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Automated plankton monitoring suggests a key role of microzooplankton and temperature for predicting dynamics of phytoplankton size classes

Running head: Environmental controls of size classes

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Author Contribution Statement

S.M, P.D.F.I., and F.P. conceptualised the study, and all authors contributed to its design. S.M., E.M., and P.N. assembled the data, and S.M. performed the analyses. S.M., M.R., E.M., S.D., S.K., and M.

B.-J. annotated images, trained the machine-learning classifier and classified the images. S.M., E.M., P.D.F.I., and F. P. drafted the manuscript; all authors provided critical and conceptual feedback (contributing roles based on https://casrai.org/credit/).

Significance Statement

Understanding the relative importance of biotic and abiotic controls of biodiversity change, in terms of taxa and traits, is critical in times of global and local anthropogenic impact on ecosystem processes. The relative importance of different mechanisms driving phytoplankton community dynamics is still debated, and might vary depending on the environmental conditions. We harnessed four years of data from an underwater imaging microscope, and ancillary monitoring sensors, to study the biotic and abiotic controls of phytoplankton size classes using machine-learning. We find that, contrary to prior expectations, large (blooming) phytoplankton are favoured by high temperature and low levels of microzooplankton. These results help us understand phytoplankton dynamics and improve the modelling of plankton food-webs, with implications for predicting plankton community structure in changing aquatic ecosystems.

Data Availability Statement

The data that support the findings of this study, and the R scripts that generated the results, are openly available from the Eawag Research Data Institutional Repository (ERIC/Open) at https://opendata.eawag.ch/. The DOI is already reserved (https://doi.org/10.25678/000BV9) and will be available online after the manuscript is accepted.

Abstract

The interplay between abiotic (resource supply, temperature) and biotic (herbivore grazing) factors determines growth and loss processes in phytoplankton through resource competition and trophic interactions, which are mediated by morphological traits like size. Here, we study the relative

importance of different grazers, water physics and chemistry on the daily net accumulation rates (AR) of six phytoplankton size classes, obtained by grouping individual organisms from natural communities based on their realised dimensions. Using a Random Forest modelling approach and four years of daily underwater imaging data, we find that the AR of small phytoplankton is mostly predicted by water temperature and herbivore grazing whereas, with increasing size, resources become more important in predicting ARs. Our results show that microzooplankton is an important predictor of AR in all phytoplankton regardless of their size, but mesozooplankton is more important for small phytoplankton forms. Our results support previous expectations and reveal surprising new patterns.

Keywords: Community dynamics, traits, imaging, machine learning, plankton, size.

Text = 2989 words

Introduction

Phytoplankton cover an enormous phylogenetic and functional diversity, and regulate essential global-scale processes and elemental cycles, such as those of carbon and nutrients (Falkowski et al. 2004). Yet, a full mechanistic understanding of phytoplankton dynamics remains elusive. Recent studies suggest the importance of quantifying both division and loss processes, or their net outcomes, when studying the environmental drivers of phytoplankton community dynamics (Behrenfeld and Boss 2018; Arteaga et al. 2020). Trophic controls play a major role in loss processes, explaining grazing defence traits and community structure (Shurin, Gruner, and Hillebrand 2006; Lima-Mendez et al. 2015; Behrenfeld et al. 2021). Additionally, trophic controls include both direct negative effects on net growth and indirect facilitation, via suppressing a competitor or grazer (Levine 1999; Lima-Mendez et al. 2015). The net rate of accumulation (AR) represents the balance between phytoplankton division rates and the sum of all loss rates (e.g., grazing, sinking, parasites)

(Behrenfeld and Boss 2018). Studying AR is essential for understanding controls of phytoplankton dynamics and for bloom prediction (Behrenfeld and Boss 2018; Isles and Pomati 2021). The AR of phytoplankton is, however, dependent on their ecological and physiological traits, and contingent environmental conditions (Litchman and Klausmeier 2008).

