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RESEARCH ARTICLE

Epiphyton phenology determines the persistence of submerged macrophytes: Exemplified in temperate shallow lakes

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Abstract

Submerged macrophytes are key components in many freshwater and marine ecosystems, contributing to ecosystem functions and services. In temperate shallow lakes, spring epiphyton shading can be decisive for submerged macrophyte development, potentially leading to macrophyte collapse and a shift to undesired, turbid conditions. Global change can alter epiphyton phenology; however, the consequences for submerged macrophytes and their stabilizing effects on clear-water conditions remain to be elucidated. Based on field data, we propose a general epiphyton shading phenology for submerged macrophytes in temperate shallow lake ecosystems. We express the temporal dynamics of epiphyton shading in terms of onset and relative increase (slope) of epiphyton development as well as epiphyton grazing impacts (onset, duration) using a Boltzmann function. This function is added to the ecosystem model PCLake+ as a customizable, macrophyte-specific shading factor. We then assess how changes in the epiphyton phenology and the presence of grazing on epiphyton affects submerged macrophyte biomass in a generic temperate shallow model lake under control and warm winter scenarios. The results from the model provide a proof-of-concept that epiphyton shading can provoke macrophyte loss and shifts between alternative equilibria. Threshold values for critical shifts depend on epiphyton shading phenology. Earlier onset and longer duration of grazing can maintain macrophytes in nutrient or climate conditions under which they would otherwise collapse. Our results show the pivotal importance of epiphyton phenology in determining lake ecosystem-wide responses stressing the need for better incorporation of epiphyton into both models and monitoring.

Submerged macrophytes are key components of most freshwater and marine shallow littoral habitats (Murphy et al. 2019). Their occurrence and biomass development are linked to numerous ecological functions and services underpinning the maintenance of good water quality (Costanza et al. 2014; Hilt et al. 2017; Janssen et al. 2021). Macrophyte seasonal development and persistence in these systems is under pressure due to anthropogenic stressors including increasing nutrient loading and climate warming (Orth et al. 2006; Botrel and Maranger 2023). These stressors can lead to increase in biomass and shifts in phenology of pelagic phytoplankton and substrate-bound epiphyton. Epiphyton consists of a functionally and taxonomically diverse community including both autotrophic (e.g., cyanobacteria, microalgae) and heterotrophic organisms (e.g., bacteria, fungi, protozoa) (Wijewardene et al. 2022) growing on, and thereby shading, submerged plant surfaces such as macrophyte stems and leaves. Pelagic phytoplankton as well as substrate-bound epiphyton compete with macrophytes for light and, to some extent, nutrients (Scheffer et al. 1997; Klančnik, Gradinjan, and Gaberščik 2015). Here, we aim to explore the effects of

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changes in the phenology of epiphyton on the persistence of macrophytes using temperate shallow lakes as example systems.

Shallow lakes and ponds represent the most abundant type of freshwaters on earth (Verpoorter et al. 2014). Submerged macrophytes can stabilize a clear-water state representing the desired ecological configuration in such systems (Scheffer et al. 1993, 2001). Increased nutrient loading can undermine the resilience of the clear state and cause a shift to a turbid, phytoplankton-dominated state. This phenomenon has been described in theory (Scheffer et al. 1993) and in real-world examples (*see* examples compiled in Scheffer and Van Nes (2007)) and is generally attributed to increasing pelagic phytoplankton development and hence stronger shading on submerged macrophytes (Scheffer et al. 1997). However, epiphyton can provide an additional and more macrophyte specific source of shading as it grows directly on the macrophytes and can form biofilms ranging from thin, nearly translucent to thick and complex mats that significantly decrease the amount and quality of light reaching the leaves it grows on (Klančnik, Gradinjan, and Gaberščik 2015). The community composition of epiphyton biofilms is known to change with season and may be specific to their macrophyte substrate, showing mutualistic, commensal, and competitive relationships with their substrate as they interact for resources or engage in chemical communication (Wijewardene et al. 2022). Overall, epiphyton has been found to be decisive for macrophyte decline under increasing nutrient loading (Phillips, Eminson, and Moss 1978; Phillips, Willby, and Moss 2016; Jones et al. 2002; Jones and Sayer 2003), can delay macrophyte recovery even when nutrient loading has been reduced (Roberts et al. 2003; Hilt et al. 2018), and affect macrophyte sensitivity to herbivory (Hidding et al. 2016).

