

The Replacement of Peridinium by Cyanobacteria in Lake Kinneret (Israel): A Commentary Review

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Abstract

The dynamics of N & P nutrient inputs and the consequent epilimnetic concentration during 1969-2018 in Lake Kinneret was studied. The consequences of their availability on algal composition were also studied. Two prominent periods were indicated: 1) Sufficient supply of N accompanied by Peridinium enhancement; 2) N deficiency and P sufficiency-induced Peridinium reduction and Cyanobacterium enhancement. The impact of Anthropocene conditions and dust deposition on N & P availability is evaluated.

Keywords

Kinneret, Peridinium, Cyanobacteria, N & P

1. Introduction

Algal community structure and nutrient availability relationships are worldwide mostly considered as the dominant factor involved in water quality protection. An enormous number of studies were carried out during the long history of limnological research. Much of the scientific effort was dedicated to field and indoor experimental research and less was carried out about standing stocks single data parameter. In other words, the physiology or eco-physiology is most commonly emphasized while nutrient standing stocks as a single type of parameters are less pronounced. This paper is an attempt at relations analysis between phytoplankton and nutrient solely as a simple trait different from complex interactions. Therefore, only macro-nutrient species of Nitrogen and Phosphorus were included. Similarly, the study of the Kinneret food web structure and energy flow pattern was based on Carbon [1]. The common approach to ecosystem structure and/or energy flow pattern research mostly includes three major evaluation types: modeling, nutrient (macro, micro, inorganic, organic, etc.) impacts or Climatological condition effects. The usage of models requires physiological features of organisms that are partly or completely the outcome of experimental measurements and their role under different physical (climate, water quality parameters) conditions. The research of the effect of a single aspect on Phytoplankton, seasonal or temporal, is not very common. The present study is supposed to focus on a small number of parameters within a restricted frame and their impact on phytoplankton densities in Lake Kinneret. To alleviate the complexity of the evaluation of the long-term data record, the statistical methods were restricted to two: simple averages and Fractional Polynomial Regressions (STATA 9). Ecophysiological, modeling, or experimental studies of Lake Kinneret phytoplankton have been carried out and documented very widely for more than 50 years. Nevertheless, here, unlike many other closely related studies, the focus is on N and P macro-nutrients, impact on the Phytoplankton assemblages, and their seasonal fate in the warm monomictic Lake Kinneret as a supportive issue to the maintenance of water quality. A similar study was documented by Edmondson and Lehman [2]. The significance of this study is aimed at analysis of the water quality deterioration supporting management improvement.

2. Material and Methods

The data that was evaluated include: Phytoplankton densities and N (TN, NO_3 , NH_4) and TP distribution in the Epilimnion of Lake Kinneret taken from the Lake Kinneret Data Base, Kinneret Limnological Laboratory, IOLR, during 1969-2001 [3] [4] [5]. Statistical evaluation methods include simple averaging and Fractional Polynomial Regression. The following regression relationships were evaluated: Phytoplankton groups (Chlorophyta, Cyanophyta, Diatoms and Peridinium) and the epilimnetic concentrations (ppm) and loads (Ton) of nutrients (TN, TP, NO_3 , NH_4); the Batimetric distribution of Nutrients; The temporal (both, monthly, and multi-annually) of nutrients and phytoplankton groups distribution. The data of nutrient concentrations in the Epilimnion as presented in all figures are based on the long term record of the Kinneret Limnological Laboratory, IOLR, and Mekorot, Water Supply Co., including sampling program and analytical analyses implementations.

3. Results and Discussion

The monthly fluctuations of nutrient concentrations in the Epilimnion of Lake Kinneret during 1969-2001 are shown in **Figure 1**. The seasonal patterns of concentrations distribution of TN and TP are similar: high level in winter followed by continuous decline to the annual Minimum in August and September. It is an outcome of several processes. External input of Nitrogen driven by precipitation and runoffs regimes; upward supply of NH_4 from the Hypolimnion as a result of De-stratification; Nitrification- NH_4 oxygenation to NO_3 ; Nitrogen fixation; particles (detritus) sedimentation; and the most relevant to the present



Figure 1. Fractional Polynomial Regressions between Monthly averages (1969-2001) of epilimnetic Nutrient (NH₄, TN, NO₃, TP) concentrations (ppm) and months.

study, algal uptake. Consequently phytoplankton dynamics is just one compartment within a complex interaction expressed as a final product entitled Total Nitrogen. Among Nitrogen forms the highest demands are due to Nitrates and Ammonium; therefore, temporal changes of Nitrogen stocks and Phytoplankton Biomass is essential.

