LIMNOLOGY and OCEANOGRAPHY

Grazing strategies determine the size composition of phytoplankton in eutrophic lakes

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Abstract

Although the general impacts of zooplankton grazing on phytoplankton communities are clear, we know comparatively less about how specific grazing strategies interact with environmental conditions to shape the size structure of phytoplankton communities. Here, we present a new data-driven, size-based model that describes changes in the size composition of lake phytoplankton under various environmental constraints. The model includes an ecological trade-off emerging from observed allometric relationships between (1) phytoplankton cell size and phytoplankton growth and (2) phytoplankton cell size and zooplankton grazing. In our model, phytoplankton growth is nutrient-dependent and zooplankton grazing varies according to specific grazing strategies, namely, specialists (targeting a narrow range of the size-feeding spectrum) vs. generalists (targeting a wide range of the size-feeding spectrum). Our results indicate that grazing strategies shape the size composition of the phytoplankton community in nutrient-rich conditions, whereas inorganic nutrient concentrations govern phytoplankton biomass. Under oligotrophic regimes, the phytoplankton community is dominated by small cell sizes and the grazers have little to no impact. Under eutrophic regimes, dominating specialist grazers push phytoplankton towards small cells, whereas dominating generalist grazers push phytoplankton towards large cells. Our work highlights that trait-based modeling, based on realistic eco-physiological trade-offs, represents a valuable tool for disentangling the interactive roles played by nutrient regimes and grazing strategies in determining the size compositions of lake phytoplankton. Ultimately, our study offers a quantitative basis for understanding how communities of lake phytoplankton may reorganize in the future in response to changes in nutrient levels and zooplankton grazing strategies.

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Phytoplankton communities perform a range of crucial functions in aquatic ecosystems, including primary production, biogeochemical cycling, and climate regulation (Naselli-Flores and Padisák 2022). In lakes, phytoplankton communities are the primary organisms that regulate water quality, a service fundamental to humans. In these ecosystems, the trait body size is a key organizing factor, and trophic interactions can be described by eco-physiological properties that are directly connected to this trait (Peters 1983; Persson et al. 1992). For example, cellular nutrient acquisition rates, cellular growth rates, and susceptibility to grazing, all depend on phytoplankton cell size (Litchman and Klausmeier 2008; Litchman et al. 2013; Marañón 2015; Hillebrand et al. 2022). The observed higher susceptibility to grazing by small cells is related to the body size of their common grazers, which are small and tend to accumulate higher total biomass than larger grazers (Kiørboe 2011; Pančić and Kiørboe 2018). These size dependencies, combined with varying environmental conditions, like nutrient availabilities, have impacts on biomass, size structure,

and composition of phytoplankton communities (Litchman and Klausmeier 2008; Finkel et al. 2010; Hillebrand et al. 2022).

Multiple environmental factors have been identified as drivers of the size composition of phytoplankton communities in lakes, they include temperature, inorganic nutrients, light, turbulent mixing, and zooplankton grazing (Kiørboe 1993; Cottingham 1999; Reynolds 2006; Zohary et al. 2021; Hillebrand et al. 2022). In the last decades, observational evidence has been accumulating on human-induced eutrophication in limnetic systems and on the rapid changes that this eutrophication has caused on the size compositions of phytoplankton communities (Hsieh et al. 2010; Pomati et al. 2020). Small cells have a higher surface-to-volume ratio that enhances their nutrient uptake capacities in nutrient-poor environments (Chisholm 1992). In contrast, large cells are characterized by lower susceptibility to grazing that reduces their grazing pressure in grazer-abundant environments (Kiørboe 2011; Pančić and Kiørboe 2018). The higher nutrient uptake capacity that in small cells comes at the expense of a higher susceptibility to grazing constitutes a fundamental and well-known eco-physiological trade-off typically invoked to explain the size structure of phytoplankton communities in various aquatic environments (Litchman et al. 2007; Ward et al. 2012; Acevedo-Trejos et al. 2015; Erdoğan et al. 2021).

Size-selective zooplankton grazers feed on different ranges of phytoplankton size classes. These different size-feeding ranges are described as grazing strategies and can be broadly categorized into two groups: (1) specialists, the group preferentially feeding on a narrow range of phytoplankton size classes, and (2) generalists, the group feeding on a broad range of phytoplankton size classes (Porter 1973; DeMott 1982). For example, copepods *Diaptomus* graze selectively on a narrow range of large *Fragilaria* spp., at around 75 μm, whereas cladoceran *Daphnia* graze on a wide range of phytoplankton, from 1 to 75 μm (Bertilsson 2003). As another example, the generalist ciliates *Strobilidium* spp. feed on a wide range of phytoplankton cell sizes, from 5 to 50 μm (Lischke et al. 2016). Although grazing experiments have demonstrated that phytoplankton communities are highly sensitive to different grazers (Bergquist et al. 1985; Levine et al. 1999; Sommer et al. 2003), we know surprisingly little about the grazing effects of specialist and generalist zooplankton on phytoplankton biomass and on the size composition of phytoplankton communities. In addition, although synergistic effects on the phytoplankton size structure caused by concurring changes in biotic and abiotic conditions have been documented (Persson et al. 1992; Cottingham 1999; Chase et al. 2002), a clear understanding of the relative contributions of the different drivers remains elusive.

By integrating different processes within a common quantitative framework, mathematical modeling has been used to unravel the interacting mechanisms shaping the size composition of phytoplankton communities in different environments (Irwin et al. 2006; Banas 2011; Ward et al. 2012). Previous size-based models (Armstrong 1994; Stock et al. 2008; Poulin and Franks 2010; Ward et al. 2012; Acevedo-Trejos et al. 2015) included allometric relationships for phytoplankton nutrient

uptake and zooplankton grazing processes. In these models, co-variations between phytoplankton cell size and eco-physiological properties, like cellular nutrient uptake rates, cellular growth rates, zooplankton grazing, and zooplankton size-selectivity, are commonly implemented using allometric functions (e.g., Hansen et al. 1994, 1997; Litchman et al. 2007; Edwards et al. 2012). Earlier size-based models showed that the dominance of small phytoplankton cells results from nutrient limitations but they also showed that the phytoplankton size structure varies heavily with changes in resource availability (Armstrong 1994; Irwin et al. 2006; Taherzadeh et al. 2017). Despite these earlier modeling efforts, the relative contribution of different allometries in shaping the size composition of phytoplankton communities remain elusive.

The grazing strategies of zooplankton constitute a current subject of modeling investigations for understanding phytoplankton community structure. With a simplified plankton model consisting of one zooplankton grazer strictly dependent on two competing phytoplankton, Cropp et al. (2017) observed that different grazing strategies had contrasting effects on the plankton dynamics. However, that model did not include properties related to plankton size. A few size-structured models investigated the contrasting effects of specialist and generalist grazers on phytoplankton size structures in chemostat settings. Fuchs and Franks (2010) found that two distinctive size-selective grazing strategies, characterized by specialist grazers feeding on suboptimal preys and by generalist grazers feeding on optimal preys, give rise to very different phytoplankton size structures. Banas (2011) showed, in qualitative terms, that multimodal phytoplankton size distributions are more likely produced by generalist grazers than by specialist grazers. Although the effects of different grazing strategies on the dynamics or the size composition of phytoplankton communities have been the object of several studies (Fuchs and Franks 2010; Banas 2011), comparatively fewer modeling investigations have been undertaken for clarifying the effects of direct interactions between grazing strategies (over a broad range of the size-feeding spectrum) and nutrient concentrations, especially in lake environments.