Morphological characteristics of phytoplankton correlate with species physiology and ecology, and, therefore with population growth and loss rates (Litchman and Klausmeier 2008; Kruk et al. 2010). Body size in particular links the principal axes of plankton resource competition and trophic interactions (Litchman and Klausmeier 2008; Marañón 2015; Andersen et al. 2016). Larger cell or colony size increases resistance against grazers, reduces the competitive ability for nutrient uptake, and increases sinking losses in stable water columns. Small cells generally possess lower sinking rates and higher maximum growth rates, and should be favoured under low nutrient conditions. Under higher temperatures, small cells can maintain higher metabolic and growth rates than larger phytoplankton because they are better competitors for nutrients due to their higher surface-to-volume ratio (Andersen et al. 2016). From the literature, general and testable expectations emerge:

- Smaller phytoplankton forms are favoured (i.e. have higher AR) under low resource conditions, and/or higher temperature and water column stability.
- Larger phytoplankton require a higher resource level than smaller forms, and/or have a competitive disadvantage under higher temperature (low AR) and are more susceptible to sinking losses under a stable water column.
- Smaller phytoplankton forms are more strongly controlled by herbivores (low AR) whereas large phytoplankton are more resistant to (size selective) grazers (high AR).

However, complex ecological interactions and the variable environmental context suggest uncertainties regarding these general and theoretical expectations. For example, long-term patterns in size-abundance relationships in Swiss lakes indicate that small phytoplankton may be favoured under

high resource levels and low temperature, whereas large (often mixotrophic) taxa prevail under low resource conditions and higher temperature (Pomati et al. 2020).

In this study we test the above expectations in a freshwater lake using high-frequency data, by investigating the temporal prevalence, relative strength and effect of (i) available resources (phosphorus, nitrogen, light), (ii) water physics (temperature, turbulence, stability), and (iii) herbivore grazers (daphnids, copepods, ciliates, rotifers), in controlling the daily accumulation rates (AR) of phytoplankton size-classes. For this goal, we use Random Forest (RF) modelling and a unique dataset of four years of daily automated *in-situ* imaging data of phytoplankton, zooplankton, and water physicochemical parameters.

Material and Methods

We monitor pelagic plankton in the size range between ~10 µm and ~ 1 cm at 3 m depth with a dual-magnification dark-field imaging microscope (Orenstein et al. 2020; Merz et al. 2021) (**Fig. 1A**), with two objectives: one for phytoplankton and small zooplankton (5.0x) and one for zooplankton (0.5x). Images are collected for 10 minutes every hour in the eutrophic Lake Greifensee (Switzerland), and we used data between May 2019 and December 2022. We removed small zooplankton from the 5.0x data using a deep-learning classifier (Kyathanahally 2023), and estimated body size as the area of the binary image mask for each phytoplankton object (Orenstein et al. 2020). Such body size estimates scale with traditional microscopy biovolume measurements (Merz et al. 2021). We binned all individual objects into 6 bins of equal length on a Log_{10} scale (**Fig. 1B, Tab. S1**) (Sprules and Barth 2016). Note that using individual-based data implies that each taxon can be found in multiple bins depending on its realised size (e.g. colony forming taxa), or due to partially cropped images (**Fig. S1** and **SI Methods**). We aggregated abundances per day per size-bin: abundances are in ROI/sec (region of interest per second), which correlates with plankton concentrations (Merz et al. 2021). We used LOESS regression to smooth the time series with $\alpha = 0.025$: we chose α to exclude

only random (temporal non-autocorrelated) noise. We calculated daily accumulation rates (AR), for each bin, as:

$$AR_i = (ln(N_{t+1,i}) - ln(N_{t,i}))$$

Where i = size-bin, N_t= abundance at time t and N_{t+1} = abundance at time t+1.

As a measure of trophic controls on phytoplankton AR, we estimated the daily abundance (ROI/sec) of daphnids, cyclopoid copepods, calanoid copepods, nauplii and rotifers (from 0.5x), and ciliates (from 5.0x) (**Fig. 1C,** taxonomic composition of classes in **Tab. S2).** We scaled zooplankton abundances to z-scores for modelling.

As abiotic predictors of AR models, we calculated thermocline and mixed layer depths, and epilimnetic temperature, from CTD profiles (rLakeAnalyzer, V1.11.4.1). We extracted the depth at 5 PAR (light penetration depth) as a proxy for light availability (**SI Methods**). Measurements of the inorganic nutrients nitrate (NO_3), ammonium (NH_4) and phosphate (P-PO_4) were performed weekly, then used to train a RF model based on CTD and Meteo data from the same dates as predictors (**SI Methods**). Nutrient levels were then predicted at the frequency of the CTD profiles and averaged to obtain daily data (**Fig. 1D**).

