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Temperature and growth strategies as the essential factors influencing the occurrence of *Stephanodiscus minutulus* (Kützing) Cleve & Möller and *Palatinus apiculatus* (Ehrenberg) Craveiro, Calado, Daugbjerg & Moestrup

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Abstract

The life cycle of diatoms and dinoflagellates enables them to produce interannually varying dominances. This variability results from life-cycle interactions, physical conditions, and inter-species competition for nutrients and light. In particular, the overall dominant species of the year can be linked to the abundances of resting stages and temperature in spring.

The aim of this study was to investigate the effects of temperature and life cycle as biotic factors on spring phytoplankton blooms caused by *Stephanodiscus minutulus* (Kützing) Cleve & Möller and *Palatinus apiculatus* (Ehrenberg) Craveiro, Calado, Daugbjerg & Moestrup, in a Hungarian shallow backwater. The composition of plankton communities exhibited a marked interannual heterogeneity. Our results suggested that a slight decrease in temperature in spring favours a spring bloom of vegetative dinoflagellates before encystment begins. However, a rapid increase in temperature results in high abundances of dinoflagellate cysts, which, in turn, leads to the dominance of diatoms. In this case, encystment starts before a pronounced dinoflagellate spring bloom is established.

Keywords: life cycle, *Stephanodiscus minutulus, Palatinus apiculatus*, spring bloom, excystment, encystment

Introduction

In temperate standing waters, phytoplankton species generally show seasonal dynamics with spring blooms yielding a major part of the annual production (Reynolds 1987a, 1987b). For most water types, temperature is one of the main controlling factors for the occurrence and dominance of phytoplankton species. However, its importance has been underestimated. Phytoplankton spring blooms in temperate waters have been generally dominated by one of two main groups: dinoflagellates or diatoms (Sommer et al. 1986, Grigorszky et al. 2000, Gligora et al. 2015). Dinoflagellates and diatoms are key groups of the freshwater phytoplankton, and, as primary producers, are particularly relevant for biogeochemical cycles and the food web.

While spring blooms are generally dominated by dinoflagellates, dominance has been gradually shifting from dinoflagellates to diatoms (Broekhuzien 1999, Jewson 1992). The reasons for the shift in dominance are not completely understood. The phenomenon of this "spring bloom type" is characteristic to Hungarian standing and running waters (Grigorszky et al. 1993, 1997, 2000, 2003), while another "type" (dominance of only centric diatoms) frequently occurred in the Danube River and its side-arms (Kiss and Genkal 1993, 1997). The dominances of both phytoplankton groups and their relative close abundances may have specific consequences for the nutrient cycling, although the physiological circumstances and life cycles of dinoflagellates and diatoms have been proposed to play an important role in governing the phytoplankton composition (Anderson 1984, Bravo et al. 2010, Drebes 1966, Durbin 1978). For example, dinoflagellates can be considered as inferior competitors to diatoms, as they have a lower photosynthetic rate (Furnas 1990, 1983). Another important fact is that besides environmental factors, changes in the timing and size of the inoculum (the cells that initialize the bloom) have been proposed as relevant factors that bring changes in the phytoplankton species composition (D'Alelio et al. 2010, Klais et al. 2011, Krempet al. 2008). The factors regulating diatom and dinoflagellate life-cycle transitions are poorly understood. The effects of nitrate and phosphate concentration on various diatom and dinoflagellate species are more or less well known and recognised as important factors in determining the abundance of species, but the effects of temperature on excystment are hardly known (Anderson 1980). Most papers focus on variables that affect the encystment, rather than the excystment process (Olli and Anderwson 2002, Heikkilä et al. 2016, Kremp et al. 2009). Nevertheless, there is a lack of knowledge of the factors regulating the cyst to vegetative cell transitions due to the difficulties of understanding their occurrence. Therefore, the objective of this study was to investigate temperature as the main variable controlling the alternation of the dominance of *Stephanodiscus minutulus* (Kützing) Cleve & Möller and *Palatinus*

apiculatus (Ehrenberg) Craveiro, Calado, Daugbjerg & Moestrup during spring blooms on interannual time scales.