Results shown in Figure 2 indicate a concentration decline of the highest nutritionally valued NH₄ and NO₃ during April months in 1969-2001 and obviously TN. Therefore, April is the maximum of the Peridinium bloomed biomass and the TN decline onwards is, therefore, the result of the temporal later decrease of its biomass. The temporal (1969-2001) changes of the concentration of TN, NO₃ and Organic Nitrogen (results are not presented) are similar: long-term decline. It is likely that sources of those nutrients are partially internal and supplemental Nitrogen demands for Peridinium are from external sources. The April data (Figure 2) indicates the similarity of NH₄ and TP temporal change of concentrations: 1969-1985, increase and decline onwards. The temporal decline of negligible external inputs of NH₄ through Jordan River inflows are shown in Figure 8. The increase of Epilimnetic TP stock (Figure 8) is probably originated not externally but internally via P mediated germinating Peridinium cysts. The cyst-mediated P supplied the demands for the bloom formation until 1985 when Peridinium density declined (Figure 5). It has to be noted that simultaneous enhancement of Chlorophyta, Cyanophyta and Diatoms accompanied the elevation of Peridinium intensity (Figure 5). The external supply of Phosphorus has also reduced significantly since the mid-1980's as a consequence of the removal of sewage (90%) and fish-pond waters (80%). The trend of increase of Epilimnetic concentration of TP was leveled off consequently. The Epilimnetic concentration



Figure 2. Fractional Polynomial Regressions between April-Monthly averages during 1969-2001 of Epilimnetic Nutrient (NH₄, TN, NO₃, TP) concentrations (ppm) and Years.

of NO_3 in the January months (Figure 3) gradually enhanced due to soil structure dryness degradation in the Hula Valley.

The evaluation of Nutrient dynamics in the Epilimnion during September months (1969-2001) (Figure 4) indicates the long-term decline of TN, NO₃ and Organic Nitrogen (data not presented). September is Summer conditions, no rain flush of Nitrates, which were mostly removed in winter. The external supply of Phosphorus is carried out and even intensified by irrigation water in summer. That is because of P-bounded linkage to organic substance breakdown under soil dryness conditions. Internal supply of P is minimal during the existence of Stable stratification in Lake Kinneret. The impact of external input enhancement of NO₃ and TP as suggested to be carried out by the seasonal effect of precipitation-runoffs is presented in Figure 3. Nevertheless, the decline of TN during the January months (Figure 3) affected Peridinium decline. The NO₃ increase in the January months (Figure 3) is just a short time case due to the early rain flushing of the free unbounded and highly available NO₃ in the Hula Peat soil stock. The decline of epilimnetic NH₄ concentration during the January months since the late 1970's is an additional support of Nitrogen reduction within the TN stock decline since the mid-1980's. The prominent dissipation of Epilimnetic Nitrogen stock (Figure 4).

3.1. TN Standing Stock and Algal Biomass (Figure 5)

What is the relation between Epilimnetic Nitrogen standing stock load and the dynamics of Phytoplankton biomass? Results presented in **Figure 5** indicate a reduction of the biomass of Chlorophyta, Diatoms and Cyanophyta in relation to the enhancement of Epilimnetic load (tons) of standing stock Nitrogen. A



Figure 3. Fractional Polynomial Regressions between January-Monthly averages during 1969-2001 of Epilimnetic Nutrient (NH₄, TN, NO₃, TP) concentrations (ppm) and Years.



Figure 4. Fractional Polynomial Regressions between September-Monthly averages during 1969-2001 of Epilimnetic Nutrient (NH_4 , TN, NO_3 , TP) concentrations (ppm) and Years.

partial exception is indicated about Diatoms density related to TN standing stock: the biomass decline is due to >1000 tons of TN while under <1000 tons of TN their biomass density increases with TN stock elevation. Contrary to the other algal groups, Peridinium biomass density is enhanced when Nitrogen standing stock is elevated. This case can be similarly expressed from an oppositional view: Peridinium biomass and TN are positively correlated while densities

of the other algal groups represent inverse relation with TN.

