Check for updates

LIMNOLOGY and OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 9999, 2021, 1–20
© 2021 The Authors. *Limnology and Oceanography* published by Wiley Periodicals LLC on behalf of Association for the Sciences of Limnology and Oceanography.
doi: 10.1002/lno.11963

Stratification strength and light climate explain variation in chlorophyll *a* at the continental scale in a European multilake survey in a heatwave summer

Daphne Donis,[1*] Evanthia Mantzouki,[1] Daniel F. McGinnis,[1] Dominic Vachon,[1,2] Irene Gallego,[1,a] Hans-Peter Grossart,[3,4] Lisette N. de Senerpont Domis,[5,7] Sven Teurlincx,[5] Laura Seelen,[5,7] Miquel Lürling,[5,6] Yvon Verstijnen,[6] Valentini Maliaka,[6,8,9] Jeremy Fonvielle,[3] Petra M. Visser,[10] Jolanda Verspagen,[10] Maria van Herk,[10] Maria G. Antoniou,[11] Nikoletta Tsiarta,[11] Valerie McCarthy,[12] Victor C. Perello,[12] Danielle Machado-Vieira,[13] Alinne Gurjão de Oliveira,[13] Dubravka Špoljarić Maronić,[14] Filip Stević,[14] Tanja Žuna Pfeiffer,[14] Itana Bokan Vucelić,[15] Petar Žutinić,[16] Marija Gligora Udovič,[16] Anđelka Plenković-Moraj,[16] Luděk Bláha,[17] Rodan Geriš,[18] Markéta Fránková,[19] Kirsten Seestern Christoffersen,[20] Trine Perlt Warming,[20] Tõnu Feldmann,[21] Alo Laas,[21] Kristel Panksep,[21] Lea Tuvikene,[21] Kersti Kangro,[21,22] Judita Koreivienė,[23] Jūratė Karosienė,[23] Jūratė Kasperovičienė,[23] Ksenija Savadova-Ratkus,[23] Irma Vitonytė,[23] Kerstin Häggqvist,[24] Pauliina Salmi,[25] Lauri Arvola,[26] Karl Rothhaupt,[27] Christos Avagianos,[28] Triantafyllos Kaloudis,[28] Spyros Gkelis,[29] Manthos Panou,[29] Theodoros Triantis,[30] Sevasti-Kiriaki Zervou,[30] Anastasia Hiskia,[30] Ulrike Obertegger,[31] Adriano Boscaini,[31] Giovanna Flaim,[31] Nico Salmaso,[31] Leonardo Cerasino,[31] Sigrid Haande,[32] Birger Skjelbred,[32] Magdalena Grabowska,[33] Maciej Karpowicz,[33] Damian Chmura,[34] Lidia Nawrocka,[35] Justyna Kobos,[36] Hanna Mazur-Marzec,[36] Pablo Alcaraz-Párraga,[37] Elżbieta Wilk-Woźniak,[38] Wojciech Krztoń,[38] Edward Walusiak,[38] Ilona Gagala-Borowska,[39] Joana Mankiewicz-Boczek,[39] Magdalena Toporowska,[40] Barbara Pawlik-Skowronska,[40] Michał Niedźwiecki,[40] Wojciech Pęczuła,[40] Agnieszka Napiórkowska-Krzebietke,[41] Julita Dunalska,[42] Justyna Sieńska,[42] Daniel Szymański,[42] Marek Kruk,[43] Agnieszka Budzyńska,[44] Ryszard Goldyn,[44] Anna Kozak,[44] Joanna Rosińska,[44] Elżbieta Szeląg-Wasielewska,[44] Piotr Domek,[44] Natalia Jakubowska-Krepska,[44] Kinga Kwasizur,[45] Beata Messyasz,[45] Aleksandra Pełechata,[45] Mariusz Pełechaty,[45] Mikolaj Kokocinski,[45] Beata Madrecka-Witkowska,[46] Iwona Kostrzewska-Szlakowska,[47] Magdalena Frąk,[48] Agnieszka Bańkowska-Sobczak,[49] Michał Wasilewicz,[49] Agnieszka Ochocka,[50] Agnieszka Pasztaleniec,[50] Iwona Jasser,[51] Ana M. Antão-Geraldes,[52] Manel Leira,[53] Vitor Vasconcelos,[54] Joao Morais,[54] Micaela Vale,[54] Pedro M. Raposeiro,[55] Vítor Gonçalves,[55] Boris Aleksovski,[56] Svetislav Krstić,[56] Hana Nemova,[57] Iveta Drastichova,[57] Lucia Chomova,[57] Spela Remec-Rekar,[58] Tina Elersek,[59] Lars-Anders Hansson,[60] Pablo Urrutia-Cordero,[60,61] Andrea G. Bravo,[61] Moritz Buck,[61] William Colom-Montero,[62] Kristiina Mustonen,[62] Don Pierson,[62] Yang Yang,[62] Jessica Richardson,[63] Christine Edwards,[64] Hannah Cromie,[65] Jordi Delgado-Martín,[66] David García,[66] Jose Luís Cereijo,[66] Joan Gomà,[67] Mari Carmen Trapote,[67] Teresa Vegas-Vilarrúbia,[67] Biel Obrador,[67] Ana García-Murcia,[68] Monserrat Real,[68] Elvira Romans,[68] Jordi Noguero-Ribes,[68] David Parreño Duque,[68]

*Correspondence: daphne.donis@unige.ch

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

Additional Supporting Information may be found in the online version of this article.

[a]Present address: Department Aquatic Ecology, Eawag Überlandstrasse, Dübendorf, Switzerland

Author Contribution Statement: D.D. analyzed and worked on data visualization, coordinated feedback from coauthors, and wrote the manuscript. E.M. coordinated the EMLS, collected data, curated the dataset, analyzed the data, and contributed to writing the manuscript. B.I. conceived the idea for the EMLS, contributed to discussions throughout the study and to the writing of the manuscript. D.M., D.V., I.G., H.-P.G., L.N.d.S.D., S.T., L.S., N.C., A.G.B., M.B., P.V., and C.C. assisted in analyzing and interpreting the dataset. The rest of the coauthors were responsible for finalizing the sampling protocols, organizing the local surveys, collecting data in their respective countries, and providing invaluable feedback on the manuscript and data analysis.

Elísabeth Fernández-Morán,[68] Bárbara Úbeda,[69] José Ángel Gálvez,[69] Núria Catalán,[70] Carmen Pérez-Martínez,[71] Eloísa Ramos-Rodríguez,[71] Carmen Cillero-Castro,[72] Enrique Moreno-Ostos,[73] José María Blanco,[73] Valeriano Rodríguez,[73] Jorge Juan Montes-Pérez,[73] Roberto L. Palomino,[73] Estela Rodríguez-Pérez,[73] Armand Hernández,[74] Rafael Carballeira,[75] Antonio Camacho,[76] Antonio Picazo,[76] Carlos Rochera,[76] Anna C. Santamans,[76] Carmen Ferriol,[76] Susana Romo,[77] Juan Miguel Soria,[77] Arda Özen,[78] Tünay Karan,[79] Nilsun Demir,[80] Meryem Beklioğlu,[81] Nur Filiz,[81] Eti Levi,[81] Uğur Iskin,[81] Gizem Bezirci,[81] Ülkü Nihan Tavşanoğlu,[81] Kemal Çelik,[82] Koray Ozhan,[83] Nusret Karakaya,[84] Mehmet Ali Turan Koçer,[85] Mete Yilmaz,[86] Faruk Maraşlıoğlu,[87] Özden Fakioglu,[88] Elif Neyran Soylu,[89] Meral Apaydın Yağcı,[90] Şakir Çınar,[90] Kadir Çapkın,[90] Abdulkadir Yağcı,[90] Mehmet Cesur,[90] Fuat Bilgin,[90] Cafer Bulut,[90] Rahmi Uysal,[90] Köker Latife,[91] Reyhan Akçaalan,[91] Meriç Albay,[91] Mehmet Tahir Alp,[92] Korhan Özkan,[93] Tuğba Ongun Sevindik,[94] Hatice Tunca,[94] Burçin Önem,[94] Hans Paerl,[95] Cayelan C. Carey,[96] Bastiaan W. Ibelings[1]

[1]Department F.-A. Forel for Environmental and Aquatic Sciences and Institute for Environmental Sciences, University of Geneva, Geneva, Switzerland
[2]Department of Ecology and Environmental Sciences, Umeå University, Umeå, Sweden
[3]Department of Experimental Limnology, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Stechlin, Germany
[4]Institute of Biochemistry and Biology, Potsdam University, Potsdam, Germany
[5]Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands
[6]Department of Environmental Sciences, Wageningen University & Research, Wageningen, The Netherlands
[7]Department of Environmental Sciences, Aquatic Ecology and Water Quality Management group, Wageningen University, Wageningen, 6708 PB, The Netherlands
[8]Society for the Protection of Prespa, Agios Germanos, Greece
[9]Department of Aquatic Ecology and Environmental Biology, Institute for Water and Wetland Research, Radboud University Nijmegen, Nijmegen, The Netherlands
[10]Department of Freshwater and Marine Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands
[11]Department of Chemical Engineering, Cyprus University of Technology, Lemesos, Cyprus
[12]Centre for Freshwater and Environmental Studies, Dundalk Institute of Technology, Dundalk, Ireland
[13]Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, Paraíba, Brazil
[14]Department of Biology, Josip Juraj Strossmayer University of Osijek, Osijek, Croatia
[15]Department for Ecotoxicology, Teaching Institute of Public Health of Primorje-Gorski Kotar County, Rijeka, Croatia
[16]Department of Biology, Faculty of Science, University of Zagreb, Zagreb, Croatia
[17]RECETOX, Faculty of Science, Masaryk University, Brno, Czech Republic
[18]Department of Hydrobiology, Morava Board Authority, Brno, Czech Republic
[19]Department of Paleoecology, Institute of Botany, The Czech Academy of Sciences, Brno, Czech Republic
[20]Freshwater Biological Laboratory, Department of Biology, University of Copenhagen, Copenhagen, Denmark
[21]Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Tartu, Estonia
[22]Tartu Observatory, Faculty of Science and Technology, University of Tartu, Tartu, Estonia
[23]Institute of Botany, Nature Research Centre, Vilnius, Lithuania
[24]Department of Science and Engineering, Åbo Akademi University, Åbo, Finland
[25]Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland
[26]Lammi Biological Station, University of Helsinki, Lammi, Finland
[27]Department of Biology, Limnological Institute, University of Konstanz, Konstanz, Germany
[28]Water Quality Department, Athens Water Supply and Sewerage Company, Athens, Greece
[29]Department of Botany, School of Biology, Aristotle University of Thessaloniki, Thessaloniki, Greece
[30]Institute of Nanoscience and Nanotechnology, National Center for Scientific Research «DEMOKRITOS», Agia Paraskevi, Attiki, Greece
[31]Research and Innovation Centre, Fondazione Edmund Mach, San Michele all'Adige, 38010, Italy
[32]Department of Freshwater Ecology, Norwegian Institute for Water Research, Oslo, Norway
[33]Department of Hydrobiology, University of Bialystok, Bialystok, Poland
[34]Institute of Environmental Protection and Engineering, University of Bielsko-Biala, Bielsko-Biala, Poland
[35]Institute of Technology, The State University of Applied Sciences, Elblag, Poland
[36]Department of Marine Biotechnology, University of Gdansk, Gdynia, Poland
[37]Department of Animal Biology, Plant Biology and Ecology, University of Jaen, Jaen, Spain
[38]Institute of Nature Conservation, Polish Academy of Sciences, Krakow, Poland
[39]European Regional Centre for Ecohydrology of the Polish Academy of Sciences, Lodz, Poland