Materials and methods

The studied backwater is situated in the Körös area, Békés county, SE Hungary (Latitude N 46^{o} 57' 14.96'', Longitude E 20^{o} 49' 18.63''). It has an area of five hectares (A_o = 5 ha), a maximum depth of 3.5 m (d_{max} = 3.5 m) and an average depth of 2 m (d_{avg} = 2.0 m). Water samples were collected monthly from January to June in 2013 and 2014. For chemical analyses and algal counts, the samples were collected with a weighted plastic tube at the deepest part of the backwater. The physical and chemical parameters were measured according to the internationally accepted analytical methods of the Hungarian water quality monitoring service (Hungarian National Standards, MSZ 12749:1993). The sediment for the cyst and spore count was collected by a Hargrave-type sediment sampler. A sub-sample was immediately fixed on the field with Lugol's iodine for subsequent algal counts with the Uterhmöhl inverted microscope technique. The microscopic investigation was performed with an Olympus-IX73 inverted and an Olympus-BX53 microscope by using phase-contrast and Nomarski-contrast technologies. The linear model was fitted to the correlation of coexistent diatom and dinoflagellate vegetative cells, diatom spores and dinoflagellate cyst. PAST (Paleontological Statistical Software Package) version 1.78 was used for the statistical analysis (Hammer et al. 2001).

Results

In both 2013 and 2014, the conductivity was relatively low, with the annual minimum values (89 and 87 μS cm^{-1}) measured in February (Fig.1.a). In both years, the conductivity began to increase in March and continued to rise throughout the months of April, May and June. The maximum conductivity (422 and 418 μS cm^{-1}) was observed in July in both years. The concentration of total phosphorus was at its maximum level in January in both years (12.6 and 11.8 μgL^{-1}, respectively), which then was strongly reduced in February (5.8 and 4.8 μg L^{-1}), and continued to decrease slightly throughout March and April (Fig.1.b). The concentration of total phosphorus did not change significantly in May and June. For 2013 and 2014, the concentration of nitrate-ion was nearly the same. The maximum nitrate-ion concentration was measured in January in both 2013 and 2014 (4.1 and 4.7 μgN L^{-1}, respectively), which slightly decreased in February (Fig.1.c). A strong reduction in the nitrate-ion concentration was measured in both years in April (1.9 and 1.8 μgN L^{-1}), while the concentration strongly increased again in May (3.9 and 4.1 μgN L^{-1}). Finally, a significant drop occurred in June when we measured the minimum concentration of nitrate-ion (0.2 and 0.18 μgN L^{-1}). The concentration of nitrite-ion was low in January in both years, and dropped to the minimum level (0.1 and 0.15 μgN L^{-1}) in February (Fig.1.d). In March, the concentration of nitrite-ion started to increase, and continued to rise in April. In May, a slight decrease was observed in the concentration of nitrite-ion in both years, but greatly increased in June to the maximum concentration of nitrite-ion (1.8 and 1.9 μgN L^{-1}). No significant differences were found in any kind of variables between the two investigated years (Table 1, Fig.1.a-d.).

Fig.1.a-d., Table 1.

In February 2013, the cysts began to excyst from which resulted the first bloom of dinoflagellates (Fig. 2.a). However, the growth in March was limited by a relatively low temperature (4 ^{o}C); the abundance of dinoflagellates decreased. With a higher temperature in April (9 ^{o}C), the concentration of vegetative dinoflagellates rapidly increased, resulting in a

second bloom of dinoflagellates at the end of April. In May, the encystment started (due to increasing temperature) and caused a decrease in the dinoflagellate bloom and an increase in cyst abundance. The cysts sank into the sediment at the bottom of the water column, where they matured until the next year. The abundance of vegetative diatoms (860-3.210 ind. L^{-1}) and spores (980-1.300 spores m^{-2}) was very low during the whole year of 2013 (Fig.2.b). In contrast, diatoms dominated in the year 2014. The year began with higher abundances of *P. apiculatus* cysts than *S. minutulus* spores. In January, the cysts of *P. apiculatus* excysted, which caused a small dinoflagellate bloom in February (Fig. 2.c). With a rapid temperature increase from March to May, the concentration of vegetative dinoflagellates decreased from 11.240 ind. L^{-1} to 2.320 ind. L^{-1}, but the encystment also started due to a further increasing temperature. This caused a decrease in dinoflagellate cyst numbers (from 69.840 cyst m^{-2} to 740 cyst m^{-2}), before a pronounced bloom could be established. From January to March, the temperature growth conditions were not favourable for diatoms (Fig. 2.d). Therefore, the spores did not transform into vegetative diatoms. In April and May, temperature became favourable and the mean growth rate of diatoms reached the highest value, and spores started to transform into vegetative diatoms. The number of vegetative diatoms grew and they formed a bloom in late May (Fig.2.). The concentrations were significantly higher compared with dinoflagellates that had already started to encyst. In early June, the growth rate decreased due to depleted nutrient conditions. Hence, the transition was reversed, and the vegetative diatoms started to transform into spores.