We use RF to estimate the relative importance of each explanatory variable on predicting phytoplankton AR per size-bin and their effects as partial dependence plots (Thomas et al. 2018). We imputed missing values (2.16%) among predictors with the function rfImpute and then trained a RF model for each size-bin, with randomForest package V4.6.14 (Liaw, Wiener, et al. 2002). To rule out overfitting, we performed cross-validation (**Fig. 1E, SI Methods**). These bin-specific RF models yielded pseudo-R^2 values of circa 60% (**Tab. S1**) (Møller and Jennions 2002).

To study both the temporal prevalence and the relative strength of AR predictors, we used a rolling-window approach: within a temporal window of 28 days, shifting forward by one week at each round, we calculated the increase in mean-squared-error (IncMSE) when disrupting (reshuffling with

replacement) the vector of values of each predictor in sequence (**Fig. 1F, SI Methods**). Predictors with high IncMSE represent important variables for the model. The relative importance of predictors (IncMSE) was then reported or averaged over time, for each size bin.

To study the partial effects of important predictors on AR, we trained an RF model with the whole dataset (to gain more confidence on inferred patterns) for each size-bin, and extracted as partial dependence plots of AR to the focal variables with the pdp package, V0.7.0 (Greenwell 2017) (**Fig. 1G**, **SI Methods**). All data analyses were performed with R, V4.1.1 (R Core Team 2021), and figures were produced using the package ggplot2, V3.3.5 (Wickham 2016).

Results

The dynamics in the abundance of phytoplankton size-bins follow the seasonal blooming succession of a temperate eutrophic lake, with peaks in spring, a trough in May (the clear water phase), and peaks in summer and early autumn (**Fig. 1A**) (Sommer et al. 2012). As expected, the smallest size-bins are more abundant than the larger ones (**Fig. 2A**). Coupled with changes in abundance, the ARs fluctuate over time highlighting the start and the end of the blooming periods (**Fig. 2B**). ARs vary substantially within and between size-bins, with larger phytoplankton showing a wider range of positive and negative ARs (**Fig. 2C**) - this may be due to the AR of bins of larger organisms, which are less abundant, being more sensitive to daily variation in numbers compared to smaller, more common phytoplankton. Large phytoplankton in fact do not show more rapid bloom dynamics compared to small (**Fig. 2A**). Among the herbivore grazers, whose trends follow the phytoplankton seasonal succession, rotifers and ciliates are the most abundant and dynamic groups (**Fig. 2D**), as expected from microzooplankton (Sommer et al. 2012). Abiotic environmental conditions in Greifensee follow the seasonal pattern of a temperate and monomictic eutrophic lake, and are reported in **Fig. S2**.

Our RF approach, based on a rolling-window analysis of size-bin time series, highlights how the environmental predictors of AR vary in their relative strength (i) over time (within size-bins) and (ii) between size-bins (**Fig. S3**). While the former can be expected in nonlinear dynamic and chaotic systems (Benincà et al. 2008; Dakos et al. 2009) and will not be discussed in detail, aggregating the relative importance of predictors over time allows us to study the variation between different size-bins (**Fig. 3**).

We find that the AR of smaller size-bins is predicted more strongly by water temperature and herbivore grazing (**Fig. 3**). Specifically, the AR of size-bins 1-3 shows a peak for low water temperature, cyclopoid and ciliate abundances (**Fig. 4**). The latter two have a clear negative effect on the AR of all phytoplankton size-bins, suggesting a strong trophic control (herbivory). In contrast, rotifers, which are important predictors for all phytoplankton irrespective of their size, have a positive effect on ARs (**Fig. 3-4**). Daphnids are relatively more important as predictors of smaller phytoplankton AR, with the expected negative effect of filter-feeding herbivores (**Fig. 3-4**). The effect of Daphnids on the AR of the two largest size bins, however, shows a more complex response curve (**Fig. 4**), suggestive of an optimum at intermediate levels of grazers - possibly an indication of indirect facilitation when daphnids are low in abundance.

With the increasing size of the phytoplankton, we note three important patterns. First, direct (light availability, phosphate and ammonium levels) and indirect (mixed layer depth) measures of resource supply become more and more important for ARs. We see that ARs saturate with increasing light intensity (depth at 5 PAR), as expected (Thomas et al. 2018), and that larger phytoplankton have a higher AR at high light levels compared to smaller forms (**Fig. 4**). Additionally, ARs show, in general, to have an optimum of mixed layer depth (correlated with thermocline depth - **Fig. S4-S5**), which may indicate that the optimal combination of light intensity and mixing (nutrient supply from the hypolimnion) for growth is between 4-8 m for all phytoplankton in the lake (Ryabov, Rudolf, and Blasius 2010). While the ARs of size-bins also display an optimum for specific levels of ammonia

(with larger phytoplankton having optima at slightly higher levels), the response of AR to phosphate variation is highly idiosyncratic depending on the size-bin: we see convex curves (akin to a Gaussian with an optimum) for the smaller size-bins, and concave for the larger ones with maxima ARs at both low and high phosphate levels (**Fig. 4**).

