms can saturate the grazing capacity of herbivores ending up in inefficient nutrient transfer within the food webs. The majority of nutrients are therefore channeled into the detritus pool, stimulating heterotrophic activity, oxygen depletion, shift in redox conditions and loss of specific biogeochemical pathways (Paerl et al., 2016). Different experimental studies described shifts in dominant biogeochemical processes that produce positive feedback on blooms and are themselves stimulated during post blooms via self-sustaining mechanisms (Gao et al., 2014; O'Neil et al., 2012). Oxic, suboxic or anoxic conditions may determine different rates of N or P recycling. Bartoli et al. (2020) have demonstrated for example that the onset of anoxia produced proportionally larger stimulation of P than N recycling, due to redox-dependent P release, ultimately leading to different stoichiometry of benthic regeneration.

Overall, the functioning of coastal lagoons is complex as it depends on the interplay between external loads, with high N:P ratios and dominating nutrient inputs in spring, internal loads, with low N:P ratios and dominating nutrient inputs during summer, the organisms processing and transferring nutrients along the food webs and local hydrology affecting nutrient import, export, and recycling. Experimental studies have explored and clarified a vast array of processes and organisms contributing to the lagoons functioning. However, they lack the capacity to produce synthetic indices of whole lagoon ecosystems functioning. Such issue can be tackled by integrating robust experimental datasets with modelling tools, specifically network models (Christian et al., 2012; Wulff et al., 2012). Network models are a type of mathematical or computational representation that uses nodes and edges to depict the relationships and interactions between different components within a system. In ecology and ecosystem studies, network models allow to map out the whole suite of material exchanges between biotic and abiotic components of a given ecosystem as they result from the transfer of energy and matter via feeding, biogeochemical and detrital pathways (Fath et al., 2007). These networks can be analysed via a suite of commonly used algorithms collectively referred to as Ecological Network Analysis (ENA) (Kay et al., 1989; Szyrmer and Ulanowicz, 1987; Ulanowicz, 2004, 1986). Through its algorithms, ENA can be used to get insights on whole system structure, activity, and development, on the structure and magnitude of cycling, on the efficiency of energy transfer through trophic levels, and on the role of indirect interactions (Baird et al., 1995; Borrett et al., 2018; Ulanowicz, 1983). Despite most networks have been based on carbon (C) as currency (Ulanowicz, 2012), several studies demonstrated the potential of targeting N transfers to investigate biogeochemical features of ecosystems (Baird et al., 1995; Christian et al., 1996; Finn and Leschine, 1980; Hines et al., 2012; Magri et al., 2018; Small et al., 2014). Comparatively, less attention has been given to the analysis of other elements such as P (Kaufman and Borrett, 2010) and even fewer studies simultaneously analysed N and P dynamics, usually compared to C (Baird et al., 2011, 2008, 1995; Scharler et al., 2015; Ulanowicz and Baird, 1999). These studies evidenced large differences in nutrient biogeochemical pathways, with N and P displaying higher trophic transfer efficiency and higher recycling rates compared to C, with most of the recycling activities that take place between lower trophic levels (Baird et al., 2008;

Scharler et al., 2015). Ultimately, the application of network tools and ENA would produce a whole system rather than a single process analysis. Moreover, the detailed and simultaneous reconstruction of N and P seasonal dynamics using network tools and ENA, embracing a multielement, modern approach, represents a promising strategy to tackle lagoon ecosystem functioning from a stoichiometric perspective.

In this study, networks for N and P flow have been compiled and analysed for the largest European lagoon, the hypertrophic Curonian Lagoon (Lithuania-Russia Federation), a microtidal enclosed system receiving nutrient-rich freshwater inputs and threatened by summer cyanobacteria hyperblooms. These blooms establish in early summer, following moderate diatom spring blooms, and persist until late autumn (Bresciani et al., 2014, 2012; Pilkaityte, 2007a; Vaičiūtė et al., 2021). The lagoon undergoes a pronounced seasonal variation in freshwater inputs in terms of discharge, nutrient loads, and stoichiometry, with large N excess in spring and large N limitation in summer (Vybernaite-Lubiene et al., 2018, 2017). These studies also revealed an unbalanced stoichiometry of internal recycling, with P regeneration in excess to N, potentially exacerbated by pelagic and benthic processes mediated by microbial communities, macrofauna, macrophytes, fish, and birds (Bartoli et al., 2021; Benelli et al., 2019; Morkune et al., 2020; Petkuviene et al., 2016; Zilius et al., 2018). Although specific biogeochemical dynamics have been analysed in numerous and diverse studies, a clear reconstruction of nutrient pathways, which connects abiotic and biotic compartments, was still missing (Bartoli et al., 2018).

Utilizing the large body of available information, spring and summer networks were compiled for the Curonian Lagoon, for both the well flushed northern transitional area, which receives most freshwater inputs and is connected to the Baltic Sea, and the southern confined area, characterized by much longer water residence time (Ferrarin et al., 2008; Umgiesser et al., 2016). These macroareas largely differed in terms of hydrodynamics, sediment composition, biogeochemical processes, and biotic communities (Zilius et al., 2018). This study aims to analyse the functioning of these two macroareas through a detailed investigation of the nutrient cycle among abiotic and biotic components, delving into areal and seasonal differences. This information allows investigating the main factors contributing to the unbalance in nutrient stoichiometry, recognized as the primary cause of cyanobacteria blooms. Structural and functional macroscopic differences between areas, seasons and nutrient cycles are examined employing synthetic indices that allow quantifying system's activity, how much of this activity is sustained by internal recycling, and the structure of internal connections. The main differences and detailed N and P mechanisms are explored through specific analyses, which allow 1) to track the fate of imported forms N and P as they pass through the system until they leave, promoting an evaluation of dominant processes; 2) to quantify N and P flows and transfer among trophic levels, assessing efficiency and losses at different stages; 3) to analyse how ecosystem components contribute to the recycling of N and P towards the dissolved inorganic pool, serving as indirect nutrient sources for primary producers. It was hypothesized that the hydrology-driven zonation and seasonality differentially affect N and P dynamics. Particularly, in the transitional area the system activity is sustained by external input, whereas the extent of internal recycling increase in the confined area, from spring to summer and from N to P. It was also hypothesized that the high primary production during summer cyanobacteria blooms saturates the grazing capacity of herbivores, leading to a crash in nutrient transfer through the food web. As a result, the role of higher trophic levels in recycling and boosting cyanobacteria blooms is relatively minor compared to the overall requirements, which are instead supported by blooms-induced biogeochemical mechanisms, involving P more than N dynamics.

2. Material and methods

2.1. Study area

The Curonian Lagoon (Lithuania-Russia Federation) is located in the south-eastern part of the Baltic Sea; with a total surface of 1584 km² it is the largest European lagoon (Fig. 1). It is a shallow (average depth 3.8 m), microtidal lagoon that is connected to the Baltic Sea by a narrow, 11 km long strait (0.4-1.1 km wide, 8-15 m depth) located in the northern corner (Fig. 1). The main freshwater input comes from the Nemunas River (also called Neman River) which accounts for ${\sim}95$ % of total inflow; it enters the central part of the lagoon and creates a unidirectional northward water flow to the strait (Ferrarin et al., 2008). The river is characterized by a seasonally variable freshwater discharge (200-2200 m³ s⁻¹), peaking during snowmelt in March and April and dropping to minimum values in August and September (Vybernaite-Lubiene et al., 2018). The river discharge and the limited water exchange with the Baltic Sea determine the freshwater character of the lagoon, with the presence of low salinity waters (generally 1-2, up to 7) limited to the northern part of the lagoon (Zemlys et al., 2013). The Nemunas inflow divides the lagoon into two macroareas: a northern transitional area and a southern confined area. The former ($\sim 404 \text{ km}^2$) is shallower (mean depth 1.75 m), it is influenced by intrusions of brackish waters and river discharge, which determine the relatively low residence time (ranging from 50 to 100 days). Coarse and sandy sediments prevail in this area. The southern confined area ($\sim 1180 \text{ km}^2$) is deeper (mean depth 3.5 m), has a residence time ranging from 100 to 250 days and it is characterized by organic-rich fine muddy deposits. Here, the water circulation is regulated mainly by wind, whose direction determines water exchanges with the transitional area (Ferrarin et al., 2008; Umgiesser et al., 2016).