Fig.2.a-d.

In 2013, *P. apiculatus* was dominant during the spring months when no other taxon occurred in significant numbers. In 2014, a diatom-dominated spring bloom occurred in April and May when *S. minutulus* was the dominant taxon.

The total number of individuals was the lowest in January 2013, followed by a slight increase in February, which was mainly caused by the *P. apiculatus* taxon. In March, the numbers fell back closer to the lowest level experienced in January (Fig.3.a.). At that time, *S. minutulus* also appeared, but only in small numbers (1.320 ind. L^{-1}). In April, the number of individuals of *P. apiculatus* reached their maximum (62.430 ind. L^{-1}), while *S. minutulus* continued to decrease (860 ind. L^{-1}). In May, the total number of individuals, including the abundance of *P. apiculatus*, strongly decreased. The Chlorophyta organisms first appeared in April, and occurred in a significant proportion in May and June. The Euglenophyta appeared in May and comprised a significant portion of the total number of individuals in June. Together with Cryptophyta, the Chlorophyta and Euglenophyta taxa became the dominant elements of the total algae numbers in June.

In 2014, we found the least number of individuals in January (Fig. 3.b), similarly to the previous year. The total number of individuals slightly increased through February and in March due to *P. apiculatus* (11.240 ind. L^{-1}). *S. minutulus* also appeared, but with a negligible number of individuals (4.680 ind. L^{-1}). In April, the total number of individuals increased, which was caused by the increased number of *S. minutulus* (19.800 ind. L^{-1}), while the number of individuals of *P. apiculatus* strongly decreased (2.320 ind. L^{-1}). In May, the total density increased significantly, mainly due to the increase in the number of individuals of Bacillariophyceae taxon (69.200 ind. L^{-1}). In May and June, *Parvodinium umbonatum* replaced *P. apiculatus* as the dominant Dinophyta species. We measured the maximum total number of individuals in June. At this time, species from the Chlorophyta, Euglenophyta, Bacillariophyta and the Dinophyta groups were dominant.

Fig. 3.a.b.

The fitted linear model indicated that there is a negative correlation between abundances of the two species (r=-0.54; p=0.07), and also a negative correlation between the resting spores of *S. minutulus* and *P. apiculatus* (r=-0.51; p=0.08) at the 10% level of significance (Fig.4).

Fig.4.

Discussion

All continents in the temperate region are characterised by the presence of shallow lakes associated with a high algal density at various times during the year (Borics et al. 2013, 2014, Grigorszky et al. 2000, Sommer et al. 1986, Padisák et al. 2003). Algal blooms have garnered major global interest during the last two decades (Hense 2010, Hense and Beckmann 2000, Hense and Burkhard 2010). Phytoplankton has 3400–4100 microalgae species of which 300 species can produce blooms (Smayda 1997). Despite the ecological importance of algal blooms, studies focusing on the period of initiation and development of the spring phytoplankton blooms, which determine the structure of the phytoplankton community, are scarce (Lewis et al. 1999, Peperzak 2006). In addition, the importance of phytoplankton species composition in small shallow lakes is almost unexplored. Only a few studies have focused on differentiating algal blooms associated with specific species from one another (Kremp at al. 2008). An improved understanding of the factors regulating bloom development can be best achieved through an analysis of inter-annual variations in bloom dynamics (Iriarte and Purdie 2004).

204 Generally, phytoplankton spring blooms were mainly dominated by cold-water diatoms and
205 dinoflagellates in temperate regions. Sometimes in the same standing water, interannually
206 varying dominances were particularly surprising, given that the maximum growth rate was
207 considered to be significantly lower for dinoflagellates than for diatoms.
208 Our studied diatom, *S. minutulus,* is a cosmopolitan species (Round 2007); it has been
209 recorded as frequent and abundant in rivers and shallow lakes with a different trophic status.
210 It is a characteristic species in the River Danube, mostly during the cold period from
211 November to April (Kiss et al. 2012).
212 Although cells of *P. apiculatus* are relatively conspicuous and readily recognisable among
213 dinoflagellates, the biology of this species has not been studied until now. The main
214 identification books (Huitfeld-Kaas 1900, West 1909, Lindemann 1919, 1928, Lefevre 1932,
215 Popovsky and Pfiester 1990) have only mentioned that this species can be frequently found in
216 various water types and can occur in the cooler regions in Europe and temperate regions. *P.*
217 *apiculatus* belongs to the group of algal species for which we have only few ecological data
218 (Grigorszky et al. 1997), although in some running and standing waters, it can be found in
219 large numbers (Grigorszky et al. 2003).
220 We have considered the fact that the cold-water dinoflagellate *P. apiculatus* and the diatom,
221 *S. minutulus* occur in high abundance in spring in order to study the relationship between life
222 cycle transitions and temperature. On interannual time scales, our results show varying
223 dominances of the investigated dinoflagellate and diatom. In January of 2013, the dormancy
224 period of the *P. apiculatus* cysts was completed and the particular 6 ^{o}C temperature was
225 favourable for excystment, thus, the cysts transformed into germinating cells. Several studies
226 have identified temperature as the main regulating factor for germination (Pfiester and
227 Anderson 1987, Bravo and Anderson 1994, Kremp and Anderson 2000). Therefore, we
228 considered the importance of temperature for the transition from cysts into germinating cells.