Second, water temperature remains among the most important predictors with increasing phytoplankton size, but with a change in the realised optimum for AR (**Fig. 3-4**). While small phytoplankton forms show an optimum at low temperatures, large phytoplankton show higher ARs at high temperatures. Lastly, and despite differences in their effects (**Fig. 5**, **Fig. S4**), microzooplankton remains, in general, the most important biotic predictor of AR across all size-bins (**Fig. 3**, **Fig. S6**). Even though in our study microzooplankton is composed of defined classes (nauplii, rotifers and ciliates), each one of them is a heterogeneous group of microorganisms belonging to different species and lineages, with large cryptic diversity in terms of physiology, life history, and size selectivity - all of which also depend on the composition of the available preys and environmental conditions.

Discussion

In line with previous studies (Andersen et al. 2016; Pomati et al. 2020), we find that AR of smaller size-bins (1-2, **Fig. 3**) is more strongly controlled by water temperature and herbivore grazing. With increasing size, we observe an increase in the relative importance of resources in predicting AR (**Fig. 3**, **Fig. S6**). Indeed, size scales positively with biomass and metabolism and, consistently with the predictions of the Metabolic Theory of Ecology, we find higher resource requirements with increasing individual size (Enquist et al. 2015; Andersen et al. 2016). We also find weak support for larger phytoplankton being favoured by deeper mixing (mixed layer depth - **Fig. 4**): this effect, however, may be confounded by the fact that deeper mixing is generally associated with upwelling of nutrients (Winder and Sommer 2012).

One important pattern emerging from our data is that microzooplankton is an essential control of AR for all phytoplankton regardless of size: we expected microzooplankton to be selective for small phytoplankton forms (Acevedo-Trejos, Marañón, and Merico 2018) but, to our surprise, they appear very important for the larger size-bins (4-5, **Fig. 3**, **Fig. S6**). Microzooplankton can exhibit varying degrees of size selectivity depending on the species and the available prey - while in general, they are supposed to prefer smaller phytoplankton sizes, their actual preference can vary from a few micrometres to several tens of micrometres (as in the case of preys such as diatoms or filamentous cyanobacteria) (Pierce and Turner 1992; Verni and Gualtieri 1997; Ger et al. 2016). Rotifers are often opportunistic omnivores, with potential trophic cascade effects (e.g., indirect facilitation) on phytoplankton by eating flagellates and ciliates (Gilbert 2022; Wilke, Ahlrichs, and Bininda-Emonds 2020; Stelzer 1998). This may explain why rotifers positively affect phytoplankton in our study.

Mesozooplankton seems to be a more important control of small phytoplankton forms (Acevedo-Trejos, Marañón, and Merico 2018). Daphnids are size-selective, grazing on phytoplankton with a size smaller than their gape, i.e., with a diameter of < 20 or 30 µm, depending on the species (Sommer et al. 2002; Zadereev et al. 2023). Calanoids and cyclopoids show differences in their feeding behaviour, with cyclopoids preying mostly on large particles, while calanoids consuming smaller particles (Burkholder and Glibert 2024). Some cyclopoid species are also primarily carnivorous (Brandl 2005). Contrary to these expectations, cyclopoids copepods in our study are important predictors for the AR of smaller-sized phytoplankton (bins 1-3). In general, mesozooplankton are also more efficient grazers and, combined with the higher encounter rates for the smaller and more abundant phytoplankton, could cause a larger grazing impact on the abundance of smaller forms, as opposed to larger, rarer and more defended phytoplankton.

We find that small phytoplankton have higher AR at low temperatures while large forms have higher AR at higher temperatures (**Fig. 4**). Previous studies reported opposite trends (Enquist et al. 2015; Acevedo-Trejos, Marañón, and Merico 2018), but a similar pattern as in this study was previously

reported in lakes (Pomati et al. 2020). These differences can be attributed to the fact that species composition within size-classes varies substantially over environmental gradients: specifically for this study, a large number of cold adapted species (e.g. diatoms, cryptophytes) can be found in the small size-bins, and many warm adapted species (e.g., colonial cyanobacteria) in the large size-bins. Cold adapted species have lower thermal optima, which leads to a steep decrease in AR when exposed to temperatures further away from their optimum (**Fig. 4**). Vice versa, warm adapted species, present in the larger size-bins, show AR that increases steadily with water temperature (**Fig. 4**, **Fig. S4**).