We present here a size-based planktonic model designed for a typical lake environment. The model includes bottom-up and top-down interactions based on previously documented data-driven allometric relationships (Hansen et al. 1994, 1997; Edwards et al. 2012). The zooplankton are characterized by two different size-feeding strategies: specialist and generalist. We use the model to investigate the effects of different combinations of size-feeding strategies on the size composition of the phytoplankton community in different nutrient scenarios. We aim to understand how biotic and abiotic processes allow for a certain phytoplankton size composition to unfold in a changing environment.

Methods

Model description

We developed a size-based plankton model for lake ecosystems based on the well-established Nutrient–Phytoplankton–

Zooplankton–Detritus framework (Fasham et al. 1990; Armstrong 1994). The model is implemented in a zero-dimensional spatial setting using a simple two-layer slab physics (Fasham et al. 1990). The upper layer, representing the ecologically active epilimnion zone, contains the planktonic ecosystem and is assumed to be well mixed. The depth of the upper layer changes dynamically and reflects the seasonally varying mixed layer depth (MLD). The bottom layer, representing the nutrient-rich and biologically inactive hypolimnion zone, contains only a fixed amount of nutrient, N_0, which replenishes the inorganic nutrient pool of the upper layer during mixing events. The planktonic ecosystem consists of different size classes of phytoplankton (P_i, with $i = 1, 2, \ldots, 150$) that for growth rely on light, $I(z)$, with z indicating depth, and inorganic nutrient, N. Phytoplankton is grazed by a zooplankton community that is structured into two size classes (Z_j, with $j = 1, 2$), representing specialist and generalist grazing strategies (Fig. 1). Dead phytoplankton and zooplankton along with a portion of the grazed

material (sloppy feeding) flow into the detritus pool, D, that gets remineralised, at a fixed rate, into the inorganic nutrient pool N. Considering nitrogen as the currency, all state variables are expressed in units of μM N. The nitrogen concentration in the nutrient pool reflects, as per standard limnology, the amount of total dissolved nitrogen available to phytoplankton.

The model captures size-dependent bottom-up and top-down interactions through allometric relationships with phytoplankton nutrient uptake and zooplankton grazing (Fig. 1). Phytoplankton and zooplankton sizes are expressed in terms of an Equivalent Spherical Diameter (ESD). The size dependencies are scaled by allometric functions of the general form: $X = \beta S^{\alpha}$, where X is an eco-physiological trait, S is the plankton size, and the parameters β and α are, respectively, intercept and exponent of the allometric functions. These functions are useful to constrain the number of free parameters in the model (Armstrong 1994). An ecological trade-off between growth ability (resource-dependent) and susceptibility to grazing emerges from the four allometric relationships encoded in the
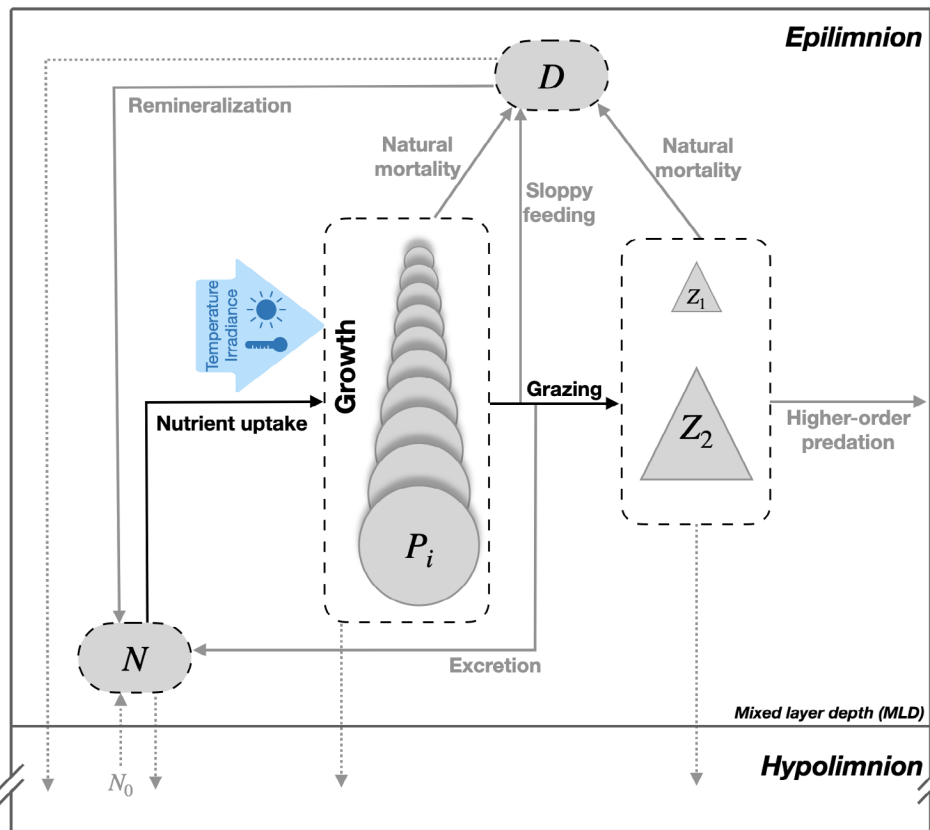

Fig. 1. Schematic representation of the size-based model. The model is implemented in a zero-dimensional spatial setting using a simple two-layer slab physics. The upper layer, representing the epilimnion, whose depth varies seasonally and is assumed to be well mixed, contains the plankton ecosystem consisting of four components: inorganic nutrients, N, phytoplankton, P, zooplankton, Z, and detritus, D. The phytoplankton community is subdivided into 150 size classes (P_i, with $i = 1, 2, \ldots, 150$) and the zooplankton community is subdivided into two size classes, Z_1 and Z_2. Black arrows represent the two size-dependent processes: phytoplankton nutrient uptake and zooplankton grazing. Gray arrows represent ecological and biogeochemical processes (solid lines) and mixing processes (dotted lines) that are size independent. The blue arrow symbol indicates the environmental forcing (i.e., temperature and irradiance) applied to the model. The loss of zooplankton to higher-order predators is density-dependent and formulated as a quadratic function. We assume that the loss of nutrients from the epilimnion is replenished through mixing events by a fixed nutrient source, N_0, in the hypolimnion.

model. These relationships are described in detail in the following subsection. All model parameters and literature sources are reported in Supporting Information Table S1.