229 The germinating cells rise up from the bottom to the upper layers of the water column, where
230 they transform into vegetative cells. The excystment process results in an initial peak into the
231 number of the cells of *P. apiculatus* in February. The relatively cold temperature limits the
232 growth rate in February and March. When the temperature rises in April (up to 9 ^{o}C), the
233 abundance of vegetative cells rapidly increases. This increase in the cell number results in a
234 second peak at the beginning of April. Certain characteristics, such as adaptation to low-light
235 conditions, mixotrophy, as well as lack of grazers, might explain the sudden appearance of *P.*
236 *palatinus*. The decrease in the number of vegetative cells at the end of May was partly caused
237 by the beginning of the encystment process when it was transformed into the resting cyst
238 stage. The cysts sink to the sediment at the bottom, where they mature until the next year,
239 when the cycle begins anew.
240 The growth of vegetative dinoflagellates starts at a lower temperature (8 ^{o}C) than their
241 encystment (14 ^{o}C). By a rapid temperature increase, encystment starts relatively early before
242 the vegetative dinoflagellates are able to build up a pronounced spring bloom. Hence, there is
243 only a short period for *P. palatinus* growth leading to a diatom-dominated spring bloom. In
244 contrast, a slow increase in temperature during spring allows vegetative growth, but delays
245 encystment. The vegetative dinoflagellates build up the pronounced bloom in spring before
246 encystments starts, leading to a dinoflagellate dominated year. Hence, the temperature
247 gradient during spring is the driving factor.
248 Some models with a complete life cycle have been developed for mainly cyanobacteria
249 (Hense and Beckmann 2006, Hellweger et al. 2008). They have been successfully applied to
250 lakes (Hellweger et al. 2008,Jöhnk et al. 2011) and coastal regions (Hense and Burchard
251 2010, Lancelot et al. 2005), demonstrating the need to include life-cycle processes in
252 ecosystem models.

253 So far, few model studies address the life-cycle processes of diatoms and dinoflagellates and
254 their interannually varying dominances (Hasle and Syvertsen 1997, Horner and Shrader 1982,
255 Kremp et al. 2008, Mann 1988). Yamamoto et al. (2002) focus on the life cycle of
256 dinoflagellates, while with regard to diatoms, they only consider their sinking dynamics. The
257 authors study seasonal dynamics, but do not address varying dominances. While Eilertsen and
258 Wyatt (2000) propose a life cycle model for both diatoms and dinoflagellates, the life cycle
259 transitions and interspecific dynamics are assumed to depend on external processes that are
260 fixed in time and quantity. Our results show interannually varying dominances of
261 dinoflagellates and diatoms, although the maximum occurrence of diatoms is three times
262 higher than dinoflagellates. We interpreted the results as the interannual variability results
263 from life-cycle interactions, temperature, and inter-species competition. The overall dominant
264 species was linked to the temperature in spring. The slowly increasing temperature favours a
265 spring bloom of vegetative *P. apiculatus* before encystment begins. Otherwise, if temperature
266 rapidly increases, it leads to the dominance of *S. minutulus* and, in this case, encystment starts
267 before the pronounced spring bloom is established.
268 The fundamental objective of community ecology is to explore the organizational patterns and
269 rules of spatially and temporally coexisting species, also known as associations. Early
270 ecological studies emphasised the importance of intra-community competition (Diamond
271 1975, Huston 1979). However, it has been proven in recent years that the dynamics of the
272 community structure cannot be explained solely on the basis of interspecies competition.
273 The only time the old model can be successfully applied is when one of the variables – for
274 example, a specific form of nutrient – is extremely scarce or extremely abundant.
275 Furthermore, it is particularly difficult to recognise the underlying causes of distribution
276 patterns if the species of interest are nearly the same in their ecological function, if they have
277 broad tolerances for a number of variables, and if the environmental conditions of their habitat

are nearly constant on a year-to-year basis. Due to studies on terrestrial organisms, more and more researchers have started to recognise that community organisation patterns are strongly dependent on the biological characteristics of the organisms. For example, in the case of algae, these biological characteristics can include their specific encystment or excystment processes.