The responses of AR to environmental predictors are mostly non-linear (**Fig. 4**). Some curves match prior expectations (e.g., responses to resources show a Monod or a Gaussian shape), others do not (e.g. temperature and P-PO_4 with both concave and convex curves). We find that the shape of these responses varies between phytoplankton size-bins, while we were expecting them to be relatively universal (Litchman and Klausmeier 2008). One explanation for this unexpected variability is that such responses may depend on the interaction between multiple drivers, and may show the expected patterns only in certain areas of a multi-parameter space. These interactions can be very complex and interdependent - e.g. responses to nutrients depend on temperature (see **Fig. S7**) (Merz et al. 2023). Alternatively, the above unexpected patterns may be due to three important caveats of our study.

First, compositional turnover of taxa within size-bins may confound some of the detected partial effects (**Fig. 4**), and possibly also some of their relative importance (**Fig. 3**): taxa composition and relative abundance change within size-bins over time (**Fig. S8**), and different taxa have different ecology and physiology. Second, the realised size, as studied here, is not the cell-size as intended in most of the previous theoretical or experimental work: the realised size, whether cell or colony size, is a plastic trait (e.g. mediated by physiological and ecological interactions). This could have influenced some of the unexpected results regarding the effects of grazers (which may target the cell inside the colony irrespective of colony size) and of abiotic factors (e.g., temperature - large taxa are colony-forming summer species). Third, the responses of size-bins could have been mediated by cell

shape. Environmental factors can influence the selection for body size and shape differently (Ryabov et al. 2021): shape variation represents a competitive strategy for medium and large phytoplankton forms to acquire an advantageous surface area-to-volume ratio (Stanca, Cellamare, and Basset 2013), or to reduce sinking velocity (Padisák, Soróczki-Pintér, and Rezner 2003).

Our results suggest that studying the dynamics of phytoplankton communities may require complementing size information with either shape and/or taxonomic identity, to increase inference of mechanisms and interactions. Additionally, we may need to refine expectations from the literature by considering that responses to biotic and abiotic environmental drivers are multidimensional and may be interdependent (Ye and Sugihara 2016). It would be important to understand how many of our expectations are confined only to certain areas of this multidimensional space by, for example, leveraging on monitoring data to infer responses of organisms in natural conditions (this study), or designing factorial experiments that explore complex interactions among environmental variables (Thomas and Ranjan 2023).

