CURRENT EVIDENCE

Changing phenology of benthic primary producers in inland waters: Current knowledge and future directions

Morgan Botrel [ID],[1]* Roxane Maranger [ID],[1] Marta Maria Alirangues Nuñez [ID],[2] Garabet Kazanjian,[3,4] Sarian Kosten,[5] Mandy Velthuis [ID],[5,6] Sabine Hilt [ID][2]

[1]Département de Sciences Biologiques, Groupe de Recherche Interuniversitaire en Limnologie (GRIL), Université de Montréal, Montréal, Québec, Canada; [2]Department of Community and Ecosystem Ecology, Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany; [3]Acopian Center for the Environment, American University of Armenia, Yerevan, Republic of Armenia; [4]Scientific Center of Zoology and Hydroecology, National Academy of Sciences of the Republic of Armenia, Yerevan, Republic of Armenia; [5]Department of Ecology, Radboud Institute for Biological and Environmental Sciences, Radboud University, Nijmegen, The Netherlands; [6]Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

Scientific Significance Statement

Benthic primary producers (BPP), including aquatic macrophytes and periphyton, in inland water littoral zones are foundational habitats that control many ecosystem processes. Given their sessile nature, BPP are also sensitive to eutrophication and climate change; however, very few long-term time series document their seasonal dynamics. This hampers our ability to assess how various, often interactive, drivers influence the timing of BPP periodic life cycle events, and thus modify ecosystem functioning. This study reviews how climate and other drivers might impact BPP phenology and provides rare evidence of strong BPP seasonal shifts associated with temperature change, supporting the need to monitor BPP more closely. We further provide insights on possible consequences of these seasonal shifts on ecosystem functioning and avenues to facilitate monitoring.

Abstract

Benthic primary producers (BPP) in inland waters, including aquatic macrophytes and periphyton, are foundational habitats that are highly sensitive to multiple human drivers of environmental change. However, long-term seasonal monitoring of BPP is limited, leaving us with little information on the cause, directionality, and consequences of the potential shifts in timing of BPP life cycle events. Here, we review the literature on the phenological changes of BPP and show that BPP respond primarily to temperature, but also to other interactive drivers related to climate change and eutrophication. In addition, we present four rare case studies where BPP display strong and earlier shifts in event timing associated with increasing temperature and discuss potential impacts