Summary

We investigated here two species whose occurrences were unaffected by the seasonal differences in nutrient availability. That the two species responded differently to spring temperature conditions, however, was based on their different life cycles. We would also like to emphasise that future studies need to focus more on the biological characteristics of organisms, including phytoplankton species. These characteristics developed through lengthy evolutionary processes so that the biotic potential of a given species – the highest possible vital index of a species when the species has its highest birth rate and lowest mortality rate – could be realised. In our view, it is paramount to consider the biological characteristics of a given species, especially species with broad tolerances, in order to better understand their occurrences.

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300 References

301 Anderson, D. M., 1980: Effects of temperature conditions on development and germination of
302 *Gonyaulax tamarensis* (Dinophyceae) hypnozygotes. – J. Phycol. **16**:166-172.

303 Anderson, D. M., 1998: Physiology and bloom dynamics of toxic Alexandrium species, with
304 emphasis on life cycle transitions. – In: Anderson, D. M., Cembella, A. D. and
305 Hallegraff, G. M., (eds.): Physiological Ecology of Harmful Algae, NATO ASI Series
306 G: Ecological Sciences 41. – Springer, pp. 29–48.

307 Borics, G., Nagy, L., Miron, S., Grigorszky, I., László-Nagy,Zs., Lukács, B. A., G-Tóth, L. &
308 Várbíró, G., 2013: Which factors affect phytoplankton biomass in shallow
309 eutrophiclakes? – Hydrobiologia **714**: 93–104.

310 Borics, G., Lukács, B. A., Grigorszky, I., László-Nagy, Z., G-Tóth, L., Bolgovics, Á., Szabó,
311 S., Görgényi, J. & Várbíró, G., 2014: Phytoplankton-based shallow lake types in the
312 Carpathian basin: steps towards a bottom-up typology. – Fundamental and Applied
313 Limnology **184**(1): 23–34.

314 Bravo, I. &Anderson, D. M., 1994: The effects of temperature, growth medium and darkness
315 on excystment and growth of the toxic dinoflagellate *Gymnodinium catenatum* from
316 northwest Spain. – Journal of Plankton Research **16**(5): 513–525.

317 Bravo, I., Fraga, S., Isabel Figueroa, R., Pazos, Y., Massanet, A. &Ramilo, I., 2010: Bloom
318 dynamics and life cycle strategies of two toxic dinoflagellates in a coastal upwelling
319 system (NW Iberian Peninsula). – Deep-Sea Research Part II **57**(3-4): 222–234.

320 Broekhuzien, N., 1999: Simulating motile algae using a mixed Eulerian-Lagrangian approach:
321 does motility promote dinoflagellate persistence or co-existence with diatoms? – Journal
322 of Plankton Research **21**(7): 1191–1216.

D'Alelio, D., D'Alcala, M., Dubroca, L., Sarno, D., Zingone, A. & Montresor, M., 2010: The time for sex: A biennial life cycle in a marine planktonic diatom. – Limnology and Oceanography **55**(1): 106–114.

Drebes, G., 1966: On the life history of the marine plankton diatom *Stephanopyxis palmeriana.* – Helgoland Marine Research **13**(1): 101–114.

Durbin, E. G., 1978: Aspects of the biology of resting spores of *Thalassiosira nordenskioeldii* and *Detonula confervacea*. – Marine Biology **45**(1): 31–37.

Eilertsen, H. & Wyatt, T., 2000: Phytoplankton models and life history strategies. – African Journal of Marine Science **22**(1): 323–338.

Furnas, M. J., 1990: In situ growth rates of marine phytoplankton: approaches to measurement, community and species growth rates. – Journal of Plankton Research **12**(6): 1117–1151.

Gligora U. M.. Žutinić P.,·BorojevićK. K.·& Plenković-Moraj A., 2015: Co-occurrence of functional groups in phytoplankton assemblages dominated by diatoms, chrysophytes and dinoflagellates. Fundamental and Applied Limnology **1872.** 101-111.

