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Do phytoplankton nutrient ratios reflect patterns of water column nutrient ratios?

A numerical stoichiometric analysis of Lake Kinneret

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Abstract

The N:P stoichiometry of a water body is one of the most commonly used indicators of its nutrient status. However, in a dynamic aquatic ecosystem the N:P stoichiometry of phytoplankton is highly variable depending on a range of factors that influence their growth. In this study, a 1D hydrodynamic-ecological model was used to examine how the internal nutrient ratios of phytoplankton relate to nutrient ratios within the water column in Lake Kinneret, Israel. We identified that seasonal patterns of the simulated dissolved inorganic N to total P (DIN:TP) ratios in the water column were a useful indicator of the N:P stoichiometry of the combined phytoplankton community. However, the internal N:P patterns of individual phytoplankton groups did not necessarily relate to DIN:TP patterns.

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Keywords: N:P stoichiometry; phytoplankton ; patterns; freshwater ecosystem; water column

1. Introduction

It is well documented that eutrophication is common in freshwater and coastal ecosystems around the world with excess nitrogen (N) and phosphorus (P) being primarily responsible for fueling primary production and excessive organic matter accumulation. Nuisance algal blooms are an increasing issue of concern and most nuisance species are adapted to high growth rates, when nutrients are in excess [1]. In

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conjunction with nutrient and chlorophyll-a concentrations, the N:P ratio of a water body is one of the most commonly used indicators of nutrient limitation and ecosystem status, and is often used as a basis to support management actions. For example, the N:P ratio of 16:1 is usually used as an indicator for studying the nutrient limitation of phytoplankton and the potential for N₂ fixation from the atmosphere [2]. While nutrients are a key driver, algal blooms are also known to be mediated by microbial interactions, however, very little is known about how the microbial interactions between zooplankton, phytoplankton and bacteria influence the overall patterns of stoichiometry within different species and trophic levels. As a result, in a dynamic ecosystem the N:P stoichiometry of organisms is highly variable [3], and are influenced by a range of factors that influence their growth. Therefore, the assumption that their internal N:P stoichiometry matches the bulk properties of the water may not be always true.

Ecological stoichiometry has emerged as a useful tool to study aquatic ecosystem interactions including algal blooms, and provides the key for interpreting trophic interactions in biogeochemical cycles [3]. Redfield's work in the world's oceans during the mid 1900's, pointed towards an almost 'universal' C:N:P ratio of marine seston [4]. This led to the assumption that the marine biota had evolved to have a similar elemental composition as their aquatic media. However, it is now well known that the C:N:P ratio of different heterotrophic and autotrophic aquatic organisms need not conform to Redfield's universal ratio. Trophic interactions and physiological controls lead to organism-specific patterns of N:P stoichiometry that may be decoupled from the water column values. Nonetheless, the idea of relative stoichiometric constancy is still widely used in limnology, and often continues to form the basis of nutrient management of freshwater systems. It is the aim of this study to explore patterns of algal internal nutrient stoichiometry compared with water column properties in a dynamic lake ecosystem.

Different organism groups vary considerably in their internal nutrient ratios in relation to the nutrients available in the environment. The degree to which organisms are stoichiometrically homeostatic is largely dependent on whether they are heterotrophs or autotrophs [3]. Heterotrophs gain the majority of their supply of C, N, and P from the same source of organic material. As a result, bacteria and zooplankton have a fairly constant N:P ratio [5]. Autotrophs support a different mechanism for their source of C compared to their source of N and P, and phytoplankton stoichiometry therefore varies considerably in response to environmental conditions, community composition, as well as species-specific intrinsic physiological processes [6]. For example, if insufficient inorganic N is available to satisfy their N:P ratios, some species will supplement N through N₂ fixation [7]. Although the optimal N:P ratio of phytoplankton ranges from 8:1 to 45:1 depending on the environmental conditions [8], it is difficult to accurately determine the uptake of different forms of N and P from the water column into phytoplankton [9].