[40]Department of Hydrobiology and Protection of Ecosystems, University of Life Sciences in Lublin, Lublin, Poland
[41]Department of Ichthyology, Hydrobiology and Aquatic Ecology, S. Sakowicz Inland Fisheries Institute, Olsztyn, 10-719, Poland
[42]Department of Water Protection Engineering, University of Warmia and Mazury, Olsztyn, Poland
[43]Department of Applied Computer Science and Mathematical Modelling, University of Warmia and Mazury, Olsztyn, 10-710, Poland
[44]Department of Water Protection, Faculty of Biology, Adam Mickiewicz University, Poznan, Poland
[45]Department of Hydrobiology, Faculty of Biology, Adam Mickiewicz University, Poznan, Poland
[46]Institute of Environmental Engineering and Building Installations, Faculty of Environmental Engineering and Energy, Poznan University of Technology, Poznan, 60965, Poland
[47]Faculty of Biology, University of Warsaw, Warsaw, Poland
[48]Department of Remote Sensing and Environmental Assessment, Institute of Environmental Engineering, Warsaw University of Life Sciences - SGGW, Nowoursynowska Str. 166, Warsaw, 02-787, Poland
[49]Department of Water Engineering and Applied Geology, Faculty of Civil and Environmental Engineering, Warsaw University of Life Sciences – SGGW, Warsaw, 02-787, Poland
[50]Department of Freshwater Protection, Institute of Environmental Protection - National Research Institute, Warsaw, Poland
[51]Department of Plant Ecology and Environmental Conservation, Faculty of Biology, University of Warsaw, Warsaw, 02-089, Poland
[52]Centro de Investigação da Montanha (CIMO), Instituto Politécnico de Bragança, Bragança, Portugal
[53]BioCost Research Group, Faculty of Science and Centro de Investigacións Científicas Avanzadas (CICA), Department of Biology, Faculty of Science, University of A Coruña, A Coruña, 15071, Spain
[54]Interdisciplinary Centre of Marine and Environmental Research (CIIMAR/CIMAR), University of Porto, Terminal de Cruzeiros do Porto de Leixões, Matosinhos, 4450-208, Portugal
[55]Research Center in Biodiversity and Genetic Resources (CIBIO-Azores), InBIO Associated Laboratory, Faculty of Sciences and Technology, University of the Azores, Ponta Delgada, 9500-321, Portugal
[56]Faculty of Natural Sciences and Mathematics, SS Cyril and Methodius University, Skopje, Macedonia
[57]National Reference Center for Hydrobiology, Public Health Authority of the Slovak Republic, Bratislava, Slovakia
[58]Department of Water Quality, Slovenian Environmental Agency, Ljubljana, Slovenia
[59]Department of Genetic Toxicology and Cancer Biology, National Institute of Biology, Ljubljana, Slovenia
[60]Department of Biology, Lund University, Lund, Sweden
[61]Department of Ecology and Genetics, Limnology, Uppsala University, Uppsala, Sweden
[62]Department of Ecology and Genetics, Erken Laboratory, Uppsala University, Norrtalje, Sweden
[63]Department of Biological and Environmental Sciences, University of Stirling, Stirling, UK
[64]School of Pharmacy and Life Sciences, Robert Gordon University, Aberdeen, UK
[65]Agri-Food & Biosciences Institute, Belfast, UK
[66]Department of Civil Engineering, University of A Coruña, A Coruña, Spain
[67]Department of Evolutionary Biology, Ecology, and Environmental Sciences, University of Barcelona, Barcelona, Spain
[68]Department of Limnology and Water Quality, AECOM U.R.S., Barcelona, Spain
[69]Department of Biology, INMAR Marine Research Institute, University of Cádiz, Cádiz, 11510 Puerto Real, Spain
[70]Catalan Institute for Water Research (ICRA), Girona, Spain
[71]Department of Ecology and Institute of Water Research, University of Granada, Granada, Spain
[72]R&D Department Environmental Engineering, 3edata, Lugo, Spain
[73]Department of Ecology, University of Malaga, Malaga, Spain
[74]Institute of Earth Sciences Jaume Almera, ICTJA, CSIC, Barcelona, Spain
[75]Centro de Investigacións Cientificas Avanzadas (CICA), Facultade de Ciencias, Universidade da Coruña, A Coruña, Spain
[76]Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Valencia, Spain
[77]Department of Microbiology and Ecology, University of Valencia, Burjassot, Spain
[78]Department of Forest Engineering, University of Cankiri Karatekin, Cankiri, Turkey
[79]Department of Animal Nutrition and Zootechnics, Faculty of Veterinary Medicine, Yozgat Bozok University, Yozgat, Turkey
[80]Department of Fisheries and Aquaculture Engineering, Ankara University, Ankara, 06110, Turkey
[81]Department of Biological Sciences, Limnology Laboratory, Middle East Technical University, Ankara, Turkey
[82]Department of Biology, Balikesir University, Balikesir, Turkey
[83]Department of Oceanography, Institute of Marine Sciences, Middle East Technical University, Ankara, Turkey
[84]Department of Environmental Engineering, Abant Izzet Baysal University, Bolu, Turkey
[85]Department of Environment and Resource Management, Mediterranean Fisheries Research Production and Training Institute, Antalya, Turkey
[86]Department of Bioengineering, Bursa Technical University, Bursa, Turkey
[87]Department of Biology, Hitit University, Corum, Turkey

[88]Department of Basic Science, Ataturk University, Erzurum, Turkey
[89]Department of Biology, Giresun University, Giresun, Turkey
[90]Republic of Turkey Ministry of Food Agriculture, Fisheries Research Institute, Isparta, Turkey
[91]Department of Freshwater Resource and Management, Faculty of Aquatic Sciences, Istanbul University, Istanbul, Turkey
[92]Faculty of Aquaculture, Mersin University, Mersin, Turkey
[93]Institute of Marine Sciences, Marine Biology and Fisheries, Middle East Technical University, Mersin, Turkey
[94]Department of Biology, Sakarya University, Sakarya, Turkey
[95]Institute of Marine Sciences, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina
[96]Department of Biological Sciences, Virginia Tech, Blacksburg, Virginia

Abstract

To determine the drivers of phytoplankton biomass, we collected standardized morphometric, physical, and biological data in 230 lakes across the Mediterranean, Continental, and Boreal climatic zones of the European continent. Multilinear regression models tested on this snapshot of mostly eutrophic lakes (median total phosphorus [TP] = 0.06 and total nitrogen [TN] = 0.7 mg L^{-1}), and its subsets (2 depth types and 3 climatic zones), show that light climate and stratification strength were the most significant explanatory variables for chlorophyll *a* (Chl *a*) variance. TN was a significant predictor for phytoplankton biomass for shallow and continental lakes, while TP never appeared as an explanatory variable, suggesting that under high TP, light, which partially controls stratification strength, becomes limiting for phytoplankton development. Mediterranean lakes were the warmest yet most weakly stratified and had significantly less Chl *a* than Boreal lakes, where the temperature anomaly from the long-term average, during a summer heatwave was the highest (+4°C) and showed a significant, exponential relationship with stratification strength. This European survey represents a summer snapshot of phytoplankton biomass and its drivers, and lends support that light and stratification metrics, which are both affected by climate change, are better predictors for phytoplankton biomass in nutrient-rich lakes than nutrient concentrations and surface temperature.

Globally, temperature, light, and nutrients are key drivers of phytoplankton blooms, but their relative importance in determining algal biomass strongly depends on the role of thermal stratification, that is, water column stability (Sverdrup 1953; Cloern 1996; Ptacnik et al. 2003; Carvalho et al. 2016). As a matter of fact, the relative importance of these drivers and interactive mechanisms between them cannot be fully resolved without including thermal stability (Winslow et al. 2017). This is particularly relevant under global processes of eutrophication and climate warming (Sinha et al. 2017) as some research foresees an allied impact of eutrophication and climate change effects in promoting harmful cyanobacterial blooms (Moss et al. 2011).

Stratification suppresses the exchange of heat and dissolved substances between the epi- and hypolimnion by reducing turbulent motions that otherwise would facilitate transport (Wüest and Lorke 2003). While the vertical structure of the water column constitutes the first response to temperature fluctuations (Sahoo et al. 2016), it also regulates the development of phytoplankton biomass by affecting light and nutrient availability (Yang et al. 2016), as well as phytoplankton settling, and therefore exerts a strong control on lake ecosystem functioning (Scheffer et al. 2001; Bartosiewicz et al. 2015).

Especially when nutrients are not limiting (e.g., in eutrophic lakes), light climate and stratification strength likely play dominant roles in regulating phytoplankton biomass (Fig. 1), and this role of light as a limiting resource has been suggested since the early days of eutrophication research (Mur et al. 1977). In general, by controlling light and nutrient availability, the underwater light climate and stratification strength determine phytoplankton growth conditions. When stratification is strong, thus suppressing fluxes from the deeper layers, mixing is restricted to the surface layer. Under such conditions, phytoplankton is constantly maintained within the euphotic zone, promoting algal growth until nutrients are depleted or other factors as grazing and sedimentation take over in controlling phytoplankton biomass (Fig. 1a; Camacho 2006; Reynolds 2006; Yankova et al. 2017). When stratification is weak, water column mixing can reach deep and nutrient rich waters, however potentially taking the algal communities beyond the euphotic zone that would limit their growth (Ibelings et al. 1994; Fig. 1b). One other ecological consequence of a strongly stratified lake is that phytoplankton may have reduced access to nutrients that remain locked in the hypolimnion (Nürnberg 1984; Posch et al. 2012; Salmaso et al. 2020). Yet, while the strength of stratification is determined primarily by light climate and heat exchange, other factors too can affect the extent and duration of the stratification, such as lake morphology (i.e., basin geometry, maximum depth and surface area) (Thompson and Schmidt 2005; Kirillin and Shatwell 2016; Magee and Wu 2017) as well as the dissolved organic and inorganic carbon content of the water, wind orientation and sheltering. Dissolved organic matter in general can have a huge impact on stratification by influencing light penetration,

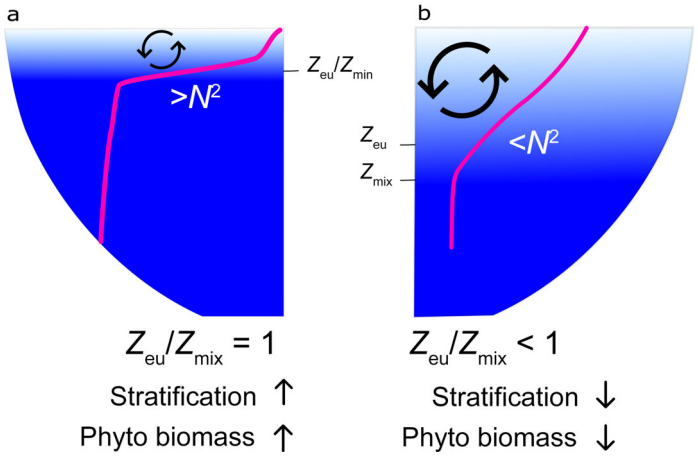


Fig 1. Schematic overview of how lake N^2 and light climate (Z_{eu}/Z_{mix}) may define phytoplankton biomass in nutrient-rich lakes. (**a**) A strong stratification ($> N^2$) allows phytoplankton to circulate well within the euphotic zone ($Z_{eu}/Z_{mix} \geq 1$)—promoting growth. (**b**) A weaker stratification ($< N^2$) allows deeper mixing, hence phytoplankton communities are highly diluted—eventually below the euphotic zone ($Z_{eu}/Z_{mix} < 1$).

and consequently surface heating, as seen in humic boreal lakes (Heiskanen et al. 2014). Wind and convection, acting on the surface mixed layer (SML), control a lake's interior diffusive fluxes regulating the physical environment experienced by phytoplankton. Important properties of the SML, such as its depth, vary widely among lakes as the result of a specific balance between factors that strengthen stratification (surface warming), and factors that disrupt or deepen the layer, such as wind shear and surface cooling (Imberger 1985; Imboden and Wüest 1995; Boehrer and Schultze 2008).

Stratification of lakes is changing under the impact of eutrophication, re-oligotrophication and climate warming (Flaim et al. 2016). For instance, in recent decades, the strength of stratification of lakes in northeastern North America has clearly increased (Richardson et al. 2017); a phenomenon that might be further enhanced by a trend of atmospheric stilling (Woolway and Merchant 2019). Analyses of the 2007 National Lake Assessment, NLA dataset (Pollard et al. 2018) showed that synergistic interactions between nutrients and temperature promoting algal or cyanobacterial developments are probable, especially in the eutrophic and hypereutrophic subsets of NLA lakes (Rigosi et al. 2014). Kosten et al. (2012) provided more support for synergistic interactions between nutrients and temperature in determining chlorophyll *a* (Chl *a*) and cyanobacterial dominance in a multilake survey along a latitudinal gradient stretching from the tip of South America to the equator. However, no lake physical variables other than surface temperature, such as density gradient or stratification strength, were included in these large-scale studies on drivers of algal biomass.

To further our understanding of the main drivers and their interactions on phytoplankton biomass across continental climatic gradients, the "grassroots" European Multi Lake Survey (EMLS) was organized during summer 2015, which coincided with the period of maximum stratification in most of the examined lakes. Data from the EMLS are publicly available (Mantzouki et al. 2018). Here, we report on the difference in Chl *a* as a proxy for phytoplankton biomass between 230 of the EMLS lakes to: (1) determine the dependency of phytoplankton biomass at the continental scale on a set of ecosystem drivers, including growth conditions (total phosphorous [TP], total nitrogen [TN], lake temperature, and light) and morphophysical properties (lake depth, surface area, light climate, and stratification strength); and (2) investigate potential interactions between these predictors that influence phytoplankton biomass.

Methods

EMLS organization

During the EMLS in summer 2015, 230 lakes were sampled across major geographical and climatic regions in Europe for various chemical, physical, and biological parameters using highly standardized sampling protocols (Mantzouki et al. 2018; Mantzouki and Ibelings 2018). All key variables were analyzed centrally (by one person on one machine) in dedicated laboratories to ensure data comparability and a fully integrated dataset.

The lake sampling site was selected as either the historical sampling point, for which long-term records exist, or the geographic center of the lake. The sampling period was defined as the warmest 2-week period of the summer, based on long-term (minimum 10 yr) air temperature data of each region. An in situ temperature profile carried out on the sampling day was used to identify and characterize the thermocline as the point where there was ≥ 1°C change of temperature per meter lake depth. An integrated water sample was obtained from 0.5 m depth to the bottom of the thermocline using a water sampler that could effectively sample the whole volume without creating intervals. In nonstratified shallow lakes, an integrated sample was drawn from 0.5 m below the lake surface to 0.5 m above the lake bottom.