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Figure 1

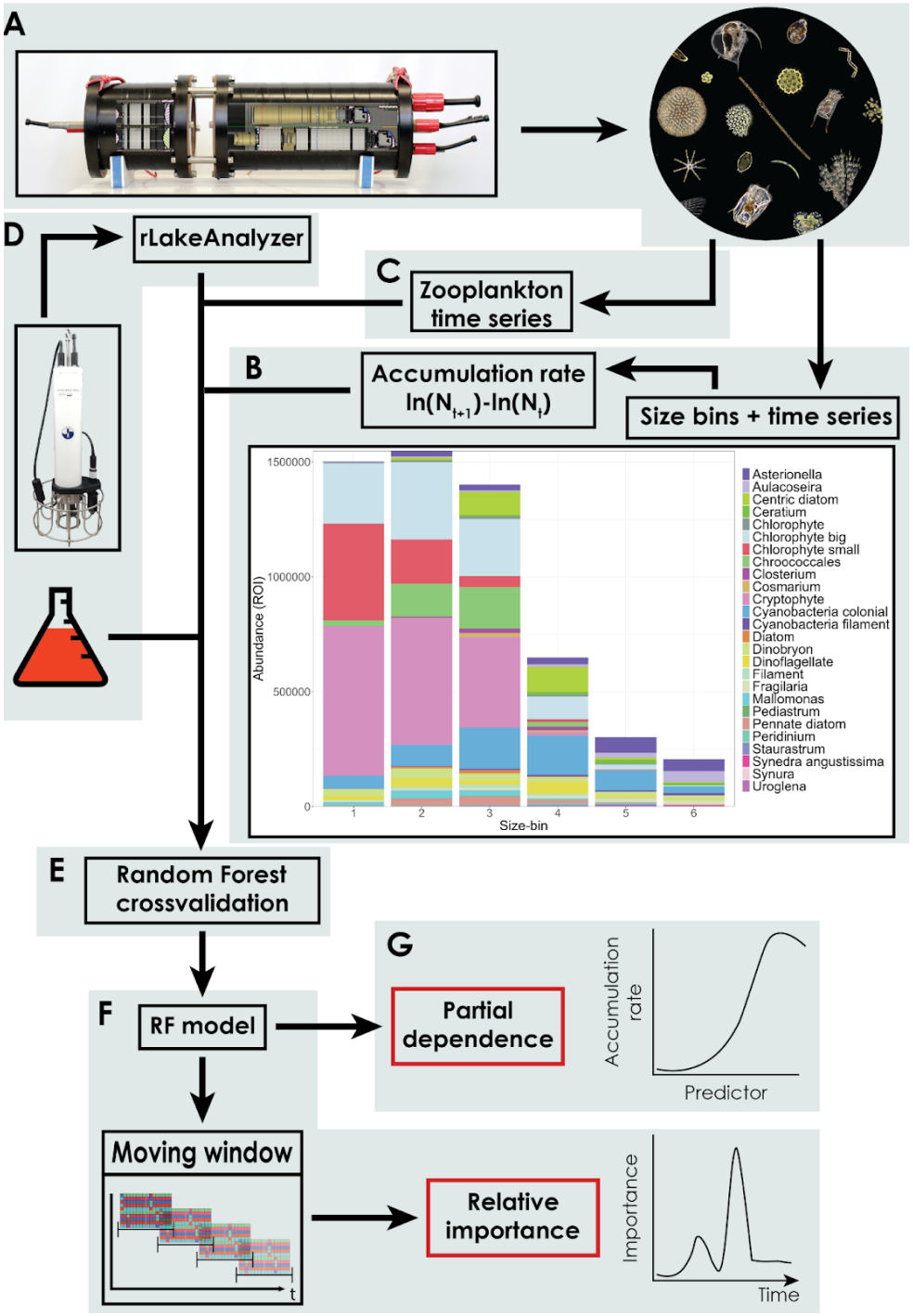

Fig 1: General workflow of the study. **A**: The underwater microscopy images phytoplankton and zooplankton automatically: traits (e.g body size) and taxonomic classification are obtained by image

processing and deep learning, respectively. **B**: Phytoplankton is assigned to 6 size-bins based on the area of each imaged object (**Tab. S2**) and daily accumulation rates (AR) are calculated based on abundances. **C**: Mesozooplankton (daphnids, cyclopoid and calanoid copepods) and microzooplankton (nauplii, rotifers and ciliates) abundance time series are also obtained from (**A**) (**Table S2**). **D**: Water physicochemical variables are extracted from CTD profiling data whereas nutrient chemistry is predicted from weekly laboratory measurements (**SI Methods**). **E**: Random Forest (RF) models are validated, and used to study the relative importance and temporal prevalence of AR predictors with a rolling-window approach (**F**). **G**: Partial effects of important AR predictors are extracted from the RF models.