Several and frequently interacting drivers control epiphyton biomass in freshwater and marine systems. Bottom-up drivers encompass limiting resources such as light and nutrients (including those associated with browning of lakes; Puts et al. 2023), which can, in turn, be forced by temperature changes (Hansson 1992; Ozersky and Camilleri 2021). The response of epiphyton biomass and community composition to nutrients and temperature, moreover, varies across seasons (Hao et al. 2020). In addition, top-down control by grazers can strongly impact epiphyton biomass (Jones and Sayer 2003; Randall Hughes et al. 2004). A wide range of algivorous and omnivorous organisms with an equally diverse array of grazing mechanisms can graze on epiphyton, including microconsumers such as protists, as well as invertebrate consumers (gastropods, amphipods, isopods, and insect larvae [Ephemeroptera, Trichoptera, Diptera] and vertebrates [algivorous fish and amphibians]; Hillebrand 2009; Vadeboncoeur and Power 2017). A review across lotic, lentic, and coastal habitats revealed that grazers removed on average 59% of the epiphyton biomass and grazer effects were stronger with increasing algal biomass and temperature and with decreasing resource availability (Hillebrand 2009). Epiphyton phenology is thus driven by abiotic factors and biotic interactions, with the latter, in turn, being modified by abiotic conditions. Consequently, epiphyton phenology can vary across years (e.g., Sand-Jensen and Søndergaard 1981; van Dijk 1993; Roberts et al. 2003). Observational and experimental studies on epiphyton and macrophyte phenology, however, are rare (Botrel et al. 2024), although lower trophic levels exhibit stronger phenological responses to climate change than higher ones (Thackeray et al. 2016). In temperate shallow lakes, model simulations suggest that shading in early June appears to be critically important for macrophyte persistence, particularly for short macrophytes such as young plants that have not yet reached the better-lit water surface, or short-stemmed species that are more susceptible to light limitation (van Nes et al. 2002). The impact of changing phenology in epiphyton shading on macrophytes and resulting knock-on effects on the ecological state of shallow lakes, however, have not yet been investigated.

Here, we extract typical epiphyton phenology patterns from field data to propose a general epiphyton phenology. We then test the effect of variation in epiphyton shading phenology on macrophyte abundance in temperate shallow lakes by adding a stand-alone and customizable epiphyton shading parameter to the lake ecosystem model, PCLake+ (Janssen et al. 2019) (Supporting Information Fig. S1). We hypothesize that epiphyton phenology in spring and summer influences the biomass and persistence of macrophyte populations in temperate shallow lakes. We specifically predict that: (1) epiphyton shading in spring leads to a collapse of submerged macrophytes, while a temporary relief from shading by grazing allows macrophyte persistence in lakes close to their critical nutrient loadings, (2) the timing of epiphyton shading onset influences macrophyte persistence, (3) timing and duration of grazing control of epiphyton shading influences macrophyte persistence, and (4) warmer springs and therefore relative changes in the timing of onset of growth seasons for macrophytes and epiphyton result in increased effects of epiphyton shading and earlier collapse of macrophytes. Using temperate shallow lakes as example, we aim at showing that explicitly including epiphyton phenology allows more comprehensive predictions of the response of submerged macrophytes to global change and hence deserves more attention in their different freshwater and marine habitats.

Materials and methods

Field data of epiphyton biomass dynamics in temperate lakes and ponds

To determine a general, qualitative phenology of epiphyton shading on submerged macrophytes in temperate lakes and ponds, we assessed studies on the seasonal development of epiphyton biomass in water bodies in six temperate locations collected between the late 1970s to early 2000s (seven growth seasons altogether). We used published data from one season each for Lake Kalgaard, Denmark (Sand-Jensen and Søndergaard 1981); Lake Veluwe, The Netherlands (van Dijk 1993); experimental ponds, USA (Moss 1976); Lake Gulbinas, Lithuania (Karosienė and Kasperovičienė 2008); and Lake Balaton, Hungary (Tóth 2013), as well as data from two consecutive seasons for Lake Müggelsee, Germany, which also allows to represent interannual variability (Roberts et al. 2003). These lakes and ponds cover a wide gradient of geographical range from 42°N to 57°N, of trophic conditions with total phosphorus concentrations ranging from oligotrophic ($17\,\mu\text{g L}^{-1}$ in the experimental ponds) to eutrophic conditions ($214\,\mu\text{g L}^{-1}$ in Lake Gulbinas), and in size from 0.0007 to 596 km^2 (*see* Supporting Information Table S1; Fig. S2 for more detailed information and a map). It should be noted that the timing of events such as the day of minimum epiphyton biomass after the onset of grazing may have changed with ongoing climate change as shown for Lake Müggelsee (Botrel et al. 2024).

Most submerged macrophyte species in temperate lakes follow an annual life cycle with storage of energy in bulbs and rhizomes and associated loss of leafy parts (the substrate for epiphyton) at the end of the growing season. In spring, macrophyte stems and leaves emerge again and often are immediately colonized by epiphyton (Hilt et al. 2018). Field data of epiphyton were based on weekly, fortnightly, or monthly sampling of epiphyton biomass from artificial substrates (plastic or glass) exposed in the lakes in early spring mimicking the start of the growing season of submerged macrophytes, or from submerged macrophytes or underwater reed stems (*Phragmites australis*). Artificial substrates are a commonly used and well-validated tool to collect epiphyton growth and composition data (van Dijk 1993; Roberts et al. 2003), in particular in eutrophic lakes where the influence of host macrophytes on their epiphytic communities is low (Eminson and Moss 1980). Moreover, biomass of epiphyton has been shown to be a predictor of shading intensity (van Dijk 1993; Köhler, Hachol, and Hilt 2010). The reported epiphyton biomasses were normalized to the maximum values of the respective lake (Fig. 1a). Based on these field observations, a general pattern of epiphyton seasonal dynamics was derived (Fig. 1b).