Considering these differences from the broader view of nutrient cycling within an aquatic ecosystem, it becomes clear that a nutrient deficiency in one group (or trophic level) will not only control the growth or decay of its own population, but also influence the composition of the entire ecosystem, and this may be independent of the stoichiometry of the available nutrients. The influence of nutrient uptake by phytoplankton on the inorganic N:P ratio of the water column is also not clear [10].

Several different types of N:P ratios have been used to understand nutrient limitation of phytoplankton, such as inorganic N:P ratios [3,10], or total N:P ratios [9,11]. Morris et al. [12] proposed that the dissolved inorganic N: total P (DIN:TP) ratio as the best index for discriminating nutrient limitation of phytoplankton. Ptacnik et al. [13] further compared a large range of different nutrient limitation indicators and confirmed that the DIN:TP ratio was the best indicator for reflecting nutrient limitation of phytoplankton in a coastal ecosystem based on its highest correlation with Chl-a. However, the abundance of phytoplankton are usually only represented by C biomass or Chl-a, and therefore the internal N (IN) and internal P (IP) content of phytoplankton are seldom measured at a high enough frequency to assess how the changes of IN:IP ratios relate to water column dynamics, preventing us from further exploring the dynamics outlined above. Aquatic ecological modelling helps us fill this gap, and in this study we used a

quantitative mechanistic model applied to Lake Kinneret (Israel), to further explore the usefulness of the DIN:TP indicator, and to determine the relationship between internal N:P ratios (IN:IP) of phytoplankton and water column N:P ratios in a dynamic aquatic environment. For this purpose we adopted the one-dimensional coupled hydrodynamic-ecological model (DYRESM-CAEDYM) that has been previously configured for Lake Kinneret and validated over a five year period (1997-2001) [14].

2. Method

2.1. Study Site and Model Overview

Lake Kinneret (Sea of Galilee) is a large monomictic lake located in the Syrian-African Rift Valley in north-eastern Israel. It covers an area of 170 km², is 21 km long and 16 km wide and has a maximum depth of 43m. The lake is of critical importance to Israel since it supplies a significant portion of the country's drinking water. A substantial body of limnological work has been published on the lake ecosystem, including application of the Dynamic Reservoir Simulation Model (DYRESM) alone, and in combination with the Computational Aquatic Ecosystem Dynamics Model (CAEDYM) [14, 15].

In this study, we applied the coupled model DYRESM-CAEDYM to Lake Kinneret, which simulates the C, N and P content of three functional groups of zooplankton, five groups of phytoplankton, and bacteria, in addition to organic and inorganic nutrient pools within the water column (Figure 1). In particular, the model simulates the stoichiometry of the following phytoplankton taxa (A1: *Peridinium*; A2: *Microcystis*; A3: *Aphanizomenon*; A4: nano-phytoplankton; A5: *Aulacoseira*), adopting a modified Droop kinetic N and P uptake model that sets the lower and upper limits on C:N and C:P ratios for each species defined by the user based on available empirical data [14]. The model captures the dynamic response of phytoplankton stoichiometry to environmental conditions and food web structure, thereby allowing us to evaluate the relationship between the IN:IP ratios of phytoplankton and the N:P ratios of the water column in the lake.

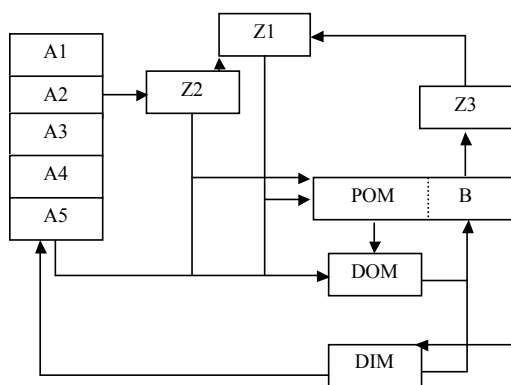


Fig. 1. Conceptual diagram highlighting the configured microbial groups and interactions in the Lake Kinneret DYRESM-CAEDYM model (A1-5: five species of phytoplankton; B: bacteria; DOM: dissolved organic matter; DIM: dissolved inorganic matter; POM: particulate organic matter; Z1: predatory zooplankton; Z2: herbivorous zooplankton; Z3: microzooplankton).