Nutrient analyses

Total phosphorus and nitrogen concentrations were assessed in unfiltered samples. Sample bottles were acid washed overnight in 1 M HCl and rinsed with demineralized water before usage. Nutrients were measured using a Skalar SAN+ segmented flow analyzer (Skalar Analytical BV, Breda, the Netherlands) with UV/persulfate digestion integrated in the system. The limit of detection was 0.02 mg L^{-1} for TP and 0.2 mg L^{-1} for TN. TP was analyzed following NEN (1986) and TN according to NEN (1990). All nutrient analyses were performed at the University of Wageningen, the Netherlands.

Pigment analyses

Pigment analysis, modified from the method described by Van der Staay et al. (1992), was carried out to determine concentrations of Chl *a* and Zeaxanthin (Zea). Measurement of Zea concentrations in the EMLS lakes were carried out with the aim of investigating cyanobacterial biomass, alongside to the general phytoplankton biomass estimate obtained with Chl *a*. Filters (45 mm diameter GF/C or /F) were freeze-dried for 6 h and then cut in half, placed in separate Eppendorf tubes, and kept on ice. A number of 0.5 mm beads and 600 μL of 90% acetone were added to each tube. To release the pigments from the phytoplankton cells and increase the extraction yield, tubes were placed on a bead-beater for 1 min and then in an ultrasonic bath for 10 min. To ensure complete extraction of the total pigment content of the filters, the bead-beater and ultrasonic bath steps were performed twice. To achieve binding of the pigments during the high-performance liquid chromatography (HPLC) analysis, 300 μL of a tributyl ammonium acetate (1.5%) and ammonium acetate (7.7%) mix were added to each tube. Lastly, samples were centrifuged at 15,000 rpm and 4°C for 10 min. Next, 35 μL of the supernatant from Eppendorf tubes were transferred into glass HPLC sampling vials. Pigments were separated on a Thermo Scientific ODS Hypersil column (250 mm × 3 mm, particle size 5 μm) in a Shimadzu HPLC, using a KONTRON SPD-M2OA diode array detector. The different pigments were identified based on their retention time and absorption spectrum and quantified by means of pigment standards. Pigment analysis was performed at the University of Amsterdam, the Netherlands.

Lake groups

Lake classification was based on climatic zone and depth type. Predicted climatic zones based on different IPCC scenarios (2000–2025; Rubel and Kottek 2010) were used to avoid the inconsistency in available digital maps, especially for areas such as the Alpine region (Rubel et al. 2017). The climatic zones were defined using the Köppen-Geiger's classification (Köppen 1900). This classification regards the main climate of the region (C = warm temperate, D = alpine), precipitation levels (f = fully humid, s = summer dry), and mean temperature (a = hot summers, b = warm summers). For easier interpretation and more statistical power, climatic regions that were of the same main climate and precipitation level were combined in three main ones: Mediterranean (Csa and Csb, n = 54 lakes), Continental (Cfa and Cfb, n = 128 lakes), and Boreal (Dfb and Dfc, n = 48 lakes) (Fig. 2). This way, only the mean temperature varied within each of the combined groups, which allowed for testing of a temperature gradient. The selection of climatic zones has a clear advantage over a latitudinal analysis, as several lakes within the Continental region are classified as Boreal lakes based on their climatic characteristics rather than their position on a latitudinal gradient (*see* Table S1 for list of EMLS lakes and corresponding climatic zone).

The EMLS lakes were categorized into shallow (< 6 m maximum depth, n = 93 lakes) and deep (> 6 m maximum depth, n = 137 lakes). This classification was used in previous snapshot surveys as an approximation for weakly or strongly thermally stratified systems (Kosten et al. 2012; Beaulieu et al. 2013).

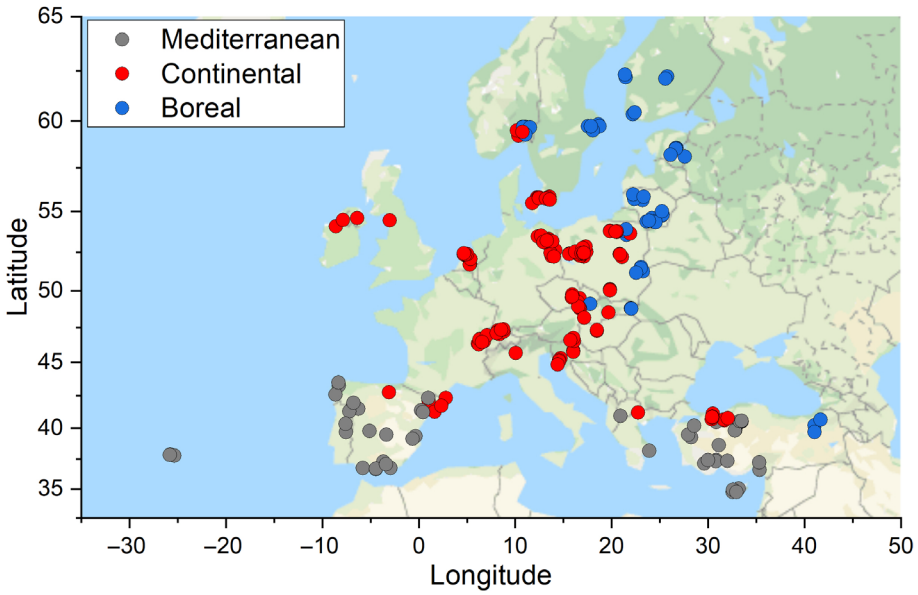


Fig 2. Location of the 230 EMLS lakes distributed over the main climatic zones of the European continent (Rubel and Kottek 2010). The Mediterranean region (n = 54) consists of Csa and Csb classes (C, warm temperate; s, summer dry; a, hot summer; b, warm summer), the Continental region (n = 128) of Cfa and Cfb (f, fully humid; rest as above), and the Boreal region (n = 48) of Dfb and Dfc (D, snow; c, cool summer; rest as above).

Table 1. List of lake variables with their units, range of values, means, medians, and standard deviations for the 230 EMLS lakes. Variables with * are included in the linear models.

Variable		Units	Range	Mean ± SD	Median
Maximum depth	maxD	m	1–310	23±41	10.00
Surface area*	SurfA	km^2	0.001–580	19±69	5
Total nitrogen*	TN	mg L^{-1}	0.1–5	1.0±0.8	0.70
Total phosphorus*	TP	mg L^{-1}	0.02–1	0.1±0.1	0.06
Surface temperature*	SurfT	°C	14.6–33	23±3.4	22.4
Average temperature	AvT	°C	13.4–33	21±3.5	20.6
Secchi depth	SD	m	0.16–10	1.8±1.7	1.19
Light climate*	Z_{eu}/Z_{mix}	-	0.02–11	1.0±1.0	0.63
Stratification strength *	N^2	s^{-2}	$3{\cdot}10^{-5}$–$3{\cdot}10^{-2}$	$5{\cdot}10^{-3}$±$4{\cdot}10^{-3}$	4.10^{-3}
Chlorophyll *a**	Chl *a*	μg L^{-1}	0.03–933	44±110	9.98
Zeaxanthin	Zea	μg L^{-1}	0.00–90	3±9.7	0.68

Statistical analysis

To disentangle the importance of various drivers of phytoplankton biomass, we applied linear regression models to six lake groups: all, deep, shallow, Mediterranean, Continental, Boreal. We (1) assessed the quality of the statistical models after excluding collinear and nonsignificant variables, (2) included groups of interactions and nominal variables as environmental predictors, and (3) discussed the three most important predictors for each model.

Response variable and environmental predictors

The response variable of all regression models was the concentration of Chl *a* obtained from the HPLC analysis, which was used as a proxy for total phytoplankton biomass (Pinckney et al. 2001; Tamm et al. 2015) and tested with the following single predictors: maximum depth (maxD), surface area (SurfA), TN, TP, surface temperature (SurfT), average temperature (AvT), Secchi disk depth (SD), light climate (Z_{eu}/Z_{mix}), and maximum buoyancy frequency (stratification strength, N^2) (Table 1).

Surface and average temperatures were determined via a water column profile with a temperature probe, taking respectively the temperature of the top 0.5 m of the water column and the average of the full profile.

Light climate was defined as the ratio of euphotic depth over mixing depth (Z_{eu}/Z_{mix}), which describes the light that phytoplankton experience while circulating through the water column (Scheffer et al. 1997). The equation $Z_{eu} = 2 \times$ SD (Secchi depth) was used to calculate Z_{eu} (equation selected as an average estimate from the range of constants reported in literature, e.g., Koenings and Edmundson 1991; Salmaso 2002; Brentrup et al. 2018). In stratified lakes, Z_{mix} was determined as the depth of the steepest density gradient (Winslow et al. 2017). In nonstratified shallow lakes, Z_{mix} matched the maximum depth and sampling depth. Water density was calculated according to the combined effects of salinity (set to 0) and water temperature based on the method of Millero and Poisson (1981).

Lake stratification is the density-induced layering of the water column (Boehrer and Schultze 2008). Strength of water column stratification was determined by the N^2 given by the Brunt Väisälä equation or buoyancy frequency, N (s^{-1}).

$$N = \sqrt{-\frac{g}{\rho}\left(\frac{\partial \rho}{\partial z}\right)}; N^2 = -\frac{g}{\rho}\left(\frac{\partial \rho}{\partial z}\right) \quad (1)$$

Buoyancy frequency is greater than zero, when a water volume (of density ρ) that is displaced vertically (z) from its initial position without heat transfer, experiences a restoring force. If $N^2 < 0$ instead, the water parcel tends to be displaced away from its initial position and the vertical water column is locally unstable. Here, we use the symbol N^2 to indicate the maximum value over the entire water column. By suppressing vertical turbulent eddies, density stratification determines the water column stability so that, in general, the greater the density gradient, the slower the diffusive exchange of water constituents between the hypolimnion and the epilimnion (Boehrer and Schultze 2008).

Three groups of interactions between some of the aforementioned variables, selected based on ecological theory and previous literature, were included as additional predictors in the models. Namely the interaction between (1) nutrients and surface temperature (Rigosi et al. 2014), (2) stratification strength and light climate (Graff and Behrenfeld 2018), and (3) surface area and light climate.

Analysis of variance

Differences in mean values of the selected variables within climatic zones and depth types were tested using one-way ANOVA. Homogeneity of variance was tested using the Levene's test from the car R package (Fox and Weisberg 2011). In case of heterogeneity, a Kruskal–Wallis test was used instead of ANOVA. Post hoc

pairwise comparisons for unequal sample sizes were performed using Tukey HSD (Honest Significant Difference) or Games–Howell test (userfriendlyscience R package; Peters et al. 2018) for homogeneous or heterogeneous variance, respectively.

Multiple linear regression model

All variables were log-transformed (natural logarithm) to obtain a normal and homogeneous distribution. Stepwise selection (backwards and forward) was used for model selection where the AIC scores were compared based on a modified equation that corrects for unequal sample size among categories (R code provided by Statoo Consulting, Switzerland). If the interaction term was significant ($p \leq 0.05$), the lower order terms were included in the equation. The most parsimonious model, in which elimination or addition of any other predictors would not improve the model by $\Delta AIC > 2$, was used for the ANOVA. The metric "lmg" of the relaimpo R package (Grőmping 2006) was used to decompose the overall R^2 of each final model into the absolute contributions of each predictor term and their interaction terms (similarly done in Rigosi et al. 2014). The relative contribution of each predictor was normalized, by forcing the sum to 100%. A bootstrapping approach was used to replicate the observed data 9999 times and determine if there were any clear differences between the predictors of the interaction terms with regards their relative contribution to the interaction term (Grőmping 2006). If those differences included zero, it indicated that the predictors were not significantly different from each other, meaning that they contributed similarly to the interaction term. When the interaction term had a significant value of $p < 0.05$ and was positive, it was interpreted as a synergistic interaction.

To avoid multicollinearity between the interactions and their main effects, we checked the variance inflation factor (VIF). If VIFs were exhibiting high numbers (VIF > 3, threshold according to (Zuur et al. 2010), we centered the interaction term with the mean of the raw variables which alleviated the collinearity problem.

We applied multiple linear regression models to test the relative importance of the selected response variables in explaining Chl *a* variance. The model applied was:

$$\text{Chl}\,a = A_0 + A_1 X_{\text{SurfA}} + A_2 X_{N2} + A_3 X_{\text{SurfT}} + A_4 X_{\text{TN}} + A_5 X_{\text{Zeu/Zmix}} + A_6 X_{N2*\text{Zeu/Zmix}} + \varepsilon \quad (2)$$

where A_0 represents the intercept term, A_1–A_6 are model parameters for each respective predictor in the models, "*" denotes the interaction between two terms, and ε is an error term. Two multiple linear regression models were applied to the entire EMLS group of lakes. Apart from the full set of environmental predictors, each of these two models included the nominal variable "depth type" or "climatic zone" (see Supplementary Material for more

Table 2. List of applied models and relative metrics. AIC does not apply correctly if number of observations is not the same, for which we rely on R^2.