Ecological model

Phytoplankton (P)

The temporal dynamics of biomass P_i for the ith phytoplankton size class is described by:

$$\frac{dP_i}{dt} = (\mu_i - \phi_P - \lambda)P_i - \sum_{j=1}^{2} G_{ij}Z_j \tag{1}$$

with

$$\mu_i = \mu_{\max_i}(S_i)\frac{N}{K_{N_i}(S_i) + N}E(T)H(I_z) \tag{2}$$

Here, μ_i describes the growth rate of phytoplankton controlled by (1) a size-scaled maximum growth rate term,

$$\mu_{\max_i}(S_i) = \beta_{\mu_{\max}} S_i^{\alpha_{\mu\max}} \tag{3}$$

(2) a size-dependent nutrient uptake term, $N/(K_{N_i}(S_i) + N)$, following Monod kinetics (1949), with $K_{N_i}(S_i)$ determined by $K_{N_i}(S_i) = \beta_{K_N} S_i^{\alpha_{K_n}}$, (3) a temperature-limited growth term, $E(T) = e^{0.063T}$, with T representing Lake Surface Temperature (LST) in °C, following Eppley (1972), and (4) a light-limited growth term $H(I_z)$ given by:

$$H(I_z) = \frac{1}{\text{MLD}}\int_{Z=0}^{Z=MLD} P_I(z)dz \tag{4}$$

The light limitation term (Eq. 4) depends on the daily MLD-averaged photosynthesis rate and is calculated by integrating the photosynthesis-irradiance relationship, $P_I(z)$, of Lewis and Smith (1983) through depth z. The function $P_I(z)$ is given by,

$$P_I(z) = \frac{\alpha_{P_I}I(z)P_{\max}}{\sqrt{P_{\max}^2 + [\alpha_{P_I}I(z)]^2}} \tag{5}$$

where α_{P_I} indicates the initial slope of the $P_I(z)$ curve, $P_{\max}$ denotes the maximum photosynthetic rate, and $I(z)$ is the irradiance I calculated at depth z based on Beer–Lambert's law,

$$I(z) = I_0 e^{-K_{\text{par}}z} \tag{6}$$

with K_{par} representing a total light attenuation coefficient due to water. I_0 is the photosynthetically active radiation (PAR) reaching the top of the lake surface (i.e., at depth $z = 0$). For numerical efficiency, we use the analytical approximation of

the integral of light limitation with depth (Eq. 4) from Anderson et al. (2015):

$$\begin{aligned} H(I) &= \frac{1}{\text{MLD}}\int_{z=0}^{z=\text{MLD}} P_I(z)dz \\ &= \frac{P_{\max}}{K_{\text{par}}\text{MLD}}\log\left(\frac{\alpha_{P_I}I_0 + \sqrt{P_{\max}^2 + (\alpha_{P_I}I_0)^2}}{\alpha_{P_I}I(z) + \sqrt{P_{\max}^2 + [\alpha_{P_I}I(z)]^2}}\right) \end{aligned} \tag{7}$$

Phytoplankton gross growth (Eq. 1) is reduced by loss terms reflecting natural mortality, ϕ_P, mixing, λ, and zooplankton grazing, $\sum_j G_{ij}Z_j$.

Zooplankton (Z)

The temporal dynamics of biomass Z_j for the jth zooplankton size class is captured by the following equation:

$$\frac{dZ_j}{dt} = \left[\varepsilon\gamma\sum_j G_{ij} - \phi_Z - \eta_Z Z_j - \lambda_z\right]Z_j \tag{8}$$

The first term describes net gain from grazing, which is regulated by sloppy feeding (ε) and assimilation efficiency (γ). The values of ε and γ are assumed constant (Hansen et al. 1997). Following Banas (2011), the grazing rate is described by the following function:

$$G_{ij} = I_{\max_j}(S_j)\frac{\delta_{ij}(S_i, S_{Z_j})P_i}{K_p + \sum_i \delta_{ij}(S_i, S_{Z_j})P_i} \tag{9}$$

where $I_{\max_j}$ is the maximum ingestion rate and K_p is the half-saturation constant for phytoplankton intake. Previous work suggested that small zooplankton graze more intensively than large zooplankton (Hansen et al. 1994). Accordingly, the maximum ingestion rate is determined based on the following allometric relationship:

$$I_{\max_j}(S_j) = \beta_{I_{\max}}S_{Z_j}^{\alpha_{I\max}} \tag{10}$$

In addition, zooplankton exhibit size-selective grazing, that is, a preference for a specific range of phytoplankton size classes (Porter 1973). This preference is captured in our model with a Gaussian function over the phytoplankton size spectrum, by the following equation:

$$\delta_{ij}(S_i, S_{Z_j}) = e^{-\left[\frac{\log_{10}(S_i) - \log_{10}\left(P_{\text{opt}_j}(S_{Z_j})\right)}{\theta_j}\right]^2} \tag{11}$$

where P_{opt_j} and θ_j are, respectively, optimum prey size and prey size tolerance. $\delta_{ij}(S_i, S_{Z_j})$ is determined by an empirical

allometric relationship (Hansen et al. 1997), $P_{\text{opt}_j}\left(S_{Z_j}\right) = \beta_{P_{\text{opt}}} S_{Z_j}{}^{\alpha_{P_{\text{opt}}}}$, and by their grazing strategies. We consider two major grazing strategies that encompass various feeding behaviors (Kiørboe 2011) in relation to the range of cell sizes preferentially targeted by the grazers, specialist, and generalist. In temperate lakes, for example, species that exhibit raptorial feeding are specialists that feed selectively on a narrow range of phytoplankton sizes, for example, nanoflagellates or copepods nauplii (Šimek and Chrzanowski 1992; Sommer et al. 2003); whereas species that show filter-feeding are generalists that feed nonselectively on a wide range of cell sizes, for example, protozoan ciliates or cladoceran daphniids (Fenchel 1980; DeMott 1982). In our model, these features are captured by considering a lower prey size tolerance (θ) for specialists than for generalists. The loss terms (Eq. 8) accounts for natural mortality (φ_Z), higher order predation (ηZ_j), and mixing (λ_z).

Nutrient (N) and detritus (D)

The temporal dynamics of nutrient, N, is given by:

$$\frac{dN}{dt} = -\sum_i \mu_i P_i + \varphi D + \varepsilon(1-\gamma)\sum_i\sum_j G_{ij}Z_j + \lambda(N_0 - N) \quad (12)$$

The first term represents the nutrient outflow due to uptake by phytoplankton. Nutrient replenishment comes from remineralization of detritus, φD, and excretion by zooplankton, $\varepsilon(1-\gamma)\sum\sum G_{ij}Z_j$. The last term, $\lambda(N_0 - N)$, describes the exchange[i] of nutrient between the upper epilimnion and the bottom hypolimnion through mixing, where N_0 is the nutrient concentration in the hypolimnion.

The pool of detritus act as a nutrient recycling station and changes according to the following equation:

$$\frac{dD}{dt} = \sum_i \phi_P P_i + \sum_j \phi_z Z_j + (1-\varepsilon)\sum_i\sum_j G_{ij}Z_j - (\varphi+\lambda)D \quad (13)$$

Physical setup

In most lake ecosystems, the exchange of materials between the ecologically active epilimnion zone (the upper layer) and the nutrient-rich biologically inactive hypolimnion zone (the bottom layer) is driven by mixing processes. In our model, mixing is expressed by the following term (Evans and Parslow 1985):

$$\lambda = \frac{\omega + h^+(t)}{MLD(t)} \quad (14)$$

where ω is the cross-thermocline mixing constant, representing diffusive mixing and $h^+(t)$ quantifies entrainment and detrainment of materials during mixing events:

$$h^+(t) = \max(0, h) \quad (15)$$

with $h = ((dMLD(t))/dt)$. All variables in the model are subject to gains and losses due to mixing (Fig. 1). Zooplankton are considered motile and hence able to avoid detrainment by maintaining themselves within the upper layer, therefore, $\lambda_z = (h/(MLD(t)))$ (*see* Eq. 8).