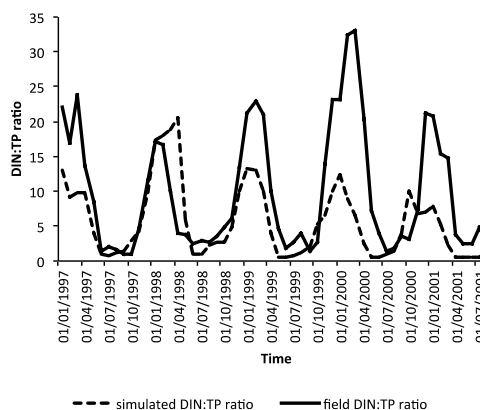


Fig. 2. Simulated water column DIN:TP ratios vs. observed DIN:TP ratios in the water column.

2.2. Calculation of Stoichiometric Ratios

Simulated water column nutrient concentrations were vertically integrated and averaged over a monthly time-step for the simulation period (1997-2001), and the mass of DIN (NH_4+NO_3) and TP variables were converted into molar DIN:TP ratios. The nutrient biomass of phytoplankton was also monthly averaged and vertically integrated. The biomass was then converted into the average IN:IP ratios for each individual phytoplankton species and the combined phytoplankton community.

To determine the relationship between the simulated IN:IP ratio patterns of phytoplankton and the DIN:TP ratio patterns of the water column in Lake Kinneret, we conducted a simple linear correlation analysis between them with different monthly time lag values, and this was done for (a) the combined phytoplankton community, and (b) each specific phytoplankton groups. To assess any seasonal differences in these patterns, the above ratios were also grouped in two classes: winter–spring (January–June) and summer–autumn (July–December).

To further explore the variability of the phytoplankton stoichiometry, a frequency analysis of the combined and individual phytoplankton IN:IP values was conducted. Due to the boom-bust nature of many species, the analysis was limited to the periods when phytoplankton biomass was considered to be significantly above the numerical lower biomass limit of the model. Therefore, the data were filtered above the threshold of 0.05mgC/L for *Aulacoseira*, or the threshold of 0.01mgC/L for *Peridinium*, *Microcystis*, *Aphanizomenon*, and nano-phytoplankton.

3. Results

3.1. Model Performance

Simulations of the physical, chemical and biological properties of Lake Kinneret with DYRESM-CAEDYM have been previously validated [14, 16]. Overall, the simulated results of the key chemical state variables (NO_3 , NH_4 , PO_4 , TN and TP) matched the seasonal trends observed in the lake. The simulated PO_4 results were lower than the field observations because field values were at, or only marginally above, the PO_4 detection level. However, the TP trend was successfully simulated [14, 16]. The main seasonal patterns of the simulated DIN:TP ratios in water column matched the observed seasonal patterns of the field DIN:TP ratios, although some discrepancies in the peak values existed (Figure 2).

3.2. Temporal Trends in N:P Stoichiometry

The simulated IN:IP ratio patterns of the combined phytoplankton community followed the DIN:TP ratio patterns of the water column (Figure 3a), with a variable time lag between these two ratio variations in different years. The time lag in 1998 was smallest, and largest in 2001. Overall, the time lag that gave the highest correlation between the DIN:TP ratios of the water column and the IN:IP ratios of the phytoplankton community was two months (Table 1). Furthermore, the magnitude of the IN:IP ratio peaks of the combined phytoplankton community compared reasonably well with the changes in the DIN:TP ratio magnitude of the water column in the different years ($R^2 = 0.36$). For example, when the DIN:TP ratio of the water column in April 1998 was 20.59 (the maximum DIN:TP ratio), the IN:IP ratio of the phytoplankton community was 57.78 in May 1998, which was also the maximum IN:IP ratio of the combined phytoplankton community. Considering the seasonality, we identified that the correlation between DIN: TP ratios and IN:IP ratios in summer-autumn for the combined phytoplankton community ($R^2=0.45$) was higher than in winter-spring ($R^2=0.34$).

