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Feces from Piscivorous and Herbivorous Birds Stimulate Differentially Phytoplankton Growth

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Abstract: Aquatic birds may impact shallow ecosystems via organic and nutrient enrichment with feces. Such input may alleviate nutrient limitation, unbalance their ecological stoichiometry, and stimulate primary production. Herbivorous and piscivorous birds may produce different effects on aquatic ecosystems due to different physiology, diet and feces elemental composition. We analyze the effects of droppings from swans (herbivorous) and cormorants (piscivorous) on phytoplankton growth via a laboratory experiment. These birds are well represented in the Curonian Lagoon, where they form large colonies. As this lagoon displays summer algal hyper-blooms, we hypothesize an active, direct role of birds via defecation on algal growth. Short-term incubations of phytoplankton under low and high feces addition produces different stimulation of algal growth, significantly higher with high inputs of cormorant feces. The latter produces a major effect on reactive phosphorus concentration that augments significantly, as compared to treatments with swan feces, and determines an unbalanced, N-limited stoichiometry along with the duration of the experiment. During the incubation period, the dominant algal groups switch from blue-green to green algae, but such switch is independent of the level of feces input and from their origin. Heterotrophic bacteria also are stimulated by feces addition, but their increase is transient.

Keywords: birds; feces; nutrients; stoichiometry; phytoplankton; bacteria

1. Introduction

Estuarine productivity can be stimulated by riverine inputs, run-off from agricultural land, point pollution sources and internal recycling. These nutrient sources can be temporally separated and may be quantitatively different [1]. Diffuse inputs, including those from rivers and agricultural land, are strongly dependent on precipitation and may, therefore, undergo pronounced seasonal variations [2]. Regarding temperate areas, for example, riverine discharge and nutrient concentrations are positively correlated and peak during autumn, winter and spring months whereas during summer, they generally attain minimum values. Concerning eutrophic shallow ecosystems, internal recycling is often the dominant mechanism sustaining primary production in the warm season, when biological components are more active [3–5]. Internal recycling results in nutrient regeneration within the system and it is generally addressed to sediments. At peak water temperatures, in fact, microbial activity or oxygen shortage may stimulate nutrient efflux from the bottom via increased mineralization or via redox-dependent release [4,6]. Besides bacteria, the macrobiota may contribute to internal nutrient recycling and primary production but its role is comparatively understudied. Aquatic birds might

be present in large colonies in estuarine systems and be quantitatively relevant as nutrient sources to the water column, via direct and indirect mechanisms. Direct mechanisms include the ingestion of food (e.g., macrofauna, fish, macrophytes) and the production of feces, which makes nutrients readily available to primary producers [7,8]. When the food is found in the same area where feces are produced, this direct mechanism is an internal recycling. When the food is found in neighbouring ecosystems (e.g., seagull colonies feeding in urban areas but nesting and excreting along the coast) this mechanism is a net nutrient import. Indirect effects include stepping on sediment and its resuspension and macrophyte grazing, which prevents nutrient uptake or sediment stabilization with roots [8,9].

Bird droppings fertilize the upper layer of the water column and soluble inorganic nutrients may stimulate fast-growing phytoplankton groups [10–12]. The organic fraction of feces might also stimulate microbial growth and activity in the water column and on the sediment surface [13,14]. Such nutrient input in some specific areas (e.g., adjacent to nesting or resting places) may represent the dominant input, largely exceeding external sources or nutrient regeneration from sediment [15–17]. Bird droppings might release different ratios of inorganic nutrients to the water column depending on the bird physiology and the ecological stoichiometry of the ingested food [18]. As compared to herbivores, piscivorous birds might produce feces enriched with inorganic phosphorus and with low N:P ratios. This may, in turn, favor the growth of algal groups like cyanobacteria, that compensate unbalanced nutrient stoichiometry (i.e., P excess) by fixing nitrogen.

We investigate with a laboratory experiment the effects produced by feces from herbivorous and piscivorous birds on microbial activity and on phytoplankton growth and community composition in the water of the Curonian Lagoon, Lithuania. Much evidence supports the relevance of birds in the biogeochemistry of the lagoon and, potentially, in supporting algal blooms [19]. First of all, this freshwater estuary displays blooms of cyanobacteria (up to 400 μg Chl-*a* L^{-1}) during summer, when external nutrient input is minimum and it is characterized by strong inorganic nitrogen and silica limitation [2,19]. The latter is due to a steep late spring-early summer decrease of discharge and of N and Si loads from the Nemunas River, the dominant freshwater input [2,6,20]. Fixation may support part of the nitrogen requirements by cyanobacteria. However, internal recycling must support the demand of other macronutrients, including P. Within biotic factors enhancing the nutrient internal recycle, birds may play a significant role. During summer, the Curonian Lagoon hosts large bird colonies, with herbivorous swans and piscivorous cormorants well represented. The consistency of the swan population was estimated in 2×10^3 individuals while nearly 6×10^3 cormorants were censused in the Curonian Lagoon, forming large colonies with 2000–3000 pairs in different areas of the Lithuanian part of the estuary and roosting and breeding along the shoreline [21,22]. Recent surveys suggest that such estimation represents a minimum number, since in August the cormorant population may peak with up to 30×10^3 individuals (Morkūnė, personal observation). Swan and cormorant droppings may reach the lagoon water directly or via runoff and increase nutrient availability, as reported in a lake with 160 breeding pairs [7]. Swans and cormorants have a different potential in terms of P input to the Curonian Lagoon due to differing population consistency and to differing potential P production, estimated in nearly 0.6 and 2.5. g P $ind^{-1}day^{-1}$, respectively [9]. Potential P input by swans to the Lithuanian part of the Curonian Lagoon may approach ~110 kg during summer (3 months period), whereas cormorants may contribute a much higher P amount, between ~1300 and ~6700 kg. Despite large differences in potential P inputs, the swan population is more sedentary than that of cormorants and may produce strong, local effects on phytoplankton, whereas the effect produced by cormorants might be diluted over much larger hunting surfaces. Relatively, potential P input by the cormorant population represents, during summer, a non-negligible fraction (10–50%) of the inorganic P summer input (~12,000 kg) by the Nemunas River, which is the main nutrient source to the Curonian Lagoon [2].