of these changes on ecosystem functioning. Given the responsive nature of BPP to multiple human drivers, we provide suggestions on how to improve basic monitoring to better understand the future impact of phenological changes of this critical habitat.
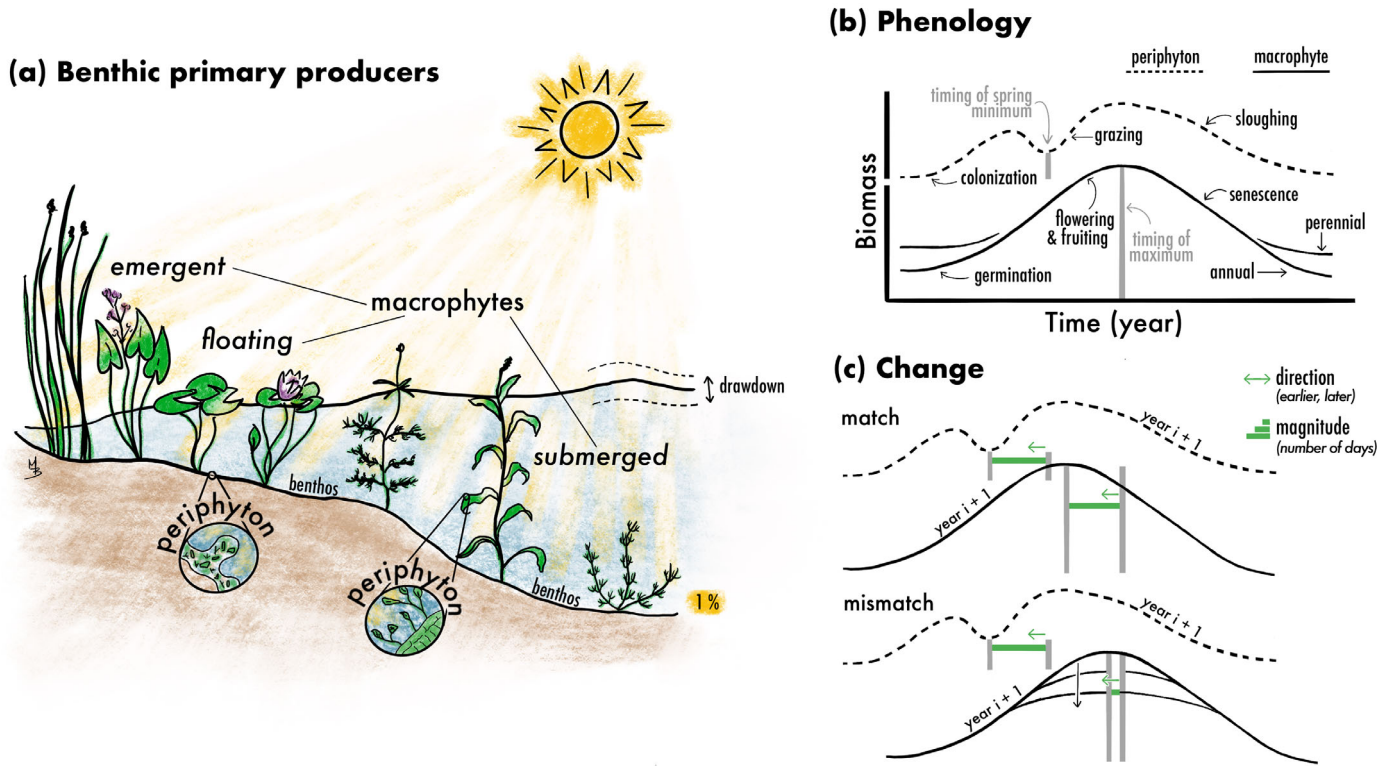
Benthic primary producers (BPP), including aquatic macrophytes and periphyton, are foundational habitats that control key functions in inland waters. These functions include food web maintenance as well as regulation of carbon, nutrients, and greenhouse gas emissions (Hilt et al. 2017). Being sessile and located at the sediment–water interface, often close to the land–water edge, BPP are also sensitive to human pressure and have been recognized as sentinels of land use change because both biomass and community composition act as indicators of eutrophication (Schneider 2007). Recent studies additionally suggest that long-term trends and seasonal dynamics in BPP abundance and reproductive traits are sensitive to climate change (Calero and Rodrigo 2019; Vadeboncoeur et al. 2021; Botrel and Maranger 2023). The complex interactions among eutrophication, climate change, and food web perturbations have been suggested as an explanation for the mysterious seasonal proliferation of benthic filamentous algae in clear, iconic large lakes such as Baikal and Tahoe (Vadeboncoeur et al. 2021). However, the underlying causes of such shifts in timing of BPP periodic life cycle events, or phenology, are poorly known. As climate change is currently altering temperature, flow, mixing regimes, and ice cover dynamics of inland waters (Woolway et al. 2020), there is an urgent need to document BPP phenological change to predict the directionality and magnitude of seasonal shifts as well as the consequences on ecosystem functioning.