Grigorszky, I., Borics, G., Padisák, J., Tóthmérész, B., Vasas, G., Nagy, S. & Borbély, G., 2003: Factors controlling the occurrence of Dinophyta species in Hungary. – Hydrobiologia **503–506**. 203–207.

Grigorszky, I., Mészáros,I., Sümegi, A. & Vasas, F., 1993: Data on regularity of occurrence of *Peridinium palatinum* Laut. – Limnological Basis and Lake Management. Proc. of the ILEC/UNEP International Training Course. 192–193.

Grigorszky, I., Nagy, S., Krienitz, L., Kiss, K. T., Mikó, H. M., Tóth,, A., Borics, G., Máthé, Cs., Kiss, B., Borbély, Gy., Dévai, Gy. & Padisák, J., 2000: Seasonal succession of phytoplankton in a small eutrophic oxbow and some consideration to the PEG model. – Verh. Internat.Verein Limnol. **27**(1): 152–156.

348 Grigorszky, I., Padisák, J., Borics, G. & Vasas, G., 1997: Data on knowledge of *Peridinium*
349 *palatinum* (Dinophyta in Körös Area (SE, Hungary). – In: Hamar, J. (ed.): The Cris-Körös
350 Rivers' Valleys, TISCIA Monograph Series, pp. 123–133.
351 Hammer, Ø., Harper, D.A.T. & Ryan, P.D., 2001: PAST: Paleontological statistics software
352 package for education and data analysis. – Palaeontologia Electronica4: art. 4, 9 pp.
353 Hargraves, P. E. & French, F., 1983: Diatom resting spores: significance and strategies. – In
354 Fryxell, G.A. (ed.): Survival strategies of the algae. – Cambridge University Press, pp.
355 49–68.
356 Hasle, G.R. & Syvertsen, E.E., 1997: Marine Diatoms (5–386). In: Tomas, C. R. (ed.):
357 Identifying Marine Phytoplankton. – Academic Press, San Diego, California, pp. 1–385.
358 Heikkilä M., Pospelova V., Forest A., Stern G. A., Fortier L. & Macdonald R. W., 2016:
359 Dinoflagellate cyst production over an annual cycle in seasonally ice-covered Hudson
360 Bay. Marine Micropaleontology. **125**, 1–24.
361 Hellweger, F. L., Kravchuk, E. S., Novotny, V. & Gladyshev, M. I., 2008: Agent based
362 modelling of the complex life cycle of a cyanobacterium (Anabaena) in a shallow
363 reservoir. – Limnology and Oceanography **53**(4): 1227–1241.
364 Hense, I., 2010: Approaches to model the life cycle of harmful algae. – Journal of Marine
365 Systems **83**: 108–114.
366 Hense, I. & Beckmann, A., 2006: Towards a model of cyanobacteria life cycle effects of
367 growing and resting stages on bloom formation of N2-fixing species. – Ecological
368 Modelling **195**(3-4): 205–218.
369 Hense, I. & Burchard, H., 2010: Modelling cyanobacteria in shallow coastal seas. –
370 Ecological Modelling **221**(2): 238–244.

371 Horner, R. & Schrader, G.C., 1982: Relative contributions of ice algae, phytoplankton and
372 benthic microalgae to primary production in nearshore regions of the Beaufort Sea. –
373 Arctic **35**: 485–503.
374 Huitfeld-Kaas, H., 1900: Die limnetischen Peridineen in norwegischen Binnenseen. – Skr.
375 Vidensk.-Selsk. Christiana, Math-Naturvidensk K1., 1-7.
376 Hungarian National Standards, MSZ 12749:1993, 1993: Felszíni vizek minősége, minőségi
377 jellemzők és minősítés. [Quality of surface water, quality characteristics and
378 classification]. Hungarian National Standards Institution.
379 Iriarte, A. & Purdie, D. A., 2004: Factors controlling the timing of major spring bloom events
380 in an UK south coast estuary. – Estuarine, Coastal and Shelf Science **61**: 679–690.
381 Jewson, D. H., 1992: Size reduction, reproductive strategy and the life cycle of a centric
382 diatom. – Philosophical Transactions of the Royal Society of London. Series B:
383 Biological Sciences **336**(1277): 191–213.
384 Jöhnk, K. D., Brüggemann, R., Rucker, J., Luther, B., Simon, U., Nixdorf, B. & Wiedner, C.,
385 2011: Modelling life cycle and population dynamics of Nostocales (cyanobacteria). –
386 Environmental Modelling and Software **26**: 669–677.
387 Kiss, K. T., 1996: Diurnal change of planktonic diatoms in the River Danube near Budapest
388 (Hungary). – Arch. Hydrobiol. Algol. Studies **80**: 113–122.
389 Kiss, K.T. & Genkal, S. I., 1993: Winter blooms of centric diatoms in the River Danube and
390 in its side arms near Budapest. – In. van Dam, H. (ed.): Twelfth International Diatom
391 Symposium. – Kluwer Academic Publishers. – Hydrobiologia **269**(270): 317–325.
392 Kiss, K. T. & Genkal, S. I., 1997: Télvégi–koratavaszi Centrales (Bacillariophyceae)
393 vízvirágzás a Dunán (1996) [Late winter - early spring bloom of centric diatoms in the
394 River Danube at (Göd (1996)]. – Hidrol. Közlöny**77**: 57-58.