Phytoplankton seasonal succession exhibits a typical pattern of eutrophic or hypertrophic systems. Diatoms dominate the spring bloom in April and May, with monthly average chlorophyll-a (Chl-a) concentration of 47 \pm 14 µg L⁻¹. After a short clear-water phase, usually in June, the biomass of N-fixing and other groups of filamentous cyanobacteria increases, peaking in August and September, with a monthly average Chl-a concentration of 96 \pm 56 µg L⁻¹ (Bartoli et al., 2018; Bresciani et al., 2014; Pilkaityte, 2007b; Vaičiūtė et al., 2021). In spring, the zooplankton community is dominated by predatory cyclopoids (Cyclops strenuus), while large herbivorous zooplankton species such as Daphnia sp. appear at the beginning of summer. Like most eutrophic water bodies, small-bodied organisms such as Chydorus sphaericus dominate the zooplankton community concomitantly with the appearance of cyanobacteria colonies (Gasiūnaitė et al., 2012; Gasiunaite and Razinkovas-Baziukas, 2004). Within the zooplankton community the main planktivorous specimens are represented by the predatory cladoceran Leptodora kindti (Lesutienė et al., 2012). Recurring phytoplankton blooms increase water turbidity, resulting in an unfavourable light climate for macrophytes, which are confined to a relatively narrow littoral belt, about 500 m wide (Zaromskis, 2002). An exception is represented by the eastern shore connecting the Nemunas Delta to the Klaipeda Strait, where the macrophyte belt is up to 5 km wide due to less turbid riverine waters (Bučas et al., 2019). Macrophytes stands host a diverse macrofauna community as compared to unvegetated sediments in the lagoon, which host a few species due to high organic matter content and low oxygen concentrations (Daunys, 2001). Oligochaetes and chironomids dominate in muddy sediments, whereas coarser sediments host also freshwater bivalves, including both native unionids and the invasive Dreissena polymorpha (Bubinas and Vaitonis, 2005; Zettler and Daunys, 2007). Almost 60 fish species have been identified in the Curonian Lagoon and among them, benthivorous fishes represent the dominant component, including Roach (Rutilus rutilus), Bream (Abramis brama), Silver bream (Blicca bjoerkna), and Ruffe (Gymnocephalus cernuus), whereas top predators are represented by Perch (Perca fluviatilis) and Pikeperch (Sander lucioperca) (Repečka, 2009, 2003). The Curonian Lagoon hosts a large waterbird community that undergoes wide seasonal



Fig. 1. Location and map of the Curonian Lagoon (Lithuania-Russia Federation, SE Baltic Sea). The black line indicates the border between the northern transitional and the southern confined area, identified from the application of the SHYFEM model (Umgiesser et al., 2016; Zemlys et al., 2013). The Nemunas River (or Neman River) is also indicated.

fluctuations both in abundance and diversity. Among the dominant species, there are mallard (*Anas platyrhynchos*), tufted ducks (*Aythya fuligula*), mute swan (*Cygnus olor*), grey heron (*Ardea cinerea*), great cormorant (*Phalacrocorax carbo sinensis*), goosander (*Mergus merganser*), black-headed gull (*Larus ridibundus*) (Morkune et al., 2020; Stanevičius, 2009; Švažas et al., 2011; Žydelis, 2001). The great cormorant represents the most abundant breeding species and during summer constitutes large concentrations along the Curonian Spit, the narrow sand dune that divides the lagoon from the sea.

2.2. Database and network construction

We constructed N and P flow networks for the transitional and the confined areas considering spring and summer conditions, for a total of 8 models. Most of the information for assembling the networks was derived from activities carried out in 2015. However, specific data (e.g., for fish community) that are not collected on a regular basis, were extracted from all the available literature spanning the last 2 decades. Surveys carried out in 2015 were selected due to the large and most complete set of data and because that year was characterized by a strong seasonal transition in the river discharge and an intense cyanobacteria bloom occurring in spring and summer, respectively. Such conditions represent a specific, recurrent feature of this hypertrophic lagoon (Vybernaite-Lubiene et al., 2018; Zilius et al., 2018). The spring networks were compiled exploiting data collected in March, April, and May, whereas data collected in July, August, and September were used to build the summer networks. June was excluded due to the high variability of chemical and biological variables across different years and the transitory conditions between spring and summer (Gasiunaite and Razinkovas-Baziukas, 2004; Pilkaityte, 2007a).

Each network consisted of 22 living and 8 non-living compartments and depicted the standing stock (or biomass) of each compartment, as well as the flow of N and P between the model compartments. The creation of the networks began with the identification of the key components of the ecosystem. For each compartment the standing stock was quantified as μ mol N or P m⁻², whereas the inter-compartmental flows, input from, and output to the outside environment were expressed as μ mol N or P m⁻² h⁻¹. The communities of the two macroareas do not overlap exactly in terms of species; nevertheless, we represented them with the same network components considering that the two zones are connected as part of the same lagoon, and differences in presence/ absence may be due to sampling outcomes rather than reflecting true different community compositions. To maintain the same model configuration, a minimum value for standing stock (1 \times 10⁻⁵ μ mol N/P m⁻²), input and output (1 \times 10⁻⁵ μ mol N/P m⁻² h⁻¹) was assumed for those species that were not in common. These small entries ensure that all eight final models have consistent structure and aggregation levels, enabling meaningful comparisons across seasons and areas, without influencing the output results of the network analysis (Baird et al., 2011, 2008, 1998; de la Vega et al., 2018b). The complete list of compartments, the detailed calculation procedures and the literature sources are reported in Supplementary materials (S1) whereas the values of standing stocks of all compartments and flows between them, imports, and exports from and to the outside environments for each network are available from the journal's electronic store as appendices (S2).

2.3. Non-living compartments

The networks resulted highly resolved as for non-living compartments: the large data set at disposal allowed in fact separating particulate from dissolved, and inorganic from organic N and P compounds, both in the water column and within the sediments (Table S1 in Supplementary Material). Seasonal concentration data of N and P compounds were derived from experimental activities carried out in 2015 at two sampling sites selected as representative of the sandy (Vidmares, N 55°41'80" E 21°43'23") and muddy (Nida, N 55°35'43" E 21°46'26") sediment types that prevail in the transitional and the confined areas, respectively (Zilius et al., 2018). At the same sites nutrient and gas (O2 and N₂) fluxes were measured both in the water column and at the sediment-water interface via the traditional approaches of light-dark bottle technique and intact sediment cores incubations (Dalsgaard et al., 2000; Strickland, 1960). The set of transformation and microbial processes between organic and inorganic, dissolved and particulate N and P compounds were directly quantified (i.e., denitrification, N-

fixation) or derived (e.g., mineralization) via the application of coefficients specific for the study areas as detailed in Zilius et al. (2018) and reported in Supplementary Material. Nutrient concentrations and processes in the Curonian Lagoon have been seasonally measured since 2010 and the reliability of data was verified by comparison with published information (Bartoli et al., 2021, 2020; Broman et al., 2021; Petkuviene et al., 2016; Zilius et al., 2021, 2015, 2014). This comparison allows us assessing whether the selected data fell within the range of previously published data or represented exceptional conditions.

Data on nutrient concentrations were collected also for an off-shore station located in the coastal area of the Baltic Sea, close to the city of Palanga (N 55°55′14″ E 21°02′40″), in the Klaipeda Strait (N 55°66′27″, E 21°13′75″) (unpublished data), and at the closing sections of the Nemunas River and of minor tributaries entering the lagoon (Vybernaite-Lubiene et al., 2018). These concentration values were combined with hydrological data to calculate all the inputs to/outputs from both the transitional and the confined areas following Vybernaite-Lubiene et al. (2022). Data on the average river discharge were provided by the Lithuanian Hydrometeorological Service, whereas water exchanges between the transitional and the confined area and between the lagoon and the Baltic Sea were derived from the results of a one-year simulation (2015) of the finite element model SHYFEM previously calibrated for the Curonian Lagoon (Ferrarin et al., 2008; Umgiesser et al., 2016; Zemlys et al., 2013).

2.4. Living compartments

Among living compartments, phytoplankton was given prominence and was divided into 5 dominant groups, which differed in terms of N:P stoichiometry, assimilation and grazing rates: Diatomophyceae and Chlorophyceae, which are more abundant in spring, non N-fixing Cyanobacteria and N-fixing Cyanobacteria, which are dominant in summer, and a final group containing the remaining classes (Table S1). The abundance, biovolume and Chl-a concentration of different groups of phytoplankton were derived from monthly samplings carried out in 2015 at Vidmares and Nida (Zilius et al., 2018) and their ranges were compared with literature data (Bresciani et al., 2012; Vaičiūtė et al., 2021, 2015). Data of Chl-a have been converted in N and P values by using C:Chl-a and C:N:P ratios specific for each phytoplankton group (Klausmeier et al., 2008; Sathyendranath et al., 2009). Concentration values were converted into standing stock values accounting for the volume of the photic zone (Petkuviene et al., 2016; Zilius et al., 2014). Phytoplankton production was quantified via the light-dark bottle incubations carried out for the determination of water column nutrient fluxes and N and P assimilation rates were derived from net production measurements using specific stoichiometric ratios (Klausmeier et al., 2008, 2004). Exudates production and phytoplankton sedimentation rates were derived from the literature on the Curonian Lagoon (Bukaveckas et al., 2019; Krevs et al., 2007).