Table 1. Summary table of IN:IP ratios of phytoplankton

	Combined	<i>Aphanizomenon</i>	<i>Aulacoseira</i>	<i>Microcystis</i>	<i>Peridinium</i>	nano-phytoplankton
Max IN:IP ratio	57.78	7.18	18.74	12.38	196.95	87.48
Min IN:IP ratio	0.38	0.33	2.21	2.21	2.21	2.21
Time Lag (months)	2	1	0	2	2	0
R ² (total)	0.36	0.51	0.10	0.06	0.11	0.22
R ² (winter-spring)	0.34	0.46	0.18	0.25	0.26	0.34
R ² (summer-autumn)	0.45	0.47	0.25	0.38	0.27	0.03

Although the simulated IN:IP ratio patterns of the combined phytoplankton community followed the DIN:TP ratio patterns of the water column, this was not the case for individual phytoplankton species. The individual phytoplankton species had various seasonal IN:IP ratio patterns and different degrees of similarity with the DIN:TP ratio peaks (Figures 3b-f). The correlation between the simulated IN:IP ratio patterns of different phytoplankton species and the DIN:TP ratio patterns of the water column and the time lags that gave the highest correlation were summarised in Table 1. Although the time lags in different years varied, the most correlated time lags for the simulated phytoplankton species ranged from 0 - 2 months. The highest correlation was found for *Aphanizomenon* with a value of 0.51. While the IN:IP ratio patterns of *Aphanizomenon* were also similar to the combined phytoplankton community, the peaks slightly lagged behind the DIN:TP ratio peaks in the water column. In addition, the variation in their magnitude did not track the observed inter-annual variation in the water column. In contrast to the *Aphanizomenon*, there was no time lag between *Aulacoseira*'s IN:IP ratio peaks and the water column DIN:TP ratio peaks, and the correlation was weak ($R^2=0.10$). Considering the seasonality, the correlation for *Aulacoseira* in summer-autumn was higher than in winter-spring. As for *Microcystis*, *Peridinium*, and nano-phytoplankton, the IN:IP ratio patterns had double peaks within each year: a major peak and a minor peak. This feature of their patterns was in contrast to the combined phytoplankton community, *Aphanizomenon*, and *Aulacoseira*, which showed only a single peak each year. The major IN:IP ratio peaks of *Microcystis*, *Peridinium*, and nano-phytoplankton occurred after the DIN:TP ratios of water column peaked. Conversely, the minor peaks in IN:IP ratios of these species occurred when the DIN:TP ratios was at its lowest level. By season, the correlations between DIN:TP ratios of water column and the IN:IP ratios for *Microcystis* and *Peridinium* in summer-autumn were higher than in winter-spring. However, the correlation for nano-phytoplankton in summer-autumn ($R^2=0.03$) was much lower than in winter-spring ($R^2=0.34$).

3.3. Averaged N:P Stoichiometry

While the previous section highlighted the differences in the temporal trends of phytoplankton stoichiometry in relation to the DIN:TP ratio, here we examined the long-term stoichiometry of individual species and associated interactions with the water column (Figure 4). The average IN:IP ratios of the phytoplankton species were quite different from each other (*Peridinium*, 107:1; *Microcystis*, 8:1; *Aphanizomenon*, 4:1; nano-phytoplankton, 47:1; *Aulacoseira*, 16:1). Given the DIM, DOM and POM were free to change, the species internal stoichiometry was quite different from both the inorganic and detrital nutrient pools in the water column. The N:P ratio of the DOM pool was 3543:1, and the N:P ratio of the DIM pool was 67:1.