Adaptation of lake ecosystem model PCLake+ to include epiphyton shading

PCLake+ is a process-based aquatic ecosystem model based on ecological interactions in temperate lakes, often used to assess eutrophication impacts on lakes and ponds and validated on a large set of Dutch shallow lakes (Janse and van Liere 1995; Janse et al. 2008; Janssen et al. 2019). PCLake+ includes key lake food-web components (Supporting Information Fig. S1) and can model ecological mechanisms, such as light competition between phytoplankton and submerged macrophytes under increasing nutrient loading which can lead to critical transitions between clear and turbid states as an emerging feature (Janse et al. 2008). Here, we used standard settings for simulating an average, temperate shallow lake with an mean depth of 2 m, a wind fetch length of 1000 m, with seasonally varying water temperature (control temperature [CT]: average 12 ± 10°C, warmer winter temperature [WWT]: average 13.5 ± 8.5°C; Mooij et al. 2007; *see* Supporting Information Fig. S3), and with evaporation and light curves reflecting average Dutch weather conditions (Janse et al. 2010). As our modeled lake is shallow, we did not invoke the option to model stratification and the hypolimnion. In PCLake+, the macrophyte growth season was initiated through temperature increase in spring (Madsen and Adams 1988; Van Wijk 1989), whereas the onset of winter storage (root allocation and shoot die-off) was defined by an integrated light threshold (Hilt et al. 2018; Janssen et al. 2019). Summer biomass of most temperate region macrophytes carries over into the following growth period in the form of winter storage rather than overwintering leafy biomass (Hilt et al. 2018). As we present a proof-of-concept, we focused on the direct effect of epiphyton shading on macrophyte development and explicitly did not (yet) include further interactions and feedbacks between other food web compartments and the epiphyton shading.

Epiphyton shading y reflects the attenuation of the incoming light by epiphyton growth ranging from none ($y=0$) to complete attenuation ($y=1$). Epiphyton shading was added to PCLake+ using a four parameter, sigmoidal Boltzmann function to achieve a steeply increasing, sigmoidal curve of proportional shading (0–1; Supporting Information Fig. S4a):

$$y=\frac{A_1-A_2}{1+e^{(x-x_0)/dx}}+A_2$$

Here, A_1 and A_2 denote the lower (here 0) and upper boundary of epiphyton shading. The center of the sigmoidal curve is defined by x_0 (here used to move the onset of the epiphyton shading curve stepwise along the spring timeline). Lastly, dx denotes a time constant to define the slope of the growth curve (here set to 2 to achieve a steep increase in shading, reflecting the fast growth of epiphyton). Hereby, phenology of and grazing impacts on epiphyton shading can be modulated in PCLake+ using the parameters of the Bolzman function.

Model scenarios

To test the influence of the timing of the onset of epiphyton shading, the epiphyton shading curve was moved up in the spring timeline by stepwise shifting the midpoint parameter dx from day 80 (i.e., 21 March) up to the day 150 (i.e., 30 May) by 10-d increments (Supporting Information Fig. S4b). The onset of the modeled macrophyte growing seasons is temperature dependent, with macrophytes responding to WWT with an earlier start to the growing season. While the real-world epiphyton growth is also temperature dependent, the shading factor in our model is currently independent of any drivers. As part of our modeling experiment, we manipulated the onset of the epiphyton shading curve relative to the macrophyte growth curve, simulating epiphyton responding earlier, equally or later to increasing temperatures than its substrate. If epiphyton shading responds earlier than the