Primary producers were also represented by microphytobenthos and another compartment including both macroalgae and macrophytes. Data on microphytobenthos biomass were derived from surficial sediment characterization (i.e., Chl-a extraction), whereas data on production and assimilation rates were derived from intact sediment cores incubations carried out for nutrient fluxes determination. Obtained data were always contrasted with literature data (Bartoli et al., 2021; Benelli et al., 2018). There was limited information on macroalgae and macrophytes abundance and distribution in the Curonian Lagoon, and there were no specific data related to 2015. Such information was therefore derived from a broad survey carried out in 2020 aimed to fill this gap (unpublished data) and compared to the available literature (Bučas et al., 2019, 2016; Feldman, 2006; Sinkeviciene, 2004; Sinkevičienė et al., 2017). Metabolic rates were calculated according to specific biomass-production rates measured in the Curonian Lagoon (Politi et al., 2021) and in similar environments (Kotta et al., 2021; Noges et al., 2010; Torn et al., 2006).

Data availability did not allow such a fine resolution for the heterotrophic compartments that were aggregated according to their community and prevalent diet (Table S1). Data on zooplankton biomass were derived from samplings carried out seasonally in 2015 both in the transitional and confined areas (unpublished data) and compared with literature values (Dmitrieva and Semenova, 2012; Gasiūnaitė et al., 2012; Lesutienė et al., 2012; Semenova, 2011). Zooplankton biomass, generally provided in μ g C L¹, was converted in N and P values by using literature ratios specific for copepods, cladocerans and rotifers (Ventura, 2006). Data on feeding intake and N and P excretion were calculated according to the metabolic model proposed by Ejsmont-Karabin (1984). For the phytoplankton and zooplankton compartments the inputs and outputs to the outside environment were also quantified. Concentration and biomass values measured at the closing section of the main rivers, at stations representative of the transitional and the confined areas and the coastal area of the Baltic Sea were combined with hydrological data as reported for non-living compartments and detailed in Supplementary Material.

Average seasonal biomass of macrofauna was derived from samplings carried out from 2015 to 2018 at different stations representative of both the transitional and the confined areas. Since these values were characterized by a high variability, to obtain the most representative average values and ranges, it was decided to consider measurements derived from all years and not just from 2015. There was no available information on bird community in 2015, therefore for the network construction data derived from visual bird surveys performed monthly during March-November 2018 in the Lithuanian part of the Curonian Lagoon have been used (Morkune et al., 2020). Data on the Russian area are not available and areal bird densities calculated for the Lithuanian area have been proportionally applied. There is a general lack of information about the fish stocks in the Curonian Lagoon and there was no specific data related to 2015. It was decided to use areal biomass values for the Lithuanian and the Russian areas that are reported for the dominant species (Repečka, 2009, 2008; Žydelis and Kontautas, 2008). The biomass values of macrofauna and fishes were initially converted in dry weight values, assuming specific dry mass/wet mass percentage ratios (Ricciardi and Bourget, 1998), and then in N and P using nutrient percentage content (Allgeier et al., 2020; Andrieux et al., 2020). The same was done for birds, which abundances were converted in biomass values using the average body mass values for each identified species reported in Dunning (2008). Consumption, excretion, and egestion rates for these groups were calculated according to specific metabolic models developed for ecosystems similar to the Curonian Lagoon as for types of species, climatic and trophic conditions (Cammen, 1980; Nagy, 2001; Palomares and Pauly, 1998; Pauly, 1989; Vanni and McIntyre, 2016). Secondary production was derived from mass balance procedures and compared with literature data (Asmus and Helgoland, 1982; Schindler and Eby, 1997; Vanni et al., 2013; Warwick et al., 1979). Diet information, when available, was derived from the literature on the Curonian Lagoon (Bubinas and Ložys, 2000; Putys and Zarankaite, 2010; Rakauskas, 2020; Rakauskas et al., 2013; Švažas et al., 2011; Žydelis and Kontautas, 2008), otherwise from studies carried out in similar environments (Fieszl et al., 2011; Gallagher and Dick, 2015; Gilbert and Servello, 2005; Jacobson et al., 2019; Kallio-Nyberg et al., 2007; Krpo-Cetković et al., 2010, Kubetzki and Garthe, 2003, Malbrouck et al., 2006; Nilsson, 2005; Pyrzanowski et al., 2019; Skóra et al., 2018; Syväranta et al., 2009). Starting from the diet composition, the amount of each prey was converted in the amount of consumed C and then N and P using the appropriate elemental ratios (Allgeier et al., 2020; Andrieux et al., 2020).

2.5. Ecological Network Analysis

The structure of each network can be represented by a matrix of exchanges, where energy or matter flows from row compartments to column compartments. Three column vectors representing imports, exports, and standing stocks for each compartment complete the input data. In contrast to the carbon (C) networks, the N and P networks do not incorporate respiration flows because they are not present in nitrogen and phosphorus metabolism. In the case of N, the process of denitrification (the microbial reduction of NO₃ to N₂) is generally considered a dissipation term. However, in this work we decided to introduce a compartment that represents N₂ in the water column and to treat exchanges between N₂ and reactive N forms (i.e., denitrification and N fixation) as exchange fluxes.

Each network was assumed to be at steady state: the sum of matter entering any given compartment equals the sum leaving the compartment (Fath et al., 2007). As the networks are reconstructed exploiting experimental data, there is inherent uncertainty associated with them. To achieve balanced flows for each compartment to be at steady state initial adjustments were made to the flows within their ranges of variation, to constraint unbalances within 15 % of each compartment throughflow (Magri et al., 2018; Scharler and Borrett, 2021). The balancing was consistently performed for both N and P networks in specific areas and seasons. Adjustments were made to the flows by acting mainly on those that were estimated, leaving the values derived from direct measurements unmodified. Subsequently, the overall balancing of the network was done by using the algorithm developed by Allesina and Bondavalli (2003). The controlled and simultaneous balancing of N and P networks, along with limiting the unbalance to 15 % of the compartmental flow, ensures that the automatic procedure results in more constrained variations in individual flows, without affecting the nutrient stoichiometry.

Once balanced, the matrices of exchanges and the column vectors were fed to the package *enaR* developed for the ecological network analysis in the R environment (Borrett and Lau, 2014; R Core Team, 2018). The ENA is a suite of different analyses based mostly on matrix algebra, which general methods have been summarized several times in the literature (Kay et al., 1989; Ulanowicz, 2004). Several metrics and indices described below were selected from the ENA outputs to completely characterize the ecosystem functioning based on the system features that they capture.

Structural and functional macroscopic differences between areas, seasons and N and P cycles were examined employing whole-system indices that reflect the system activity, recycling, and internal connection. The ecosystem size and activity were estimated by the total system throughflow (TST), which represents the total amount of medium flowing through the network; it is computed as the sum of all flows, including inputs, outputs and inter-compartmental flows (Finn, 1976; Kay et al., 1989). Higher TST values indicate a larger or more active system. The TST can be partitioned into acyclic and cyclic flows. A cycle represents a series of transfers among compartments that form a closed path exiting from one compartment and returning to it without crossing any compartment twice. The cycling analysis allows assessing the structure and the magnitude of cycles within the system and to quantify the total amount of material that flows through cycles of various lengths. The Finn cycling index (FCI) is calculated from the ratio between the cycled flow and the TST (Baird and Ulanowicz, 1989; Finn, 1980). This index quantifies how much of the total system activity is sustained by internal recycling (Baird et al., 2011; de la Vega et al., 2018a). The Average Path Length (APL) represents the average number of compartments that a unit of matter imported from the outside visits before leaving the system (Finn, 1976). The APL is defined as (TST-Z)/Z, where Z is the sum of all exogenous inputs (Kay et al., 1989). Higher values are indicative of a more developed and connected system, characterized by longer pathways. TST, FCI and APL are all network metrics returned by the enaFlow function in enaR.

The Lindeman Spine (Ulanowicz and Kemp, 1979) collapses a complex ramified network into a linear sequence of transfers from one trophic level to the next. We carried out this analysis, using the Trophic Aggregation algorithm (*enaTroAgg* function); it informs about how much matter or energy each level receives from the preceding one and from the outside environment, as well as the fraction that each trophic level loses through export or recycles back to the detritus pool. This analysis allows calculating the efficiency of nutrient transfer from each level to the next, whereas the overall systems trophic efficiency was calculated as the geometric mean of trophic efficiency of single transfers (Baird et al., 2011). In carbon networks the first trophic level is represented both by autotrophs and detritus pool, whereas in nutrient networks the first level is represented by dissolved and particulate pools of N or P, with primary producers shifted to the second level since they consume dissolved N and P.