Lake group	Multilinear model	*N* lakes	R^2	AIC
(1) All-a	Chl $a = -9.06 - 0.23$ (SurfA) $- 0.31$ (N^2) $+ 3.36$ (SurfT) $+ 0.46$ (TN) $+ 0.47$ (Z_{eu}/Z_{mix}) $+ 0.18$ (N^2*Z_{eu}/Z_{mix}) $-$ 0.90 (Cont) $-$ 2.06 (Med)	230	35%	842.43***
(2) All-b	Chl $a = -2.44 - 0.15$ (SurfA) $- 0.11$ (N^2) $+ 1.12$ (SurfT) $+ 0.31$ (TN) $+ 0.45$ (Z_{eu}/Z_{mix}) $+ 0.19$ (N^2*Z_{eu}/Z_{mix}) $+ 1.17$ (Shallow)	230	30%	856.65**
(3) Shallow	Chl $a = 0.33$–0.05 (SurfA) $- 0.17$ (N^2) $+ 0.48$ (SurfT) $+ 0.78$ (TN) $- 0.09$ (Z_{eu}/Z_{mix}) $+ 0.12$ (N^2*Z_{eu}/Z_{mix})	93	31%	Na
(4) Deep	Chl $a = -0.65 - 0.14$ (SurfA) $+ 0.07$ (N^2) $+ 0.84$ (SurfT) $+ 0.01$ (TN) $+ 1.13$ (Z_{eu}/Z_{mix}) $+ 0.29$ (N^2*Z_{eu}/Z_{mix})	137	12%	Na
(5) Med.	Chl $a = -17.035 - 0.23$ (SurfA) $- 0.029$ (N^2) $+ 5.26$ (SurfT) $+ 0.40$ (TN) $+ 0.83$ (Z_{eu}/Z_{mix}) $+ 0.22$ (N^2*Z_{eu}/Z_{mix})	54	45%	Na
(6) Cont.	Chl $a = -5.40 - 0.26$ (SurfA) $- 0.33$ (N^2) $+ 1.88$ (SurfT) $+ 0.47$ (TN) $+ 0.23$ (Z_{eu}/Z_{mix}) $+ 0.12$ (N^2*Z_{eu}/Z_{mix})	128	25%	Na
(7) Bor.	Chl $a = -15.65 - 0.15$ (SurfA) $- 0.005$ (N^2) $+ 6.05$ (SurfT) $+ 0.41$ (TN) $+ 2.77$ (Z_{eu}/Z_{mix}) $+ 0.62$ (N^2*Z_{eu}/Z_{mix})	48	43%	Na

* $P \leq 0.05$.
** $P \leq 0.01$.
*** $P \leq 0.001$.

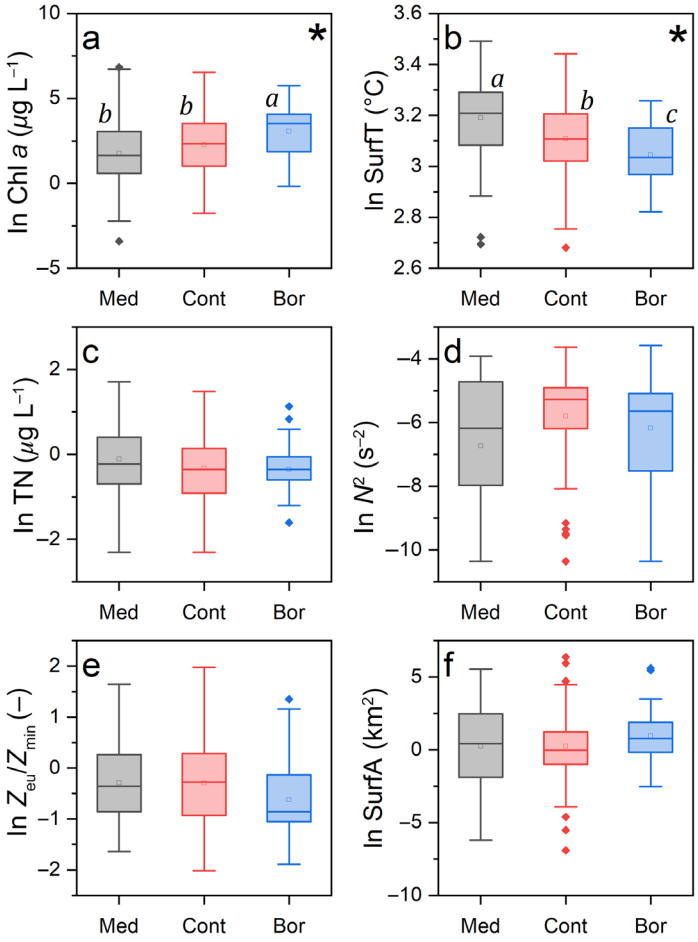


Fig 3. EMLS log-transformed response variable, (**a**) Chl *a*, and significant predictors: (**b**) surface temperature, (**c**) total nitrogen, (**d**) maximum buoyancy frequency (stratification strength), (**e**) light climate (Z_{eu}/Z_{mix}), and (**f**) surface area, averaged over climatic zones. Significant differences at the 0.05 level are marked with *. Different italic letters indicate significant differences among categories (Tukey test; $p < 0.05$).

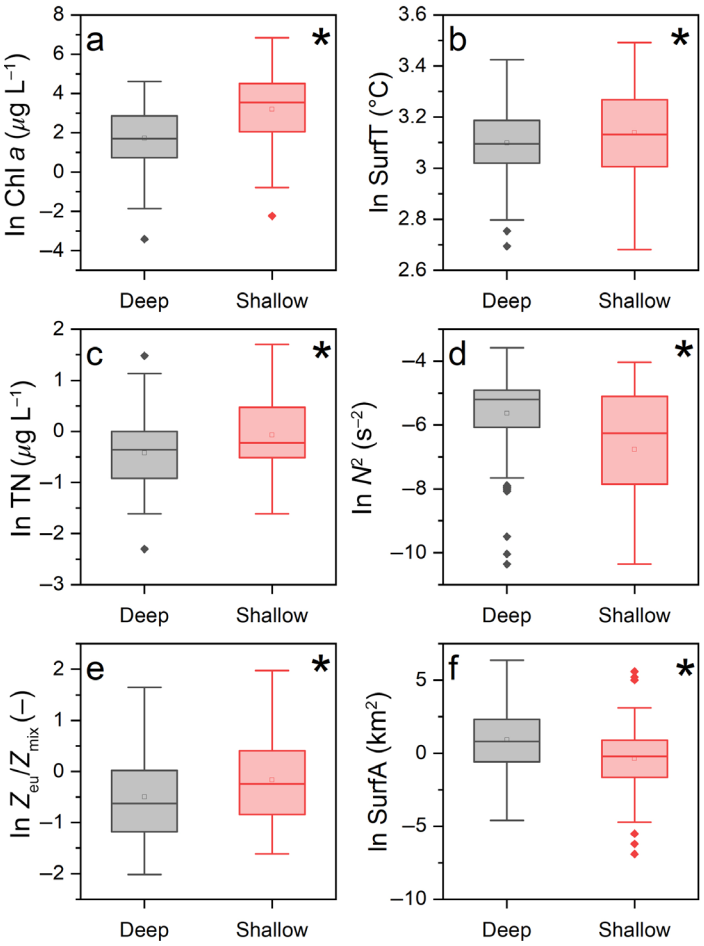


Fig 4. EMLS log-transformed response variable (**a**) Chl *a*, and significant predictors: (**b**) surface temperature, (**c**) total nitrogen, (**d**) maximum buoyancy frequency (stratification strength), (**e**) light climate (Z_{eu}/Z_{mix}), and (**f**) surface area, averaged over depth type. Significant differences at the 0.05 level are marked with *.

detail). These nominal variables comprehend the lake subsets to which the same multilinear regression model that was further applied, that is, deep, shallow, Mediterranean, Continental, Boreal (Table 2).

Results

Response variable and environmental predictors

The EMLS lake data cover a wide range of morphological, physical, chemical, and biological values (Table 1). The median measured TP was 60 $\mu g\ L^{-1}$, and according to Carlson trophic state index (TSI) 85% of the lakes were classified as eutrophic (TSI > 50). EMLS lakes were largely represented by eutrophic conditions (70%) also when calculating the TSI on basis of Secchi disk depth (median SD = 1.2 m), while TSI based on Chl *a* concentration (median Chl *a* = 10 $\mu g\ L^{-1}$) leads to 54% of lakes being classified as eutrophic.

Significant collinearity was observed between maximum depth and surface area, and between surface temperature and average temperature (Fig. S1). VIFs of maximum depth and average temperature were higher than 3, thus they were removed from subsequent analyses. Secchi depth was also removed in favor of using the light climate variable, Z_{eu}/Z_{mix}.

All the variables were found to be significant, except for TP, and the interactions TN*SurfT and SurfA*Z_{eu}/Z_{mix}, which therefore never appeared as Chl *a* variance predictors.

Lake groups: Climatic zone and depth type

Climatic zone

ANOVA was performed on the three climatic zone groups, composed by 54 Mediterranean, 128 Continental, and 48 Boreal lakes (Fig. 3; Table S2).

Mean Chl *a* concentrations were significantly higher in the Boreal lakes (mean ln ± 1 SD, 3 ± 1 $\mu g\ L^{-1}$) compared to

Continental (2.2 ± 1 $\mu g\ L^{-1}$) and Mediterranean (1.7 ± 2 $\mu g\ L^{-1}$), while no significant difference was found between Continental and Mediterranean lakes (Fig. 3a; Table S2).

Depth type

The EMLS dataset is composed of 93 shallow and 137 deep lakes (> 6 m). Response variable, Chl *a*, and all of the predictors used in the statistical models of the EMLS significantly differed between deep and shallow lakes (Fig. 4; Table S2). Chl *a*, SurfT, TN, and Z_{eu}/Z_{mix} were all higher for shallow lakes, whereas deep lakes showed a stronger stratification strength (N^2) and greater surface area than shallow ones.

Drivers explaining Chl *a* at the continental scale

The applied models significantly explain a proportion of the variability in Chl *a* ($p \leq 0.001$; Table 2), with the model applied to Mediterranean lakes explaining the highest variability (R^2 = 45%), closely followed by the model applied to Boreal lakes (R^2 = 43%) with Continental lakes further behind (R^2 = 25%), while the model applied to deep lakes explained the lowest variability (R^2 = 12%), compared to R^2 = 31% for shallow lakes. Based on AIC comparison, the nominal variable "climatic zone" is more significant than "depth type" in explaining the variance of algal biomass (Table 2). Nevertheless, the lake group "depth type" explained more of the overall R^2 compared to "climatic zone" (37% vs. 26%; Table S3).

When the model included the nominal variable "climatic zone" among the predictors, it resulted as the strongest predictor for algal biomass with 26% of the model R^2 explained, closely followed by stratification strength (24%), and with a significant but smaller contribution of TN (13%; Table S3). Similarly, when "depth type" was included, it resulted as the most significant predictor (37%); however, it was much more important than the second most significant predictor (stratification strength, 18%), that was closely followed by light climate (15%; Table S3).

The 230 lakes dataset allows us to carry out the same analysis separately on each group of lakes corresponding to the explanatory categories, climatic zone, and depth type, to gain more insights on the summer drivers of phytoplankton biomass for this set of lakes.

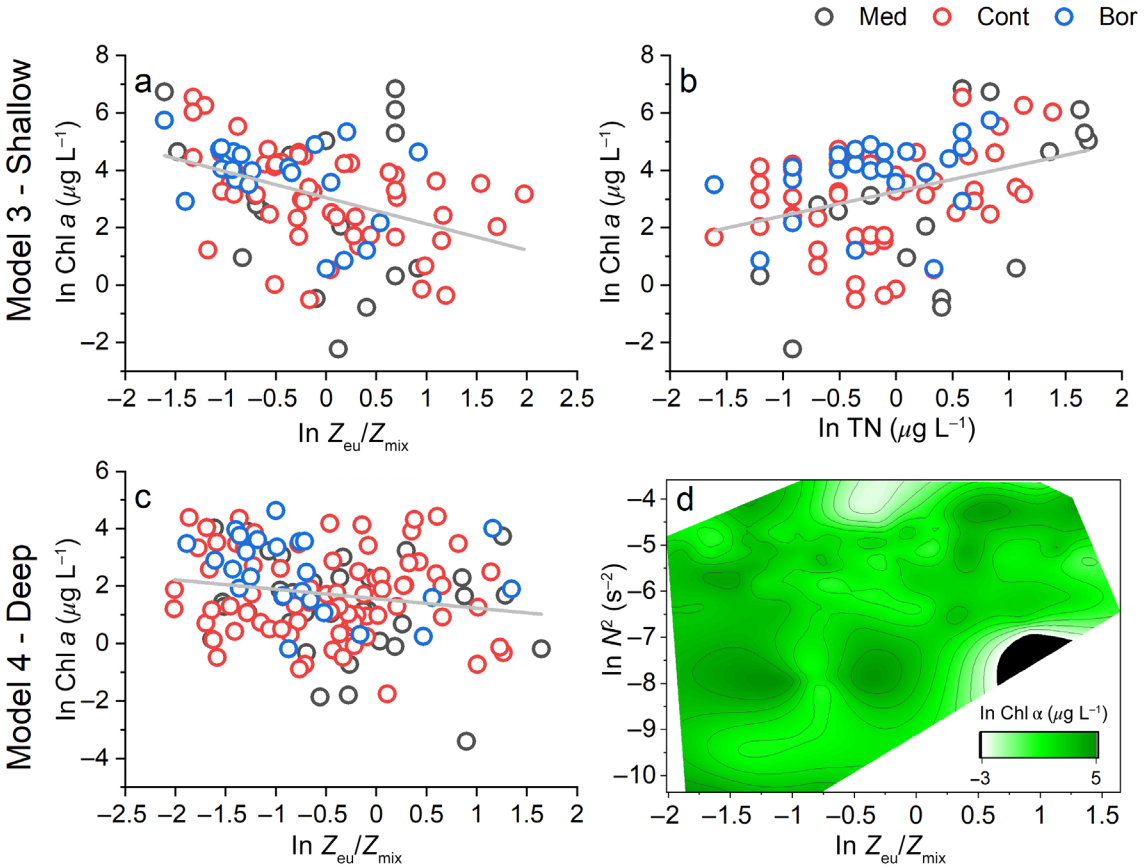


Fig 5. First two significant predictors for Chl *a* in lake group model 3 (shallow) and model 4 (deep). (**a**, **b**) Light climate, Z_{eu}/Z_{mix}, and TN explain respectively 46% and 33% of Chl *a* variance in EMLS shallow lakes (model R^2 = 31%). (**c**, **d**) Light climate, Z_{eu}/Z_{mix}, and its interaction with stratification strength, $N^2{*}Z_{eu}/Z_{mix}$, explain respectively 32% and 29% of Chl *a* variance in EMLS deep lakes (model R^2 = 12%). All variables are plotted as to the statistical models, that is, natural logarithm (ln). See Table S4 for relative contribution and significance of all predictors.