3.2. TP Standing Stock and Algal Biomass (Figure 6)

Results shown in **Figure 6** with regard to Algal Biomass and TP relations are similar to those with TN standing stock: the decline of the biomass of Chlorophyta



Figure 5. Fractional Polynomial Regressions between annual averages of Phytoplankton groups Biomass (g/m²) (Peridinium, Chlorophyta, Diatoms, Cyanophyta) and years during 1969-2001.



Figure 6. Fractional Polynomial Regressions between Multi-annual (1969-2001) averages of Phytoplankton (Chlorophyta, Cyanophyta, Diatoms, Peridinium) densities (g/m²) and Epilimnetic loads (Ton) of Total Nitrogen (TN).

and Cyanophyta when TP stock is >20 tons while the decrease of Diatoms is started when TP is >40 tons. The similarity of TP and TN relations to Peridinium biomass density reflects two different traits: Peridinium biomass increase as a result of TP elevation or vise versa the increase of Peridinium Biomass is the reason for the TP elevation through the P-cysts mediation. The second option is likely more relevant. Peridinium life cycle includes the blooming status during the late winter-spring-early summer when dormant cysts are produced. These large and heavy cysts are settled down to the Phosphorus reach bottom sediments. The cysts incorporate P from the sediments and during the next season they germinate into motile vegetative form, which conveys P into the Epilimnion for the benefit of the biotic (Chlorophyta, Cyanophyta and Diatoms) demands for bio-available P. The insufficient Nitrogen stock for Cyanophyta is completed by their capability to maintain Nitrogen-fixation. Conclusively, the supply of the key macro-nutrient of P is carried out by Peridinium and when this algae is under the constraint of Nitrogen deficiency there is a decline of P as well. Peridinium, unlike Cyanophyta, is unable to complete its Nitrogen demands by fixation from the atmosphere and, therefore, responded to N deficiency through Biomass decline.

Dust deposition as a significant source of Phosphorus is documented [6] [7] [8] [9]. The evaluation of dustfall impact on the Epilimnetic-bioavailable-P concentration requires an insight into the wind regime (velocity and direction) in the Kinneret region (Serruya, S. 1978). Unlike what is documented for external inputs of Nitrogen, which represents prominent periodical changes, external supply of Phosphorus fluctuated less. **Table 1** represents the monthly averages of wind directions (Degrees) and velocities (m/s) during 1969-1975 [10].

Table 1. Monthly averages (1969-1975) of Wind velocity (m/s) and Direction (Degrees:
North = 360 or 0; South = 180). Hourly values were averaged to Monthly and mul-
ti-annual means (Data source is [10].

Month	Direction (Degrees)	Velocity (m/s) (SD)
1	60	3.0 (0.4)
2	293	2.8 (0.6)
3	275	2.8 (0.4)
4	269	3.3 (0.4)
5	266	3.8 (0.4)
6	270	4.5 (0.5)
7	267	5.1 (0.5)
8	266	4.6 (0.5)
9	267	3.8 (0.4)
10	270	3.1 (0.3)
11	301	2.8 (0.4)
12	230	3.1 (0.5)

Wind information was published [3] as colored graphical charts from which it was possible to define the period and daytime of the occurrence of maximal gust velocity ranges (**Table 2**): The periodical frame was defined between June and August and the daytiming—15:00-17:00, which is the typical Summer Westerly gusts.

Results in Table 1 and Table 2 indicate the absence of significant changes within the long-term (multi-annual) monthly and daily patterns of wind (gusts) regime. Therefore, the fluctuations of Epilimnetic P concentrations can not be attributed solely to wind mediated-P transported by dustfall [6] [7] [8] [9]. The dependence between the changes of Epilimnetic-P and wind regime is probably latent and internal conditions are more effective driven forces. The stable long-term regime of the dust carrier wind documented by Seruya, S. [10] and IOLR-KLL1's reports (2004-2018) justify allocating different sources of Phosphorus. Significant anthropogenic changes were carried out in the Hula Valley: drainage and agricultural developments that might cause P-rich dust matter inputs into the lake. Nevertheless, Zarka et al. [9] stated that the sources of P-rich dust particles are not necessarily cultivated fields, cattle farms or intensive pasture areas. Moreover, the effectiveness of P-rich dust carrier is probably not due to the westerly directions. It is, therefore, suggested that the Epilimnetic TP concentration seasonal dynamics (Figure 1) is driven by internal sources (P-mediated Peridinium Cysts) and probably to a lesser extent by inputs of dustfall originated from Dolomite and Feldspar substances. If, as previously hypothesized, import of P to the Epilimnmion is mostly due to deposition of wind carrier dust, it should