Numerical experiments

The phytoplankton community is composed of $n = 150$ size classes sequentially spaced on a $\log_{10}$ basis, from 1 to $100\,\mu m$. Herbivorous zooplankton are composed of two size classes, $5\,\mu m$ (Z_1) and $200\,\mu m$ (Z_2), respectively. All the variables are initialized at low concentrations, $0.01\,\mu M\,N$ (Supporting Information Table S1). Default parameter values are reported in Supporting Information Table S1, unless specified otherwise in the different experiments.

MLD, LST, and PAR are forcing variables in our model, that is, external environmental data used as input to the model. For LST and PAR, we selected a set of averaged weather data for lakes around 40°N from 1991 to 2011 from Layden et al. (2015), *see* Supporting Information Fig. S1A. According to the mean lake depth of eight Swiss lakes (Pomati et al. 2020), the seasonal variation of MLD ranges from 2.5 m to 80 m. We adopted a theoretical mixing pattern for MLD based on sinusoidal functions with varying frequencies over a 1-yr time period (*see* Supporting Information S1; Fig. S1B). Varying frequencies allowed us to perform numerical experiments with contrasting mixing patterns.

We performed numerical experiments by systematically varying the combinations of parameter values controlling grazing strategies and nutrient levels in combination with mixing frequencies (Table 1). Furthermore, we adopted a set of data-driven allometric relationships derived from a rich compilation of over 120 freshwater phytoplankton species and

Table 1. Conditions considered for the different numerical experiments. The experiments are created by changing the values of parameters defining (1) grazing strategies and (2) environmental conditions (nutrient level and mixing frequency). All experiments are based on the same set of allometric relationships presented in Supporting Information Table S1.

Scenarios of grazing strategy	Nutrient level	Mixing frequency
SS: Dominant and subordinate specialist	Oligotrophic: $1\,\mu M\,N$	Constant: No mixing
SG: Dominant specialist and subordinate generalist	Eutrophic: $15\,\mu M\,N$	Medium: 4 mixing events yr^{-1}
GS: Dominant generalist and subordinate specialist	Hypertrophic: $50\,\mu M\,N$	High: 12 mixing events yr^{-1}
GG: Dominant and subordinate generalist		

28 zooplankton species (Hansen et al. 1994, 1997; Edwards et al. 2012). These allometries were adopted in previous models (e.g., Banas 2011) and represent a realistic range of parameters for prominent freshwater species. With the assumed allometric scaling for $\mu_{\max i}$ and $K_{N i}$, the system configures small phytoplankton cells as faster growers and gleaners, such that they can grow at high rates under low nutrient levels (Fig. 2A,C). With the assumed allometric scaling for $I_{\max j}$ and the density-dependent grazing formulation (Eq. 9), the small zooplankton, Z_1, is the dominant grazer, whereas the large zooplankton, Z_2, is the subordinate grazer because, being characterized by a higher ingestion rate, Z_1 accumulates more biomass than Z_2 when enough food is available (Fig. 2B). The allometric scaling for $P_{\mathrm{opt} j}$ determines that Z_1 grazes on cells smaller than those grazed by Z_2. Therefore, small phytoplankton are limited by the top-down control more strongly than their larger counterparts (Fig. 2D). This constitutes an eco-physiological trade-off whereby the more effective nutrient uptake by small cells is counteracted by a stronger grazing pressure from the dominant grazer. Conversely, the larger phytoplankton cells, those that are less effective in taking up nutrients, will experience a weaker grazing pressure.
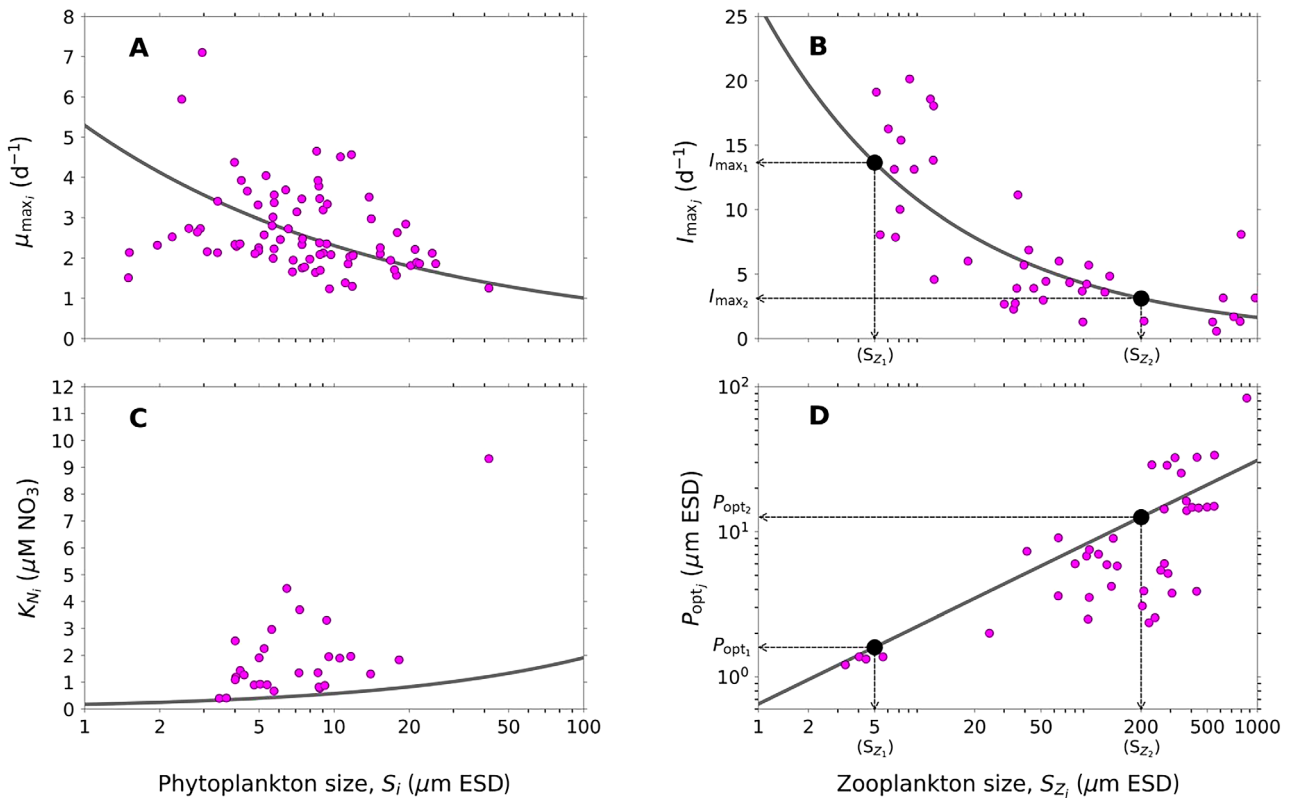
Different scenarios of grazing strategies

We examined different scenarios of grazing strategies for the two size-selective zooplankton groups, the dominant Z_1 and the subordinate Z_2. The four grazing scenarios are dominant and subordinate specialists (SS, Fig. 3A), dominant specialist and subordinate generalist (SG, Fig. 3B), dominant generalist and subordinate specialist (GS, Fig. 3C), and dominant and subordinate generalists (GG, Fig. 3D). These scenarios capture different distributions of grazing pressures on the different phytoplankton size classes (Fig. 3). We consider prey size tolerances, θ_j, of 0.2 and 0.5 for the specialist and the generalist, respectively (Supporting Information Table S1). These four grazing scenarios are further varied in combination with different nutrient levels and mixing frequencies (Table 1).