Kiss, K.T., Klee, R., Ector, L. & Ács, É., 2012: Centric diatoms of large rivers and tributaries in Hungary: morphology and biogeographic distribution. – Acta Bot. Croat. **71**(2): 1–53.

Klais, R., Tamminen, T., Kremp, A., Spilling, K. & Olli, K., 2011: Decadal-scale changes of dinoflagellates and diatoms in the anomalous Baltic Sea spring bloom. PLoS ONE, 6:e21567. doi:10.1371/journal.pone.0021567.

Kremp, A. & Anderson, D. M., 2000: Factors regulating germination of resting cysts of the spring bloom dinoflagellate *Scrippsiella hangoei* from the northern Baltic Sea. – Journal of Plankton Research. **22**(7): 1311–1327.

Kremp, A., Tamminen, T. & Spilling, K., 2008: Dinoflagellate bloom formation innatural assemblages with diatoms: nutrient competition and growth strategies in Baltic spring phytoplankton. – Aquatic Microbial Ecology **50**(2): 181–196.

Kremp, A., Rengefors, K., Montresor, M., (2009): Species specific encystment patterns in three Baltic cold-water dinoflagellates: The role of multiple cues in resting cyst formation. Limnology and Oceanography. **54** (4) 1125–1138.

Lancelot, C., Spitz, Y., Gypens, N., Ruddick, K., Becquevort, S., Rousseau, V., Lacroix, G. & Billen, G., 2005: Modelling diatom and *Phaeocystis* blooms and nutrient cycles in the Southern Bight of the North Sea: the MIRO model. – Marine Ecology Progress Series **289**: 63–78.

Lefevre, M., 1932: Monographie des espčces d'eau douce du genere Peridinium. Arc. Bot. Mem. Caen. **2**(5): 1–208.

Lewis, J., Harris, A., Jones, K. & Edmonds, R., 1999: Long-term survival of marine planktonic diatoms and dinoflagellates in stored sediment samples. – Journal of Plankton Research **21**(2): 343–354.

419 Lindemann, E., 1918: Untersuchungen über Süβwasser peridineen und ihre Variationsformen.
420 – Arch. Protistenkunde **39**: 209–264.
421 Lindemann, E., 1928: Neue peridineen. – Hedwigia. **68**: 291–296.
422 Mann, D. G., 1988: Why didn't Lund see sex in *Asterionella*? A discussion of the diatom life
423 cycle in nature. – In: Round, F. (ed.): Algae and the Aquatic Environment. – Biopress,
424 pp. 383–412.
425 Olli K. & Anderson D. M., 2002: High encystment success of the dinoflagellate *Scrippsiella*
426 *cf. lachrymosa* in culture experiments. – Journal of Phycology. 21(1): 145–156.
427 Padisák J., Borics, G., Fehér, G., Grigorszky, I., Oldal, I., Schmidt, A. & Zámbóné-D., Zs.,
428 2003: Dominant species, functional assemblages and frequency of equilibrium phases in
429 late summer phytoplankton assemblages in Hungarian small shallow lakes. –
430 Hydrobiologia. **502**: 157–168.
431 Peperzak, L., 2006: Modelling vegetative growth, gamete production and encystment of
432 dinoflagellates in batch culture. – Marine Ecology Progress Series **306**: 143–152.
433 Pfiester, L. A. & Anderson, D. M., 1987: Dinoflagellate reproduction. – Botanical
434 Monographs. – Blackwell Scientific Publications **21**(14): 611–648.
435 Popovsky, I. & Pfiester, L., 1990: Dinophyceae (Dinoflagellida) Süsswasserflora von
436 Mitteleuropa Band 6. p. 272.
437 Reynolds, C. S., 1987a: Community organization in the freshwater plankton. – *In*: Gee, J., H.,
438 R., Giller, P. S. (ed.): The organization of communities, past and present. – Blackwell
439 Scientific Publication – London, pp.297–325.
440 Reynolds, C. S., 1987b: The response of phytoplankton communities to changing lake
441 environments. Swiss J. Hydrol. **49**: 220–236.
442 Round, F., Crawford, R. & Mann, D., 2007: The diatoms: biology and morphology of the
443 genera. – Cambridge University Press., pp.760.