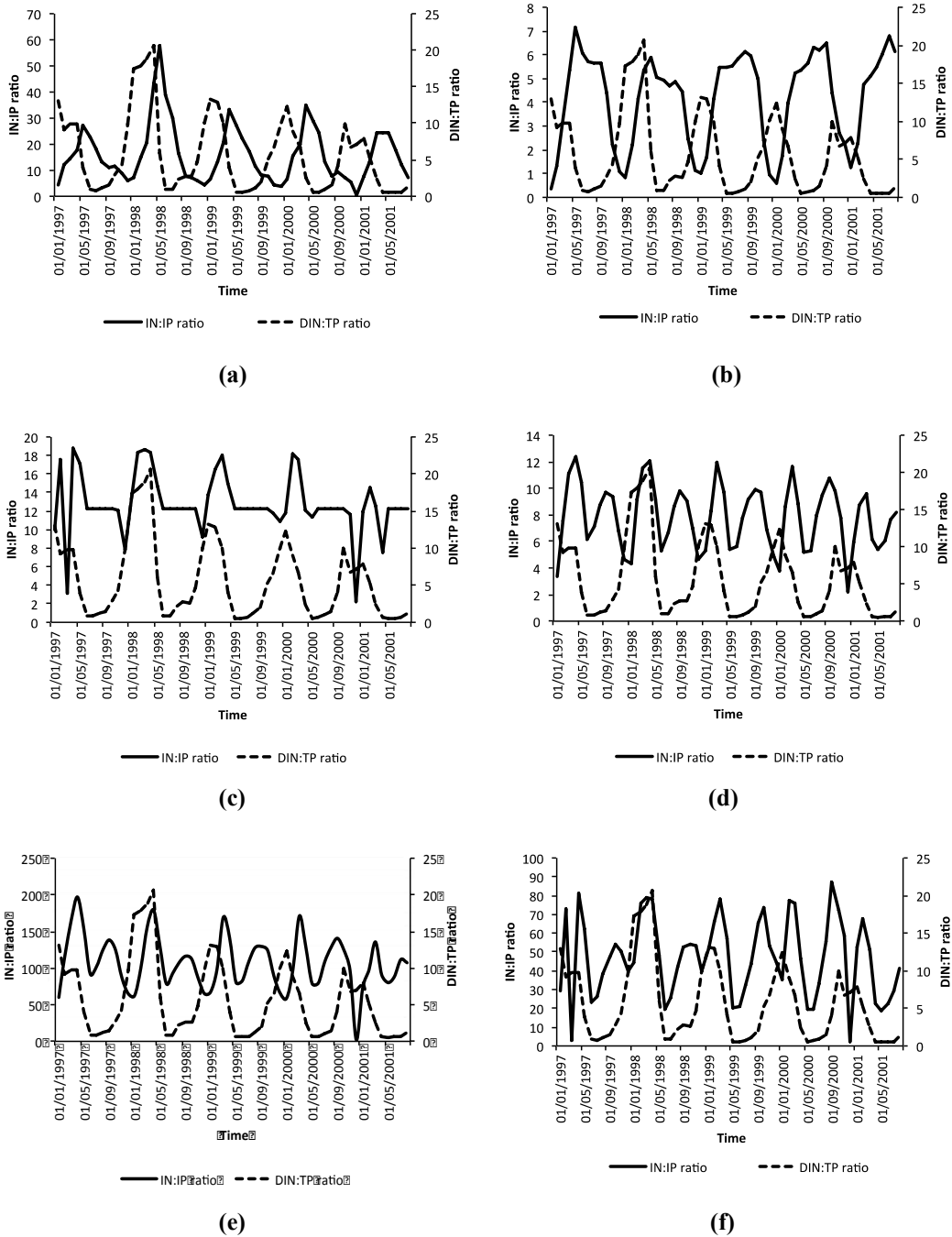


Fig. 3. Simulated IN:IP ratios of phytoplankton vs. DIN:TP ratios of water column (a) the combined phytoplankton community; (b) *Aphanizomenon*; (c) *Aulacoseira*; (d) *Microcystis*; (e) *Peridinium*; (f) nano-phytoplankton.