The lack of knowledge on BPP phenological change is mostly due to the patchy nature of BPP that makes their monitoring more tedious compared to planktonic organisms. Whether in lentic or lotic systems, BPP are phototrophs that grow attached to the lit surfaces at the bottom of the littoral zone, below the high-water mark and above 1% of incident light (Fig. 1a). This interface includes the shoreline but also the sediment in contact with water and can cover either a proportion of, or an entire ecosystem, as is the case for some rivers and shallow lakes. Aquatic macrophytes are the macroscopic vegetation in the littoral zone, and include macroalgae (such as charophytes), mosses, as well as herbaceous vascular plants (angiosperms and pteridophytes) of various growth forms according to their tolerance to immersion. Periphyton is the biofilm composed of algae, bacteria, and detritus that forms on any submerged substrate and that can sometimes be detached from the bottom, creating floating mats (e.g., metaphyton of filamentous algae). When BPP are monitored, they are typically sampled only once per year at most (Birk et al. 2012), and repeated seasonal measurements are almost inexistent. Littoral habitats of lakes are known to be

less studied compared to open waters (Vander Zanden and Vadeboncoeur 2020), and as a result, very few long-term BPP phenological time series exist. Thus, we have little information on the cause and manner of the shifts in the timing of BPP life cycle events in this critical habitat.

Despite this gap in knowledge, information on BPP phenology exists, mainly from detailed annual studies that measured biomass accrual through time (Fig. 1b; Biggs 1996; Wetzel 2001a). During the growing season, BPP biomass typically increases in a sigmoidal fashion reaching a seasonal maximum. The peak biomass is followed by a decreasing phase where loss processes dominate due to, for example, senescence or tearing and sloughing from hydrologic disturbances. For macrophytes, the seasonal pattern can be observed for annuals but also for the many perennials that maintain belowground organs throughout the year, raising the biomass at the start and end of the growing season (Wetzel 2001a). In tropical settings, macrophyte biomass is often strongly governed by seasonal changes in hydrology (e.g., Giorgi et al. 2005; Tabosa et al. 2012). Phenology can also be followed by the timing of various events throughout macrophyte life cycles, such as germination, flowering, seed production, or turion formation (i.e., winter bud). For periphyton, the exponential growth phase in temperate lakes can be interrupted in spring or early summer due to biomass loss from macroinvertebrate grazing (Wetzel 2001b; Roberts et al. 2003) similar to the clear-water phase observed in open waters caused by zooplankton grazing on phytoplankton. Onset and duration of this interruption can be assumed to respond to changes in climate or food webs (Fig. 1b).

The timing of BPP life cycle events and biomass dynamics can be expected to shift in different directions, be it earlier or delayed, and vary in magnitude in response to climate change (Fig. 1c). The biological events of primary producers tend to occur earlier with increasing temperature and are delayed with higher precipitation. For terrestrial plants, expected shifts are around -4 to -0.5 d°C^{-1}, and -0.5 to 1 d mm^{-1} of rain, while for phytoplankton they are among the most variable at around -6 to 6 d°C^{-1} and -1 to 5 d mm^{-1} (Thackeray et al. 2016). This higher variability of phytoplankton shifts reflects the complex nature of climate impacts on inland waters affecting water temperatures and levels, nutrient availability, as well as hydrodynamics (e.g., stratification, waves, water residence time), which all influence the timing of phytoplankton life cycle events. In addition, phenological shifts vary in magnitude with trophic levels (Thackeray et al. 2016), potentially leading to a mismatch between primary producers and consumers. For plankton, those phenological asynchronies have been widely investigated (Gronchi et al. 2023), while for BPP, this knowledge is lacking despite potentially massive ecosystem consequences. A prominent example for