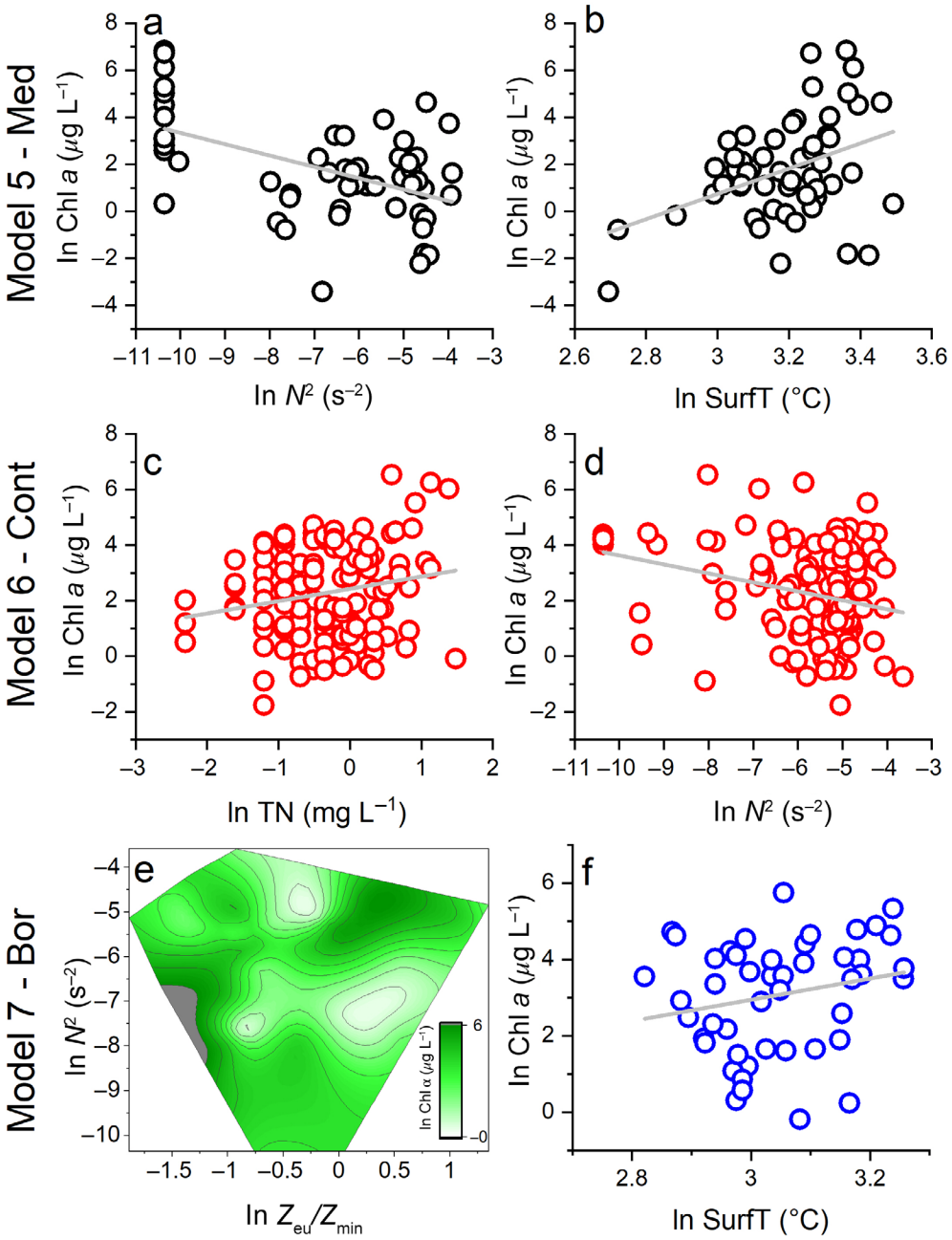


Fig 6. First two significant predictors for Chl *a* in lake group model 5 (Mediterranean), model 6 (Continental), and model 7 (Boreal). (**a**, **b**) Stratification strength, N^2, and surface temperature, SurfT, explain respectively 46% and 24% of Chl *a* variance in EMLS Med lakes (model $R^2 = 45\%$). (**c**, **d**) TN and N^2 explain respectively 35% and 29% of Chl *a* variance in EMLS Cont lakes (model $R^2 = 25\%$). (**e**, **f**) Light climate, interaction with stratification strength, $N^2{*}Z_{eu}/Z_{mix}$, and SurfT explain respectively 34% and 21% of Chl *a* variance in EMLS Boreal lakes (model $R^2 = 43\%$). All variables are plotted as to the statistical models, that is, natural logarithm (ln). See Table S5 for relative contribution and significance of all predictors.

Shallow vs. deep lakes

Light climate was the most important variable explaining Chl *a* variance in both shallow and deep lake subsets (46% and 32%, respectively; Fig. 5a,c). Stratification strength was also a significant contributor for both lake types, either individually (14%, shallow lakes; Table S4), or in synergistic interaction with light climate (29%, deep lakes; Fig. 5d). However, for shallow lakes, TN played a more significant role than stratification (33%; Fig. 5b) while not appearing as a significant predictor of algal biomass in the deep lakes subset.

Mediterranean vs. Continental vs. Boreal lakes

When applying the model to the different climatic zones, the strength of the stratification appeared as a strong

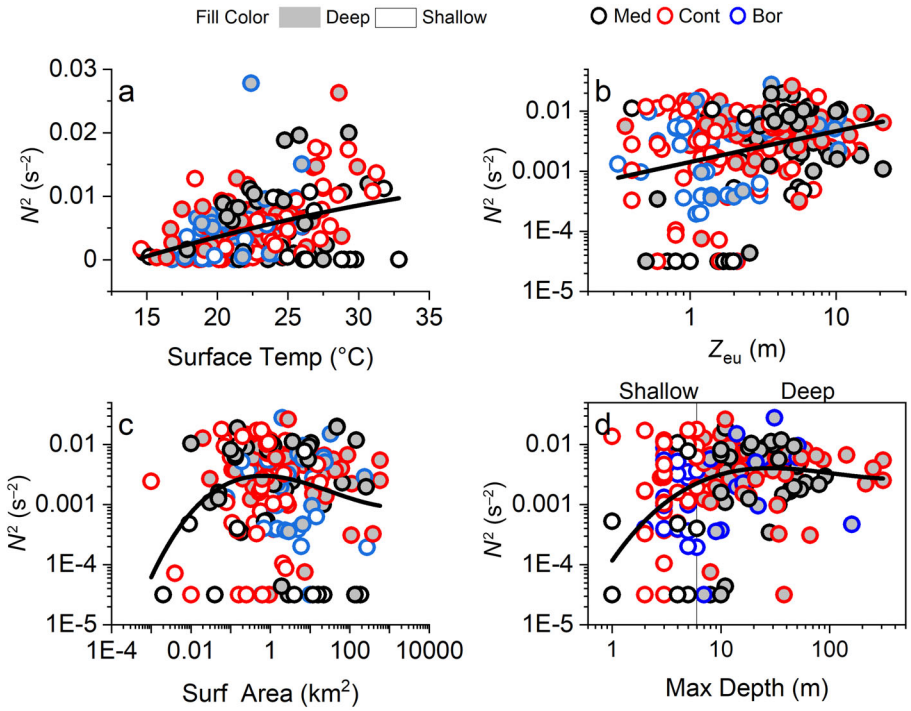


Fig 7. Relationships between N^2 and (**a**) surface temperature, 2nd-order polynomial fit, $R^2 = 0.14$; (**b**) euphotic depth, 2nd-order polynomial fit, $R^2 = 0.06$; (**c**) surface area, 3rd-order polynomial fit, $R^2 = -0.08$; (**d**) maximum depth, 4th-order polynomial fit, $R^2 = 0.2$. All polynomial fit are significantly better than function $y =$ constant at the 0.05 level.

predictor, either individually (Med. 46% and Cont. lakes 29%; Fig. 6a,d) or in interaction with light climate (Boreal lakes 34%; Fig. 6e). In Mediterranean and Boreal lakes, surface temperature was also a strong predictor of algal biomass (24% and 21%, respectively; Fig. 6b,f) but not for Continental lakes (Table S5). Instead, nutrients were the most significant predictors of Chl *a* (34%) for Continental (Fig. 6c), while being less important for Boreal lakes (14%) and not important for Mediterranean lakes (Table S5).

Relationship between stratification metrics

Within the EMLS lakes, we analyzed the relationship between stratification strength and some of the drivers, that is, temperature, light penetration, and lake morphology. As already shown, Mediterranean lakes, while being on average the warmest, did not have the highest average stratification strength (Fig. 3d). When looking at the entire dataset (Fig. 7), the polynomial fit between the maximum N^2 and surface temperature was significant ($p < 0.001$) but weak ($R^2 = 0.14$; Fig. 7a), indicating that only for a relatively small number of the EMLS lakes, higher surface water temperatures at the sampling time corresponded to a stronger stratification. An even weaker relationship ($R^2 = 0.06$) was observed between stratification strength and light penetration depth (Z_{eu}; Fig. 7b). As for the morphological features, the relationship observed between maximum N^2 and surface area (Fig. 7c), was much weaker ($R^2 = 0.08$) than between maximum N^2 and maximum lake depth ($R^2 = 0.2$). Here, the 4th-order polynomial fit followed the effect of temperature on N^2 for increasing lake depths, reaching a plateau for lakes deeper than ~ 20 m (Fig. 7d).

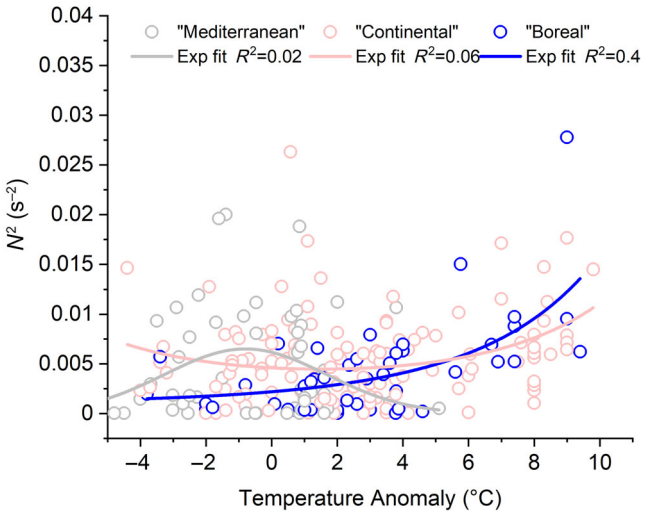


Fig 8. Eight-day average temperature anomaly at the sampling site and sampling period in relation to the lake stratification strength for the EMLS climatic zone subsets, Continental (gray), Mediterranean (light pink), and Boreal (blue). All best fits are given by exponential curves, with the one for Boreal lakes being the most significant ($R^2 = 0.4$).

Air temperature anomaly

The summer of 2015 was the third warmest summer (after 2003 and 2010) since 1880 in Europe (GISTEMP, NOAA online data). During the sampling period in 2015, 70% of EMLS lakes experienced a positive temperature anomaly of 1.9°C ± 3.4°C (average ± 1 SD, based on each lake 8-d temperature average compared to 10-yr average for the same 8 d). However, when looking at each climatic zone separately, 96% of Continental lakes and 87% of the Boreal lakes experienced a positive temperature anomaly of 3.8°C ± 2.6°C and 3.7°C ± 2.9°C, respectively. In contrast, only 53% of the Mediterranean lakes experienced a positive temperature anomaly, of 1.4°C ± 1°C. The remaining 30% of the total, 4% of Continental, 13% of Boreal and 47% of Mediterranean are lakes that showed a negative deviation from the long term average.

Hence, at the time of sampling, the great majority of Continental and Boreal lakes experienced a strong temperature increase compared to the long-term average levels, which was not the case for Mediterranean lakes. Compared to the other regions, Boreal lakes as well showed the strongest exponential relationship between the experienced temperature anomaly and stratification strength (Fig. 8).