444 Smayda, T. J., 1997: Bloom dynamics: physiology, behaviour, trophic effects. What is a
445 bloom? A commentary. – Limnology and Oceanography **42** (5/2): 1132–1136.
446 Sommer, U., Gliwicz, Z. M., Lampert W. & Duncan A., 1986: The PEG-model of seasonal
447 succession of planktonic events in fresh waters. – Archiv für Hydrobiologie **106**: 433–
448 471.
449 Tedesco, L., Vichi, M. & Thomas, D. N., 2012: Process studies on the ecological coupling
450 between sea ice algae and phytoplankton. – Ecological Modelling **226**: 120–138.
451 Yamamoto, T., Seike, T., Hashimoto, T., & Tarutani, K., 2002: Modelling the population
452 dynamics of the toxic dinoflagellate *Alexandrium tamarense* in Hiroshima Bay, Japan. –
453 Journal of Plankton Research **24**(1): 33–47.
454 West, G.S., 1909: A biological investigation of the Peridinieae of Sutton Park. Warwickshire.
455 – New Phytologist **8**: 181–196.
456

457 Tables and figures captions

458 Table 1. The main physical and chemical variables in 2013 and 2014.

459 Fig.1.a-d. The main investigated variables in 2013 and 2014. Fig. 1.a. Conductivity. Fig. 1.b.

460 Total phosphorus. Fig. 1.c. Nitrate. Fig.1.d. Nitrite.

461 Fig.2.a-d.Fig.2.a. Seasonal distribution of water temperature, vegetative cells and cysts of

462 *Palatinus apiculatus in 2013*.Fig.2.*b.* Seasonal distribution of water temperature, vegetative

463 cells and spores of *Stephanodiscus minutulus* in 2013.Fig.2.c.Seasonal distribution of water

464 temperature, vegetative cells and cysts of *Palatinus apiculatus in 2014*.Fig.2.*d.* Seasonal

465 distribution of water temperature, vegetative cells and spores of *Stephanodiscus minutulus* in

466 2014.

467 Fig.3.a.b. Fig.3.a. Seasonal changes of the main algal taxonomic groups in 2013. Fig.3.b.

468 Seasonal changes of the main algal taxonomic groups in 2014.

469 Fig.4. The linear model fitted to the correlation of coexistent vegetative cells of the

470 investigated two species (A) and their resting cysts and spores (B). Data are in logarithmic

471 values.

472

2013	Mean	Range	Standard deviation	Mean	Range	Standard deviation
		2013			2014	
Temperature (^{o}C)	12.7	4.8-21.1	4.8	13.2	4.6-22,4	5.1
pH	7.4	7.0-7.8	0.30	7.5	7.1-7.9	0.34
Conductivity (μS cm^{-1})	213.0	89.0-422.0	29	229.0	87.0-418.0	27
Secchi depth (m)	1.8	1.5-3.2	0.3	1.9	1.4-3.4	0.3
Oxygen (mg L^{-1})	9.1	7.14-10.8	1.8	8.9	6.85-11.4	1.9
Calcium (mg L^{-1})	6.2	6.0-6.4	0.2	6.3	6.0-6.5	0.2
Magnesium (mg L^{-1})	1.6	0.93-2.24	0.42	1.8	0.90-2.52	0.43
Sodium (mg L^{-1})	3.4	3.0-4.3	0.22	3.6	3.1-4.6	0.25
Potassium (mg L^{-1})	0.42	0.39-0.45	0.03	0.43	0.40-0.47	0.03
Sulphate (mg L^{-1})	1.56	0.98-2.28	0.71	1.63	0.94-2.20	0.68
Total P (μgP L^{-1})	5.6	3.2-12.7	2.7	5.4	3.7-11.8	2.5
Nitrate (μgN L^{-1})	3.7	0.20-4.1	0.7	3.8	0.18-4.7	0.8
Nitrite (μgN L^{-1})	0.8	0.1-1.8	0.28	0.7	0.15-1.9	0.25

473

474 Table 1.