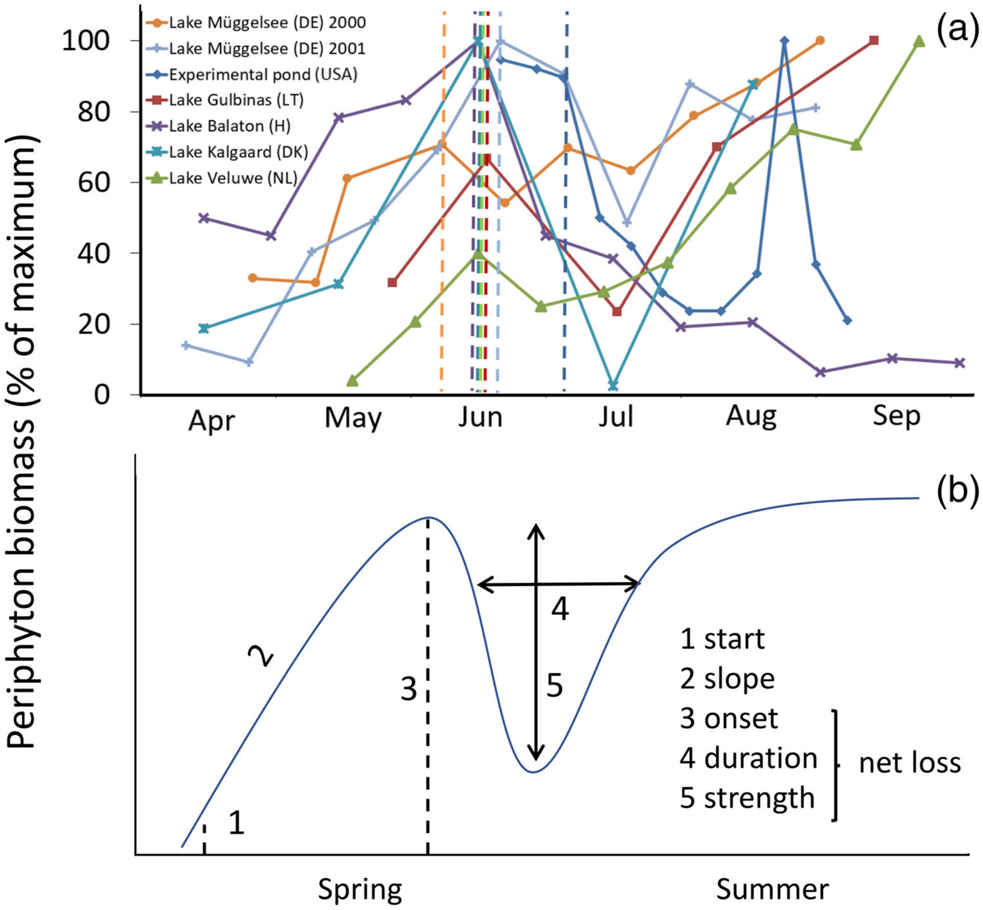

Fig. 1. (**a**) Observed epiphyton biomass phenology (normalized to the respective maximum biomass) with onset of epiphyton net loss (dashed lines) based on published field data of temperate lakes and experimental ponds: Müggelsee: Roberts et al. (2003); Experimental Lake: Moss (1976); Lake Gulbinas: Karosienė and Kasperovičienė (2008); Lake Balaton: Tóth (2013); Lake Kalgaard: Sand-Jensen and Søndergaard (1981); and Lake Veluwe: van Dijk (1993). (**b**) A general model of epiphyton spring–summer phenology on submerged macrophytes in temperate systems derived from field data in panel (**a**). An initial period of fast growth in spring is followed by a net loss period due to grazing. Toward summer, the epiphyton regains net biomass gain with the highest values observed in mid/late summer. Note that spatial and temporal variability occurs in the cardinal events such as in (1) the start, (2) slope of the growth curve, as well as the (3) onset, (4) duration, and (5) strength of the net loss period.

macrophytes, this can result in epiphyton shading occurring as soon as macrophyte substrate becomes available and hence starting immediately with a value greater than 0 (Supporting Information Fig. S4b). This is a relatively realistic artifact of the method and can also be observed in the field when macrophyte leaves are colonized by epiphyton as soon as they emerge (Hilt et al. 2018). Periods of top-down control (i.e., grazing) on epiphyton were introduced as periods of no net-change in epiphyton shading by providing the parameter *dx* in the form of a time series rather than a singular value. Grazing periods were set to start relative to the midpoint of the epiphyton shading curve at 10-d increments starting at − 10 d to + 20 d relative to the midpoint (Supporting Information Fig. S4c). Additionally, we manipulated the *dx* time series to set grazing period duration to either 5, 10, 15, or 20 d (Supporting Information Fig. S4d). In this way, we simulated the different net effects of potential changes in the phenology of periphyton grazers and their predators in response to warming (Kazanjian et al. 2018 and references therein).

We collected two sets of results from the model. First, we calculated load-response curves of macrophyte biomass to epiphyton shading as average macrophyte biomass during one summer period (day 150–210) when the adapted PCLake+ model output has reached equilibrium. Model runs reached equilibrium before year 25, hence we consistently used the summer period average of year 25. This average summer macrophyte biomass was plotted against the epiphyton shading proportion to assess the location of forward and return shifts as well as the size of the hysteresis space (Fig. 2a). Therewith, we (a) defined the P-loading condition to be used for further modeling based on whether it allowed an epiphyton shading driven regime shift (Supporting Information Fig. S5), and (b) assessed the maximum proportion of epiphyton shading tolerated by the macrophytes under different onset timings of epiphyton growth to inform the choice of the A_2 parameter of the Boltzman function under CT (Fig. 2b, c) and WWT conditions (Supporting Information Fig. S6). Second, to capture the full extent of transient dynamics in the response of macrophyte biomass development to epiphyton shading timing as well as timing and duration of grazing on epiphyton, we computed 25-yr time series. We assessed three parameters indicative of macrophyte response to changes in the epiphyton phenology, namely 25-yr cumulative biomass of macrophytes (g dry weight [DW] m^{-2}) and planktonic phytoplankton chlorophyll *a* (mg Chl *a* m^{-3}) in summer (June, July, and August) as well as time to macrophyte population collapse (years to collapse; i.e., the first year in which the biomass of macrophytes was reduced to less than 10 g DW m^{-2} during the macrophyte growth period). These transient model runs included different epiphyton shading curve onset times (a) without top-down control (i.e., no grazing on epiphyton) and (b) with top-down control whereby the grazing phase had varied onset times and durations. Given the temperature threshold for the start of the macrophyte growth season in PCLake+, the macrophyte growth period started on day of year 104 in the CT scenario, and day of year 90 in the WWT scenario, while the growth period ended on day of year 285 in either temperature scenario.