Therefore, it can be assumed that internal recycling by birds may represent an important nutrient source to the lagoon during summer, when the Nemunas River discharge and nutrient inputs are minimal [2]. We analyze with a laboratory experiment the effects produced by bird droppings on microbial activity and phytoplankton growth in the water of the Curonian Lagoon. We hypothesize

that, due to different diets, feces from herbivorous and piscivorous birds have different elemental composition and produce different effects on the phytoplankton growth and community composition by releasing dissolved inorganic nutrients (N, Si and P) with different stoichiometry.

2. Materials and Methods

2.1. Sampling Procedure and Microcosms Set Up

Bird feces, phytoplankton and water were collected from the Curonian Lagoon (Lithuania) in early August 2018. A week before the beginning of the experiment, on August 3rd, aquatic bird feces were collected from a great cormorant colony (*Phalacrocorax carbo*) located in the Curonian Spit and from a mute swan (*Cygnus olor*) resting place located along the lagoon shoreline (Figure 1). The feces were air-dried, crushed and ground to fine powder by ceramic mortar and pestle in the laboratory. A subsample of dried and powdered feces was analyzed for P content (see next paragraph) whereas the rest was used in the experiment.

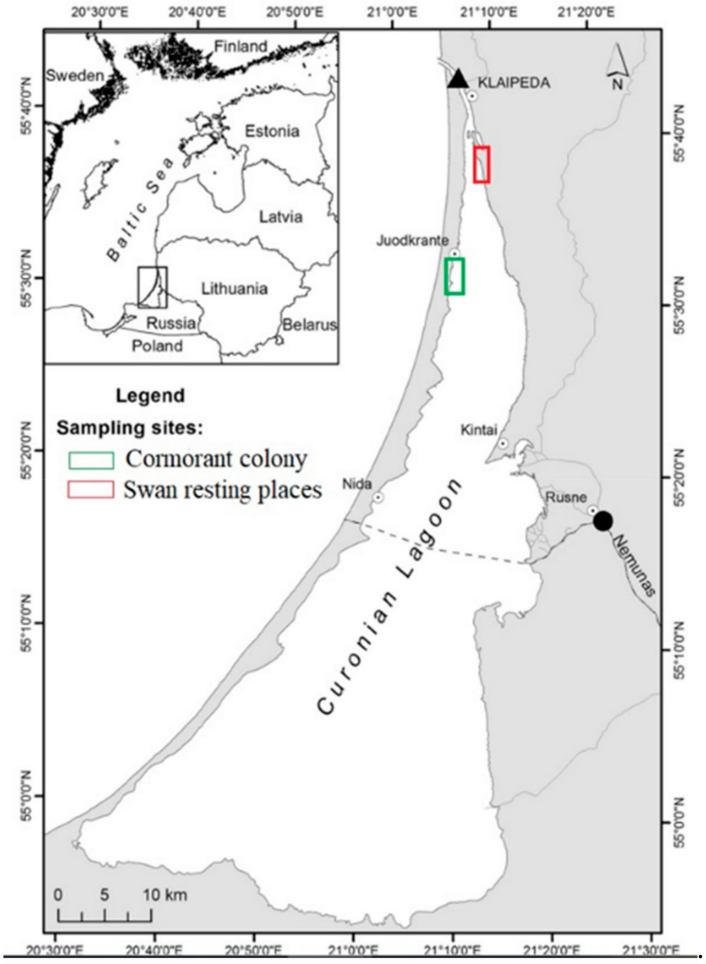


Figure 1. Map of the Curonian Lagoon with the areas indicated where the feces of cormorants and swans were collected.

Nearly 50 L of water was collected from the central part of the Curonian Lagoon on August 8th, and filtered in situ with a 55 µm mesh plankton net to concentrate, by a factor of 40, algal cells in a final volume of 1.25 L. Simultaneously, 20 L of surface water (0.3 m depth) was collected, transported to the laboratory and filtered through GF/F filters (pore size 0.7 µm).

In situ concentrations of chlorophyll *a* and inorganic nutrients were 86 ± 7 μg Chl-*a* L^{-1}, 1.2 ± 0.3 μM N-NO_x^-, 1.3 ± 0.0 μM N-NH_4^+, 0.5 ± 0.2 μM PO_4^{3-}, 4.8 ± 1.5 μM SiO_2. Just before the start of the experiment, on August 9th, 25 mL of the algal concentrate was diluted by a factor of 40 in 1 L of filtered water from the lagoon and transferred to acid-washed plastic bottles (n = 15) to have a final concentration of algal cells similar to that in situ (75 ± 10 μg Chl-*a* L^{-1}) in each bottle. One g of powdered feces from the two bird species was dissolved and mixed in 100 mL of distilled water to prepare 2 stock solutions of concentrated cormorant and swan feces. Taken from literature data on P content in bird feces (0.5< x <1%), expected concentrations of total P in the stock solutions were between ~ 50 and ~ 100 mg P L^{-1}. The experimental design consisted of 3 bottles that served as a control, 6 bottles with 1 mL of the feces stock solution (low addition, 3 bottles with swan feces (SL) and 3 bottles with cormorant feces (CL) and 6 bottles with 10 mL of the feces stock solution (high addition, 3 bottles with swan feces (SH) and 3 bottles with cormorant feces (CH) (Figure 2).

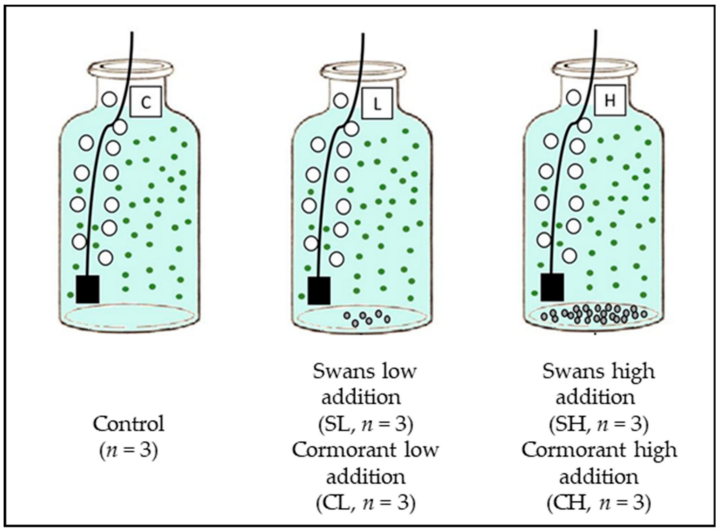


Figure 2. The experimental design consisted of three treatments. Controls (C, n = 3) had no bird feces added; swans and cormorant low feces added (SL, n = 3 and CL, n = 3) and swans and cormorant high feces added (SH, n = 3 and CH, n = 3). See the text for more details.