Nutrient levels and mixing frequencies

To investigate how different resource inputs and frequencies of mixing events select dominant phytoplankton size classes, we perform experiments based on different levels of nutrients supplied from the bottom layer (N_0) and based on different frequencies of mixing through the water column. The designated nutrient levels reflect oligotrophic, eutrophic, and

Fig. 2. Data-driven allometric relationships considered in our model. (**A**) maximum nutrient uptake rate, $\mu_{\max i}$, and (**C**) half-saturation constant for nutrient uptake, $K_{N i}$, for a given phytoplankton size class S_i ($i = 1, 2, \ldots, 150$). (**B**) maximum ingestion rates, $I_{\max j}$ and (**D**) optimal prey size, $P_{\mathrm{opt} j}$ for a given zooplankton size class S_{Z_j} ($j = 1, 2$). The black circles denote the value of $I_{\max}$ (13.7 and 3.1 d^{-1}) and P_{opt} (1.6 and 12.6 μm) adopted for Z_1 and Z_2. The data in (**A**) and (**C**) are from Edwards et al. (2012) and the data in (**B**) and (**D**) are, respectively, from Hansen et al. (1997) and Hansen et al. (1994).
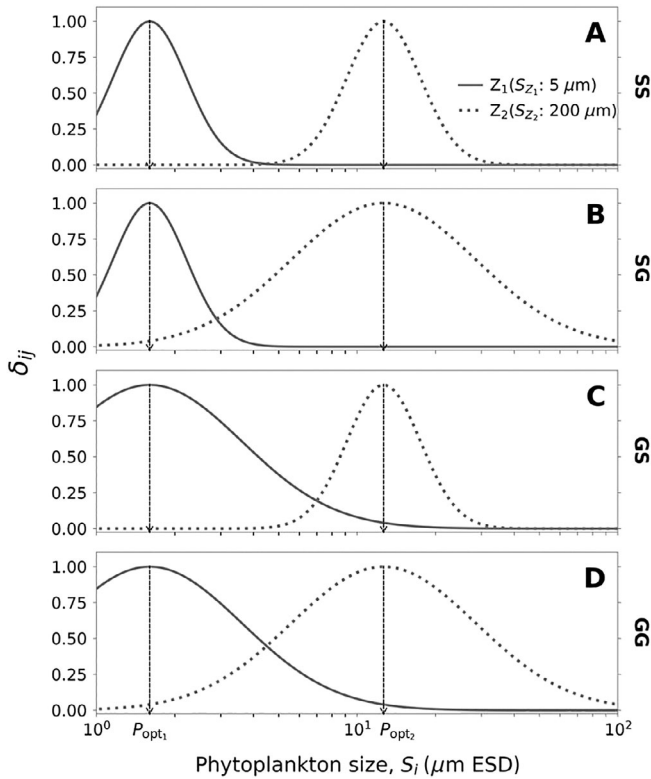
Fig. 3. Zooplankton grazing strategies considered in our model. These strategies are defined by the grazing preferences, $\delta_{ij}\left(S_i, S_{Z_j}\right)$, of the small ($Z_1$, $S_{Z_1} = 5\,\mu$m ESD, with $P_{opt_1} = 1.6\,\mu$m ESD, solid lines) and the large (Z_2, $S_{Z_2} = 200\,\mu$m ESD, with $P_{opt_2} = 12.6\,\mu$m ESD, dotted lines) zooplankton on the different phytoplankton size classes, S_i. The different preferences reflect four scenarios of grazing strategies: (**A**) dominant and subordinate specialists (SS), (**B**) dominant specialist and subordinate generalist (SG), (**C**) dominant specialist and subordinate generalist (GS), and (**D**) dominant and subordinate generalists, GG. Dashed arrows denote the optimal prey size, P_{opt}, for each zooplankton size class (*see* Fig. 2D).

hypertrophic conditions corresponding, respectively, to 1, 15, and $50\,\mu$M N (Table 1). The mixing frequencies reflect constant, medium, and high mixing corresponding, respectively, to no mixing, 4 mixing events per year, and 12 mixing events per year (Table 1 and Supporting Information Fig. S1B).

Analyses of macro-ecological properties

We run the model with repeated annual forcing for 10 yr. Our analyses are based on the results obtained in the 10th year when the model has reached steady annual cycles. The results for each grazing strategy scenario are analyzed in terms of two community-aggregate phytoplankton properties: total biomass and mean cell size (biomass-weighted), S_w, which is given by:

$$S_w = \frac{\sum_i^n P_i S_i}{\sum_i^n P_i} \tag{16}$$

where n is the total number of size classes. The value of S_w represents the dominance of a range of size classes instead of a single size class.

Sensitivity analyses

We investigated the sensitivity of our model results with respect to the zooplankton community structure and the parameters characterizing the two allometric relationships considered in our model (i.e., the maximum phytoplankton growth rate, $\mu_{\max i}$, and the maximum zooplankton ingestion rate, $I_{\max j}$, *see* Supporting Information S2). For the zooplankton community structure, we tested a varying number of grazers (i.e., four, six, and eight) over a broader zooplankton size range (from 5 to $2000\,\mu$m). With this broader size range, the grazing pressure fully covers the entire phytoplankton size spectrum (Supporting Information Fig. S2). For the allometric scaling, we tested variations of $\pm 50\%$ in the two size-scaling exponents, $\alpha_{\mu_{\max}}$ and $\alpha_{I_{\max}}$ (Supporting Information Fig. S3A,B). We conduct the sensitivity analyses for a subset of environmental conditions: the combination of medium mixing frequency and eutrophic or hypertrophic condition.

Results

Effects of nutrient levels and mixing frequencies on community size composition

Under all grazing strategies, regardless of mixing frequencies, oligotrophic conditions produce a median daily total biomass of less than $0.3\,\mu$M N with an annual variation of less than $0.6\,\mu$M N (Fig. 4A–D; Supporting Information). Biomass increases with increasing nutrient levels and mixing frequencies. The highest median biomass and largest annual variation are obtained under the most extreme conditions: hypertrophic nutrient levels combined with high mixing frequencies (Fig. 4A–D).

In the absence of mixing, oligotrophic and eutrophic systems respond similarly to different grazing strategies and are characterized by a persistent dominance of the smallest size class (1 μm ESD) throughout the year (Fig. 4E–H). Only hypertrophic systems show intermediate size classes, in the range of 3–5 μm ESD (Fig. 4E–H). The presence of mixing produces larger mean cell sizes in eutrophic and hypertrophic systems, especially when generalist grazing is the dominant feeding strategy (Fig. 4G,H). Moving from oligotrophic to eutrophic and hypertrophic conditions and with increasing mixing, we observe an increase in the mean cell size of the phytoplankton community from 1 to 60 μm ESD (Fig. 4E,H). These results highlight the positive effect of nutrient levels on total biomass and mean cell size and show that the impact of different mixing regimes depends on the specific grazing strategy.