The Output Environ Analysis (enaEnviron function) allows calculating the proportion of any internal exchanges ascribed to a unitary input of matter/energy (Fath and Patten, 1999; Patten et al., 1976). Each import is considered separately, and the results are additive. If applied to nutrient networks it can be used to track the fate of a unit of the imported nutrient, as it passes through the system until it leaves it. Results indicate how often imported nutrients pass through each pathway or process. These frequencies are portrayed as percentages and values >100 reflect rapid recycling within the system. In this study, the focus was on the fate of a unit of dissolved inorganic N or P imported into the system, as such import represents the most significant and readily available source of N and P for phytoplankton. Results from this analysis allowed to quantify the frequency with which N or P were assimilated by phytoplankton before being exported and to determine in which forms they left the systems, providing an evaluation of the dominant processes (Christian and Thomas, 2003; Small et al., 2014).

The Total Dependency Analysis allows assessing the dependency of any compartment on any other compartment activity, through direct and indirect pathways. The algorithm used in this analysis is included in the enaFlow function, and produces a matrix in which the coefficients express the fraction of each compartment's throughflow that previously resided in another compartment (Kay et al., 1989; Szyrmer and Ulanowicz, 1987). This analysis can be used to depict the extended diet (or the main sources of uptake) of a species or compartment, not only considering direct relationships but also indirect ones. This study focused on the dependency of phytoplankton. The only direct inputs to phytoplankton are inorganic and organic N or P dissolved in the water column, whereas any positive values related to the other compartments indicated their contribute to the recycling of N and P towards the dissolved inorganic and organic pools, serving as indirect nutrient sources for primary producers. The diagonal elements of the dependency matrix quantify the fraction of the throughput that returns to every compartment.

2.6. Uncertainty analysis

To assess the robustness of ENA results, an uncertainty analysis was performed according to Hines et al. (2018), which allows quantifying how the combined errors in all the estimated flows propagate through index calculations. This uncertainty analysis relies on a Linear Inverse Modelling coupled with a Markov Chain Monte Carlo approach (LIM-MCMC) to sample multiple plausible solutions from a solution space bounded by the input data equalities and inequalities. Each network solution is considered plausible if it contains variables that meet massbalancing criteria and fall within the defined range of the uncertainty values. This uncertainty analysis has been performed by the enaUncertainty function, which is included in the enaR package for R (Borrett and Lau, 2014). This function uses the original network model, along with uncertainty ranges, to generate the inputs needed to LIM analysis. This analysis produces plausible model sets using the limSolve package and the xsample function (Soetaert et al., 2009). This function randomly sample solution space for 1,000 iterations, using a random walk. The jump length is automatically set at a reasonable value according to the size of the solution space and a "mirror" algorithm uses the inequality constraints as "reflecting planes" along which jumps are reflected back into the solution space (Van den Meersche et al., 2009). According to the

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LIM-MCMC approach with the *limSolve* package, each variable used was sampled assuming a uniform distribution of the uncertainty ranges assigned to each network flow (Soetaert et al., 2009). LIM results are finally converted back into network objects for further analysis with *enaR* functions, and the set of 1,000 plausible models were solved with this approach (Hines et al., 2018). This allowed calculating the distribution for each output of the ENA. Differences between the population of indices calculated for the transitional and confined area and for the spring and the summer season have been tested by the non-parametric effect size statistic introduced by Cliff (1993). This method was selected because previous studies showed that parametric tests like Student's *t*-tests could identify differences even for tiny effects (Tecchio et al., 2016). This statistic estimates the probability that a randomly selected value in one sample is higher than a randomly selected value in

the second sample minus the reverse probability. The calculated values range from -1 and + 1, with positive values indicate that all values in sample 1 are larger than all values in sample 2, and vice versa, 0 indicates stochastic equality, whereas ± 1 indicate completely disjointed distributions. Significant differences were identified using threshold values provided by Romano et al. (2006): negligible if the Cliff delta (δ) was <0.147, low if <0.33, medium if <0.474, or large if >0.474. Medium and large effect sizes have been considered to be indicative of a significant trend.



Fig. 2. Total system throughflow (TST), Finn Cycling Index (FCI), and Average Path Length (APL) calculated from N (plots a, c, e, respectively) and P (plots b, d, f, respectively) networks. Plots display both values derived from initial networks (red triangles) and the indices distributions derived from the application of the uncertainty analyses (grey boxes). Abbreviations indicate: NTSP (N network-Transitional area-SPring), NCSP (N network-Confined area-SPring), NTSU (N network-Transitional area-SUmmer), NCSU (N network-Confined area-SUmmer), PTSP (P network-Transitional area-SPring), PCSP (P network-Confined area-SPring), PTSU (P network-Transitional area-SUmmer), PCSU (P network-Confined area-SUmmer).

3. Results

3.1. Flow analysis

The TST values, calculated from the N and P networks, revealed striking differences between areas, seasons and nutrients (Fig. 2a and b). Values ranged from around 3,370 to 10,470 μ mol m⁻² h⁻¹ for N networks

a) NTSP

and from around 150 to 615 μ mol m⁻² h⁻¹ for P networks and differed by a factor of nearly 20 between the two nutrients. In spring, TST values for N networks were significantly higher in the transitional area compared to the confined area (the distribution of the indices was completely disjoint, $\delta = 1$), while P networks displayed an opposite behaviour, with larger fluxes in the confined area ($\delta = -0.665$, large effect). Both N and P networks in summer exhibited a substantial increase in TST values



Fig. 3. The Lindeman Spines of N and P networks in spring (a) and summer (b). All values are in µmol N or P m⁻² h⁻¹. The roman numbers inside the boxes indicate the discrete trophic levels, whereas the percentage values indicate the fraction of the input to the same trophic level that is transferred to the next one. Solid black arrows indicate nutrients transfer through trophic levels, red diagonal arrows on the top of the boxes indicate inputs from the outside, green grounding symbols on the bottom indicate outputs to the outside. The dashed black arrows indicate the amount of nutrients returned to the detrital pool. Abbreviations indicate: NTSP (N network-Transitional area-SPring), NCSP (N network-Confined area-SPring), PTSP (P network-Transitional area-SPring), PCSP (P network-Confined area-SPring), NTSU (N network-Transitional area-SUmmer), NCSU (N network-Confined area-SUmmer), PTSU (P network-Transitional area-SUmmer), PCSU (P network-Confined area-SUmmer), PCSU (P network-Confined





compared to spring, with the confined area showing a more pronounced rise and higher values (in all cases the distribution of the indices was completely disjoint, $\delta = -1$). Specifically, in the transitional area, N and P values increased by 131 % and 167 %, respectively, while in the confined area by 240 % and 265 %, respectively.

The percentage of TST involved in recycling, quantified by FCI, increased from the transitional to the confined area, from spring to summer, and from N to P (Fig. 2c and d). In both seasons, the transitional area recycled <10 % of N and slightly more (13 %) of P. This indicates that almost 90 % of the imported nutrients were exported to the outside without being involved in cycling. Seasonal FCI values for the confined area ranged from 35 % to 50 % for N, and from 61 to 63 % for P in spring

and summer, respectively. The APL followed the same trend of FCI and was linearly correlated with it (Fig. 2e and f, data on linear correlations not shown). APL values revealed that within the transitional area, most of N and P cycled over short path lengths, involving <3 compartments, whereas within the confined area, nutrients were transferred over longer loops, with values ranging from 6 to 15, with the latter characterizing the P network in summer. The distribution of the plausible indices, derived from the application of the uncertainty analysis, allowed us to observe significant differences between areas and between N and P networks for both FCI and APL indices (in all cases the distribution of the indices was completely disjoint, $\delta = \pm 1$). Differences between seasons were significant for both areas for N networks (Fig. 2c–e, $\delta = -1$). For P

networks seasonal differences were significant for the confined area (Fig. 2d–f, δ = - 0.683 for FCI and δ = - 0.807 for APL), but not for the transitional area (δ = - 0.108 for the FCI and δ = 0.311 for APL).

3.2. Lindeman spine

Fig. 3a and b display the Lindeman Spines, which help us understanding the distribution of the total flow of N and P along the trophic web. The imports from and exports to the outside environment, as well as the amount of nutrients returned to the detrital pool, are shown. In all networks, up to nine integer trophic levels were identified. However, after the sixth level, the amount of nutrients transferred to the next levels was <0.001 μ mol N or P m⁻² h⁻¹ and such flows (and levels) are not represented in the figures.