Fig. 1. BPP are photosynthetic organisms that grow attached at the bottom (the benthos) of the littoral zone in inland waters and include aquatic macrophytes of different growth forms (emergent, floating, submerged) and periphyton attached to sediment, stones or macrophytes (**a**). The upper limit of the littoral is the high-water mark within the drawdown zone and the lower limit corresponds to 1% incident light. BPP phenology, usually measured from biomass accrual, typically displays a sigmoid growth pattern followed by a decreasing phase over a year (**b**) and is also expressed by sequential biological events (curved arrows). Various deviations from the typical unimodal pattern can be observed (straight arrows). BPP phenology can change by displaying a shift in timing across years, this shift can vary in direction and magnitude with different BPP types responding in synchrony (match) or asynchrony (mismatch) to climate change (**c**). Mismatch can result in negative consequences, for example, earlier periphyton growth and shading could diminish submerged macrophyte survival and growth.
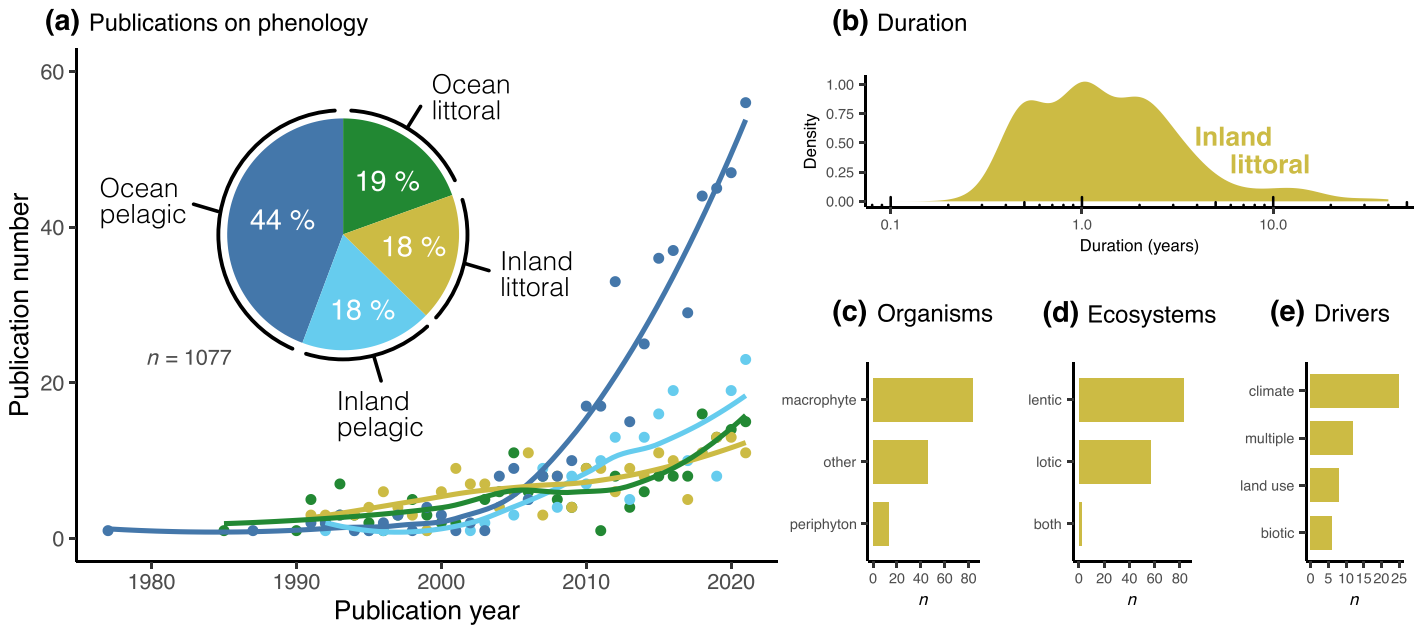
interactions among BPP is the effect of periphyton shading on submerged macrophytes that can cause their decline and shift shallow lakes to a turbid equilibrium (Scheffer et al. 1993; Phillips et al. 2016) providing fewer ecosystem services (Janssen et al. 2021). Asynchronous shifts in the timing of periphyton shading and macrophyte growth in response to climate change can thus have cascading effects on the entire ecosystem. In addition, shifts driven by climate change are likely to interact with other human impacts, particularly those that limit BPP growth such as nutrient inputs in lentic ecosystems and light and flow regimes in lotic ones (Bernhardt et al. 2022). To our knowledge, the consequences of shifts in BPP timing on ecosystem functioning have not been investigated.