Low and high additions are conservative estimates of realistic feces inputs to the water in the proximity of colonies, but much lower inputs near bird resting places (Petkuviene, unpublished data). The high addition (0.1 g of feces dry weight per liter) simulated a condition in which 100% of droppings generated by the two colonies reached the water surface, whereas the low addition (0.01 g of feces dry weight per liter) simulated a condition in which only 10% of the produced droppings reached the water. Low and high additions also simulated the effect produced by birds in areas with densities of ~0.01 and 0.1 ind m^{-2}, respectively. Such densities are much lower than those generally found in resting places within the Curonian Lagoon (Morkūnė, personal observation).

After feces addition, experimental bottles were transferred into a 150 L aquarium filled with water and each bottle was provided with gentle air bubbling to maintain the particulate matter and the algal material in suspension and to ensure 100% saturation during the whole experiment duration. The aquarium was placed outside, under natural temperature and illumination conditions. Water sub-samples for the analyses of inorganic nutrients, the heterotrophic bacterial abundance, chlorophyll *a* (Chl-*a*) and algal groups were collected at the beginning of the experiment, just after feces addition (T_0) and after 24 h (T_1), 48 h (T_2), 72 h (T_3) and 96 h (T_4).

2.2. Nutrients, Phytoplankton and Heterotrophic Bacteria Analysis

Dissolved inorganic nutrient concentration (DIN = NO_3^-+NO_2^-+NH_4^+, DIP = PO_4^{3-}, DSi = SiO_2), the dominant algal groups (green algae, blue-green algae, diatoms, cryptophytes) and their total

biomass (μg Chl-*a* L^{-1}), and the heterotrophic bacterial abundance were analyzed from each bottle replicate and on each sampling date. Sampled water (40 mL) was always replaced with in situ filtered water. An exponential growth equation was used to calculate from experimental values of Chl-*a* the phytoplankton specific growth rate in the different treatments:

$$B_f = B_i \times e^{tr} \quad (1)$$

where B_f and B_i (μg L^{-1}) are the final and initial Chl-*a* concentrations in the water of each treatment, respectively, and proxies of phytoplankton biomass; r is the specific growth rate (day^{-1}) and t is the incubation time (day).

Water samples were filtered through GF/F filters (pore size 0.7 μm), transferred into 10 mL PE tubes for later analyses and frozen immediately (−20 °C). Dissolved nutrients were measured with a 4-channel continuous flow analyzer (San++, Skalar) using standard colorimetric methods [23]. Nitrate (NO_3^-) was converted into nitrite (NO_2^-) via cadmium reduction and the NO_x^- (NO_3^- + NO_2^-) pool was analyzed via diazotization [23]. Dissolved ammonium (NH_4^+) was analyzed manually by means of the salicylate-hypochlorite method, using nitroprusside as a catalyst [24].

Total inorganic P (IP) of bird feces was extracted from dried and powdered material, whereas total P (TP) was extracted from ashes after ignition at 550 °C and 1 M HCl extraction. Organic phosphorus (OP) was calculated as the difference between TP and IP. TP and IP were measured spectrophotometrically with the molybdate–ascorbic acid method [25].

Phytoplankton community composition was determined by means of a fluoroprobe (FluoroProbe II, © bbe Moldaenke GmbH, Schwentinental, Germany). The probe measures fluorescence emitted by Chl-*a* following excitation of photosynthetic accessory pigments specific to each 'spectral' group. The fluoroprobe allows estimation of the proportional contributions of four spectral phytoplankton groups (green algae, blue-green algae, cryptophytes, diatoms) expressed as μg L^{-1} of Chl-*a* [26].

Heterotrophic bacteria (aerobic and facultative anaerobic) were enumerated using heterotrophic plate count methodology using Plate count agar. Serial dilutions were done to assess the bacterial colony forming units (CFU L^{-1}) in collected water samples.

Taken at T_3 from each treatment were the dominating heterotrophic bacteria colonies for further analyses. Identification and confirmation of the genus of the bacteria were based on molecular characterization. The employed molecular method was partial sequencing using the 16S rRNA gene as a target for the identification of bacteria. Fragments of 16S rDNA (positions 341–907) were amplified by PCR using the primer set 341F (5′-CCTACGGGAGGCAGCAG-3′) and 907R (5′-CCGTCAATTC(AC)TTT(AG) AGTT-3′). The amplification of the microorganism's DNA was done at the Marine Research Institute of Klaipeda University and outsourced to Baseclare Netherlands for sequencing. The closest relatives for all retrieved sequences were determined by comparison using the BLAST function (http://www.ncbi.nlm.nih.gov/BLAST/). Phylotypes were defined as sequences showing ≥98% homology to each other.

Differences among the concentration and stoichiometry of inorganic nutrients, Chl-*a* concentrations, bacterial counts and phytoplankton specific growth rates in the different treatments were tested via analysis of variance (ANOVA) on repeated measurements (Sigma Plot 12.0 (Systat Software Inc., San Jose, CA, USA)).

3. Results

3.1. Effects of Bird Feces Addition on Inorganic Nutrients and Chl-a Concentrations

Along the course of the experiment, water temperature in the incubation tank varied between 25 and 32 °C (T_0 to T_2) and between 19 and 21 °C (T_3 and T_4). Such variations reflected different illumination conditions: bright sky in the first half of the experiment and cloudy weather in the second half.

Added cormorant feces contained 4.0 mmol of TP per gram of feces dry weight and 58% of TP was in the organic form. Swan feces had a lower TP concentration (0.31 mmol P g^{-1} feces dry weight) and more than 75% was organic.