Maximal Gust Velocity Range (m/s)	Year
5 - 8	2004
6 - 9	2005
6 - 9	2006
5 - 8	2007
4 - 6	2008
4 - 6	2009
6 - 8	2010
6 - 9	2011
3 - 5.5	2012
5 - 9	2013
6 - 9	2014
6 - 9	2015
4 - 9	2016
5 - 8	2017
4 - 7	2018

Table 2. Range of wind velocity (m/s) during the Summer (June-August) months at 15:00-17:00 daily afternoons (IOLR Annual Reports 2004-2018).

lead conclusively to an increase of Epilimnetic P concentration during the summer months (June-August; Table 1, Table 2). Nevertheless, during these months the P concentration declines and increases from October (Figure 1) through January by sedimentation of P-rich Dolomite or Feldspar dominated dust particles [9] from local substances in the vicinity. Partial support for this suggestion is given in **Table 1** [10], indicating a Northern-Easterly wind direction in January. Conclusively, the dynamics of Epilimnetic P concentration is driven to a lesser extent by dust deposition and mostly attributed to internal sources and Jordan waters import, and the role of wind regime is minor. Data shown in Figure 2 indicates an increase of P concentration during the April months of 1969-1985 when the Peridinium biomass was high before the temporal decline of Peridinium. After 1985, the successful implementation of sewage and fishpond waste removal gradually reduced Nitrogen supply, which deteriorated the growth rate of Peridinium. The elevation of Epilimnetic-P concentration in the January and September months was probably caused by De-stratification process and upward Hypolimnetic supply. Data presented in Figure 8 indicates the contribution of TP by sewage and Fishpond wastewater, which was eliminated in the late 1980's when decline was documented.

3.3. Temporal Fluctuations of Nutrient Loads (Figure 7)

Results in Figure 7 indicate continuous Nitrogen shortage during 1970-2001 while the standing stock of TP is increasing. Nevertheless, the seasonal fluctuations of TN and TP are similar but occur under different mechanisms: High TN in winter is the outcome of precipitation regime causing NO_3 importing from



Figure 7. Fractional Polynomial Regressions between Multi-annual (1969-2001) averages of Phytoplankton (Chlorophyta, Cyanophyta, Diatoms, Peridinium) densities (g/m²) and Epilimnetic loads (Ton) of Total Phosphorus (TP).

the Peat soil and the beginning of elevation in October as a result of NH₄ flux from the Hypolimnion driven by De-Stratification caused by air temperature decline driving water cooling mechanism. The high level of TP in the winter months (January-May) is the result of Peridinium-cyst-mediated Phosphorus transfer. The decline of TP in summer is the result of Peridinium crashed die-off bloom and sedimentation of dead cells accompanied by low-river discharges, which convey small quantities of P from the drainage. The seasonal dynamics of algal biomass density (**Figure 8**) indicates a decline of Peridinium in summer due to a lack of Nitrogen accompanied by an outbreak of nitrogen fixation-capable Cyanophyts. The nitrogen seasonal deficiency is the result of biomass decline of diatoms while a slight summer recovery of Chlorophyts occurs. The fluctuated biomass densities of phytoplankters-excluded Peridinium are slightly enhanced, representing a narrow range of variations but significant to analyzed trend of changes.

3.4. Batimetrical Distribution of Epilimnetical Nutrients (Figure 9)

Batimetrical distribution of Epilimnetic nutrients is shown in **Figure 9**. Nitrate concentrations are declining between surface and 15 m as a result of algal uptake while the increase between 15 - 20 m is probably caused by NH_4 oxygenation to NO_3 by Photosynthetic Bacteria (Chlorobium phaeobacteroides) [11] [12] and accompanied nitrifiers during De-Stratification process. The low concentration of NH_4 in shallow layers of 0 - 15 m is the result of nitrification, and an increase below 15 m is due to the flux from the gradual De-stratified Hypolimnion. The



Figure 8. Fractional Polynomial Regressions between monthly (upper panels) and annual (lower panels) averages of Epilimnetic Loads (Ton) of Total Nitrogen (TN) (left), Total Phosphorus (TP) (middle) and NH_4 (right) inputs through Jordan inflow and years (1969-2001).