Here, we review current information on drivers, directionality, magnitude, and consequences of changes in BPP phenology in inland waters. We report four rare long-term and experimental case studies where freshwater macrophytes and periphyton display strong shifts in their phenology associated with temperature change. We also provide examples of technologies to facilitate future seasonal monitoring of BPP as

a base for an improved understanding of freshwater ecosystem response to global change.

What information on BPP phenology is available and what are the drivers of change?

To explore the information available on BPP phenology in inland waters and compare it to more traditional pelagic efforts (Vander Zanden and Vadeboncoeur 2020), we conducted a literature search on the use of the term phenology across aquatic ecosystems (marine and inland) and habitats (pelagic and benthic). The search was conducted 26 January 2023 on Web of Science Core collection in the titles, abstracts and keywords. To have a total number of papers on the phenology per ecosystem (ocean and inland waters) and habitat type (littoral and pelagic; Fig. 2a), we did four queries. For a given ecosystem habitat combination, keywords describing other ecosystem/habitat where excluded (e.g., phenolog* AND inland waters AND littoral NOT ocean NOT pelagic; phenolog* AND inland waters AND pelagic NOT ocean NOT littoral) resulting in a total of 1077 studies. Papers looking at multiple habitat ecosystem were less than 20% of all papers on aquatic organism

Fig. 2. Presence of the term "phenology" in publications across aquatic ecosystem and habitat types (**a**) as well as information breakdown for inland water littoral habitats (**b–e**). The density plot (**b**), which express the frequency distribution, is truncated at 50 yr for clarity (one observation afterwards), and drivers (**e**) correspond to broad environmental factors explaining variation in either periphyton or macrophytes. *n*, number of publications.

phenology. Exact keywords are described in the online data repository (Botrel et al. 2023*b*).

We found that despite increasing interest on the topic of phenology in aquatic ecosystems in the last decade, much of the research has focused on the pelagic ocean, while inland waters and littoral habitats have received less attention (Fig. 2a). When unpacking information for littoral habitats in inland waters (Fig. 2b–e), only two-third of the studies (142 out of 212) actually deal with phenology of benthic aquatic organisms, with the majority of those being on BPP (95) and the remaining on other organisms, mostly macroinvertebrates (Fig. 2c). The observational time frame is also overwhelmingly short with a median duration of 1 yr, and only six studies lasted longer than 10 yr (Fig. 2b). Of the latter, only one reported seasonal shifts in timing of BPP (14 yr, Hou et al. 2019), while the others either used phenological curves as methods (Han et al. 2018; Hou et al. 2018; Luo et al. 2020), reported early successional species in sediment archives (Michelutti et al. 2020), or looked at macroinvertebrates (Mahato and Johnson 1991). The knowledge gap is even more pronounced for periphyton and in lotic systems (Fig. 2c,d). More information is available in lentic systems and for plants in part due to developments in remote sensing techniques, with about a third of the macrophyte studies considering multiple growth forms and the remaining looking exclusively at a specific type (41% submerged, 8% floating, 19% emergent).

Yet despite the lack of long-term data, information on potential drivers of shifts in BPP seasonal timing are available