Effects of different grazing strategies on community size composition

Our result shows that total biomass levels and annual fluctuations of biomass depend weakly on grazing strategies
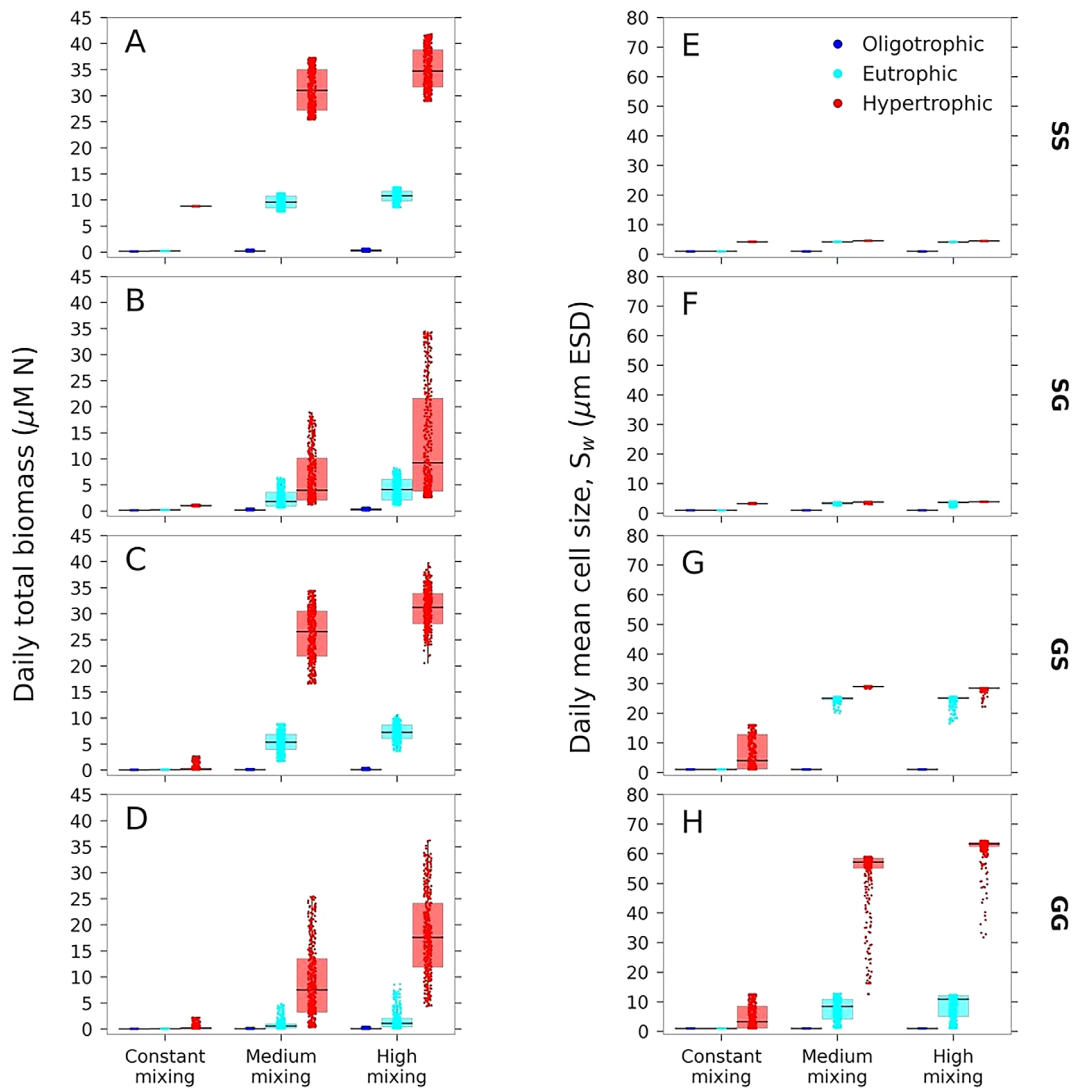
Fig. 4. Model results (number of data points = 365, one data point for every day of the last year of model run) of phytoplankton total biomass (**A–D**) and mean cell size (**E–H**) on a daily basis and under different grazing strategies (GG, dominant and subordinate generalist; GS, dominant generalist and subordinate specialist; SG, dominant specialist and subordinate generalist; SS, dominant and subordinate specialists), different nutrient conditions (i.e., oligotrophic: 1 μM N, blue dots; eutrophic: 15 μM N, cyan dots; and hypertrophic: 50 μM N, red dots), and different mixing frequencies (constant: no mixing; medium: 4 mixing events yr^{-1}; high: 12 mixing events yr^{-1}). The size of the boxplots denotes the first quartile (25th percentile) and the third quartile (75th percentile). The line in the middle of the boxplots marks the median (50th percentile). The maximum, median, and annual ranges of total biomass and mean cell size are shown in Supporting Information.

(Fig. 4A–D). By contrast, different grazing strategies produce distinctive patterns of mean cell size, especially under highly perturbed environmental conditions, that is, hypertrophic conditions combined with high mixing frequencies. The low median ($\leq$ 4.5 μm) and low variation ($\leq$ 2 μm) in mean cell size produced by a dominant specialist under all environmental conditions show that small phytoplankton cells dominate the community throughout the year regardless of nutrient levels and mixing frequencies (Fig. 4E,F; Supporting Information). In systems with a dominant generalist, nutrient levels have a stronger influence on the median and annual variations of mean cell size. Under scenario "GS," the mean cell size

increases from 1 to over 20 μm ESD when moving from oligotrophic to eutrophic and hypertrophic conditions (Fig. 4C). Among all grazing scenarios, scenario "GG" produces the highest mean cell size, more than 57 μm ESD (Fig. 4H; Supporting Information). In addition, "GG" yields the largest annual variations in mean cell size (Fig. 4H). In summary, a dominant specialist produces phytoplankton communities dominated by small cells, narrow size variations, and low sensitivity to nutrient and mixing conditions; whereas a dominant generalist produces phytoplankton communities dominated by large cells, broad size variations, and high sensitivity to nutrient and mixing conditions.
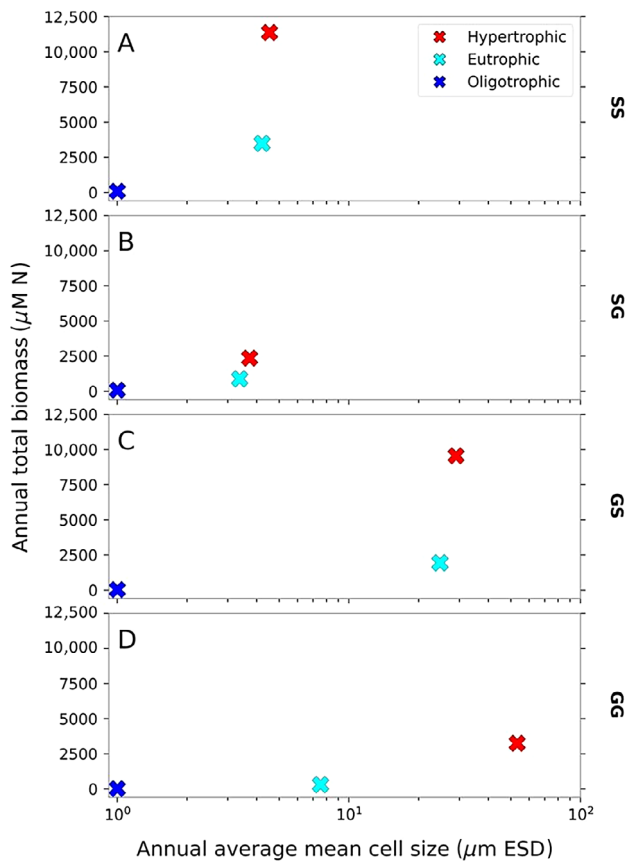
Fig. 5. Annual total biomass vs. annual average mean size under different grazing strategies and different nutrient conditions. For these runs, the mixing frequency is fixed to medium.