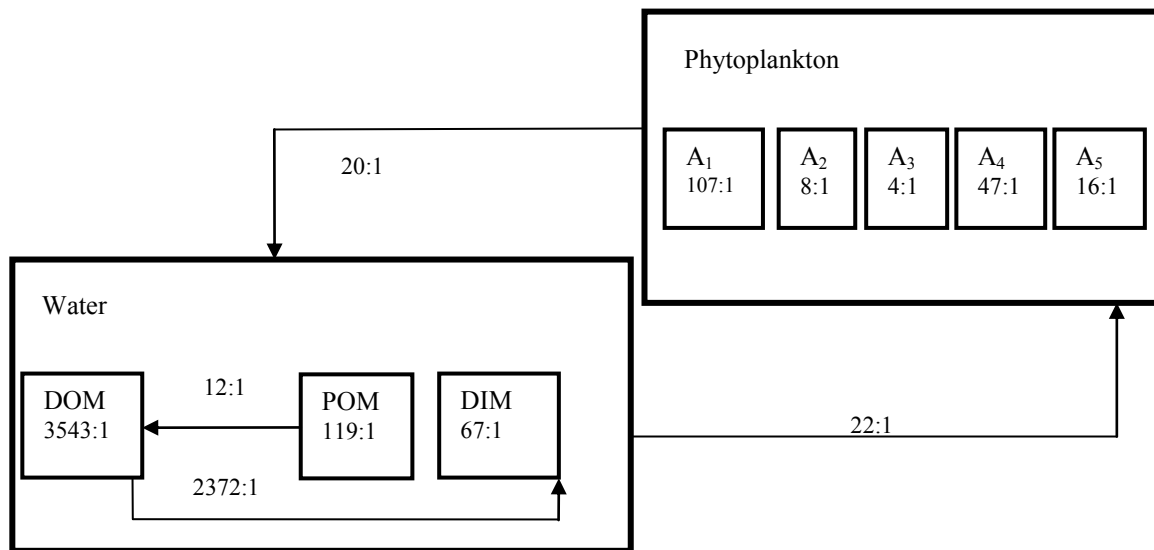
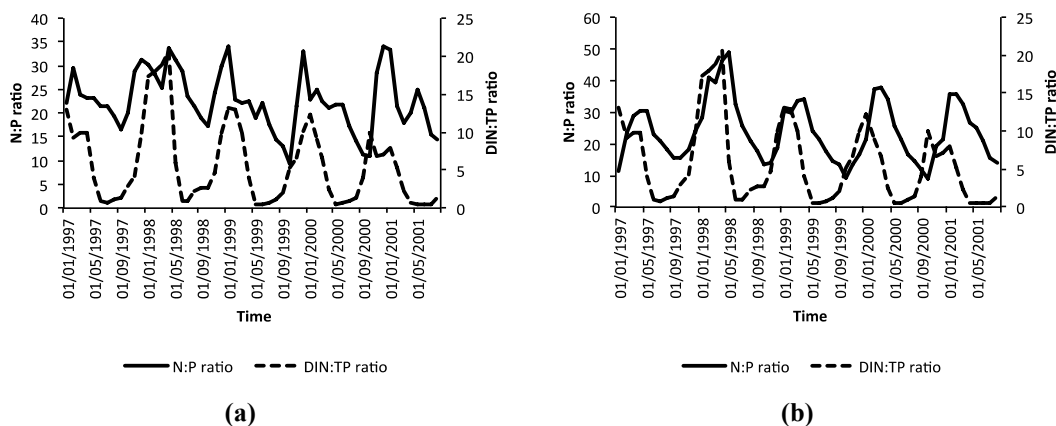


Fig. 4. Summary diagram of the average N:P stoichiometry for phytoplankton and nutrient pools within the water column.

The differences of N:P stoichiometry in the nutrient pools resulted in different N:P ratios for the nutrient flux pathways in the water column. For the internal nutrient cycling processes, the average nutrient uptake N:P ratio for the combined phytoplankton community was 22:1, and the average excretion N:P ratio of the combined phytoplankton community was 20:1. The phytoplankton uptake and excretion nutrient ratios linked the water column stoichiometry and the combined phytoplankton stoichiometry, and there was significant seasonal variation in the N:P ratio of these flux pathways (Figure 5). Both the uptake and excretion N:P ratio patterns of the combined phytoplankton community followed the DIN:TP ratio patterns of the water column. The difference was that the N:P ratio of the excretion from the combined phytoplankton community exhibited a minor time lag (1-2 months).