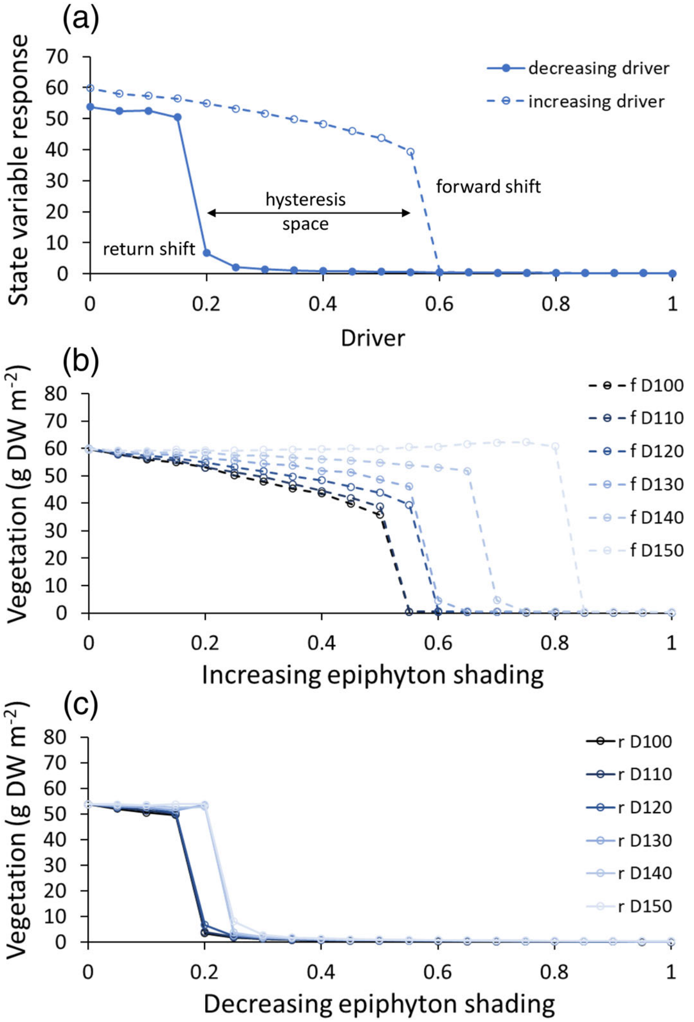

Fig. 2. (**a**) A load-response curve of a state variable (here vegetation dry weight [g dry weight (DW) m^{-2}]) at equilibrium under a gradually increasing or decreasing driver (here epiphyton shading) showcasing a hysteresis. Internal stabilizing feedback in the clear water state allows submerged vegetation to tolerate high levels of epiphyton-mediated shading before the vegetation collapses and the lake shifts to a turbid state (forward shift, dashed line). A return of macrophytes to the system (return shift, solid line), however, requires a reduction far below the shading level on which the forward shift occurred as the system is stabilized by a different feedback loop due to high pelagic phytoplankton shading. The hysteresis space between these two tipping points covers the range of shading conditions at which either vegetation state can occur and at which a stronger perturbation can shift the system from one state to another. Assessment of the influence of the onset date of epiphyton shading on the tolerance of submerged vegetation to epiphyton shading showed (**b**) later onset of epiphyton growth resulted in a much higher tolerance to epiphyton shading by the macrophytes. However, (**c**) a return of macrophytes from a turbid system required a very strong reduction of epiphyton shading.

Results

Field data on epiphyton phenology in temperate shallow lakes

Field data of different European temperate lakes and experimental ponds in the United States revealed a general qualitative pattern of epiphyton biomass development in spring and summer (Fig. 1a) which was translated into a model (Fig. 1b). In spring, epiphyton biomass increased rapidly. Following this initial growth, many lakes showed a period of net loss of epiphyton biomass varying in its timing (onset), strength, and duration. The timing of the onset of the net loss period varied among lakes as well as among years in the same lake (Müggelsee) by several weeks and started between early June and July. The duration of the net loss period also varied between 1 and 6 weeks. Generally, this was followed by another period of net gain. Usually, maximum epiphyton biomass was reached in summer (apart from Müggelsee 2001 and Balaton) (Fig. 1a).

Model adaptation captures effects of epiphyton shading as a regime shift driver

In the CT scenario, the load-response curves across a range of P-loading scenarios showed that the adapted PCLake+ model successfully captured effects of epiphyton shading as regime shift driver (Fig. 2). Forward and return tipping points and the width of the hysteresis space were sensitive to the P-loading scenario (Supporting Information Fig. S5). In the lowest P-loading scenario (0.0001 g P m^{-2} d^{-1}), the modeled lake maintained macrophyte biomass up to 95% epiphyton shading and required very little reduction in shading to allow macrophytes to return. With increasing P-loading, however, the collapse of macrophytes occurred at increasingly lower epiphyton shading thresholds and the return of macrophytes required increasingly stronger reduction of shading (Supporting Information Fig. S5). The hysteresis space was largest at a P-loading of 0.0025 g P m^{-2} d^{-1}; therefore, we used this loading scenario for all further analyses.

Effects of timing of epiphyton shading onset on epiphyton shading threshold

In the CT as well as the WWT scenario, the load-response curves along a gradient of maximum epiphyton shading showed that the timing of the onset of the epiphyton shading curve affected the amount of shading the modeled lake could tolerate before collapse of the macrophytes (Fig. 2b), as well as the amount of shading reduction necessary to allow the return of macrophytes (Fig. 2c). In both temperature scenarios, earlier development of epiphyton shading resulted in macrophyte collapse at lower maximum epiphyton shading levels and required stronger reduction of the epiphyton shading before macrophytes could recover. In the CT scenario, the hysteresis space was widest for the epiphyton shading curve with day 120 (April 30) midpoint. In the WWT scenario, the model lake tolerated relatively more maximum epiphyton shading (A_2) before macrophytes collapse (Supporting Information Fig. S6) than in the CT scenario (Fig. 2b). Based on these results, we chose to assess the effects of grazing on epiphyton on the persistence of macrophytes in the virtual lake using a maximum shading of 0.55 in the CT scenario, and 0.6 in the WWT scenario to operate in the space where (temporary) relief from epiphyton shading could make the difference between loss and maintenance of macrophytes in the lake.