Figure 2

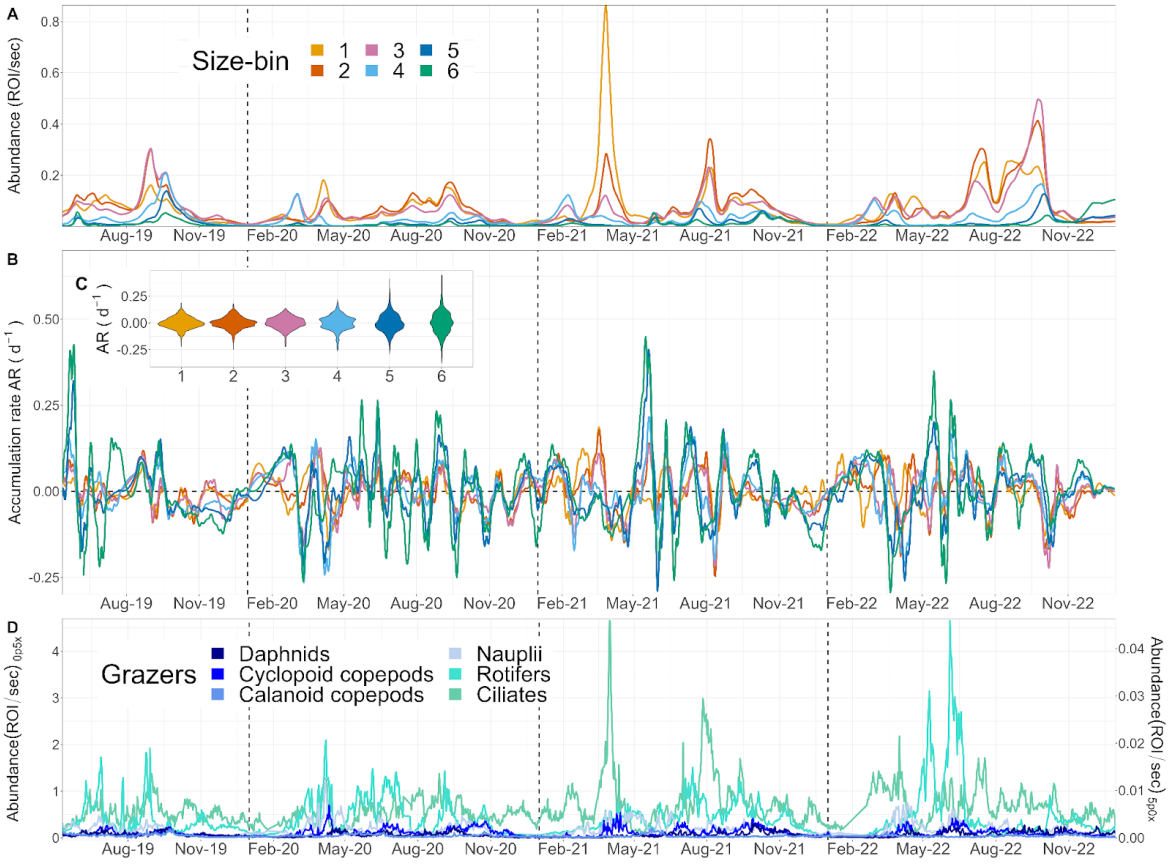

Fig. 2. Temporal dynamics of plankton in Greifensee (2019-2022). Vertical dashed lines mark January 1st of each year. **A)** Daily abundance of phytoplankton size-bins (smoothed, see Methods). **B)** Daily accumulation rate (AR) of size-bins. **C)** Overall distribution of AR for each size-bin. **D)** Daily zooplankton abundance (ciliates are on the right-side Y-axis because they were monitored through the 5.0x objective).