In both the N and P networks, the inputs to the first trophic level were sustained through a combination of external inputs (indicated by the red arrows) and recycling processes from the higher trophic levels (indicated by the dashed black arrows). In the transitional area most of the nutrient inflow to the first level consisted of external inputs, representing 82 % and 71 % of the total N input in spring and summer, respectively, and approximately 50 % of total P in both seasons. In the confined area, the amount of nutrients imported from the main tributary and the transitional area represented only a minor portion of the total input to the first level, ranging from 19 to 36 % for N and from 7 to 11 % for P, with higher values observed in spring.

For both N and P networks, the available nutrients were transferred to primary producers (transfers from the first to the second level) with higher efficiency in the confined area (ranging from 63 to 83 % for N and from 88 to 94 % for P) compared to the transitional area (from 15 to 52 % for N and for 42 to 52 % for P). In the transitional area, the amount of N and P imported from the outside to the second level increased from 60 % in spring to 72 % in summer. In contrast, for the confined area, this amount remained consistently below 15 % in both seasons.

The grazing efficiency (transfers from the second to the third level) within the transitional area for both N and P ranged from 16 to 19 %, with minimal seasonal differences. Within the confined area, these values decreased compared to the transitional area, and for both nutrients, they halved from spring to summer (from 10 to 5 % for N and from 8 to 4 % for P, respectively). The remaining portion was either exported to the outside or returned to the first level, with the latter process being dominant within the confined area and increasing from spring to summer.

For higher trophic levels, P was more effectively transferred to and used by consumers compared to N. The systems trophic efficiency ranged from 12 to 18 % for N and from 20 to 22 % for P.

3.3. Output Environ Analysis

Dissolved inorganic nitrogen (DIN), comprising ammonium (NH_4^+) , nitrite (NO₂), and nitrate (NO₃), is expected to exit the system in various forms. These include inorganic or organic forms dissolved in the water column (indicated as output from the DIN_w and DON_w compartments, respectively), particulate organic forms (output from PON_w), to be permanently stored in the sediment (output from PNs), or to be removed as N2 gas produced by denitrification primarily occurring within the sediment. The latter process is represented here as output from the inorganic N dissolved in pore water (DIN_{pw} compartment). The probability that a unit of imported DIN is exported through one of the designated processes is illustrated in Fig. 4a. It reveals that in spring >80 % of the DIN imported into the transitional area left the system in the same form as it entered, whereas about 5 % was permanently removed through sediment storage or denitrification, and the remaining portion was exported to the outside as phytoplankton (indicated as output from Phyto compartment, derived from the sum of the output from the five compartments representing different phytoplankton groups). In the same season, in the confined area, the proportion of N



Fig. 4. Probability that a unit of imported DIN_w (a) and DIP_w (b) is exported from the transitional or the confined area as one of the indicated forms. Abbreviations indicate: NTSP (N network-Transitional area-SPring), NCSP (N network-Confined area-SPring), NTSU (N network-Transitional area-SUmmer), NCSU (N network-Confined area-SUmmer), PTSP (P network-Transitional area-SPring), PCSP (P network-Confined area-SPring), PTSU (P network-Transitional area-SUmmer), PCSU (P network-Confined area-SUmmer).

exported as DIN_w represented a minor portion compared to the transitional area (30 %), whereas the export in particulate forms increased, both as PON_w and phytoplankton, as well as DON_w. Concurrently, the contribution of permanent removal processes such as sediment storage (17 %) and denitrification (10 %) increased. In summer, in both areas, the amount of N exported as particulate organic N (including both Phyto and PON_w) increased, peaking at 83 % in the confined area, while the contribution of permanent removal processes (including export as PN_s and DIN_{pw}) decreased, representing <3 % in both areas.

In spring dissolved inorganic phosphorous in the water column (DIP_w) was mainly exported from the transitional area as phytoplankton (36 %) and DIP_w (27 %), whereas about 26 % was accumulated within sediments (PP_s) (Fig. 4b). In the same area, the amount exported as DIP_w decreased in summer, and the accumulation within the sediment become negligible, while the amount exported as particulate organic forms (including both Phyto and POP_w) augmented. In the confined area, in both seasons, most of the imported DIP_w was exported as POP_w or phytoplankton, representing about 85 % and 93 % of total exports in spring and summer, respectively.

The Output Environ Analysis also allowed us calculating how many times a unit of DIN_{w} or DIP_{w} loaded into the networks was incorporated into the phytoplankton compartments before being exported (Fig. 5a and b). The frequency of phytoplankton uptake of a unit of imported N was <1 for the transitional area, both in spring and summer. Values for the confined area increased from 1.25 in spring to 2.96 in summer, partly sustained by the uptake of DON_w resulting from recycling



Fig. 5. Frequency at which phytoplankton used a unit of DIN_w (a) or DIP_w (b) imported in the transitional or the confined area, before being exported. Abbreviations indicate: NTSP (N network-Transitional area-SPring), NCSP (N network-Confined area-SPring), NTSU (N network-Transitional area-SUmmer), NCSU (N network-Confined area-SUmmer), PTSP (P network-Transitional area-SPring), PCSP (P network-Confined area-SPring), PTSU (P network-Transitional area-SUmmer), PCSU (P network-Confined area-SUmmer).

processes. The frequency of uptake increased for P in both areas, but values within the transitional area remained below 1, whereas within the confined area, they exceeded 4 both in spring and summer.

3.4. Total Dependency Matrices

The Total Dependency Matrices illustrate the contribution of different compartments to the recycling of N (Fig. 6) and P (Fig. 7) towards the dissolved inorganic and organic pools and indirectly to the activity of phytoplankton (obtained by averaging values of the five compartments representing different phytoplankton groups) both in spring and summer. In the transitional area during both seasons, <20 % of the phytoplankton production was sustained by DIN_w and DON_w. These components only in summer were related to mineralization processes within the water column (dependency on PON_w) and within the sediments (dependency on PON_s, DOP_{pw} and DIP_{pw}) (Fig. 6a and b). In both spring and summer, the sum of all dependency values was <100, indicating that primary producers' activity was sustained by input from

the outside environment.

Within the confined area, in both seasons, the dependency of phytoplankton activity on DON_w and DIN_w ranged from 68 to 76 %. In spring, these compartments were primarily sustained by PON_w (50 %) and, to a lesser extent, by PON_s and DON_{pw} (18 %). The contribution of sediment mineralization processes increased in summer, with dependency values reaching about 32 % for PON_s, DON_{pw}, and DIN_{pw}. In spring, the self-dependency of the pooled phytoplankton compartments almost equalled the values of dissolved N. These values in summer reached 105 %, suggesting high recycling activity. Higher values of dependency on phytoplankton compared to PON_w suggested that these compartments contributed to recycling not only through water column loop among phytoplankton – PON_w – DON_w – DIN_w, but also through secondary pathways as exudates production, settlement of organic matter that sustain sediment mineralization or feeding, and consumer-mediated recycling by higher trophic levels.

Dependency matrices derived from P networks of the transitional area displayed similar trends both in spring and summer (Fig. 7a and b). In both seasons, as for N, <25 % of phytoplanktonic production was sustained by DOPw and DIPw. Most of the water column dissolved P derived from POP_w, but the relative contribution of sediment processes slightly increased from spring to summer. Within the confined area, >75 % of phytoplankton production was sustained by the water column loop among POPw, DOPw, and DIPw. The contribution of sediment mineralization processes (POPs - DOPpw - DIPpw) was about 35 % in both seasons. Dependency values related to pooled phytoplankton compartments increased from spring (130 %) to summer (155 %). Compared to N networks the dependency values on living compartments increased, particularly those on herbivorous zooplankton, chironomids, oligochaetes, predators and benthivorous fishes. These dependency values ranged from 10 to 28 % in spring, with the highest value on chironomids, and from 10 to 25 % in summer, with the highest value on herbivorous zooplankton.

4. Discussion

4.1. A single lagoon integrating two contrasting macroareas

This study organizes, models, and synthesizes the outcomes of extensive experimental research carried out in the Curonian Lagoon over the last 30 years. Unlike previous investigations that focused on single compartments, organisms, or processes, this study offers a comprehensive analysis of coupled N and P seasonal dynamics in the transitional and confined areas of the Curonian Lagoon. The added value of the ENA is its helicopter view that integrates abiotic and biotic dynamics and produces synthetic descriptors of ecological functioning, N and P cycling and trophic performances. The results of the ENA suggest marked differences between the two nutrient pathways in the transitional and confined areas. In the transitional area, high riverine water and nutrient inputs, particularly in spring, result in limited retention and cycling through the food webs, leading to large export. This area exhibits riverine-like behaviour with passive drifting of not-assimilated and nottransformed nutrients, which are eventually transferred to the sea. Conversely, confinement in the southern lagoon area likely plays a major role in unbalancing the equilibrium between internal recycling and external loading. The former set of processes largely outweighs the latter, especially during summer, and more for P than N.