from interannual, comparative, experimental, and modeling studies (51 studies out of the 95 studies on BPP). The main driver emerging from our literature synthesis was climate (Fig. 2e). The exact climate-related factors explaining phenology varied, but were in majority related to temperature (e.g., Handley and Davy 2005; Andresen et al. 2018; Turnage et al. 2018). However, the specific phenological response to temperature could not be simply summarized due to the lack of standardized methods to report BPP phenology. Indeed, a variety of phenological response variables were reported across studies (Table 1). These were mostly productivity metrics describing the size and development of communities or individuals (biomass, cover, counts), rates of changes (growth, senescence) and greenness, but some studies also included macrophyte traits or counts of sexual and asexual organs and leaf responses to herbivory. Only 14 studies reported specific events in BPP life cycles, with 2 of those tracking shifts in the timing of these events (Andresen et al. 2018; Hou et al. 2019), both of which were found to be related to temperature. For example, Andresen et al. (2018) predicted the green-up dates of two emergent macrophytes in the Arctic from accumulated degree days and estimated that this event is 16 d earlier over the last 70 yr (1946–2016, -0.2 d yr^{-1}). Likewise, timing of phenophases (i.e., development stages, from emergence or flowering to senescence) was related to accumulated degree days in a latitudinal comparison with earlier onset of events in Spain compared to Switzerland (Calero et al. 2017). Despite the clear temperature effect, other climate-related factors additionally explained phenology. This was mostly hydrologic regime

Table 1. Summary of phenological response variables recorded across 51 studies where we could also identify drivers of BPP phenology. "Flower" and "seed" are used widely to include charophyte reproductive organs and oospores, respectively.

	Type of response	Type of variable or organ	Phenological response variables	Occurrence	Total
Macrophytes	Sexual reproduction	Flower	Flower count (number, density, presence, proportion of individual with, proportion per shoot, length)	12	39
			Inflorescence count (number, density)	3	
			Flowers per inflorescence/individual	2	
		Fruit	Fruit count (number, presence, proportion of individual with)	4	
			Fruit water content	1	
		Seed	Seed count (number, presence, density, biomass)	5	
			Seed setting rate per infructescence	1	
			Seed per fruit (number, mass ratio)	2	
			Seed C : N	1	
			Ripe seed or fruit (%)	2	
			Seeds germinating (%)	6	
	Asexual reproduction and storage	Turion and tuber	Turion count (number, density, biomass)	4	20
			Turion C : N	1	
			Tuber count (number or density, proportion of plants with)	4	
		Rhizome	Rhizome shape (volume, diameter, length)	2	
			Rhizome water content	1	
			Rhizome starch content	1	
		Other	Adventitious roots (number of plants with)	1	
			Root crowns density	2	
			Stolon density	2	
			Allocation of nonstructural carbohydrates in organs	2	
	Production and senescence	Density	Whole biomass	6	75
			Above ground biomass	5	
			Below ground biomass	2	
			Above water biomass	1	
			Allocation of biomass to multiple organs	2	
			Necromass	1	
		Change	Growth rate	6	
			Senescence rate	2	
		Occupancy	Cover classes in plots (%)	5	
			Whole ecosystem cover (%, classes or not)	3	
			Volume inhabited (%)	2	
			Occurrence	2	
		Size	Areal cover	4	
			Mat thickness (floating species)	1	
			Shoot (height or length)	8	
		Shape	Internodal length	1	
			Leaves width or length	3	

Table 1. Continued

Type of response	Type of variable or organ	Phenological response variables	Occurrence	Total
	Development	Bud count (number, per plant)	2	
		Number of surviving plants or seedlings	3	
		Lateral development (branching, length of secondary branch)	1	
		Stem, leaves or seedling count (number, number per plant, %)	8	
		Peak abundance (NDVI and LAI)	2	
	Greenness	Leaf Area Index (LAI)	2	
		Green-Excess Index (GEI)	1	
		Normalized Difference Vegetation Index (NDVI)	2	
Defense and herbivory	Leaf damage and composition	Leaf C : N ratio	2	6
		Leaf sclereid abundance	1	
		Leaf water content	1	
		Leaf area damaged	1	
		Biomass per leaves removed by herbivores	1	
Events		Timing of phenological stages (e.g., sterile plant, fruit, etc. to senescence)	7	20
		Start of season (day)	4	
		Peak of season (day)	2	
		End of season (day)	3	
		Maximum growth (day)	1	
		Growing season length	1	
		Flowering period	2	
Periphyton	Production	Chlorophyll *a*	3	14
		Colony development (absent, present, blooming)	1	
		Height of filament	1	
		Cover classes in plots (%)	2	
		Gross primary productivity (GPP)	3	
		Nutrient uptake rate	1	
		Chemical composition (C, N, amino acid, fatty acids, sterols)	1	
		Enzyme activity	1	
	Successional stage	Species composition	1	