Pigments analysis

Measurement of Zea concentrations in the EMLS lakes were carried out with the aim of investigating cyanobacterial biomass. A strong linear relationship was found between Zea and Chl *a* (R^2 = 0.6; Fig. S3) indicating that higher Chl *a* concentrations systematically corresponded with higher concentrations of Zea.

Discussion

Drivers explaining phytoplankton biomass at the continental scale

Several studies have focused on the effects of nutrients and warming on phytoplankton in more than one lake (table S1 in Salmaso and Tolotti 2021). This is of particular concern for resolving the climate warming effect on lakes and the positive feedbacks on eutrophication of lakes (Sinha et al. 2017; Deng et al. 2018). However, thermal stratification, which will likely increase with climate warming (Woolway and Merchant 2019), is an important feature governing lake ecosystems as it affects both nutrient availability and light climate (Schwefel et al. 2016), generating complex feedbacks for the biota (Mesman et al. 2021). The importance of these factors may dominate when lakes are not nutrient limited.

We have applied a set of multiple regression models to 230 European lakes (54–85% of which were eutrophic depending on the criterion applied) to test the dependency of Chl *a* on phytoplankton growth resources (nutrients, temperature, and light climate) and morphophysical lake properties (surface area, stratification strength), including interactions between specific predictors. Our results indicate that physical properties of a lake, such as stratification strength and light climate (expressed as the ratio of euphotic to mixing depth), are the strongest ecosystem drivers for phytoplankton biomass for this set of mostly nutrient-rich lakes, at the sampling time. It is possible, however, that a different result would be obtained from the same dataset in a different time of the year.

In a similar fashion to the present work, an earlier study on 1076 US lakes (Rigosi et al. 2014), showed that surface temperature, nutrients, and their interaction were the main phytoplankton biomass predictors. Interestingly, their results showed that the largest part of the variance in Chl *a* for the subset of eutrophic and hypereutrophic lakes was explained by a synergistic interaction between nutrients and temperature. Our study moves a step forward and highlights the fact that additional variables need to be considered when collecting lake "snapshots" at a continental scale. The analysis presented here indicates that nutrients, temperature, and light should not be the only algal growth conditions to be considered. We show that when lake stratification metrics are included, we can gain insights into the lake physics mechanisms that promote phytoplankton biomass growth and potentially improve the development of predictive tools.

Moreover, our statistical analysis indicates that surface temperature alone should not be used as a proxy for stratification strength. Indeed for a multilake survey, it is necessary to estimate lake stability (N^2) as a variable that comprises the lake thermal "history," and therefore gives insight into the environmental conditions that the phytoplankton have experienced during the recent past. Such information is easily attained with a temperature profile and is extremely relevant when looking at ecosystem functioning, as thermal structure and light penetration determine the physical constraints of the photosynthetic biomass distribution in the water column. These constraints also determine to what extent specific phytoplankton features adapted to life in a stable water column, such as the pigment composition (e.g., presence of phycoerythrin in deep chlorophyll maxima), and buoyancy regulation (e.g., gas vesicles, motility, shape adaptations) may favor specific algal groups.

Shallow vs. deep lakes

In the EMLS, most of the lakes were eutrophic which may explain the predominant importance of light climate (Z_{eu}/Z_{mix}) for algal biomass variance in both shallow and deep lakes. We therefore assume that, for nutrient-rich lakes, phytoplankton rather than inorganic suspended solids determine underwater light extinction (Scheffer et al. 1997), which subsequently determines phytoplankton biomass.

Although light climate was the most important factor for both EMLS depth types, we observed a relatively greater importance of light climate in shallow rather than deep lakes (explaining 46% and 32% of the variation, respectively), which may be explained by the fact that shallow lakes exist in two clearly distinct states, clear vs. turbid. Mechanisms directly linked to the underwater light climate, for example,

high cyanobacterial biomass and benthivorous fish stirring up the sediment, provide varying degrees of resilience to the turbid state (Scheffer et al. 1997). In contrast, macrophytes stabilize the clear water state, and light penetration that reaches the sediment is vital for their development (Ibelings et al. 2007). With 72% of the shallow EMLS lakes having a Secchi depth of less than 0.8 m, we could argue that the majority are in a turbid state, be it stable or not. This may go some way to explain the critical role of light in determining biomass of algae in EMLS shallow lakes.

TN is the second-most important predictor for Chl *a* in shallow lakes (33%) which, together with the general absence of TP as significant predictor for Chl *a* variance, suggests that for the 230 EMLS lakes, the commonly found linear relationship between TP and Chl *a* does not hold true (Vollenweider 1968). This is in line with previous studies on nutrient-rich lakes suggesting that (1) a positive linear TP–Chl *a* relationship exists only at intermediate concentrations of TP (0.004–0.23 mg L^{-1}; Quinlan et al. 2020) and (2) nitrogen becomes limiting for phytoplankton under high TP, especially over shorter temporal scales (Filstrup et al. 2014).

A eutrophic status of a lake, however, does not mean that nutrients cannot be limiting for dense phytoplankton, with a large demand to sustain a high biomass. Yet, the condition of nutrient limitation (in our case nitrogen) could be seen as an effect driven by Z_{eu}/Z_{mix} (first predictor). Especially for shallow lakes, when this ratio becomes smaller, the mixed layer exceeds the euphotic zone and nutrients from the sediment are likely to be resuspended. We may easily see a more direct relationship between Chl *a* and light climate than with the nutrient abundance, because light climate, by revealing the recent mixing history, is a more integrative indicator of nutrient availability than the nutrient content of a single water sample, especially for productive shallow lakes.

For deep lakes, light climate and its synergistic interaction with water column stability had a similarly important contribution to the overall R^2, explaining Chl *a* variance (32% and 29% for Z_{eu}/Z_{mix} and N^2, respectively). High algal biomass increases turbidity, which can increase water temperature in the surface layer through increased heat absorption (Ibelings et al. 2003), and thus reinforce stratification (Paerl and Huisman 2008). Reinforced stratification through increased turbidity implies that phytoplankton is maintained within the euphotic zone offering a potential explanation of how light climate can interact synergistically with water column stability ($Z_{eu}/Z_{mix} > 1$; Fig. 1a). However, in a strongly stratified lake, nutrients may remain available in the hypolimnion even when they are depleted in the epilimnion, so that deeper mixing, also of short duration, enhances the likelihood that phytoplankton gains access to this pool of nutrients. In deep, well-stratified lakes, it is also relatively common to find algal biomass maxima (a.k.a. deep chlorophyll maximum [DCM]) at the crossroads of light from above and nutrients from below (Leach et al. 2018). On the other hand, if stratification is weak and mixing can reach deeper layers, it will take the algal communities beyond the euphotic zone reducing algal growth ($Z_{eu}/Z_{mix} < 1$; Fig. 1b). A deeper mixed layer will allow light to reach greater depths by diluting epilimnetic phytoplankton over a larger volume of lake water, thus increasing light penetration. This extended euphotic depth will likely, however, not make up for light limitation due to a deeper mixing depth, so the ratio Z_{eu}/Z_{mix} would still decrease when water column stability decreases (Fig. 1b), exacerbating the light limitation of phytoplankton growth.

In contrast to the shallow lakes, in EMLS deep lakes neither TP nor TN appeared as a significant predictor of algal biomass, possibly because of the higher likelihood of light limitation mentioned above. Interestingly, another difference between EMLS shallow and deep lakes was that the surface area explained a significant 22% of the overall Chl *a* variance of deep lakes, while did not explain the Chl *a* variance for the shallow lakes (Table S4). This might be due to the fact that the surface area becomes important considering its direct relationship with lake wind exposure, which can influence the water column mixing depth in deep lakes, hence the availability of light and nutrients for phytoplankton (Fig. 1). Although wind exposure was not included in this study, EMLS lake area correlated with depth (Fig. S1a), and was therefore indirectly related to the water column thermal structure. Indeed, EMLS lakes with larger surface areas tended to be deeper (Fig. 4f) and more stable (Fig. 4d), and this may have favored phytoplankton's access to light, in particular when nutrients are not—or less of—a limiting factor, for example, when DCMs are formed where phytoplankton has access to nutrients in the hypolimnion (Leach et al. 2018).

Mediterranean vs. Continental vs. Boreal lakes

When EMLS lakes were clustered by climatic zone, stratification strength appeared as a strong predictor for Chl *a*, either individually (Mediterranean 46% and Continental lakes 29% variation explained) or in synergistic interaction with light climate (Boreal lakes 34%). Stratification strength was thus a dominant factor promoting phytoplankton optimal growth conditions, interacting with the availability of nutrients and light, as discussed. Light climate interaction with water column stratification was a strong factor for Boreal lakes phytoplankton growth (Fig. 6e) possibly due to their tendency to be richer in humic substances and consequently darker (Kutser et al. 2005; Kelly et al. 2018).

Phytoplankton biomass in Continental lakes seemed to exhibit a higher degree of nitrogen dependency (Fig. 6c); however, we cannot exclude that those lakes in other regions were in a similar state, since as discussed above, predictors like light climate can possibly encompass nutrient limitation. On the other hand, the comparatively lower Chl *a* content of Mediterranean lakes (Fig. 3a) seems to indicate that, at the time of sampling, these lakes were experiencing a better nutrient–phytoplankton balance than Continental lakes.

The best predictor for algal biomass: Stratification strength or lake depth?

Stratification strength decreased in importance when splitting the dataset into depth types, which may indicate that depth-type itself explained algal biomass variance. This is also suggested by the fact that all predictors were significantly different between deep and shallow lakes (Fig. 4), and some important environmental factors have a different effect on these two clusters. Wind has generally a larger effect on temperature structure and stability of shallow lakes, because the wind-induced mixing allows heat to be transferred throughout the entire water column (Nõges et al. 2011). Furthermore, shallow lakes respond more directly to short-term weather variations (Arvola et al. 2009; Deng et al. 2018). For deep lakes that have a higher heat retention and potential energy, greater wind speeds are required to drive mixing during the summer months, resulting in greater stability (Boehrer and Schultze 2008). Fetch and dominant wind direction and intensity are also important in determining stratification strength in deep lakes (Wetzel 2001), although these data were not collected for this study. However, given the consistently higher N^2 observed for EMLS deep lakes (Fig. 4d), we can assume that sufficiently strong and long-lasting winds were not present at each sampling site during—or shortly prior to—the sampling period to modify the aforementioned scenario of deep lakes that are more strongly stratified than shallow lakes.

Depth and N^2 may therefore be confounding variables because, at least for this dataset, lake depth can explain most of the variation in stratification trends. Nevertheless, whether lake maximum depth or stratification strength is actually the most significant predictor of Chl *a* in the overall EMLS dataset, the message remains unchanged: lake morphophysical properties are essential when investigating phytoplankton biomass responses to environmental changes.

Relationship between stratification metrics

Given the importance of stratification strength as a predictor of Chl *a* variance at the European continental scale, we analyzed the relationship between this variable, represented by maximum N^2, and the environmental and morphological characteristics that act on the density gradient of a lake (surface temperature, light penetration depth, maximum depth, and surface area).

Surface temperature

Stratification strength responds directly to changes in water temperature, yet each lake will need a certain number of warm days with relatively low wind speed to develop stratification, which also depends on lake morphological factors. The reason for the weak correlation observed between maximum N^2 and surface temperature (Fig. 7a) may be that deep and shallow lakes are equally represented, and while deep lakes are more strongly stratified, the shallow lakes had the highest surface temperature (Fig. 4b,d). The absence of a strong correlation between stratification strength and surface temperature is further confirmed by the absence of any trend between stratification strength and climatic zone (Fig. 4d).

Moreover, the fact that shallow and Mediterranean lakes had the highest surface temperature, but the weakest stratification confirms that surface temperature can be a misleading indicator for stratification strength, especially for snapshot surveys as shown in previous studies on large datasets (Read et al. 2014; Winslow et al. 2017).

Light penetration depth

Changes in light absorption by the dissolved and suspended content of a lake affect the vertical distribution of heat and resulting stratification (Andrew et al. 2008; Rinke et al. 2010). We did not observe, however, a distinct relationship between stratification strength and light penetration (Fig. 7b). The reason why this relationship is not stronger may be that the effect of light on stratification is more evident in time series than in spatial gradients. This is because light-induced heat diffusion in the water column and its temporal variability has a stronger effect on the duration of the stratification than on its absolute value. Indeed, more transparent lakes (Secchi transparency > 5 m) tend to maintain a seasonal thermal stratification for a longer duration than more turbid ones (Richardson et al. 2017), therefore remaining stable longer. Assessing whether this is the case is not possible with a summer snapshot sampling design, although it was observed that light penetration can drive the depth of the mixed layer. This is suggested for the EMLS dataset by a moderate linear relationship ($R^2 = 0.35$) between the depth of the epilimnion, or mixed layer, and the euphotic depth (Fig. S2).

Maximum depth and surface area

We observed a relationship between N^2 and both the lake maximum depth and lake surface area (Fig. 7c,d). The shape of the polynomial fit shows that the linearity of stratification strength with lake maximum depth holds until lake depths of $\sim$ 20 m, because of the physical limit dictated by the thermal diffusivity of water. This relationship may confirm that N^2 and depth are interdependent in determining resource availability for the algal communities.