Many coastal lagoons have confined stagnant zones prone to anoxia and dystrophy but they occupy a minor fraction of the total surface. This contrasts with the Curonian Lagoon, where the confined area accounts for roughly 60 % of the total lagoon surface. ENA results suggest that higher recycling depends on interplaying processes, including high rates of primary production saturating the grazing capacity, high sedimentation rates fuelling microbial activities, consumers-mediated recycling overcoming nutrient limitation, and redox-dependent nutrient release mechanisms (Bartoli et al., 2020; Benelli et al., 2019; Petkuviene et al.,



Fig. 6. Phytoplankton dependency on N (%) in spring (a) and summer (b). Abbreviations indicate: NTSP (N network-Transitional area-SPring), NCSP (N network-Confined area-SPring), NTSU (N network-Transitional area-SUmmer), NCSU (N network-Confined area-SUmmer).



Fig. 7. Phytoplankton dependency on P (%) in spring (a) and summer (b). Abbreviations indicate: PTSP (P network-Transitional area-SPring), PCSP (P network-Confined area-SPring), PTSU (P network-Transitional area-SUmmer), PCSU (P network-Confined area-SUmmer).

2019; Zilius et al., 2018, 2014).

4.2. Lagoon hydrology differently drives seasonal N and P dynamics

Results of ENA align with experimental and theoretical outcomes of several studies (Bartoli et al., 2020; Ferrarin et al., 2008; Remeikaitė-Nikienė et al., 2017; Vybernaitė-Lubienė et al., 2022; Zilius et al., 2018, 2014). They demonstrate that hydrology plays a pivotal role in differentiating N and P dynamics within both the transitional and confined area. The primary differences regard the amount of nutrients delivered to the two areas and the time it takes for these nutrients to be processed, including the main pathways they follow within food webs and the rate at which they are recycled.

The nutrient-specific differences between the N and P pathways become apparent through variations in whole system indices. The TST index, which represents the overall system activity, exhibits a contrasting seasonal pattern. In the spring, TST values for N networks are significantly higher in the transitional area compared to the confined one, whereas TST values for P networks are higher in the latter. During the summer, there is a significant increase in values in both areas, with the most substantial rise occurring in the confined area, resulting in the highest recorded values. In both seasons, for both N and P, TST values in the transitional areas are associated with low recycling rates. This suggests that the overall system activity is not primarily supported by internal processes, but it is rather driven by external nutrient loads. The nutrient load to the transitional area, as well as to the entire lagoon, is mainly delivered by the Nemunas River and, as the freshwater discharge, it is characterized by a high seasonal variability, with loads peaking in spring, and reaching minimum values in summer (Vybernaite-Lubiene et al., 2018, 2017). The river flows into the central part of the lagoon, creating a northward unidirectional flow towards the Baltic Sea (Ferrarin et al., 2008). Dominant wind patterns regulate water exchanges between the transitional and confined areas. However, the former serves as the primary source of nutrients for the confined area, exceeding the input from the minor tributaries, even though it transfers only a minor portion of the total received load (Vybernaitė-Lubienė et al., 2022). Using 2015 data, the nutrient input-to-surface ratio for the two areas has been calculated. The results revealed that the transitional area received N and P loads from 6 to 10 times higher than the confined area, with these differences being more pronounced in spring, thus explaining the higher observed TST.

The configuration of the lagoon, along with variations in river discharge and changes in prevailing winds, contributes to significant spatial and temporal variability in its water residence time. The transitional area is characterized by the lowest residence time, with the minimum value recorded close to the Nemunas Delta in the spring (< 20 days) (Ferrarin et al., 2008; Umgiesser et al., 2016). The high influx of river water and nutrients, especially during spring, along with the low residence time, lead to limited retention and cycling through the food webs, resulting in significant export. Findings from the Lindeman Spine suggest that the majority of the nutrient load is not assimilated by primary producers and it is not incorporated into the food web, leaving the lagoon largely unaffected. This is especially true for N in the spring, for which <15 % of total input is assimilated by primary producers, while about half of the total P inputs were assimilated by primary producers. This is primarily due to the N:P stoichiometry of external loads, which in spring ranges from 120 to 200, and exceeds the theoretical Redfield ratio, suggesting large N excess or P limitation (Vybernaite-Lubiene et al., 2018, 2017). In summer, despite the reduction in external riverine inputs, TST values increase for both N and P, partially explained by the slight increase in recycling processes. The significant input observed at the second level of the Lindeman Spine suggests that the decrease in dissolved N and P input from the Nemunas River is partly counterbalanced by phytoplankton-associated organic N and P, likely originating from the confined area, which acts as a nutrient source (Vybernaitė-Lubienė et al., 2022).

In the southern lagoon area, confinement likely plays a major role in unbalancing the equilibrium between external loading and internal recycling. Internal recycling processes become dominant, especially during the summer, as evidenced by the increase in TST values, which align with FCI. These findings are in agreement with the seasonal variations in water residence time, which during summer exceeds 200 days in most of the confined area (Umgiesser et al., 2016). In this area, despite the lower nutrient input, the longer residence time enables more efficient N and P assimilation by primary producers compared to the transitional area. The longer the residence time, the greater the processing time during which nutrient can be repeatedly cycled through uptake, sedimentation of organic matter, mineralization, and permanent or temporary removal though different mechanisms, including absorption, precipitation, and nutrient specific bacterial processes (i.e., coupled nitrification-denitrification) (Seitzinger et al., 2006). This explains the more diverse results observed in the Output Environ Analysis, depicting the fate of a unit of imported N or P for the confined area compared to the transitional area, particularly during spring.

Hydrology alone cannot explain the Curonian Lagoon functioning as this factor has significant interactions with the seasonality, attributable to increasing water temperature, daylength, and biological activity. Hydrology also influences the sediment texture, composition, and organic matter accumulation, all of which affect sediment processes and retention capacity (Zilius et al., 2012). During the transition from spring to summer, the significant reduction in Nemunas River discharge coincides with a large increase in nutrient fluxes, particularly in the confined area. Nitrogen and P cycling undergo a different regulation resulting in distinct pathways. In both areas, for example, the seasonal increase in P fluxes is comparatively higher than that of N. Such difference between the two nutrients is due to a number of element-specific features, including their different origin (i.e., mostly allochthonous for N, largely internal for P) and their pathways (i.e., the presence of a dissipative process as denitrification, connecting the water compartment to the atmosphere for N and the absence of a similar process for P). Further details on the contrasting pathways of N and P in the two areas will be discussed in the following paragraphs.

4.3. A survey in N and P biogeochemistry supporting ENA outcomes

4.3.1. Nutrient dynamics in the transitional area

The Output Environ Analysis results suggest that during spring, the combination of a high N load and rapid water turnover, likely leads to the passive transport of DIN across the transitional area to the Baltic Sea, where it is exported in the same form as it enters the system. The assimilatory uptake by primary producers, denitrification (output from the DIN_{pw} compartment) and sediment storage (output from the PNs compartment) together accounted for only a small portion of DIN exports and were scarcely noticeable compared to the total import. In a variety of transitional ecosystems, N temporary or permanent removal has been demonstrated to be strictly related both to water residence time and loading (Nixon et al., 1996; Seitzinger et al., 2006). Several studies report linear correlation between phytoplankton production and residence time, in particular for periods <50 days (Delesalle and Sourniat, 1992). Biomass accumulation occurs when the residence time exceeds the phytoplankton doubling time, which, according to the literature, typically ranges between 1 and 9 days, with higher values observed in environments characterized by nutrient limitation (Ferguson et al., 2004; Malone and Chervin, 1979). Although these values are lower compared to the average spring residence time in the transitional area, it is likely that the high areal nutrient load saturates the uptake capacity of primary producers. The same is true for denitrification, which is the primary process responsible for N removal in transitional ecosystems (Asmala et al., 2017; Seitzinger, 1990; Sharples et al., 2017). Denitrification has been demonstrated to be positively related to N loadings with increasing rates until reaching an asymptotic threshold, due to saturation of the microbial enzymatic activity (Dong et al., 2000; Magri et al.,

2022; Ogilvie et al., 1997). These threshold values largely differed among analysed systems and depend on biological and environmental variables, as well as differences in acute or chronic nutrient loading. In the transitional area, characterized by sandy and flushed sediments with low organic matter content, it is likely that the low potential denitrification is overwhelmed by the significant influx of NO₃ (Bartoli et al., 2021).