Interactive effect of timing and length of epiphyton grazing on macrophytes

To assess the effects of presence of a grazing period, its timing (onset) and duration (*see* Fig. 1b), we produced multiple time series by running the model for a gradient of epiphyton shading curve midpoints for epiphyton development from early to relatively late in the season (CT: D100–D150, WWT: D80–D110) with variable grazing period onset and duration scenarios. In both, the CT (Fig. 3) and the WWT (Fig. 4) scenarios, an earlier onset of the grazing period relative to the midpoint of the epiphyton shading curve allowed a higher average summer biomass development of macrophytes, particularly so when the epiphyton shading also started early in the season (Figs. 3a, 4a). Equally, longer grazing periods were more beneficial for the average summer biomass development of macrophytes, particularly in scenarios with earlier development of epiphyton shading (Figs. 3b, 4b). Furthermore, earlier and longer grazing periods in scenarios with early epiphyton development allowed macrophytes to persist longer in the lake (Figs. 3c, d, 4c, d). Overall, late in the season development of epiphyton shading had less impact on the biomass development and persistence of (already established) macrophytes in the model lake and, subsequently, respite from shading due to a grazing period had little added effect. The 25-yr average summer biomass of pelagic phytoplankton showed the opposite pattern. Early onset and longer duration of epiphyton grazing events in the scenarios with early development of epiphyton coincided with lower development of phytoplankton biomass more than late onset or short duration of grazing events (Fig. 5a, b). Generally, late development of epiphyton shading had less effect on overall lower phytoplankton development irrespective of onset and duration of grazing periods. Overall, the main differences between results in the CT and WWT scenarios concern the importance of timing with a general shift of all dynamics to earlier in the year in the WWT scenario.

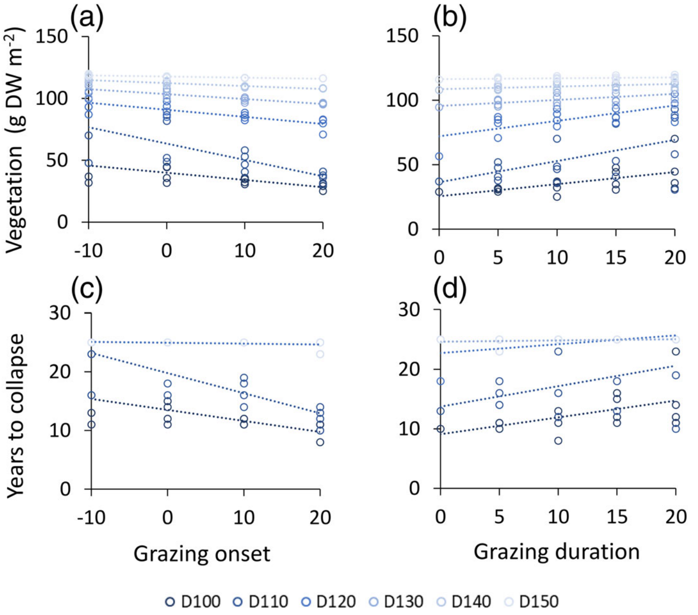

Fig. 3. Scatter plots along a gradient of epiphyton shading curve midpoints (day [D] 100–150; blue shades) in presence of a grazing event in the control temperature scenario. (**a**) The 25-yr average summer biomass of macrophytes (g dry weight [DW] m^{-2}) against onset of the grazing period relative to the midpoint of the shading curve. The spread of points along the *y*-axis for each shading curve set reflects the influence of the duration of the grazing period (5, 10, 15, and 20 d). (b) The same 25-yr average summer biomass of macrophyte data against the duration of the grazing event. The spread of points along the *y*-axis for each shading curve set reflects the relative onset of the grazing period (− 10, 0, 10, and 20 d). (**c**) Years until macrophytes disappear during the growth period from the model lake in response to the relative onset of the grazing period. (**d**) Years until macrophytes disappear during the growth period from the model lake in response to the duration of the grazing period.

Discussion

Our model results support the hypothesis that epiphyton shading in spring can drive the collapse of submerged macrophytes in temperate shallow lakes when critical shading levels are surpassed. Subsequently, macrophyte restoration needs a stark reduction of epiphyton shading to values far below the ones at which the system tipped into the turbid state. This leads to a hysteresis along an epiphyton shading gradient. The timing of epiphyton shading onset is decisive in this process, the later in the season the epiphyton shading starts, the more shading is tolerated before submerged macrophytes collapse. Our model results also suggest that grazing on epiphyton can alleviate the impact of epiphyton shading and allow macrophyte persistence in the modeled lake even above critical nutrient loading. As hypothesized, timing and duration of top-down control by grazing on epiphyton influences macrophyte long-term persistence in the modeled shallow lake. The earlier and the longer top-down control of epiphyton occurs, the more beneficial it is for summer macrophyte biomass and overall persistence of macrophytes in a lake. Warmer winters allow an earlier onset of macrophyte growth based on temperature cues. When modeling a range of onset dates of epiphyton shading, a higher shading proportion may be tolerated before macrophytes collapse. Overall, WWTs did not necessarily lead to lower macrophyte biomass or an earlier collapse of the macrophyte population per se (against our hypothesis), the interaction with timing of epiphyton shading onset and the timing and duration of grazing on epiphyton was more decisive in our model exercise. While our results provide a proof-of-concept showcasing the potential influence of epiphyton shading, future research will need to link epiphyton development to its biotic and abiotic control factors in the model to allow capturing the interactions fully.