We also find that oligotrophic systems are typically characterized by small cells and low biomass with small differences between grazing scenarios (Fig. 5). In contrast, in non-oligotrophic systems, a dominant specialist and a dominant generalist selects for, respectively, nano-cells (i.e., 3–5 μm ESD, Fig. 5A,B) and micro-cells (i.e., > 20 μm ESD, Fig. 5C,D). This result highlights the importance of grazing strategies on the size composition of the phytoplankton community in eutrophic environments.

Sensitivity analysis

Varying the zooplankton community structure or the allometric scaling relationships revealed the important role played by grazing strategies on the size composition of the phytoplankton community in eutrophic environments. In contrast, an increase in the number of grazers (i.e., from 2 to 8) or changes in the allometric relationships (i.e., ± 50% changes in $\alpha_{\mu_{max}}$ and $\alpha_{I_{max}}$) mostly controls total phytoplankton biomass. More specifically, total phytoplankton biomass declines when the number of grazers increases from 2 to 8 and this decline in biomass varies with nutrient concentrations and grazing strategies (Supporting Information Fig. S4). In hypertrophic conditions,

varying the allometric scaling for maximum growth rate and maximum ingestion rate, via the parameters $\alpha_{\mu_{max}}$ and $\alpha_{I_{max}}$, respectively, affects primarily the total biomass of phytoplankton (Supporting Information Fig. S5). Specifically, a higher $\alpha_{\mu_{max}}$ and a lower $\alpha_{I_{max}}$ increase the total biomass; whereas a lower $\alpha_{\mu_{max}}$ and a higher $\alpha_{I_{max}}$ decrease the total biomass. The phytoplankton mean size does not change appreciably when varying these parameters. There is an exception for scenario "GG" when $\alpha_{\mu_{max}}$ is reduced. Under this condition, the community composition shifts towards intermediate cell sizes (Supporting Information Fig. S5D,H). In summary, the sensitivity analysis shows that our results are robust with respect to the specific parameter values chosen for characterizing the assumptions most relevant to our study, i.e. in relation to allometries and grazing pressure.

Discussion

The way phytoplankton communities respond to environmental changes has important consequences on the water quality and the health of aquatic ecosystems. The cell size composition of phytoplankton communities is related to fundamental eco-physiological processes and has impacts on energy fluxes, food-web structure, and ecosystem functioning (Litchman and Klausmeier 2008). We investigated variations in community-aggregate phytoplankton biomass and mean cell size under different combinations of nutrient levels, mixing conditions, and zooplankton grazing strategies. The grazing strategies are defined in our study by the range of cell sizes targeted by the grazers. We find that in non-oligotrophic lakes, where regular mixing takes place during the year, the size composition of the phytoplankton community is primarily shaped by the grazing strategy dominating the zooplankton community or, in other words, by the strategy (specialist vs. generalist) of the small grazer. In contrast, the maximum phytoplankton biomass is primarily controlled by nutrient availability and mixing conditions.

Effects of nutrient level on phytoplankton biomass

In our model, the nutrient levels are co-determined by nutrient concentrations, ranging from oligotrophic to hypertrophic conditions, and mixing frequencies, ranging from no mixing events to 12 mixing events per year. We find that high nutrient concentrations and high mixing frequencies increase total phytoplankton biomass and produce large annual variations in biomass. Nutrients in lakes are supplied in pulses from the hypolimnion to the biologically active epilimnion by vertical mixing events (Imboden and Wüest 1995). These nutrient pulses constitute a crucial physical control for the abundance and biomass production of phytoplankton in lakes (Sommer et al. 2012), such that large seasonal variations in nutrients and mixing support high fluctuations in phytoplankton biomass (Reynolds et al. 2000). Several empirical models supported a positive linear relationship between the logarithmically transformed

values of annual mean nutrients and chlorophyll *a* (Chl *a*) concentrations, taken as a proxy of phytoplankton biomass (McQueen et al. 1989; Reynolds et al. 2000; Phillips et al. 2008). A disruption of the synergistic link between high mixing frequencies and high nutrient concentrations can lead to drastic reductions in lake primary production (Yankova et al. 2017). Ecosystem models showed a tight relationship between phytoplankton dynamics and nutrient pulses when the phytoplankton community is controlled primarily by bottom-up regulation (e.g., Taherzadeh et al. 2017). By considering size-selective grazing interactions in our model, we find that the pattern of phytoplankton biomass generally follows nutrient levels but is refined by the specific grazing regime (generalist vs. specialist) considered in nutrient-repleted conditions. This leads to different annual biomass levels between grazing scenarios.

Effects of nutrient level on phytoplankton size composition

Apart from regulating phytoplankton biomass, nutrient inputs also govern phytoplankton mean cell size. The mean cell size in our model results reflects the range of dominant size classes in the community. We find a consistent dominance of small cells ($\cong 1\,\mu m$ ESD) under weak environmental perturbations typical, for example, of meromictic lakes (characterized by rare mixing events) or of oligotrophic lakes (characterized by low grazing pressures). Previous size-based models, which used linear allometric scaling to describe phytoplankton growth, captured similar size ranges under low resource levels and weak top-down regulations but in chemostat settings (e.g., Irwin et al. 2006; Poulin and Franks 2010; Banas 2011; Taherzadeh et al. 2017). The tendency towards small size classes under low nutrient concentrations or mild grazing pressure is also found in model studies of the global ocean in tropical regions (Ward et al. 2012) or when two-layer slab models (like the one adopted here) are applied along broad environmental gradients (Acevedo-Trejos et al. 2015). Such patterns are attributed to the high nutrient affinity (i.e., the low half-saturation constant for nutrient uptake) of small cells (Armstrong 1994; Banas 2011; Acevedo-Trejos et al. 2015) or to the low nutrient storage requirement (Irwin et al. 2006; Taherzadeh et al. 2017), which provides small cells with a competitive advantage in systems characterized by low nutrients (Grover 1991). In nature, the strong dominance of pico-phytoplankton is often observed in oligotrophic environments, whereas a high proportion of large cells (more than $20\,\mu m$ in ESD) are usually found under eutrophic conditions (Chisholm 1992; Ward et al. 2012; Cloern 2017; Hillebrand et al. 2022). However, the results from our data-driven size-based model show that nutrient competition is not the only factor affecting the size composition of the phytoplankton community in nutrient-rich and well-mixed conditions. We show that the phytoplankton size composition is primarily regulated by the specific grazing strategy (specialist vs. generalist) dominating the zooplankton community.