In spring, the riverine load is characterized by a large P limitation (Vybernaite-Lubiene et al., 2018, 2017). Unlike N, a relative larger portion of P is assimilated by primary producers, enters the water column recycling loop, and is exported in organic form, both dissolved and particulate. A substantial portion of the exported DIP occurred via sediment storage. To simplify the Fig. 4, the category referred to as particulate phosphorus in sediment (PPs) encompasses both the organic and inorganic constituents, along with the microphytobenthos, with the latter prevailing in spring. The same output for the microphytobenthos compartment was observed for N, but it was less pronounced as compared to the overall N pool. Microphytobenthos acts as a temporary nutrient reservoir and has been shown to play a significant role in driving benthic fluxes in the transitional area (Bartoli et al., 2021; Benelli et al., 2018; Zilius et al., 2012). An active benthic algae community colonized littoral sandy sediment due to the shallow water column and the high light availability, especially in spring. Benthic algae exert control on nutrient concentrations through the uptake of pore water solutes diffusing from the sediment to the water column, thereby reducing internal recycling. They also compete with pelagic producers for nutrients and contribute to increase water clarity (Bartoli et al., 2003; Sundbäck et al., 2000).

Apart from microphytobenthos activity, in estuarine and shallow ecosystems, P dynamics are closely linked to manganese (Mn) and iron (Fe) compounds. Oxidized Fe and Mn bind and co-precipitate DIP in solid phase (Canfield, 1994). Some of these compounds are redox sensitive and O₂ shortage conditions induce metals reduction and the consequent release of reactive P (Viktorsson et al., 2013). The terrigenous material transported by the Nemunas River contains elevated concentrations of microbially reducible Mn⁴⁺ and Fe³⁺, which have been demonstrated to act as a natural geochemical buffer against P release in the transitional area, even under anoxic conditions (Bartoli et al., 2020; Petkuviene et al., 2016). Therefore, it is likely that in the river plume area, a portion of reactive P released by mineralization processes could be retained within sediments. This retention is facilitated by the high hydrodynamics in the area and the combined influence of microphytobenthos and bioturbating fauna, which help preserve oxidized Mn and Fe pools (Zilius et al., 2015). In summer, both N and P dynamics are primarily driven by primary producers' uptake in the water column, representing the main form of nutrient export. However, internal recycling remains relatively limited during this period.

4.3.2. Nutrient dynamics in the confined area

Within the confined area the longer residence time increases the magnitude and relevance of internal processes, resulting in a more diverse picture of exports depicted in the Output Environ Analysis. Both water column primary production and remineralization rates intensified compared to the northern area, resulting in increased export of dissolved and particulate organic N forms, including phytoplankton. Nitrogen assimilation by primary producers, the subsequent deposition of phytodetritus and the sediment storage represent an important mechanism for the permanent N removal. The sediment storage is not due to microphytobenthos activity, which is limited by low light penetration in deeper and turbid water (Bartoli et al., 2021; Zilius et al., 2014). Net retention was likely due to decoupled rates of organic matter sedimentation and degradation and to large benthic nitrate consumption sustaining microbial respiration and growth (Lin and Stewart, 1997; Luque-Almagro et al., 2011). Muddy sediments display higher denitrification rates in comparison to sandy sediments in the transitional area and are sustained by large availability of both high-quality organic matter from

phytoplankton and water column nitrate (Bartoli et al., 2021; Zilius et al., 2018).

Unlike N, which is partly removed by benthic processes, assimilative uptake by phytoplankton represented in spring the main process driving DIP export. This lagoon area on an annual base acts as a net sink of water column DIP, but a source of particulate P, sustained also by P released from sediments (Vybernaite-Lubiene et al., 2022). Sediment storage, in contrast to the transitional area, does not serve as pathway of DIP export. Muddy sediments display ten times higher P content compared to sandy ones and most of the pools that bind P are reactive and more sensitive to bottom water chemical changes (Petkuviene et al., 2016). Experimental studies showed that despite the high DIP concentration in pore water, inorganic P regeneration from sediments is generally limited (Petkuviene et al., 2016; Zilius et al., 2015). The largest DIP effluxes were occasionally measured in summer, after large bloom and sedimentation events increasing benthic respiration and leading to negative sediment redox, and to the exhaustion of oxidized Mn and Fe sedimentary pools (Bartoli et al., 2020; Zilius et al., 2015). These events are particularly significant since the specific conditions that favor P release produce little effects on benthic N cycling. Indeed, organic sediments display low rates of nitrification, due to low O₂ concentration, and low rates of ammonium efflux when the activity of macrofauna is inhibited by chemically reduced conditions (Bartoli et al., 2021). Since these large DIP effluxes were reported occasionally, they are not included in this study, which is based on average seasonal rates and adopts a conservative approach that excludes the outliers. However, their relevance is potentially high, since they could contribute to further unbalance the N: P recycling ratio obtained from ENA. Furthermore, they might trigger the water column blooms-collapse-blooms cycles, in specific areas identified as hotspots, sustaining, and prolonging this phenomenon over time (Vaičiūtė et al., 2021).

In summer, in both areas, a major fraction of imported N and P was exported in particulate organic form, mostly as living phytoplankton, and cyanobacteria in particular (Vybernaite-Lubiene et al., 2017; Zilius et al., 2018, 2014). When the macroscopic colonies of *Aphanizomenon flos-aquae* dominated among the primary producers, the proportion of settleable Chl-*a* significantly decreased, due to the positive buoyancy capacity of these organisms (Bukaveckas et al., 2019). These negligible settling rates further favor the export of algal biomass and phytodetritus, resulting in lower retention through sedimentation and burial, or benthic removal processes (Vybernaite-Lubiene et al., 2017; Zilius et al., 2014).

4.4. Pelagic nutrient turnover, high primary production, and limited transfer along the food web

Total Dependency Analysis has been used to quantify the direct and indirect contributions of benthic and pelagic compartments as nutrient sources for phytoplankton. The pelagic production in shallow coastal ecosystems is generally supported by sediment mineralization processes (Fisher et al., 1982; Tobias et al., 2003). In the Curonian Lagoon the results from the dependency matrices show that the recycling of particulate and dissolved nutrient from the sediment (dependency on DIN_{pw} or DIP_{pw} compartments) contributed to a minor share of phytoplankton requirements, ranging from 1 to 30 % for both N and P. The primary source of nutrients for phytoplankton is represented by the water column loop, involving phytoplankton, particulate organic N or P, and dissolved organic and inorganic N or P. This is mainly due to the high turnover rates in the water column, driven by organic matter oxidation and assimilation. Previous experimental measurements and mass balances carried out in this site demonstrated that sediment regeneration and additional inputs (e.g., cyanobacteria-mediated N2 fixation) accounted for a minor portion of phytoplankton requirements (Broman et al., 2021; Zilius et al., 2018, 2014). In different shallow lakes or coastal ecosystems, the water column regeneration has been reported to exceed both tributaries input and sediment regeneration. This

phenomenon is recognized as a direct consequence of eutrophication, resulting in a transition from benthic to pelagic processes (Li and Reardon, 2017; Mccarthy et al., 2016, 2013).

The high rates of water column recycling can be partly attributed to a limited control of primary production by herbivores. The Lindeman Spine shows that the efficiency of nutrient transfer from primary producers to herbivores, in both areas and seasons, for either N or P, is <20 %. The high rates of primary production likely saturate the grazing efficiency, bringing about low transfer of nutrient to higher trophic levels and the majority of nutrient channeled into the detritus pool. This phenomenon is particularly evident in the confined area, where Chl-a concentration and production are generally higher, and especially during the summer, when the percentage of N and P transfer decreases to <5 %. The carbon flow and pathways in the Curonian Lagoon, as well as in four other south-eastern Baltic coastal ecosystems, have already been analysed using the software ECOPATH on annual networks (Christensen et al., 2005; Tomczak et al., 2009). All these eutrophic ecosystems displayed low trophic transfer efficiency, and the turbid Curonian Lagoon displayed the highest primary production and the lowest trophic transfer efficiency (7 %). These results can be attributable to the dominance of filamentous and inedible cyanobacteria, which are not efficiently grazed by the planktivorous communities (Heymans et al., 2014; Karpowicz et al., 2020). The lowest nutrient transfer efficiency across the food web was indeed recorded in summer within the confined area, where nonfixing and N2-fixing cyanobacteria, together constituted >80 % of total phytoplankton.

Previous studies have demonstrated that the shift from diatoms to cyanobacteria is followed by a decline in grazing efficiency, dropping from 34 % to 8 % of net primary production in the transitional area and from 60 % to 4 % in the confined area (Bartoli et al., 2018; Semenova and Aleksandrov, 2009). The differences between the values reported in the literature and the grazing rates estimated in this study may, in part, be attributed to the lack of a specific compartment for microzooplankton (size category 20-200 μ m), which in this study was considered as part of the microbial loop among phytoplankton and non-living compartments due to a lack of data. Microzooplankton has been shown to significantly contribute to overall grazing and play a significant role in biomass accumulation control, particularly in spring, when the largest differences were recorded (Griniene et al., 2016).