Figure 9. Fractional Polynomial Regressions between monthly averages (1969-2001) of algal (Chlorophyta, Diatoms, Cyanophyta, Peridinium) Densities (g/m^2) and month.

combination of triple processing of NH_4 upward flux, external inputs of NO_3 and Nitrification is essentially reflected by the Batimetric distribution of TN. The prominent decline of TP between 0 - 15 m indicates the upper Peridinium high biomass density and the poor P load renewal from other sources.

3.5. Peridinium, TP and TN Seasonal Matching

The role of the combined impact of P and N on Kinneret algal assemblages and particularly Peridinium was documented previously [13] [14] [15]. Results shown in Figure 10 & Figure 11 define the seasonal onset and die-off of the Peridinium bloom with the respective response to epilimnetic stocks of TN and TP. The monthly fluctuations of the biomass density indicate an onset development from October to the April Maximum and die-off from April to the minimum in August-October. The peak of Epilimnetic TN stock is matching the maximum of the Peridinium biomass. The seasonal die-off of the Peridinium biomass is matched with the decline of the Epilimnetic TN stock. Contrary to those TN-Peridinium relations, the increase of epilimnetic TP stock is matched with high Peridinium density. It is likely that two different dynamic traits are indicated: the external import of Nitrogen enhances Peridinium growth rate and its elevation is indicated as supplemented algal cells contributing cyst-mediated Phosphorus to the Epilimnion. An indicated prediction suggests that the rate of TN stock Die-off (exponent value, Figure 12) is higher as the Nitrogen load is increased.

4. Conclusive Summary

This paper is an attempt at an evaluation of the dependant/independent paradigm



Figure 10. Fractional Polynomial Regressions between multi-annual (1969-2001) averages of nutrients (TN, TP, N0₃, NH₄) concentration (ppm) and depth (m).



Figure 11. Fractional Polynomial Regression (upper panels) between Peridinium Biomass (g/m^2) and Epilimnetic concentrations (ppm) of TN (upper left panel) and TP (upper right panel). Lower Panel: Trend of changes (LOWESS) (0.8) of Monthly averages of Peridinium Biomass (g/m^2) during 1969-2001.



Figure 12. The Die-off rate of Nitrogen Load in Lake Kinneret (whole water column) between maximum (March) and Minimum (August) Vs the Exponent of TN dissipation which was taken from the Regression Equation (R^2 and p values are given).

of an everlasting dilemma: Between phytoplankton composition and nutrient concentrations, who is the boss? Algal community structure responds to the concentration of the nutrients or the contrary: is the concentration of nutrients the outcome of the structure and density of the algal assemblages? The answer given here confirms nutrients as independents. Nitrogen and Phosphorus loads are defined here as predictors of dominating Peridinium or Cyanobacteria. The processes of algal consumption and impact of other conditions impact are excluded.

A prominent decline of TN standing stock in the Epilimnion of Lake Kinneret was documented during 1969 to 2001. A direct positive relation was found between the standing stocks of TN and the Peridinium biomass. Because Peridinium was dominant, the total Phytoplankton biomass is also a dependant of TN. Contrary to Peridinium, the biomass of Cyanophyta increased with respect to the decline of all Nitrogen species concentration. Is TN standing stock a unique initiator of Cyanobacterial enhancement? TN decline initiated Nitrogen deficiency, which is favored by Cyanobacteria due to their capabilities to maintain the fixation of atmospheric Nitrogen [16]-[22]. During the history of Kinneret Phytoplankton research, there were several investigations aimed at the attractive issue of pinpointing the chemical elements or compounds that enhance the growth rate of Peridinium or Cyanobacteria. Two elements were considered: Cuprum (Cu) and Selenium (Se). The study of the Cu impact was not thoroughly developed but that of Se was widely studied [23] [24] [25] [26] by an earlier data confirming Se as a limiting factor of Peridinium growth. The content of Se in the Hula Valley peat soil and the Jordan River were documented (Nishri and Gavrieli 2019). Nevertheless, the particular study of 95 elements included in the Mendeleev's periodic table and a vast number of natural compounds is much