(a)

(b)

Fig. 5. N:P ratios of phytoplankton nutrient uptake (a) and excretion (b) versus water column DIN:TP ratio

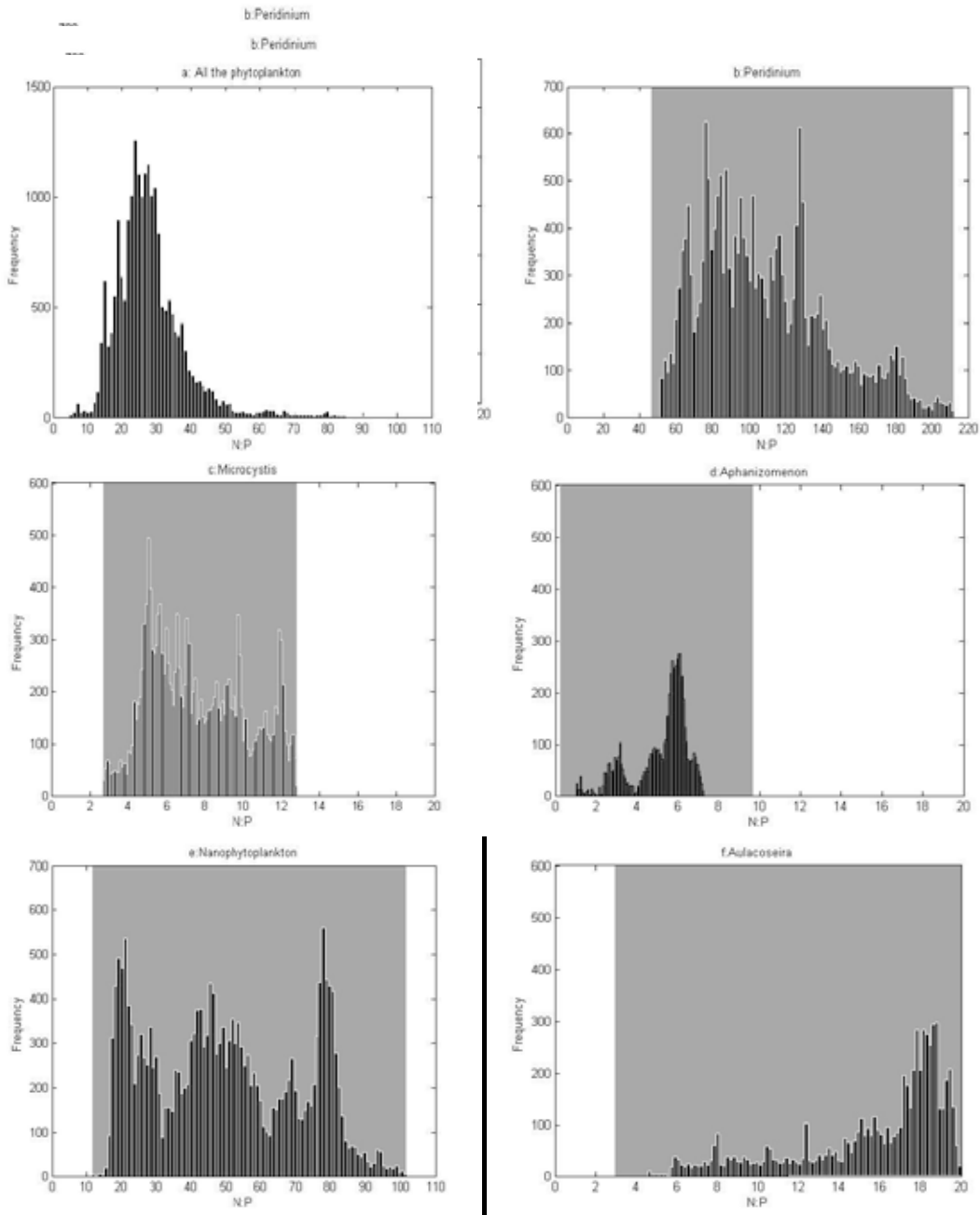


Fig. 6. Frequency histograms of IN:IP ratios (a) the combined phytoplankton community and (b-f) individual phytoplankton species. Note that the shaded box indicates the user defined IN:IP range configured for each species.