The low transfer efficiency observed at higher trophic levels may be partly attributed to the prevalence of benthivorous species, sustained by the detritus chain, over planktivorous species, sustained by the grazing chain. This pattern is evident among fish species, with benthivorous individuals, whose diet is supported by deposit-feeding macrofauna, dominate the community (Bubinas and Ložys, 2000). Similarly, within the macrofauna higher transfer efficiency values recorded in the transitional area can be attributed to the dominance of filter-feeding bivalves (e.g. *Dreissena polymorpha* and native unionids), in contrast to the confined area where deposit-feeding oligochaete and chironomids primarily dominate (Zettler and Daunys, 2007).

Low nutrient transfer efficiency in the pelagic compartment of the transitional area determines large export of energy and matter to the sea, limiting the filter and reactor service that generally characterizes coastal ecosystems. In the confined area organic matter and nutrient inputs to the benthic compartment occurs, producing a cascade of negative consequences on oxygen availability, macrofauna abundance and diversity, capacity of microbial consortia to process organic inputs and exhaustion of geochemical buffers, affecting system resilience to stress. Inefficient pelagic nutrient transfer across the network makes therefore also benthic processes inefficient and not linear, producing positive feedback on the pelagic compartment (Cloern, 2001; Viaroli et al., 2008).

4.5. Cyanobacteria and consumers induce higher P recycling

A few studies have simultaneously described the dynamics of C, N, and P in aquatic ecosystems using network analysis (Baird et al., 2011,

2008; Scharler et al., 2015; Scharler and Avers, 2019; Ulanowicz and Baird, 1999). These studies consistently reported high recycling rates for both N and P compared to C, with P generally exhibiting higher recycling rates than N. In a study carried out in the Sylt-Rømø Bight ecosystem, Baird et al. (2008) attributed these differences to N dissipation processes (primarily N2 and N2O production via denitrification), which lack equivalents in P transformations. This hypothesis was confirmed in a later study where the authors analysed sub-systems within the same marine basin without considering denitrification and observed a variable ratio between N and P recycling rates (Baird et al., 2011). The results of the present study display the same pattern, with higher recycling for P compared to N. However, when the FCI values for N are normalized by those of P, the ratio shows high variability, ranging from 0.29 to 0.8, and in both areas the values increase from spring to summer. This increase corresponds to decreased denitrification rates and reaches a maximum value in the confined area, which in summer undergoes minimal denitrification rates due to the low availability of nitrate in the water column and of O₂ in sediments, suppressing nitrification coupled to denitrification (Bartoli et al., 2021; Zilius et al., 2018)

The variations in denitrification rates alone cannot fully account for the significant differences in the estimated FCI values between N and P. Variations in the recycling rates of N and P have been attributed to stoichiometric differences in N to P ratios of heterotrophic organisms along the food web (Scharler et al., 2015). Heterotrophic organisms incorporated proportionally more N and P than C, and more N or P depending on their limiting resources. Highest recycling rates have been reported for the nutrient that showed the highest trophic transfer efficiency and was considered the limiting resource (Vanni, 2002). In the Curonian Lagoon, higher recycling rates are associated with heterotrophic organisms (e.g., herbivorous zooplankton, chironomids, benthivorous fishes) for P networks, which also exhibit higher trophic transfer efficiency. Consumer-mediated nutrient recycling plays a central role in meeting the nutrient requirement of primary producers in nutrient limited systems, as observed in the mangrove island analysed by Scharler et al. (2015). In the present study, although these values represented minor fractions of external inputs or water column regeneration rates, they contributed to explain the differences in the dynamics of N and P.

Recent studies have been conducted in the Curonian Lagoon, to assess the potential contribution of waterbirds to overall P recycling (Morkune et al., 2020; Petkuviene et al., 2019). The Curonian Lagoon hosts a high diversity and large number of waterbirds, with the great cormorant being the most abundant breeding species in summer (Morkune et al., 2020; Putys and Zarankaite, 2010; Švažas et al., 2011). In two different studies, Morkune et al. (2020) and Petkuviene et al. (2019) demonstrated that waterbirds, and particularly piscivorous birds as the great Cormorant, can significantly contribute to the P balance and stimulate the algal blooms in the Curonian Lagoon. These birds release large amounts of P through their excretion, estimated to range from 1 to 12 % of the total P load delivered by the Nemunas river, with the peak contribution in summer, when riverine discharge is minimum. However, the results from ENA contrast these findings, as they suggest that bird excretion plays a minor role as a P source for phytoplankton. One potential explanation for these differences is that the cited study only examined bird recycling in relation to external inputs, while the Dependency Analysis results consider the contribution of birds compared to the overall system recycling activity. It's worth noting that these results may be somewhat underestimated as the real consistency of bird populations in the Russian area was estimated according to Lithuanian records and not directly quantified. Nonetheless, it is important to underline that, as discussed for sediment regeneration, large colonies of piscivorous birds likely have a large local impact that can lead to confined blooms rapidly expanding to cover larger surfaces, fuelling the bloom-collapsing-bloom mechanism (Bresciani et al., 2014; Vaičiūtė et al., 2021).

For birds, as well as for other groups of organisms that may play a fundamental role in the recycling of N and P like fish, there is a general lack of information regarding the actual population size, both in the Lithuanian and, especially, in the Russian area. To achieve the same level of detail as it has been attained here for non-living compartments, more research is required to obtain adequate population inventory and functional roles.

5. Conclusions

The results of this study highlight substantial differences in N and P dynamics between the two areas of the Curonian Lagoon, characterized by different hydrological conditions. The norther transitional area, regardless of the season, receives a large amount of nutrients, primarily as dissolved forms from the Nemunas River in spring and as particulate forms from the southern confined area in summer. The high flushing rate in this area limits the contribution of internal processes to nutrient cycling. In contrast, in the southern area smaller nutrient inputs are coupled with longer water residence time. This promotes across the two seasons the recycling and reuse of both N and P, but also N loss through denitrification (in spring) and P regeneration favored by oxygen shortage (in summer).

Despite the high rates of primary production, the ENA results indicate a low nutrient transfer efficiency to higher levels in the food web. This suggests that phytoplankton itself maintains and promotes blooms, particularly during the summer, through the microbial loop, which connects assimilation and recycling processes. The low trophic transfer efficiency, especially in the confined area, translated into excess organic matter to the benthic compartment, further emphasizing the importance of internal recycling processes. Since the confined area covers more than half of the entire lagoon's surface, this cascade of negative effects impairs the resilience of the whole ecosystem. The potential for extensive internal recycling may in the short term, offset the effectiveness of any management measures implemented to reduce external loads, whereas the forecasted increase in water temperature during the summer due to climate change may further promote the confinement or the extension of the stagnant sector.

The findings of this study provide a comprehensive view of the N and P circulation within the two areas of the lagoon. The identified spatial and temporal differences contribute to deepening our understanding of mechanisms promoting cyanobacteria blooms. Further efforts should aim to enhance the model resolution and to address hotspots where the mechanisms governing the bloom-collapse-bloom cycle can be better constrained and clarified.

CRediT authorship contribution statement

Monia Magri: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Writing - original draft, Writing - review & editing. Cristina Bondavalli: Conceptualization, Methodology, Validation, Writing - original draft, Writing - review & editing. Marco Bartoli: Conceptualization, Funding acquisition, Supervision, Validation, Writing - original draft, Writing - review & editing. Sara Benelli: Data curation, Writing - original draft, Writing - review & editing. Mindaugas Žilius: Data curation, Writing - original draft, Writing - review & editing. Jolita Petkuviene: Data curation, Writing original draft, Writing - review & editing. Irma Vybernaite-Lubiene: Data curation, Writing – original draft, Writing – review & editing. Diana Vaičiūtė: Data curation, Writing - original draft, Writing - review & editing. Evelina Griniene: Data curation, Writing - original draft, Writing - review & editing. Petras Zemlys: Data curation, Writing - original draft, Writing - review & editing. Rasa Morkune: Data curation, Writing - original draft, Writing - review & editing. Darius Daunys: Data curation, Writing - original draft, Writing - review & editing. Sabina Solovjova: Data curation, Writing - original draft, Writing - review & editing. Martynas Bučas: Data curation, Writing -

original draft, Writing – review & editing. Zita Rasuole Gasiūnaitė: Data curation, Writing – original draft, Writing – review & editing. Artūras Baziukas-Razinkovas: Data curation, Supervision, Writing – original draft, Writing – review & editing. Antonio Bodini: Conceptualization, Funding acquisition, Methodology, Supervision, Validation, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

I have shared the data as csv files at the Attach File Step.

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Appendix A. Supplementary data

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