less realistic than the investigation of smaller number of nutrients. Therefore, the research into the impact of macro-nutrients (N, P, C) is preferable. Nishri and Gavrieli [27] documented the results of a study about the relations between nutrient contents in the Jordan River inflows, which is the donor, and Lake Kinneret, which is an acceptor of nutrients. They documented linkage between Jordan River flood regimes and Peridinium bloom formation. Until 1993, Peridinium was dominant and hydraulic modifications were related to extremity of the bloom. They also suggested a linkage between hydraulic fluctuations and the implementation of the Hula Project accomplishment. The mixotrophic trait of Peridinium was considered as also related to the hydraulic fluctuations and to underground water migrations in the Hula Valley. The patchy habitat of the Peridinium blooms was linked to a higher level of macro-nutrients (N, P, C) within the bloom stain [27]. The bloom containing water mass migration was considered as enhanced renewal of required nutrients' availability. The intensive inputs of allochtonous organic Nitrogen and Carbon might, therefore, be the reason for the recorded heavy blooms of Peridinium during the 1970's and most of the 1980's [27]. Moreover, the anthropogenic implementation of sewage and fishpond waste removal caused the decline of Nitrogen inputs and Cyanobacteria enhancements onwards. The Nitrogen deficiency as stimulator of N₂-fixer Cyanobacterium blooms is prominently accepted. The impact of Selenium inputs is a partial confusion. The Hula Peat soils are Se-rich substrate and Se is a limiting factor of Peridinium growth rate [23] [24] [25] [26]. The most available chemical derivate of Se is 4+ value, which is the dominant form in the Jordan River waters [27]. Nevertheless, prior to the draining of Lake Hula and surrounded swamps, the chemical trait of the peat soil was reductive and Peridinium bloomed intensively, but presently soil conditions are oxidative and, therefore, limitation of Se is not doubtful.

5. The Multi-Parameter Dilemma

The impact of Selenium (Se) on the growth rate of Peridinium was thoroughly investigated (Rodhe 1978; Lindstrom 1980; Nishri and Sukenik 2012; Nishri *et al.* 1999). The Hula peat soil source of Se was documented by Nishri and Gavrieli [27]. The most common chemical form of Se in the Jordan River is Se⁴⁺. It has to be taken into account that the Peat Soil was water-covered until the late 1950's under reductive conditions. It is suggested that before the draining of Hula Water (old Lake Hula and swamps), the input of Se to Lake Kinneret was intensive as was the consequent Peridinium bloom formation. Between the late 1950's and 1993, Se supply from the peat soil into the lake smoothly continued supporting Peridinium bloom formation. Nevertheless, during the 1990's the bloom-favored condition of Nitrogen input declined. The quantitative regime of Se merit from the Peat soil into the lake is yet unknown. Nevertheless, Nishri and Gavrieli (2019) reported high concentrations of Se⁴⁺ in the River Jordan waters. Consequently, it is suggested that the limiting factor for Peridinium growth rate in

Lake Kinneret is Nitrogen (several species: DIN, TDN, etc.). During 1957-1993, Se was probably commonly supplied but Nitrogen declined. Consequently, Nitrogen was the limiting factor that caused the reduction of Peridinium. Moreover, from 1993 onwards, several cases of heavy flooding were recorded, followed by Peridinium outbreak caused by Nitrogen enhancement from external supply. Several parameters are known as prominently demanded by Peridinium bloom production: the compounds produced via the Calcite precipitation process [27] DIC, and Se⁴⁺ and others (Cuprum was also predicted). Nevertheless, it is insufficient to indicate short-term parameters as impact factor, while Nitrogen reduction was defined as a long-term condition that also influenced other Phytoplankters. The impact of N, P, C, and Se (including different Se forms) on the Peridinium growth rate was confirmed as sole or any mixed parameters, but only long-term deficiency effect as sole element of Nitrogen was documented. The advantageous novelty of the study is aimed at comprehensive presentation of long term record of data monitoring as a solid contribution for future management implementation.

Conflicts of Interest

The author declares no conflicts of interest regarding the publication of this paper.

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