In order to understand the frequency distribution of the IN:IP ratios of the phytoplankton, frequency histograms for the IN:IP ratios were analyzed (Figure 6 a-f). The IN:IP ratio peaks of the combined phytoplankton community was slightly higher than Redfield ratio (16:1), suggesting Lake Kinneret is P-limited in general. The IN:IP ratios of *Peridinium* ranged widely from 50:1 to 210:1, and the five year average IN:IP ratio was 107:1. The IN:IP ratio distribution of *Microcystis*, nano-phytoplankton and *Aulacoseira* fell within a narrower range but the mean matched their five year averages well.

4. Discussion

4.1. Model Performance

Given the complexity of environmental factors affecting phytoplankton dynamics, the model successfully captured the seasonal variability in nutrient dynamics and phytoplankton biomass. The simulated biological variables were generally lower than the field data due to the limitation of patchy nature and complex biological processes [14]. Many factors may limit the accuracy of model predictions for the N:P ratios of phytoplankton blooms, including the inappropriate use of experimental data for comparisons, the complexity and scale of ecosystems, the level and type of the nutrient inputs and the spatial heterogeneity in environmental conditions [10].

4.2. N:P Stoichiometry of Phytoplankton Community

Our use of the coupled model to analyze the stoichiometric variations in the phytoplankton community in Lake Kinneret shows that the internal nutrient limitation patterns of the entire phytoplankton population reflects the water column nutrient ratios in the dynamic freshwater environment. This further supports the Sterner and Elser's hypothesis based on laboratory experimental results [3, 17], which suggests that the IN:IP ratios of phytoplankton should match the supply nutrient ratios of the ecosystem. Ptacnik et al. [13] has also suggested the DIN:TP ratio is the best nutrient limitation indicator for predicting the biomass of phytoplankton. Here we confirm that the DIN:TP ratio is closely correlated to the nutrient limitation of phytoplankton when a time lag is considered between nutrient uptake and biomass accumulation.

However, the internal N:P ratio patterns of individual phytoplankton species did not necessarily relate to DIN:TP ratio patterns, since different species have different seasonal IN:IP ratio patterns relative to the DIN:TP ratios of the water column. The internal nutrient ratio patterns simulated for *Aphanizomenon* matched the DIN:TP ratio patterns in the water column more closely than the other species. As N₂ fixing cyanobacteria are mainly dependent on total N:P ratios [18], low N:P ratios have been shown to contribute to *Aphanizomenon* blooms in Lake Kinneret [19]. *Aphanizomenon* may take one month to adjust its internal nutrient ratios when nutrient changes in the water column. This may explain why the IN:IP ratios of *Aphanizomenon* occur when the DIN:TP ratio reaches the minimum level. In contrast, *Aulacoseira* takes a shorter period of time to adjust its internal nutrient ratios in response to the changes of the DIN:TP ratios in water column, which fits with the observation of winter *Aulacoseira* blooms in Lake Kinneret [20]. The IN:IP ratio patterns of *Microcystis*, *Peridinium*, and nano-phytoplankton are characterised by annual double peaks, which suggests that their internal nutrient ratios reflect the nutrient supply ratios in the water column not only at high DIN:TP ratios but also at low ratios. The double peaks each year illustrate that the nutrient ratio is not the only factor that can influence the internal nutrient limitation patterns of phytoplankton. Other environmental factors, such as temperature [21], light [22], food-web structure [23] and anthropogenic factors [20], can also mediate the internal nutrient limitation patterns of phytoplankton.

Overall, the results of the present study indicate that the stoichiometry of the total phytoplankton biomass in Lake Kinneret is closely related to the nutrient status of the water column. This improved understanding of the relationship between the internal N:P ratios of phytoplankton and the N:P ratios of the water column can help develop more accurate nutrient limitation metrics and ecological models for predicting algal blooms in aquatic ecosystems. The results also highlight that simply inferring the limitation of particular species based on the water column nutrient stoichiometry may be misleading. Therefore, it is important to consider seasonal changes of nutrient limitation functions and compare the correlations between the internal N:P ratios of phytoplankton groups and the inorganic N:P ratios, the total N:P ratios, and the DIN:TP ratios of the water column to provide an effective means to manage water quality in lake ecosystems.

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