Ammonium concentration displayed statistically significant differences among treatments (ANOVA on repeated measures, F = 456.8, $p < 0.05$) and along the course of the experiment (ANOVA on repeated measures, F = 619.3, $p < 0.05$) (Figure 3a). Regarding all treatments, with CH as the exception, NH_4^+ concentrations displayed an initial increase, from 1.5 ± 0.2 µM measured at T_0 to ~18 µM measured at C, SL, SH, and CL at T_2. During the cormorant high treatment (CH), feces addition resulted in instantaneous NH_4^+ release (~20 µM at T_0) and in a further increase up to 56.5 ± 1.5 µM measured at T_2. Afterwards, NH_4^+ concentrations showed a moderate (C, SL, SH) or steep decrease (CL, down to 2.4 ± 1.8 µM, and CH, down to 3.7 ± 1.8 µM measured at T_4) (Figure 3a).

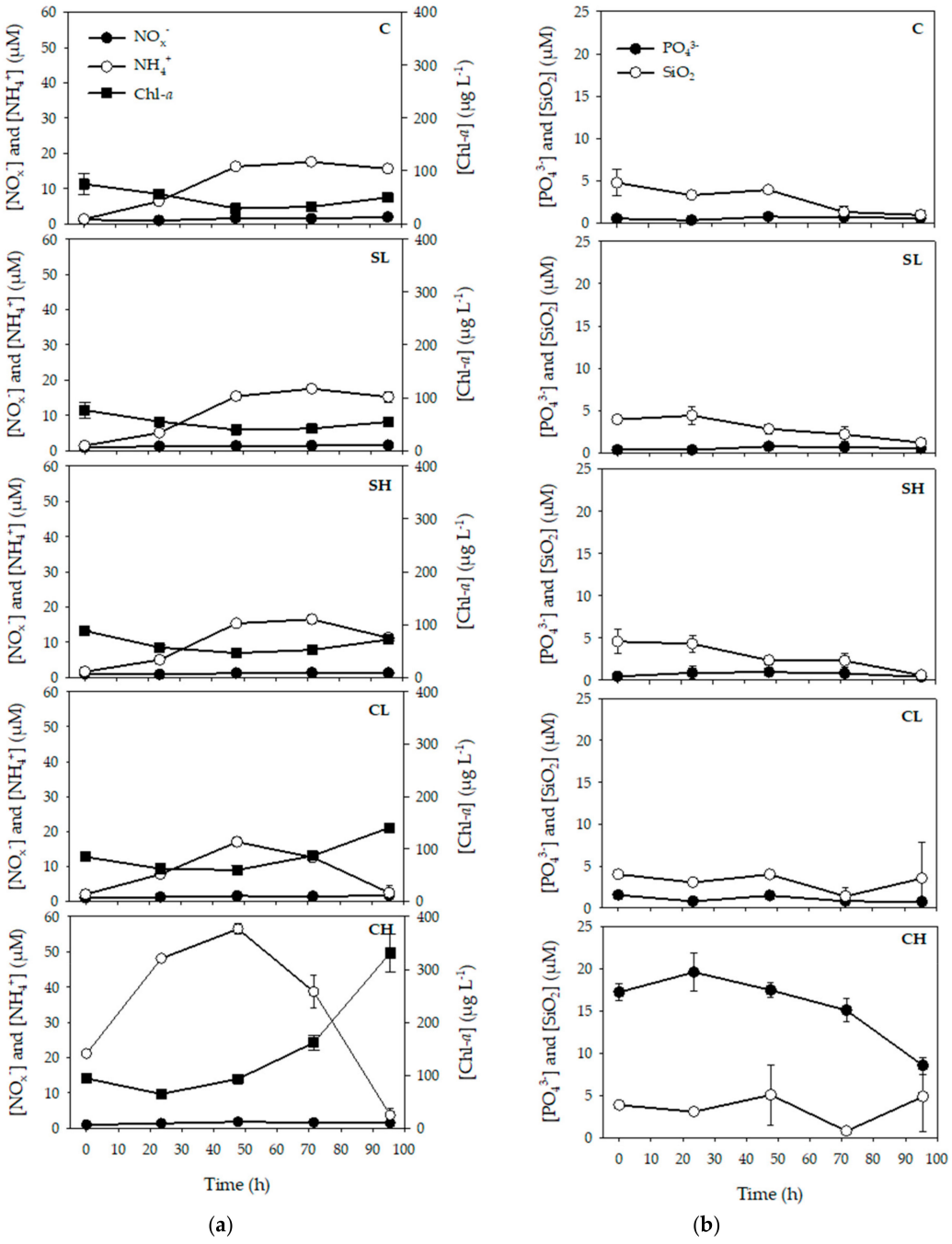


Figure 3. Dissolved inorganic N and Chl-*a* concentrations (**a**) and dissolved inorganic P and Si concentrations (**b**) measured in the 5 treatments every 24 h for 4 days (T_0 to T_4). Averages and standard deviations (n = 3) are reported.

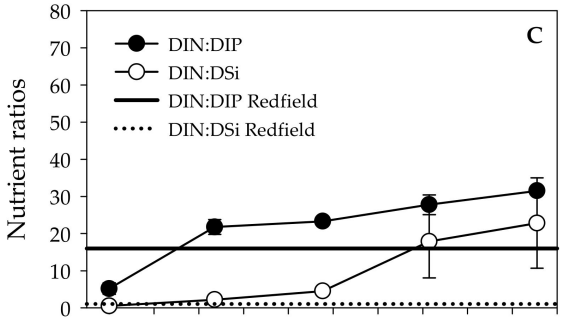
Added feces did not produce measurable effects on the oxidized forms of inorganic nitrogen NO_2^- and NO_3^-, which were pooled together as NO_x^- (Figure 3a). They always displayed low concentrations (<2 μM) with no significant differences among treatments and along the course of the experiment (ANOVA on repeated measures, F = 1.3, p >0.05).

The addition of feces produced significantly different effects on the concentrations of Chl-*a* in the various treatments and on their temporal trends (ANOVA on repeated measures, F = 171.9, $p < 0.05$ and F = 132.9, $p < 0.05$, respectively) (Figure 3a). During C, SL and SH treatments, initial Chl-*a* concentrations (75.2 ± 19.9 μg L^{-1}) displayed a decreasing temporal trend and was nearly halved at T_2. During CL and CH treatments, Chl-*a* concentrations underwent a slight initial decrease but thereafter increased exponentially, up to 330.9 ± 36.5 μg L^{-1} measured in CH at T_4. Only at CL and CH the concentrations of Chl-*a* at the end of the experiment were significantly higher than those measured at T_0.