EMLS lakes with a greater area were on average deeper and had a more stable water column (Fig. 4d,f). Therefore, surface area of the EMLS dataset was directly correlated with maximum depth and was used as the only morphological variable in the statistical models. However, the relationship between surface area and N^2 was not strong (Fig. 7c), possibly because a larger surface area does not necessarily mean a greater wind exposure, which is largely determined by the lake's orientation toward the dominant wind direction and lake topography. Clearly, as for the underwater light regime, analyzing the effect of wind exposure on the thermal structure is not

possible with a single observation, but would require a water column temperature time series.

Temperature anomaly: 2015, an unusually hot summer

As expected, Mediterranean lakes had higher surface temperatures than Boreal ones (Fig. 3a,b). However, Boreal lakes exhibited a significantly higher Chl *a* concentration than Mediterranean lakes, while lakes in both climatic zones had comparable nutrient concentrations (Table S2). This seems to confirm the importance of factors other than temperature (lower in Boreal lakes) or nutrients (similar) driving phytoplankton biomass, especially water column stability in relation to the light climate. Indeed, while Boreal lakes are known to stratify intermittently during summer (Kirillin and Shatwell 2016; Woolway and Merchant 2019), the heat wave likely intensified the stratification strength in the Boreal lakes more strongly than in other regions, given that the region experienced the largest temperature anomaly (Fig. 8). This may have favored the conditions shown in Fig. 1a and supported by our model results, that is, the interaction between light climate and stratification strength is the main Chl *a* driver for Boreal lakes (Fig. 6e).

As several studies addressed the relationship between light, nutrients, and temperature effects on primary producers in Boreal regions (Zwart et al. 2016; Bergstrom and Karlsson 2019), alternative explanations may apply too. Although it is not possible to generalize, such observations are crucial to generate ideas and stimulate future research. It is possible that a higher abundance of mixotrophs in Boreal lakes may help to explain the higher Chl *a* in that region, since Hansson et al. (2019) demonstrated that the success of mixotrophs is correlated with the elevated colored dissolved organic matter content of Boreal lakes. It is also interesting to note that Mantzouki et al. (2018) found that for the same EMLS dataset, the variety of toxins produced by cyanobacteria increased with latitude, which possibly may have reduced the grazing pressure in Boreal lakes, contributing to higher Chl *a*.

Cyanobacteria like it warmer?

Zea is frequently used as a pigment to indicate cyanobacterial biomass (Bianchi et al. 2000; Glibert et al. 2004; Przytulska et al. 2017; Ewing et al. 2020), although it is found both in cyanobacteria and in chlorophytes (Deshpande et al. 2014; Ibelings et al. 2016). In this study, we do not provide microscopy results to confirm the correspondence between cyanobacteria and Zea; therefore, the following discussion is presented with a degree of caution, and mainly serves to stimulate further ideas, eventually contributing to a deeper understanding of the worldwide increase in cyanobacterial blooms.

The strong correlation between Zea and Chl *a* EMLS (Fig. S3) indicated that higher Chl *a* concentrations systematically corresponded with higher concentrations of Zea, which may suggest that water column stratification and light climate are the main drivers for cyanobacterial growth in eutrophic lakes, as they are for overall phytoplankton. Moreover, cyanobacteria have evolved specific traits like buoyancy and accessory pigments that renders them specifically well adapted to stably stratified conditions (Huisman et al. 2018). Consequently, the fact that light climate was the main driver for both lake depth types (Fig. 4) may confirm that at high nutrient levels, light becomes limiting for cyanobacterial development (Ganf and Oliver 1982; Bouterfas et al. 2002; Huisman et al. 2004).

Considering the high temperature anomaly experienced in Boreal regions at the sampling time, the significance of a positive interaction between water column stability and light climate in promoting cyanobacteria in the Boreal lakes during a record hot summer supports the general observation that "blooms like it hot" (Paerl and Huisman 2008). In the context of climate change—and rapid warming at high latitudes—perhaps a more appropriate rephrasing is "blooms like it warmer than usual," since the Boreal lakes were still cooler than the Mediterranean lakes, yet the temperature anomaly was higher as were Zea levels. Among the EMLS subset of lakes with detectable Zea (which are 172 over the total 230 of this study), almost all (95%) of the Boreal lakes experienced a higher positive T-anomaly ($\sim 4°C \pm 2.5°C$). Evidently, more detailed integrated lab-field studies, including both ecological and evolutionary aspects, are needed to resolve this issue.

Future scenario and management strategies

Among the Chl *a* predictors of this study, lake surface temperature and water column stratification are expected to have the strongest impact on lake ecosystems in a warming future (O'Reilly et al. 2015; Kraemer et al. 2017). Both variables were significant drivers for trends in phytoplankton biomass across climatic gradients in Europe. Thus, since lake water column stability will likely increase with a warming climate (Oleksy and Richardson 2021), bloom-forming cyanobacteria in particular will be further promoted given their typical dependence on buoyancy that makes them particularly well adapted to a stable water column (Steinberg and Hartmann 1988; Paerl and Paul 2012).

Although we concur with Ibelings et al. (2016) that any sustainable approach controlling cyanobacterial blooms has to be rooted in nutrient reduction, our present analysis underlines the potential effectiveness of additional measures that weaken the future strengthening of lake stratification, which is demonstrated here to play such a critical role in determining differences in lake phytoplankton and cyanobacterial biomass. It may be essential, for instance, to include measures like artificial lake mixing (Visser et al., 2016) to mitigate algal (and cyanobacterial) blooms.

Conclusions

Nutrients and light are the fundamental resources for phytoplanktonic biomass, even in nutrient rich lakes, such as the

ones represented in this study; however, results from the EMLS analysis show that Chl *a* variance is better predicted by light climate and stability metrics. These predictors are also strong indicators of the epilimnetic nutrient load and of the light experienced by the algal biomass prior to sampling. This explains why in this nutrient-rich lake dataset, light climate was the most important variable explaining Chl *a* variance in both shallow and deep lakes, with the difference that, only for deep lakes the optimum condition for photosynthetic biomass was obtained when stratification operated in a synergistic interaction with light climate. The dominance of light climate and the absence of TP as significant predictor for Chl *a* variance confirms that: (1) when TP levels are high as in the average EMLS, light and nitrogen become limiting resources for phytoplankton and (2) light climate, as metric for the recent history of water column mixing, is a powerful indicator for nutrient availability, and needs to be included in similar studies.

Furthermore, our analysis of this pan-European dataset shows that shallow and Mediterranean lakes exhibit the highest surface temperature, although the weakest stratification, confirming that lake surface temperature does not necessarily correlate with lake stratification strength. Consequently, especially for snapshot surveys, a lake temperature profile should be preferred over surface temperature data as it is a more sensible indicator for stratification strength and ecological response to warming.

Finally, among the 230 European lakes, we observed a significant exponential correlation between temperature anomaly and the stratification strength only for Boreal lakes that, incidentally, had the highest Chl *a* concentrations; a notion deserving further attention in light of most rapid increases in warming taking place at high latitude regions. This, coupled with the fact that, for mildly to hyper-eutrophic lakes, light climate and water column stratification are the most important drivers determining phytoplankton biomass, may serve to better plan and implement lake management and mitigation strategies.

References

Andrew, J. T., and others. 2008. Cooling lakes while the world warms: Effects of forest regrowth and increased dissolved organic matter on the thermal regime of a temperate, urban lake. Limnol. Oceanogr. **53**: 404–410.

Arvola, L., and others. 2009, 2010, p. 85–101. *In* D. G. George [ed.], The impact of the changing climate on the thermal characteristics of lakes. Springer Science+Business Media B.V.

Bartosiewicz, M., I. Laurion, and S. MacIntyre. 2015. Greenhouse gas emission and storage in a small shallow lake. Hydrobiologia **757**: 101–115.

Beaulieu, M., F. Pick, and I. Gregory-Eaves. 2013. Nutrients and water temperature are significant predictors of cyanobacterial biomass in a 1147 lakes data set. Limnol. Oceanogr. **58**: 1736–1746.

Bergstrom, A. K., and J. Karlsson. 2019. Light and nutrient control phytoplankton biomass responses to global change in northern lakes. Glob. Chang. Biol. **25**: 2021–2029.

Bianchi, T. S., E. Engelhaupt, P. Westman, T. Andren, C. Rolff, and R. Elmgren. 2000. Cyanobacterial blooms in the Baltic Sea: Natural or human-induced? Limnol. Oceanogr. **45**: 716–726.

Boehrer, B., and M. Schultze. 2008. Stratification of lakes. Rev. Geophys. **46**: 1–27.

Bouterfas, R., M. Belkoura, and A. Dauta. 2002. Light and temperature effects on the growth rate of three freshwater algae isolated from a eutrophic lake. Hydrobiologia **489**: 207–217.

Brentrup, J. A., and others. 2018. The potential of high-frequency profiling to assess vertical and seasonal patterns of phytoplankton dynamics in lakes: An extension of the Plankton Ecology Group (PEG) model. Inland Waters **6**: 565–580.

Camacho, A. 2006. On the occurrence and ecological features of deep chlorophyll maxima (DCM) in Spanish stratified lakes. Limnetica **25**: 453–478.

Carvalho, F., J. Kohut, M. J. Oliver, R. M. Sherrell, and O. Schofield. 2016. Mixing and phytoplankton dynamics in a submarine canyon in the West Antarctic Peninsula. J. Geophys. Res. Oceans **121**: 5069–5083.

Cloern, J. E. 1996. Phytoplankton bloom dynamics in coastal ecosystems: A review with some general lessons from sustained investigation of San Francisco Bay, California. Rev. Geophys. **34**: 127–168.

Deng, J., and others. 2018. Climatically-modulated decline in wind speed may strongly affect eutrophication in shallow lakes. Sci. Total Environ. **645**: 1361–1370.

Deshpande, B. N., R. Tremblay, R. Pienitz, and W. F. Vincent. 2014. Sedimentary pigments as indicators of cyanobacterial dynamics in a hypereutrophic lake. J. Paleolimnol. **52**: 171–184.

Ewing, H. A., and others. 2020. "New" cyanobacterial blooms are not new: Two centuries of lake production are related to ice cover and land use. Ecosphere **11**(6): e03173.

Filstrup, C. T., and others. 2014. Regional variability among nonlinear chlorophyll-phosphorus relationships in lakes. Limnol. Oceanogr. **59**: 1691–1703.

Flaim, G., E. Eccel, A. Zeileis, G. Toller, L. Cerasino, and U. Obertegger. 2016. Effects of re-oligotrophication and climate change on lake thermal structure. Freshw. Biol. **61**: 1802–1814.

Fox, J., and S. Weisberg. 2019. An R Companion to Applied Regression, Third edition. Sage, Thousand Oaks CA.

Ganf, G. G., and R. L. Oliver. 1982. Vertical separation of light and available nutrients as a factor causing replacement of green-algae by blue-green-algae in the plankton of a stratified lake. J. Ecol. **70**: 829–844.

Glibert, P. M., and others. 2004. Evidence for dissolved organic nitrogen and phosphorus uptake during a cyanobacterial bloom in Florida Bay. Mar. Ecol. Prog. Ser. **280**: 73–83.

Graff, J. R., and M. J. Behrenfeld. 2018. Photoacclimation responses in subarctic Atlantic phytoplankton following a natural mixing-restratification event. Front. Mar. Sci. **5**: 209. doi:10.3389/fmars.2018.00209

Grőmping, U. 2006. Relative Importance for Linear Regression in R: The Package relaimpo. Journal of Statistical Software, Foundation for Open Access Statistics vol. 17(i01).

Hansson, T. H., H.-P. Grossart, P. A. del Giorgio, N. F. St-Gelais, and B. E. Beisner. 2019. Environmental drivers of mixotrophs in boreal lakes. Limnol. Oceanogr. **64**: 1688–1705.

Heiskanen, J. J., and others. 2014. Effects of cooling and internal wave motions on gas transfer coefficients in a boreal lake. Tellus B **66**: 1–16.

Huisman, J., G. A. Codd, H. W. Paerl, B. W. Ibelings, J. M. H. Verspagen, and P. M. Visser. 2018. Cyanobacterial blooms. Nat. Rev. Microbiol. **16**: 471–483. doi:10.1038/s41579-018-0040-1

Huisman, J., and others. 2004. Changes in turbulent mixing shift competition for light between phytoplankton species. Ecology **85**: 2960–2970.

Ibelings, B. W., M. Bormans, J. Fastner, and P. M. Visser. 2016. CYANOCOST special issue on cyanobacterial blooms: Synopsis—a critical review of the management options for their prevention, control and mitigation. Aquat. Ecol. **50**: 595–605.

Ibelings, B. W., B. M. A. Kroon, and L. R. Mur. 1994. Acclimation of photosystem II in a cyanobacterium and a eukaryotic green alga to high and fluctuating photosynthetic photon flux densities, simulating light regimes induced by mixing in lakes. New Phytol. **128**: 407–424.

Ibelings, B. W., M. Vonk, H. F. J. Los, D. T. van der Molen, and W. M. Mooij. 2003. Fuzzy modeling of cyanobacterial surface waterblooms: Validation with NOAA-AVHRR satellite images. Ecol. Appl. **13**: 1456–1472.