Effects of grazing strategy on phytoplankton size composition

We find that communities of grazers dominated by specialists favor nano-phytoplankton (i.e., small cells, 3–5 μm ESD) by suppressing the competitive pico-phytoplankton, whereas communities of grazers dominated by generalists favor micro-phytoplankton (i.e., large cells, more than 20 μm ESD) by suppressing the competitive pico- and nano-phytoplankton. Since in-situ investigations on the separate effects of size of grazers and size-feeding ranges of grazers on phytoplankton communities are rare (Weithoff and Beisner 2019), these two factors are often confounded in lake observations, thus direct comparisons with natural systems are difficult. However, lake enclosure experiments from two small lakes in Michigan, USA, found that the grazing of copepods and rotifers (specialists) favors a phytoplankton community characterized by small cells (Bergquist et al. 1985). Our results show that specialist grazers favor small phytoplankton only in the absence of dominant (small-sized) generalist grazers. When we consider generalist grazers as dominant, our results agree with the observation in small eutrophic lakes in Germany (Lischke et al. 2016), where the high abundance of ciliates (*Strobilidium* spp.), which are generalists grazers known for their voracious feeding on pico- and nano-phytoplankton, favors large phytoplankton like diatoms. Generally, in natural environments, the dominance of specialist or generalist grazers interchanges seasonally, it is thus expected that the size compositions of phytoplankton communities are determined by the interactive effects of available nutrients and the dominant grazing strategy (Weisse 1991; Sommer et al. 2012). To disentangle the influence of primary factors in a simplified environment, an earlier size-based model investigated the effects of specialist and generalist grazers on the phytoplankton size composition in a chemostat setting (Banas 2011). The model showed a shift from small to intermediate phytoplankton cell sizes as the grazing community transitioned from purely specialist to purely generalist. While in general agreement with the results from Banas (2011), our two-grazer model framework considers, additionally, the interactive effects of specialist and generalist strategies with nutrient levels. We are thus able to clarify that the effects of different grazing strategies become prominent in eutrophic conditions and that the dominant grazing strategy is crucial in determining the size compositions of phytoplankton. On a broader level, our results provide first theoretical insights on how the relative composition of specialists and generalists in a community of grazers could regulate the transfer of energy from the inorganic nutrient pool to higher trophic levels.

Generality of our results and future research directions

In our model, the size composition of the zooplankton community is structured into two primary size classes characterized by different grazing strategies and a specific set of allometric relationships. We acknowledge that even in small lakes

there could be more than just two zooplankton size classes and that they may exhibit body sizes larger than those considered here (e.g., up to 2000 μm for microzooplankton). We also acknowledge that our results are based on a specific set of allometric relationships. Even if these relationships are derived from laboratory data, size scaling may show higher variability in nature. Our sensitivity analysis, however, confirmed that the control of the dominant grazing strategy over the phytoplankton size composition is robust with respect to the number of grazers and to the different allometric relationships considered. When we increase the number of grazers in the model, we observe mainly a decrease in total phytoplankton biomass to less than 5000 μM N. Increasing the number of grazers in our model enhances the size diversity of zooplankton. As a form of functional diversity, a higher size diversity for the grazers would normally lead to a stronger grazing control on the biomass of the phytoplankton community (Duffy 2002; Ye et al. 2013). The decrease in total biomass we found is consistent with the reference levels of biomass required by the EU Water Framework Directive (Poikāne et al. 2010) for classifying the trophic conditions of European deep lakes or reservoirs (i.e., more than 15 m deep). These reference levels of biomass are based on a rich compilation of chlorophyll-a data and centre in the range 1.5–2.2 μg Chl a L^{-1}, corresponding to the biomass values of 3500–5000 μM N shown in our results (Supporting Information Fig. S4).

In natural systems, multiple nutrients (carbon, nitrogen, and phosphorus) can co-limit phytoplankton growth (Gaedke et al. 2002; Klausmeier et al. 2004). Since specific elemental requirements are related to specific cell sizes (Finkel et al. 2010), grazing pressure can affect the stoichiometry of phytoplankton communities by selecting organisms with specific nutritional values (Mandal et al. 2018). For example, in laboratory experiments, daphnia showed higher grazing rates when exposed to phosphorus-limited phytoplankton than when exposed to phosphorus-rich phytoplankton (Mandal et al. 2018). Future research efforts could focus on understanding how the interactive effects of phytoplankton stoichiometry and grazing pressure modify the size compositions of phytoplankton communities in lakes.

The size-based framework presented here is one way among many to model the size composition of phytoplankton communities. Our trait-based model uses a morphological trait, that is, phytoplankton cell size, that is a predicted outcome, that is, a state variable, rather than a fixed input parameter, of the model (Klausmeier et al. 2020). This type of model does not require to specify species or group identities. With minimal complexity, the model is thus capable of producing a consistent range of predictions and allows for systematic assessments of the outcomes in relation to data-driven allometric assumptions. In our model, the grazing of zooplankton on phytoplankton depends on a size-based assumption from earlier empirical studies. This assumption can vary across species.

Our model does not resolve specific feeding modes of certain zooplankton species (e.g., ambushing feeding, filter feeding) or the interactions with higher trophic levels (e.g., carnivores or omnivores). The feeding behaviors of copepods can affect the bottom-up control on phytoplankton and the intraguild predatory interactions between copepods and ciliates can modulate the grazing pressure on phytoplankton (Wollrab and Diehl 2015). Fish predation has important impacts on the zooplankton size structure and also this aspect can impact on the grazing forces that shape the phytoplankton community and can regulate the trophic transfer efficiencies in whole-lake food-webs (Carpenter et al. 1985; Jeppesen et al. 2000; Iglesias et al. 2011). The investigation of these aspects in the context of a more complex planktonic ecosystem or even at the level of larger food-web models constitutes obvious next directions for research.

Conclusions

We presented a size-based modeling study that combines a set of empirically-derived allometric relationships and zooplankton grazing strategies. Our results support the importance of nutrient concentrations in regulating maximum phytoplankton biomass and highlight, for the first time, the relevant role played by grazing strategies, in terms of different size-feeding ranges (specialist vs. generalist), in controlling the size compositions of phytoplankton communities in eutrophic lakes. Different lines of development could be considered in the future for refining our understanding of phytoplankton community structures in freshwater ecosystems. For example, one might consider incorporating size dependencies in relation to temperature-related physiological properties of phytoplankton growth. The effects of temperature on the size composition of phytoplankton communities are of great relevance, especially under the current context of global environmental change (Zohary et al. 2021). Temperature influences phytoplankton dynamics directly via growth rate responses and indirectly via competition for resources and zooplankton grazing (Eppley 1972; Rhee and Gotham 1981; Winder and Schindler 2004). Two-way interactive effects of temperature and nutrient availability on phytoplankton dynamics or on plankton interactions have been explored in an enclosure experiment (Berger et al. 2007), in a laboratory experiment (Striebel et al. 2016), and in a 5-yr mesocosm experiment (Yvon-Durocher et al. 2015). The three-way interactive effects of temperature, nutrients, and grazing in lakes are complex and difficult to disentangle with observational data alone (Pomati et al. 2020). Size-based models, like the one used here, constitute complementary tools for investigating the mechanisms shaping phytoplankton community structures. In this respect, we hope that by making our model available as open-source software will not only foster reproducibility and transparency but also speed up flow of ideas and scientific progress in lake ecosystems.

Data availability statement

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Conflict of Interest

None declared.