The concentrations of PO_4^{3-} varied among treatments and along the course of the experiment. Regarding C, SL and SH, PO_4^{3-}, concentrations varied between 0.5 and 1.1 μM, without significant temporal trends and significant differences among treatments. The low and high addition of cormorant feces resulted in an instantaneous solubilization of mineral P. Occurring at time zero, these two treatments exhibited an increase of PO_4^{3-} concentrations, which were 3 and 32 times higher than those measured in the control treatment, respectively. ANOVA on repeated measurement suggested that differences among treatments were significant (F = 745.4, $p < 0.05$), with much higher PO_4^{3-} concentrations (15< x <20 μM) measured in CH at T_0 and T_1, thereafter halving at T_4 (Figure 3b).

Dissolved silica concentrations underwent significant temporal variations, but they were similar among treatments (ANOVA on repeated measures, F = 8.5, $p < 0.05$ and F = 0.4, p >0.05, respectively). Taking place at C, SL, and SH, SiO_2 concentrations displayed a decreasing temporal trend, from ~ 4 to <1 μM. Occurring at CL and CH, SiO_2 concentration temporal trends were more erratic, with a marked decrease measured at T_3 followed by an increase to final concentrations similar to those measured at T_0.

The DIN:DIP and DIN:DSi ratios displayed similar increasing trends along the course of the experiment in C, SL, and SH treatments (Figure 4). Particularly, DIN:DIP averaged ~ 5 and suggested N limitations at T_0 and thereafter it increased to ~ 30 suggesting P limitation at T_4. The DIN to DSi ratios at T_0 were slightly above one and increased to final values between 16 and 20, suggesting an increasing Si limitation. The addition of cormorant feces produced a strong effect on nutrient ratios, which differed significantly from the other treatments and underwent different temporal trends (F = 115.4, $p < 0.05$; F = 51.7, $p < 0.05$, respectively) (Figure 4). Concerning CL, the DIN:DIP ratio increased slightly over the 16 threshold value (T_3) but thereafter it decreased. Regarding CH, the DIN:DIP ratio was constantly <4, suggesting an invariable and strong inorganic N limitation. Reactive silica was limiting algal growth as DIN:DSi ratios in both CL and CH were generally above the 1.07 threshold for Si limitation with a peak in T_3 (~ 18 and ~ 50, respectively) coinciding with a transient Si depletion.



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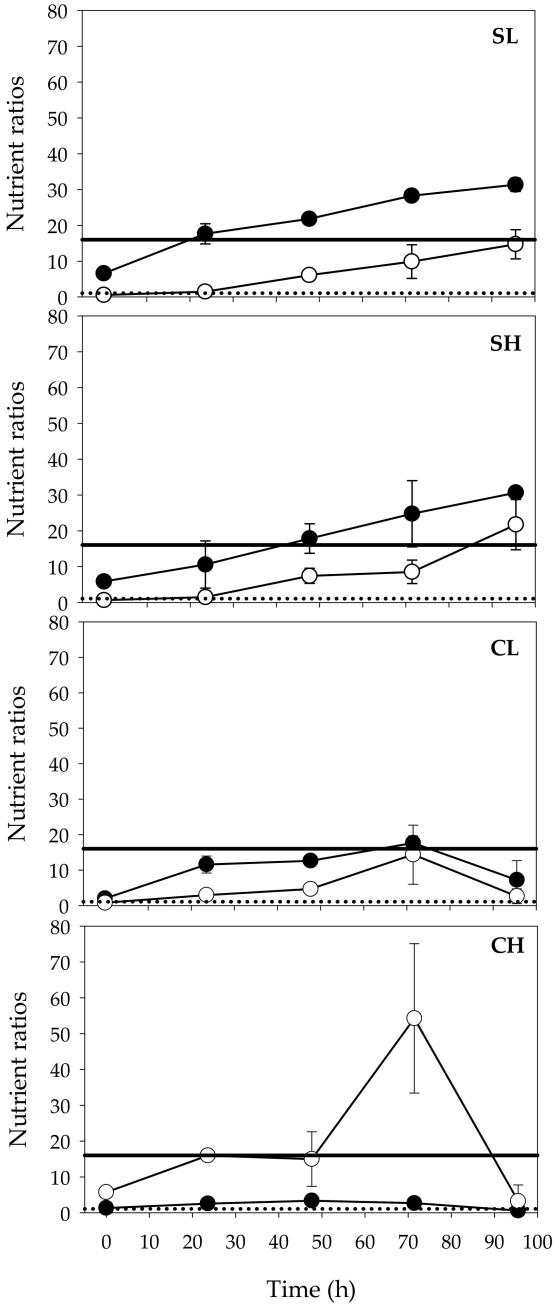


Figure 4. Temporal trend of nutrient stoichiometry (DIN:DIP and DIN:DSi ratios) calculated for the 5 treatments every 24 h for 4 days (T_0 to T_4). Continuous and dotted reference lines indicate the theoretical Redfield ratios (16 for DIN:DIP and 1.07 for DIN:DSi). Averages ± standard deviations (n = 3) are reported.

3.2. Phytoplankton Community Changes

Calculated phytoplankton growth rates were negative in all treatments between T_0 and T_1 and between T_1 and T_2, with CH as the exception (Figure 5). Thereafter, growth rates turned all positive, with an increasing trend between T_3 and T_4 and significant differences among treatments. These results suggest that phytoplankton growth was suppressed at the beginning of the experiment (T_1, T_2) resulting in a decrease of algal biomass. They also suggest that algal growth recovered after 48 h in C, SL, SH and CL treatments. High cormorant feces addition (CH) stimulated phytoplankton growth after 24 h, with the instantaneous growth rate peaking at 0.72 day^{-1} between T_3 and T_4 and doubling rates calculated for the other treatments.