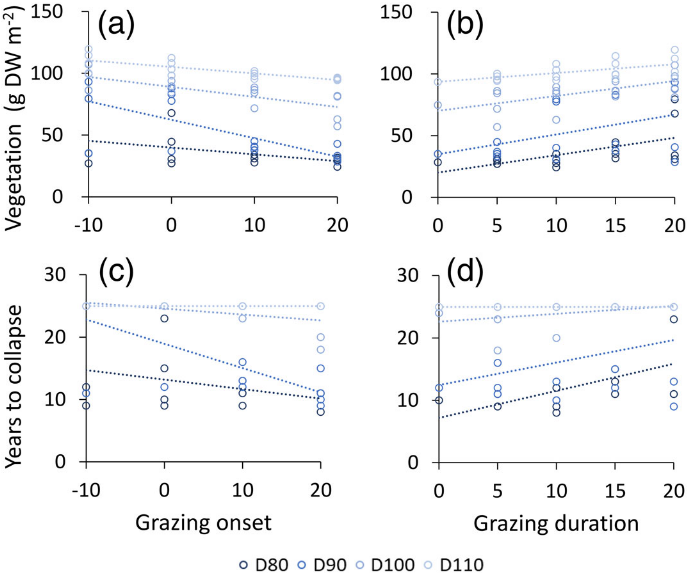

Fig. 4. Response of submerged macrophyte biomass and resilience in the warmer winter temperature scenario. The 25-yr average summer biomass of macrophytes (g dry weight [DW] m^{-2}) relative to (**a**) timing of the grazing period, and (**b**) duration of the grazing event. Years until macrophytes disappear during the growth period from the model lake along a gradient of epiphyton shading curve midpoints (day [D] 80–110; blue shades) in response to (**c**) the relative onset of the grazing period and (**d**) the duration of the grazing period.

General epiphyton phenology

The annual process of community assembly with all major external factors and internal interactions shaping communities,

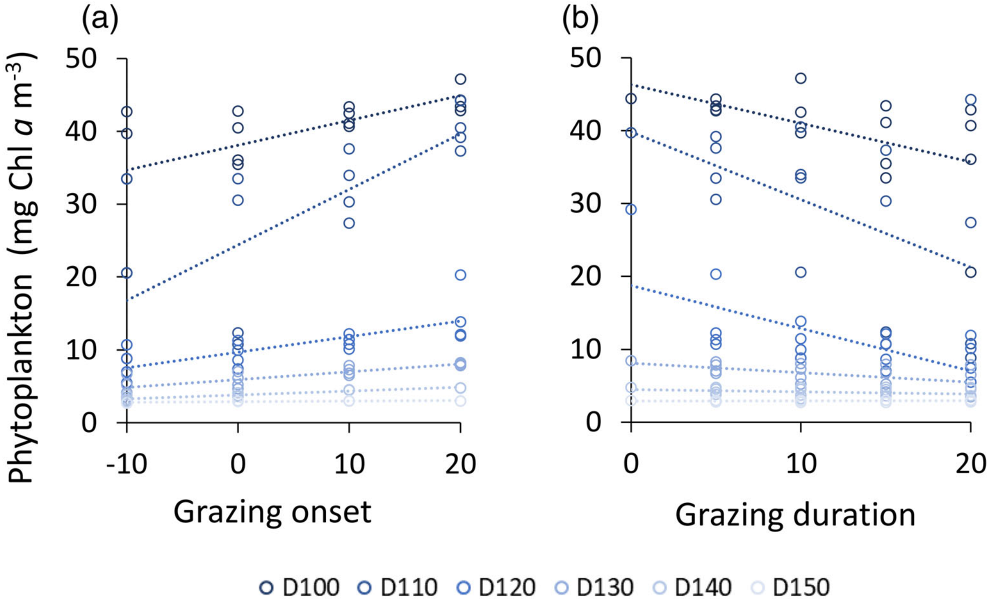

Fig. 5. The 25-yr average summer pelagic phytoplankton biomass (mg chlorophyll *a* [Chl *a*] m^{-3}) along a gradient of epiphyton shading curve midpoints (day [D] 100–150; blue shades) in presence of a grazing event and under the control temperature scenario relative to the (**a**) onset of the grazing period and (**b**) duration of the grazing event.