altering water level, velocity, chemistry, and hydroperiod (e.g., Fernandez-Zamudio et al. 2018; Brahney et al. 2021), or the interaction of temperature with hydrology (Calero et al. 2018; Calero and Rodrigo 2019). The variability of explanatory factors is analogous to the high variability in the magnitude of shifts per degree observed for phytoplankton (Thackeray et al. 2016), reflecting the complex nature of climate impacts on inland waters.

Similarly to climate, land use change influences BPP phenology through temperature and hydrologic regimes, such as flow control through dam creation (Power 1992;

Hutchinson 2019; Yang et al. 2020) and thermal pollution from mine heap leachate (Chmura and Molenda 2012; Fig. 2e). Land use also explained phenological changes related to resource acquisition, such as modification of pH and nutrients (Toth 2018; Simao et al. 2021) and fluctuations in light availability from fine particles interception (land slide, Villa et al. 2020). Interestingly, we found that changing biotic interactions were reported to affect BPP phenology in six studies (Fig. 2e), notably through interspecific competition for light. For example, shading by the free-floating duckweed in a mesocosm experiment modified submerged charophyte morphology and

decreased reproductive capacity, resulting in an earlier peak of reproductive organ density (Van Onsem and Triest 2021). Conversely, increased light availability through changes in riparian vegetation canopy associated with stochastic weather events explained an increase in gross primary production by macroalgae in streams altering the overall growing season (Roberts et al. 2007; Mulholland et al. 2009). Other plant influences on BPP phenology included changes in community structure through the arrival of invasive plants (Toth et al. 2019; Torso et al. 2020; Glisson et al. 2022), adaptation through hybridization (Glisson and Larkin 2021), and