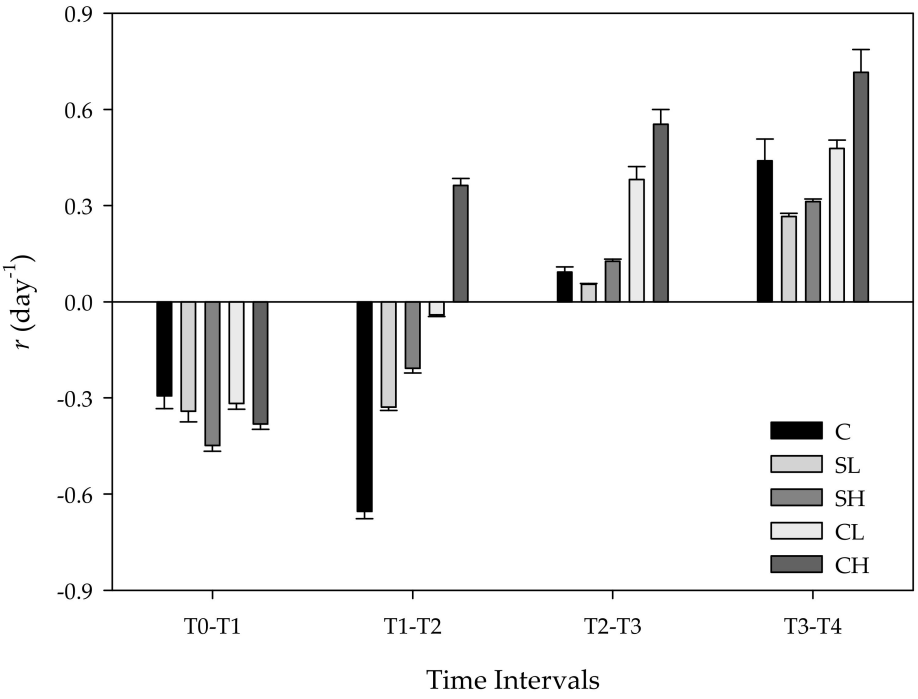
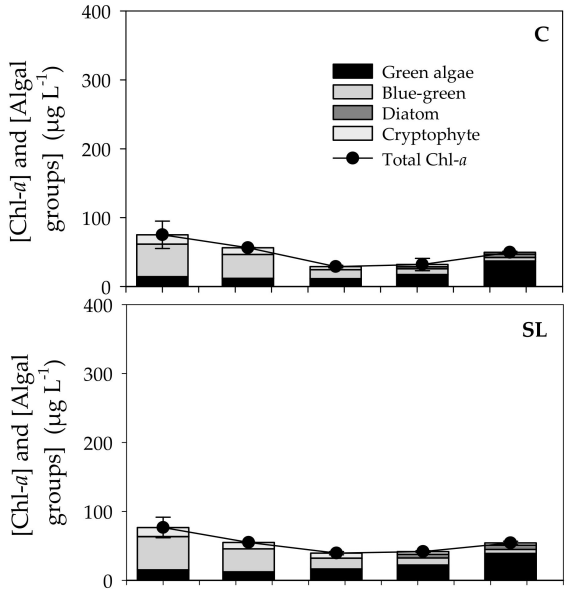


Figure 5. Phytoplankton growth rates measured in the 5 treatments and in 4 time intervals along the course of the experiment. Averages ± standard deviations (n = 3) are reported.

Results from the fluoroprobe allowed for analyzing of the share of the total amount of Chl-*a* in the 4 main algal groups (Figure 6). The relative dominance of these phytoplankton groups within the algal community changed along the course of the experiment in all treatments. Occurring at the beginning of the experiment, blue-green algae dominated the phytoplankton community of all treatments. However, along the incubation period, the relative abundance of blue-green algae decreased by 3–10 folds. Concurrently, the share of green algae within the algal community increased, accounting for up to 71–91% of the total at T_4.



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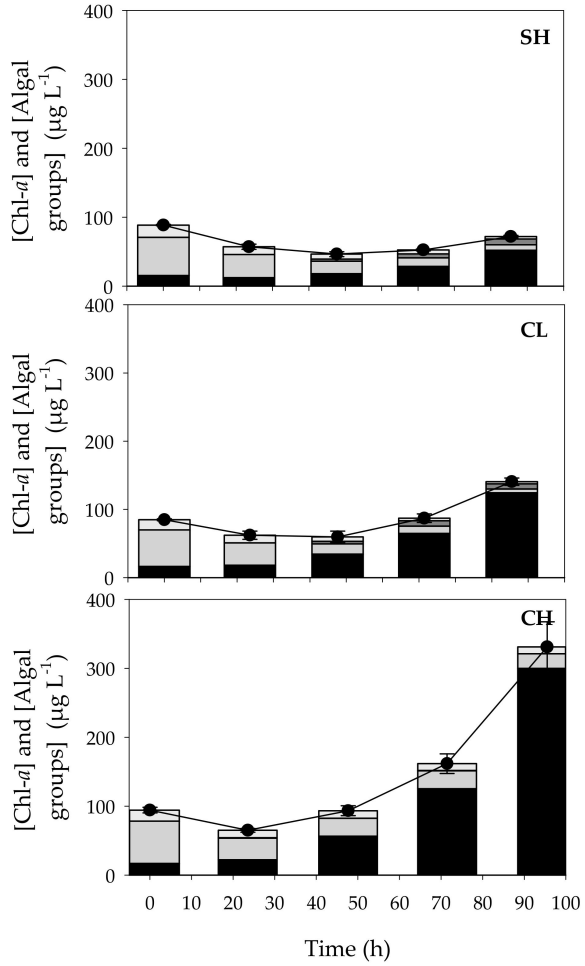

Figure 6. The composition of the phytoplankton community in the 5 treatments along the course of the experiment is reported, together with the Chl-*a* concentrations. Average values of Chl-*a* ± standard deviations (n = 3) are reported.

3.3. Heterotrophic Bacteria Abundance

Heterotrophic bacteria abundance displayed a transient, exponential increase between T_0 and T_1 and, thereafter, decreased steeply without significant differences among treatments (Figure 7). Happening at T_1, the highest heterotroph concentration (3912×10^6 CFU L^{-1}) was measured in the treatment with a high addition of swan feces, and the lowest (2280×10^6 CFU L^{-1}) in the control treatment.

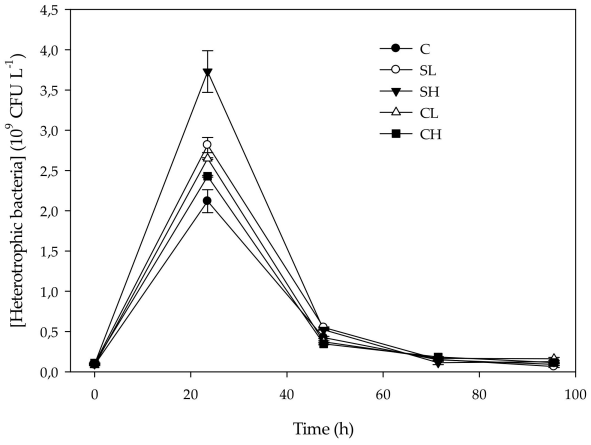

Figure 7. Concentrations of heterotrophic bacteria measured in the 5 treatments along the course of the experiment. Averages ± standard deviations (n = 3) are reported.