Figure 3

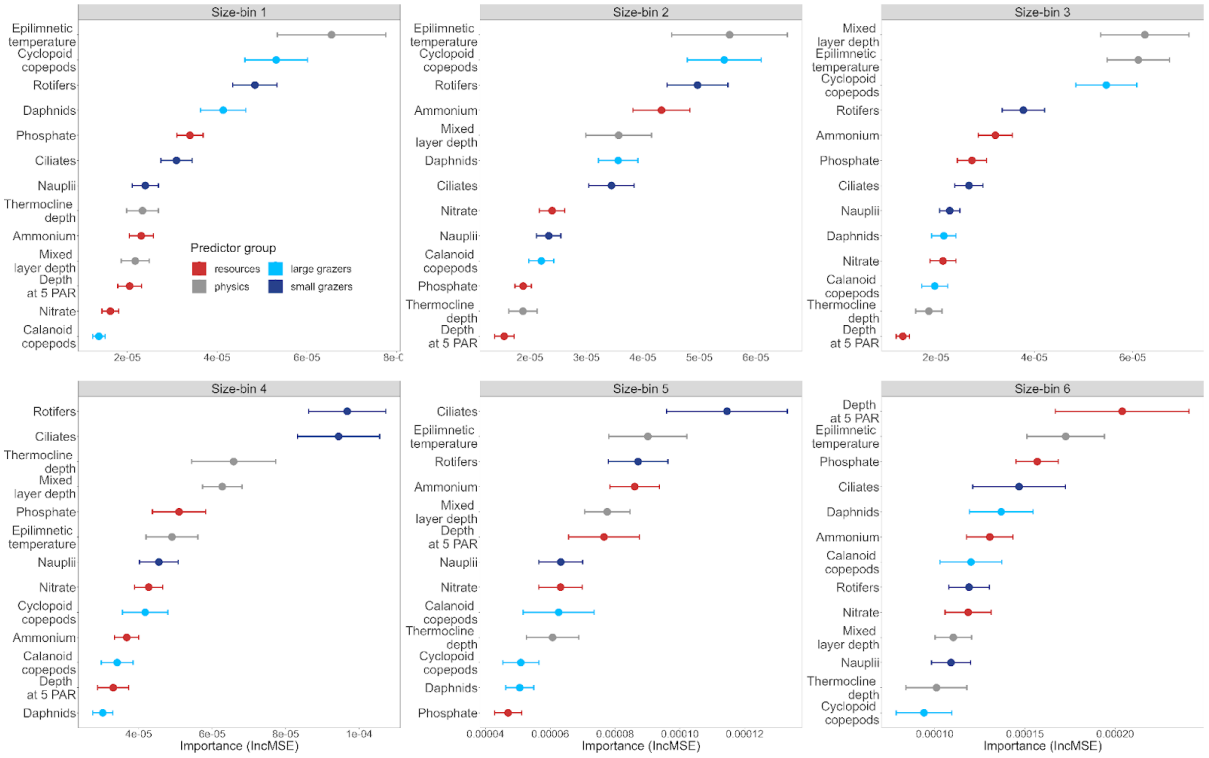

Fig. 3. Overall mean importance (IncMSE ± standard error) of each predictor over the entire study period for each size-bin. Colours indicate types of predictors: grey = water physics, red = resources, light blue = mesozooplankton, dark blue = microzooplankton.

Figure 4

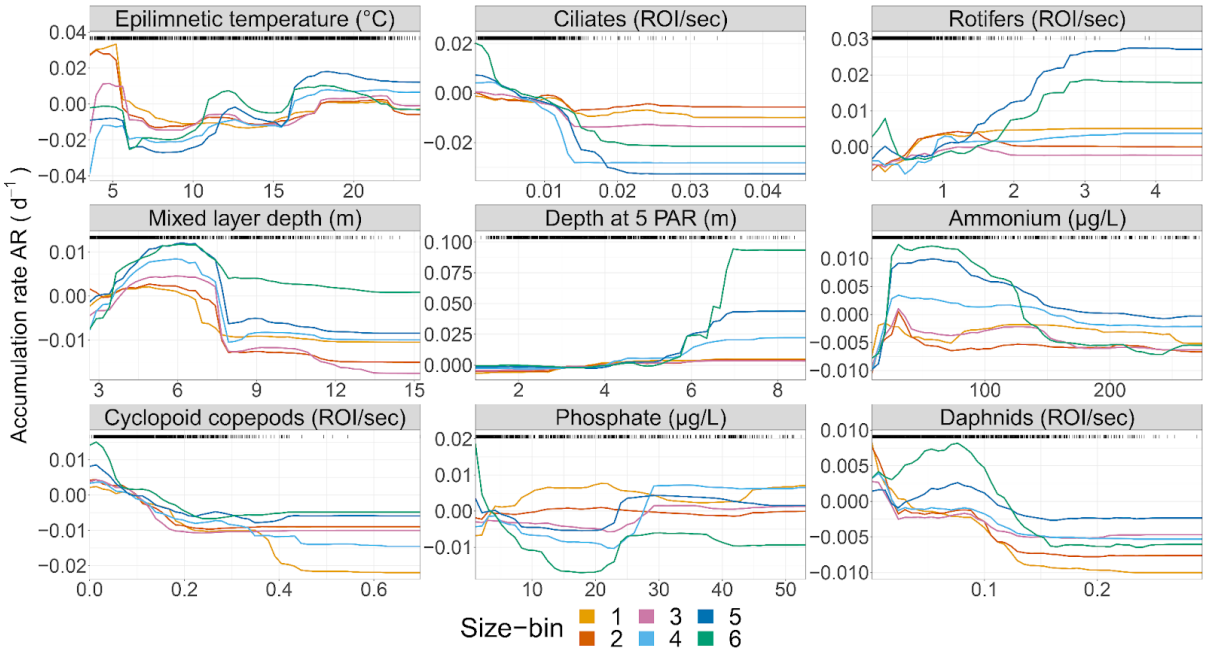

Fig. 4. Partial effects of the most important predictors (other predictors, see **Fig. S4)**: these dependencies emerge from predicting the response (AR) over varying levels of the chosen variable (X-axis, in the plot title) while holding the other variables in the RF model at their medians over the entire dataset. Each line represents one size-bin (colours as in **Fig. 1**). The distribution of observed data points is shown as black bars on top of each graph: high data-dense areas hold more confidence in the prediction.