Ibelings, B. W., and others. 2007. Resilience of alternative stable states during the recovery of shallow lakes from eutrophication: Lake Veluwe as a case study. Ecosystems **10**: 4–16.

Imberger, J. 1985. The diurnal mixed layer. Limnol. Oceanogr. **30**: 737–770.

Imboden, D. M., and A. Wüest. 1995. Mixing mechanisms in lakes. *In* Physics and chemistry of lakes. Springer-Verlag.

Kelly, P. T., C. T. Solomon, J. A. Zwart, and S. E. Jones. 2018. A framework for understanding variation in pelagic gross primary production of lake ecosystems. Ecosystems **21**: 1364–1376.

Kirillin, G., and T. Shatwell. 2016. Generalized scaling of seasonal thermal stratification in lakes. Earth Sci. Rev. **161**: 179–190.

Koenings, J. P., and J. A. Edmundson. 1991. Secchi disk and photometer estimates of light regimes in Alaskan lakes - effects of yellow color and turbidity. Limnol. Oceanogr. **36**: 91–105.

Kosten, S., and others. 2012. Warmer climates boost cyanobacterial dominance in shallow lakes. Glob. Chang. Biol. **18**: 118–126.

Kraemer, B. M., T. Mehner, and R. Adrian. 2017. Reconciling the opposing effects of warming on phytoplankton biomass in 188 large lakes. Sci. Rep. **7**: 1–7.

Köppen, W. 1900. Versuch einer klassifikation der klimate, vorzugsweise nach ihren beziehungen zur pflanzenwelt. Geographische Zeitschrif **6**: 657–679.

Kutser, T., D. C. Pierson, L. Tranvik, A. Reinart, S. Sobek, and K. Kallio. 2005. Using satellite remote sensing to estimate the colored dissolved organic matter absorption coefficient in lakes. Ecosystems **8**: 709–720.

Leach, T. H., and others. 2018. Patterns and drivers of deep chlorophyll maxima structure in 100 lakes: The relative importance of light and thermal stratification. Limnol. Oceanogr. **63**: 628–646.

Magee, M. R., and C. H. Wu. 2017. Response of water temperatures and stratification to changing climate in three lakes with different morphometry. Hydrol. Earth Syst. Sci. **21**: 6253–6274.

Mantzouki, E., and B. W. Ibelings. 2018. The principle and value of the European Multi Lake Survey. Limnol. Oceanogr. Bull. **27**: 82–86.

Mantzouki, E., and others. 2018. A European Multi Lake Survey dataset of environmental variables, phytoplankton pigments and cyanotoxins. Sci. Data **5**: 180226.

Mesman, J. P., and others. 2021. The role of internal feedbacks in shifting deep lake mixing regimes under a warming climate. Freshw. Biol. **66**: 1021–1035.

Millero, F. J., and A. Poisson. 1981. International one-atmosphere equation of state of seawater. Deep-Sea Res. A Oceanogr. Res. Pap. **28**: 625–629.

Moss, B., and others. 2011. Allied attack: Climate change and eutrophication. Inland Waters **1**: 101–105.

Mur, L. R., H. J. Gons, and L. Van Liere. 1977. Some experiments on the competition between green algae and blue green bacteria in light-limited environments. FEMS Micobiol. Lett. **1**: 335–338.

Nõges, P., T. Nõges, M. Ghiani, B. Paracchini, J. Pinto Grande, and F. Sena. 2011. Morphometry and trophic state modify the thermal response of lakes to meteorological forcing. Hydrobiologia **667**: 241–254.

Nürnberg, G. K. 1984. The prediction of internal phosphorus load in lakes with anoxic hypolimnial. Limnol. Oceanogr. **29**: 111–124.

Oleksy, I. A., and D. C. Richardson. 2021. Climate change and teleconnections amplify lake stratification with differential local controls of surface water warming and deep water

cooling. Geophys. Res. Lett. **48**: e2020GL090959. doi:10.1029/2020GL090959

O'Reilly, C. M., and others. 2015. Rapid and highly variable warming of lake surface waters around the globe. Geophys. Res. Lett. **42**: 10773–10781.

Paerl, H. W., and J. Huisman. 2008. Climate. Blooms like it hot. Science **320**: 57–58.

Paerl, H. W., and V. J. Paul. 2012. Climate change: Links to global expansion of harmful cyanobacteria. Water Res. **46**: 1349–1363.

Peters, G. J. Y. 2018. Userfriendlyscience: Quantitative analysis made accessible (R package version 0.7-1071). doi:10.17605/osf.io/txequ

Pinckney, J. L., T. L. Richardson, D. F. Millie, and H. W. Paerl. 2001. Application of photopigment biomarkers for quantifying microalgal community composition and in situ growth rates. Org. Geochem. **32**: 585–595.

Pollard, A. I., S. E. Hampton, and D. M. Leech. 2018. The promise and potential of continental-scale limnology using the U.S. Environmental Protection Agency's National Lakes Assessment. Limnol. Oceanogr. Bull. **27**: 36–41.

Posch, T., O. Köster, M. M. Salcher, and J. Pernthaler. 2012. Harmful filamentous cyanobacteria favoured by reduced water turnover with lake warming. Nat. Clim. Change **2**: 809–813.

Przytulska, A., M. Bartosiewicz, and W. F. Vincent. 2017. Increased risk of cyanobacterial blooms in northern high-latitude lakes through climate warming and phosphorus enrichment. Freshw. Biol. **62**: 1986–1996.

Ptacnik, R., S. Diehl, and S. Berger. 2003. Performance of sinking and nonsinking phytoplankton taxa in a gradient of mixing depths. Limnol. Oceanogr. **48**: 1903–1912.

Quinlan, R., and others. 2020. Relationships of total phosphorus and chlorophyll in lakes worldwide. Limnol. Oceanogr. **66**: 392–404.

Read, J. S., and others. 2014. Simulating 2368 temperate lakes reveals weak coherence in stratification phenology. Ecol. Model. **291**: 142–150.

Reynolds, C. S. 2006. The ecology of phytoplankton. Cambridge Univ. Press.

Richardson, D. C., and others. 2017. Transparency, geomorphology and mixing regime explain variability in trends in lake temperature and stratification across northeastern North America (1975-2014). Water **9**: 442.

Rigosi, A., C. C. Carey, B. W. Ibelings, and J. D. Brookes. 2014. The interaction between climate warming and eutrophication to promote cyanobacteria is dependent on trophic state and varies among taxa. Limnol. Oceanogr. **59**: 99–114.

Rinke, K., P. Yeates, and K. O. Rothhaupt. 2010. A simulation study of the feedback of phytoplankton on thermal structure via light extinction. Freshw. Biol. **55**: 1674–1693.

Rubel, F., K. Brugger, K. Haslinger, and I. Auer. 2017. The climate of the European Alps: Shift of very high resolution Köppen-Geiger climate zones 1800–2100. Meteorol. Z. **26**: 115–125.

Rubel, F., and M. Kottek. 2010. Observed and projected climate shifts 1901-2100 depicted by world maps of the Köppen-Geiger climate classification. Meteorol. Z. **19**: 135–141.

Sahoo, G. B., A. L. Forrest, S. G. Schladow, J. E. Reuter, R. Coats, and M. Dettinger. 2016. Climate change impacts on lake thermal dynamics and ecosystem vulnerabilities. Limnol. Oceanogr. **61**: 496–507.

Salmaso, N. 2002. Ecological patterns of phytoplankton assemblages in Lake Garda: Seasonal, spatial and historical features. J. Limnol. **61**: 95–115.

Salmaso, N., and M. Tolotti. 2021. Phytoplankton and anthropogenic changes in pelagic environments. Hydrobiologia **848**: 251–284.

Salmaso, N., and others. 2020. Responses to local and global stressors in the large southern perialpine lakes: Present status and challenges for research and management. J. Great Lakes Res. **46**: 752–766.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature **413**: 591–596.

Scheffer, M., S. Rinaldi, A. Gragnani, L. R. Mur, and E. H. van Nes. 1997. On the dominance of filamentous cyanobacteria in shallow, turbid lakes. Ecology **78**: 272–282.

Schwefel, R., A. Gaudard, A. Wüest, and D. Bouffard. 2016. Effects of climate change on deepwater oxygen and winter mixing in a deep lake (Lake Geneva): Comparing observational findings and modeling. Water Resour. Res. **52**: 8811–8826.

Sinha, E., A. Michalak, and V. Balaji. 2017. Eutrophication will increase during the 21st century as a result of precipitation changes. Science **357**: 405–408.

Steinberg, C. E. W., and H. M. Hartmann. 1988. Planktonic bloom-forming cyanobacteria and the eutrophication of lakes and rivers. Freshw. Biol. **20**: 279–287.

Sverdrup, H. U. 1953. On conditions for the vernal blooming of phytoplankton. ICES J. Mar. Sci. **18**: 287–295.

Tamm, M., R. Freiberg, I. Tonno, P. Noges, and T. Noges. 2015. Pigment-based chemotaxonomy—a quick alternative to determine algal assemblages in large shallow eutrophic lake? PLoS One **10**: e0122526.

Thompson, R. K. C., and R. Schmidt. 2005. Ultra-sensitive alpine lakes and climate change. J. Limnol. **64**: 139–152.

Van der Staay, G. W. M., A. Brouwer, R. L. Baard, and F. van Mourik. 1992. Separation of photosystems I and II from the oxychlorobacterium (prochlorophyte) Prochlorothrix hollandica and association of Chlb binding antennae with PS II. Biochim Biochim. Biophys. Acta **1102**: 220–228.

Visser, P. M., B. W. Ibelings, M. Bormans, and J. Huisman. 2016. Artificial mixing to control cyanobacterial blooms: A

review. Aquatic Ecology **50**: 423–441. doi:10.1007/s10452-015-9537-0

Vollenweider, R. A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters with particular reference to nitrogen and phosphorus as factors in eutrophication. OECD. Paris. Tech. Report DA5/SCII/68 27, 250 p.

Wetzel, R. G. 2001. Water movements. Limnology (Third Edition). Academic Press; 93–128. doi:10.1016/B978-0-08-057439-4.50011-3

Winslow, L. A., J. S. Read, G. J. A. Hansen, K. C. Rose, and D. M. Robertson. 2017. Seasonality of change: Summer warming rates do not fully represent effects of climate change on lake temperatures. Limnol. Oceanogr. **62**: 2168–2178.

Woolway, R. I., and C. J. Merchant. 2019. Worldwide alteration of lake mixing regimes in response to climate change. Nat. Geosci. **12**: 271–276.

Wüest, A., and A. Lorke. 2003. Small-Scalehydrodynamics Inlakes. Annu. Rev. Fluid Mech. **35**: 373–412.

Yang, Y., W. Colom, D. Pierson, and K. Pettersson. 2016. Water column stability and summer phytoplankton dynamics in a temperate lake (Lake Erken, Sweden). Inland Waters **6**: 499–508.

Yankova, Y., S. Neuenschwander, O. Koster, and T. Posch. 2017. Abrupt stop of deep water turnover with lake warming: Drastic consequences for algal primary producers. Sci. Rep. **7**: 13770.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution, **1**: 3–14.

Zwart, J. A., and others. 2016. Metabolic and physiochemical responses to a whole-lake experimental increase in dissolved organic carbon in a north-temperate lake. Limnol. Oceanogr. **61**: 723–734.

Acknowledgments

The authors acknowledge COST Action ES 1105 "CYANOCOST – Cyanobacterial blooms and toxins in water resources: Occurrence impacts and management" and COST Action Global Change Biology ES 1201 NETLAKE – Networking Lake Observatories in Europe" for contributing to this study through networking and knowledge sharing with European experts in the field. We acknowledge the members of the Global Lake Ecological Observatory Network (GLEON) for their collaborative spirit and enthusiasm that inspired the grassroots effort of the EMLS. E.M. was supported by a grant from the Swiss State Secretariat for Education, Research and Innovation to Bas Ibelings and by supplementary funding from University of Geneva. We thank Wendy Beekman for the nutrient analysis. We thank Pieter Slot for assisting with the pigment analysis. We thank Dr. Ian Jones for valuable feedback on an earlier version of the manuscript. We thank the Leibniz Institute of Freshwater Ecology and the Aquatic Microbial Ecology Group for logistic and technical support of J. Fonvielle and H.-P. Grossart, and the Leibniz Association for financial support. H.P. was supported by the US National Science Foundation (1840715, 1831096). A.C.'s work was funded by the Spanish Agencia Estatal de Investigacion and EU funds through the project CLIMAWET (CGL2015-69557-R). The collection of data for Lough Erne and Lough Neagh were funded by the Department of Agriculture, Environment and Rural Affairs, Northern Ireland. We are grateful to Kristiina Vuorio from the Freshwater Centre of the Finnish Environment institute for her help in organizing, collecting and analysing samples by the University of Jyväskylä and to Gerald Dörflinger from the Water Development Department of Cyprus for his assistance with the sampling in Cyprus and for granting the CUT team permission to use WDD's equipment. Finally, we would like to thank the numerous other assistants that helped realizing each local survey. Open access funding provided by Universite de Geneve.

Conflict of Interest

None declared.

Submitted 24 September 2020
Revised 01 July 2021
Accepted 08 October 2021

Associate editor: Catherine M. O'Reilly