The analyses of the cultivated bacteria based on 16S showed that, during T_3, heterotrophic bacteria were dominated by *Flavobacteria*, *Cytophagia*, and *Betaproteobacteria* in all treatments.

4. Discussion

Large colonies of aquatic birds have the potential to affect, via droppings, the water quality of aquatic ecosystems [27–30]. They may affect microbial communities [29,31–34], increase nutrient availability [15,35–38] and stimulate phytoplankton or macrophyte growth [39,40]. Results from our experiment suggest that feces from herbivorous and piscivorous aquatic birds may produce different effects on dissolved inorganic nutrient concentrations, their ecological stoichiometry, and phytoplankton growth rates, but not on algal community composition and bacterial enrichment. These effects may change depending on the bird food sources, seasonality and bird residing period in the water or in its proximity [18]. Herbivorous bird species generally produce N-rich feces, with N:P ratios varying from 6 to 58 [41], whereas feces from piscivorous birds are rich in P [42,43]. These differences have implications for nutrient stoichiometry. During our experiment, low and high addition of swan feces produced little effect on nutrient concentrations, on their relative availability and on algal growth, which were similar to those measured in the control treatment. The addition of cormorant feces, on the contrary, and in particular the high addition of it, resulted in much higher concentrations of ammonium and orthophosphate in the water column and produced a significant stimulation of phytoplankton growth.

Waterbirds are demonstrated to contribute substantially to nutrient inputs to lakes. Seasonally, their inputs may represent 50–69% of C, 27–40% of N and 70–75% of P external loads [37,38,42]. During nesting, breeding and roosting periods, waterbirds are delivering guano directly to the water or depositing it on the soil/trees. Later on, these deposits reach the water with run-off or via groundwater [7]. After microbial degradation residuals from feces are slowly broken down, associated nutrients can be released from the coagulates for periods of 14–21 days [14,44]. Additionally, mineralization processes on settled feces may alter the redox conditions of soils and sediments and favour the chemical release of bound P. All these aspects are important for aquatic ecosystems like the Curonian Lagoon, where large colonies of waterbirds are located along the perimeter of the lagoon and where summer blooms of N-fixing cyanobacteria suggest P excess [19,45]. Long-term monitoring of the Curonian Lagoon water demonstrates strong summer N and Si limitation for algal growth due to minimum nutrient inputs from the watershed of the Nemunas River [2]. During summer, most nutrients are present in the water column as particulate forms, stocked in phytoplankton biomass [2,20]. Under specific circumstances, with limited inputs from the watershed, algal growth and algal community composition may depend on internal recycling and on the relative abundance of recycled nutrients [45,46]. Zilius et al., [47,48] and Petkuviene et al., [6] demonstrated that sediments in the Curonian Lagoon are playing an important role in supplying nutrients, especially phosphorus, but not enough to satisfy requirements from growing algae. Bartoli et al., [19] suggested the idea of multiple drivers of cyanobacterial blooms in the Curonian Lagoon, enhancing P inputs or its mobility from different ecosystem compartments and further unbalancing the N:Si:P stoichiometry. Aquatic birds are hypothesized as one of the drivers of cyanobacteria blooms due to their large numbers and their demonstrated direct and indirect effects on nutrients [49]. Nutrients associated with aquatic bird feces may prime local blooms [40]. Such blooms may trigger a cascade series of events including light limitation in the water column, high pelagic respiration, water stratification, and sediment anoxia, resulting in a large bottom release of P bound to Fe, increasing the extent and duration of blooms. Such a sequence of events was demonstrated to occur in the Curonian Lagoon under calm weather periods [6,50]. Monthly observation of waterbirds in the Curonian Lagoon demonstrated that piscivorous birds are the dominant population during the spring–summer period, leading to relevant input of phosphorus to water as compared with other birds (Morkune, personal communication). Alternative approaches, like the ecological network analysis applied to phosphorus at the whole lagoon level, may allow calculating which fraction of algal bloom is supported by water birds.

Results from the present experiment demonstrate that swan or cormorant feces addition did not produce direct or indirect effects on reactive silica concentration and suggest slow release of Si from the feces. Swan or cormorant feces addition also did not affect the oxidized forms of N, likely due to the absence of nitrites or nitrates in the added feces or significant nitrification in the water column during the four-day incubation. Water analyses revealed in T_1 some ammonium availability in all treatments, but such ammonium was quantitatively assimilated by phytoplankton rather than nitrified. Under conditions of nutrient limitation, phytoplankton may inhibit the activity of N-bacteria via the production of specific chemicals; something similar is reported for illuminated sediments where microphytobenthos inhibit processes like denitrification [51]. The low and high addition of swan feces also produced limited effects on ammonium and reactive phosphorus, as concentrations at T_1 were similar to those of the control treatment. Waterbird feces generally contain elevated amounts of total N and P [17,27], but our results suggest that the contribution of reactive, inorganic forms to these total pools may largely vary among birds. Most of N and P in added swan feces were likely organic and poorly reactive. However, as demonstrated for grazing waterfowls, swans may control the biomass of aquatic vegetation and indirectly act upon phytoplankton growth. Macrophyte removal, in fact, results in minor direct control of nutrients via uptake and higher nutrient availability to phytoplankton. Moreover, rooted macrophytes may promote via radial oxygen loss oxidized chemical conditions in the rhizosphere and, therefore, promote N loss via coupled nitrification and denitrification and P retention within sediments, by favoring its co-precipitation with iron oxides [52,53].