including the role of physical factors, grazing, and nutrient limitation, has been studied and described in detail for plankton both in freshwater (Sommer et al. 2012) and marine systems (Ji et al. 2010 and references therein). Climate warming-induced phenology shifts such as the earlier occurrence of diatom blooms or peak abundances of *Daphnia* populations in spring (Adrian, Wilhelm, and Gerten 2006) have frequently been shown for lake plankton and have contributed to a general understanding of taxon and ecosystem responses to climate warming (De Senerpont Domis et al. 2013; Thackeray et al. 2016). In contrast, knowledge on epiphyton phenology is limited (Botrel et al. 2024) and a general model equal to the Plankton Ecology Group model (Sommer et al. 2012) is lacking. This is surprising given the importance of epiphyton for macrophyte biomass (*see* introduction), but also for lake nutrient cycling and food web structure (Vadeboncoeur and Steinman 2002). The qualitative pattern we suggested for epiphyton biomass development of temperate lakes in spring and summer resembles phytoplankton dynamics in eutrophic, temperate lakes with a peak biomass in spring followed by a decline termed clear-water phase for phytoplankton (Sommer et al. 1986). A comprehensive comparison of phytoplankton and epiphyton phenology, however, has not been performed yet. Our literature data were taken from total series with an accumulation of epiphyton on substrates over time. Studies comparing such total epiphyton dynamics with interval series show that the latter have a similar general qualitative pattern in spring and early summer. Two-week epiphyton can absorb up to 80% of photosynthetically active radiation (e.g., van Dijk 1993; Roberts et al. 2003), so a complete escape of submerged macrophyte leaves from shading by rapid growth is not possible.

Integration of epiphyton phenology into lake ecosystem model

Extensive and rigorous testing of many combinations of abiotic conditions as well as onset and duration of grazing periods on epiphyton phenology and its effects on submerged macrophytes is not possible in experimental or observational studies and thus requires the use of models. Epiphyton shading of macrophytes, however, is often neglected in lake ecosystem models (Sachse et al. 2014). In macrophyte growth models such as the sagopondweed growth analysis (Hootsmans 1994; Hidding et al. 2016) or Charisma (van Nes et al. 2003), epiphyton shading has been included as a predefined fraction reducing the photosynthetically active radiation. In our adapted version of the ecosystem model PCLake+, we model epiphyton shading and regulate it by the choice of the Boltzmann curve parameters, which allows us to simulate seasonal dynamics with a customizable timing, curve, and maximum shading. While this approach allows testing of multiple scenarios and predicting general trends, it does not take the various strategies of different macrophyte species to cope with shading such as photosynthetic acclimation or shoot elongation into account (Hootsmans, Santamaría, and Vermaat 1995) and it does not link epiphyton dynamics to any abiotic or biotic drivers. However, linking epiphyton dynamics to water temperature, nutrient availability, and grazer dynamics is needed for allowing feedback loops and more realistic predictions of its influence on the response of macrophytes and shallow lake ecosystems to climate change. Calibration and validation of such models requires experimental studies testing the effects of warming on epiphyton phenology (e.g., Kazanjian et al. 2018; Hao et al. 2020; Cheng et al. 2022) and field data on seasonal epiphyton development in lakes, ideally as part of long-term monitoring programs (Botrel et al. 2024). These should also take the intricate interactions between lake morphometry into account, in particular depth, and biotic selection and grazing interactions determining epiphyton community composition and occurrence (Puche et al. 2021).

Timing of epiphyton shading

Our study has focused on spring and early summer in temperate lakes, when epiphyton shading phenology appears to be important for bottom-dwelling, but also for annual tall-growing macrophyte species with sprouts emerging from seeds or winter storage organs (van Nes et al. 2002). In summer, tall-growing species can partially escape epiphyton shading by concentrating their biomass near the better-lit water surface (Sand-Jensen et al. 2008). Our model results primarily serving as a proof-of-principle showcase that an earlier development of epiphyton shading in spring leads to lower cumulative macrophyte biomass production and to a faster collapse of the macrophyte community in control as well as WWT scenarios. Including the diversity of submerged macrophyte growth forms and strategies to cope with reduced light availability and their specific interactions with epiphyton communities will be valuable future directions of research. The same holds for the phenology of epiphyton grazers. Our model results showcased that grazing early on in the development of epiphyton shading has the most beneficial effects for the establishment and long-term persistence of macrophytes, both under control and WWT scenarios. Kazanjian et al. (2018) showed in fishless mesocosm experiments that periphyton grazing in spring occurred earlier in warmed treatments as compared to controls. However, for predicting the response of shallow lake ecosystems to changes in the environmental conditions, fully linking the phenology of epiphyton grazers and their predators to would be needed in lake ecosystem models. Lake restoration efforts would gain from such modeling insights to highlight that macrophyte restoration in lakes may thus not only require reduced nutrient loading, but in addition may gain from controlling the predators of epiphyton grazers.

Conclusion

Globally, loss of submerged macrophytes is a common problem not only in lakes (Zhang et al. 2017; Botrel and

Maranger 2023), but also in marine shallow littoral areas with, for example, major declines in seagrasses (Orth et al. 2006). The critical role of epiphyton phenology for submerged macrophyte development shown in our study implies that shallow lake restoration measures should not only target epiphyton biomass but also take epiphyton phenology into account. Changes in epiphyton phenology potentially also affect macrophyte presence, productivity, and diversity of higher trophic levels in other freshwater and marine littoral habitats of different climate zones and thus deserve increased attention in future monitoring, experimental studies, and modeling.

Author Contributions

Alena S. Gsell, Sven Teurlincx, and Sabine Hilt co-led the manuscript and contributed equally. Alena S. Gsell, Sven Teurlincx, and Sabine Hilt came up with the research question and designed the approach. Sven Teurlincx provided the model. Sabine Hilt and Marta M. Alirangues Nuñez provided the field data. Alena S. Gsell conducted the model analyses. All authors wrote and edited the manuscript.

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Conflicts of Interest

None declared.

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Supporting Information

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

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