Cormorant feces resulted in a large increase of ammonium and reactive phosphorus in the water, the latter in excess to the former. We calculated from the instantaneous increase of the 2 nutrients in the water that nearly 0.8% and 0.6% of cormorant feces in dry weight were in the form of NH_4^+ and PO_4^{3-}, respectively. Previous studies [15] have demonstrated that aquatic birds may represent a major N and P source for aquatic environments and may alter the cycle of these elements by largely enhancing their internal recycling. Cormorants satisfy nearly 90% of their food requirements with fish predated from the Curonian Lagoon [54,55] and may, therefore, recycle large inorganic N and P amounts associated with their preys. During our experiment, at T_4, the ammonium released from cormorant feces was quantitatively taken up by phytoplankton, whereas PO_4^{3-} concentrations halved as compared to initial values but remained elevated (nearly 10 μM). These results might be important in the Curonian Lagoon as PO_4^{3-}-rich cormorant droppings may favor N-fixing cyanobacteria and because these piscivorous birds exceed swans in number by a factor of 12.

Results from this study do not support the hypothesis that bird feces determine significant effects on algal communities since, in all conditions during the four days and without significant differences among treatments, green algae became dominant over the other groups. Such an outcome may be related to the simplified experimental conditions as compared to the natural environment and to the short incubation time. Water temperature is an important factor that may affect the growth rates of algal groups. Cyanobacterial growth, for example, peaks at around 30 °C, while green algae growth peaks at 23–25 °C [56]. High temperatures measured at T_1 and T_2 in the incubation tank decreased at T3 and T4 due to cloudy weather, thus such a temperature drop may have favored the growth of green algae at the expense of cyanobacteria. Light is another important factor in shaping the composition of the phytoplankton community. Low irradiance can favor cyanobacteria growth [57–60], and this is the summer condition of the Curonian Lagoon, with high water turbidity and low light penetration. Under these circumstances, the presence of different accessory pigments and the structural organization of their light-harvesting antenna allow cyanobacteria to absorb green light, normally remaining as an unabsorbed portion of photosynthetically-active radiation in the dense community [61], whereas during high irradiance, most of the cyanobacteria are more sensitive to photoinhibition than green algae, which can limit their growth favoring *Chlorophyta* dominance [62]. Since the incubation tank we used was transparent, large light availability may have favored the growth of green algae at the expense of cyanobacteria.

Occurring at the beginning of the experiment, temporary stress was produced in the algal community, resulting in heterotrophic bacteria growth in all treatments, including the control.

Such a bacterial peak was limited in time and likely due to dissolved organic carbon release by phytoplankton [63]. Coinciding with such an initial decline of phytoplankton biomass and growth of heterotrophs, we measured the accumulation of ammonium in the water of all treatments. After heterotrophic bacteria decrease, the phytoplankton community recovered. Some hypotheses are that heterotrophic bacteria and smaller phototrophs out-compete the filamentous cyanobacteria in phosphorus uptake when nitrogen and carbon are available [64]. The highest abundance of bacteria was observed in all treatments after 24 h, and the highest increase was observed in the SH treatment, where the highest amount of organic matter in the feces was expected. The growth dynamics of bacteria in our treatments were related to the amount of yellow substances, a proxy of dissolved organic matter (DOM), but not to the nutrient concentration. It is known that heterotrophic bacteria are the dominant organisms in aquatic habitats metabolizing DOM. Uptake of DOM is the first step in the microbial loop that ultimately mineralizes about 50% of primary production [65,66].

Different studies demonstrated that the presence of birds was associated with a significant increase in the number of coliform bacteria in littoral areas [67–70]. A recent study stresses the important role of cormorants for fecal pollution in the Curonian Lagoon [34]. Besides affecting water quality, microbes may increase organic matter biodegradation, assimilate nutrients and compete with phytoplankton [71,72]. During our experiment, the bacteria diversity assessed after 70 h, showed that microbial communities were dominated by *Flavobacterium*, *Flectobacillus* (*Cytophaga–Flavobacteria*) and *Commamonas* (*β-proteobacteria*). *Cytophaga–Flavobacteria* are particularly common in many oceanic habitats and are among the most abundant bacterial groups. Generally, *β-proteobacteria* are the most abundant group in freshwater systems, although *Cytophaga–Flavobacteria* can dominate some freshwater environments or can be abundant in sediments. These bacteria may have a specialized role in DOM uptake and degradation. Cultured isolates of *Cytophaga–Flavobacteria* are well known to be proficient in degrading biopolymers such as cellulose and chitin, which represent part of the high molecular mass (HMW) fraction of DOM [65,66,73]. Regarding P-enriched environments, *β-proteobacteria* can become dominant and appear to act as successful opportunistic competitors for nutrients [74].

Grazing pressure is another important factor in promoting cyanobacteria dominance rather than other algae species. It has been observed that zooplankton such as *Daphnia* prefers to eat other species of algae rather than cyanobacteria [75], resulting in a low top-down control. This competitive advantage was controlled and set to zero in our experiment, as the water was filtered to remove the largest zooplankton. As such, we might have favored the growth of green algae and diatoms.

An important outcome of the experiment is that unbalanced nutrient stoichiometry (DIN:DIP) alone is not, even in the short-term, the only condition leading to the dominance of N-fixing cyanobacteria over other phytoplankton groups. Other physical, chemical and biological conditions co-regulate algal community dynamics. Vybernaite–Lubiene et al., [2] have demonstrated in the Curonian Lagoon regular N and Si limitation during summer months, but such limitation is not always coupled to summer cyanobacterial blooms. During our experiment, a longer incubation period would have allowed for testing of the effects of heavily unbalanced stoichiometry (strong N and Si limitation and DIP abundance at T_4 in the CH treatment, the more interesting for our purposes).

5. Conclusions

Different swan and cormorant diets produce feces that release different amounts of inorganic nutrients to the water. Piscivorous cormorant feces increased the concentrations of dissolved reactive P and affected the DIN:DIP stoichiometry; they also stimulated the growth of phytoplankton. Previous studies suggest that summer nutrient stoichiometry and algal concentrations, in the Curonian Lagoon, overlap those of the present experiment. Feces additions were also realistic for different lagoon areas where dense bird colonies rest, feed or hunt. This study does not directly link bird droppings to the Curonian Lagoon hyper-blooms but provides evidence that birds, and piscivorous cormorants in particular, may support P demand by blooming phytoplankton. Individual P production, multiplied by the estimated consistency of the bird population, represent, in fact, non-negligible fractions of

the main external input to the lagoon. Moreover, feces are mostly dropped on the surface, photic water layer where released inorganic nutrients are immediately bioavailable to phytoplankton. Future experimental efforts in this direction should be done in situ, for example using phytoplankton bioassays and along transects from bird colonies/resting places to control areas and should be maintained for longer periods.

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