sex-specific seasonal variation (Hoffmann et al. 2014). In terms of interactions with fauna, event timing was altered by changes in herbivory (Franceschini et al. 2010; Pinero-Rodriguez et al. 2021) including gut passage of seeds favoring earlier germination (Figuerola et al. 2005). Multiple interacting drivers, as reported in a quarter of the studies, appeared responsible for BPP seasonal shifts. The only available long-term study (14 yr) using historical satellite images clearly associated the interactive effect of climate and land use change to shifts in the timing of macrophyte emergence above water in 25 lakes, with variable direction and magnitude in shifts (Hou et al. 2018). Thus, more attention clearly needs to be paid to interactive driver impacts on BPP phenology.
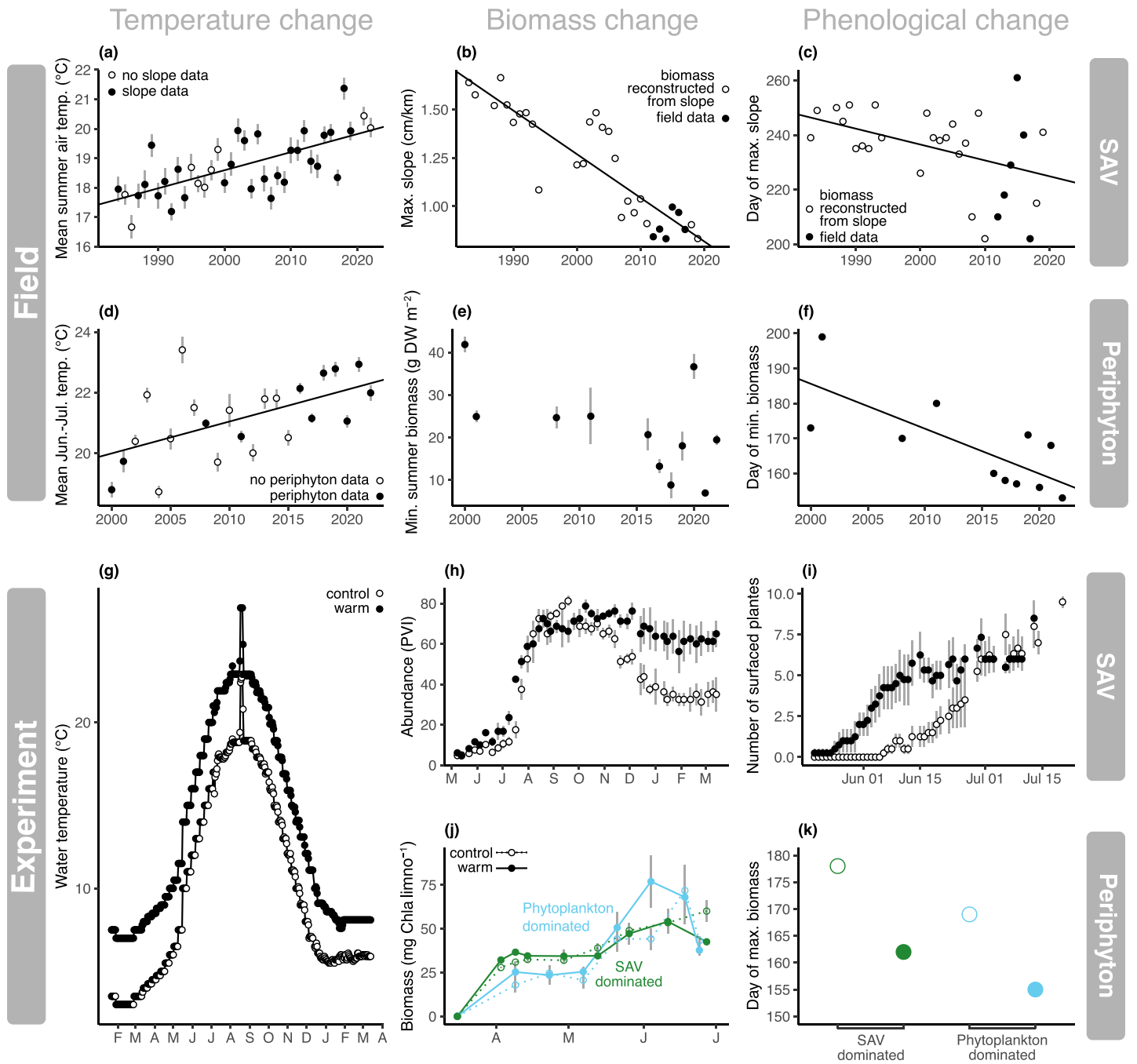
Insights from rare long-term data and experimental evidence on BPP seasonality

To further investigate the drivers, directionality, and magnitude of changes in BPP phenology, we compiled evidence from our field and experimental work on the sensitivity of aquatic macrophytes and periphyton to climate change and other interacting drivers. Our first example comes from submerged aquatic vegetation (SAV) meadows in Lac Saint-Pierre (LSP), a fluvial lake (area: ~ 400 km^2, mean depth: 3 m) along the Saint Lawrence River in Quebec, Canada (Fig. 3a–c). Due to the fluvial nature of the meadows, SAV biomass could be estimated from the slope of surface water elevation between upstream and downstream gauging stations because, like a dam, higher biomass obstructs more flow in a predictable manner. Using signal decomposition analysis, this biomass signal was disentangled from others captured by water level slope (i.e., tides, waves), and validated with 6 yr of comprehensive biomass measures (Botrel et al. 2022). We then used this approach to reconstruct detailed SAV growth patterns from historical water level data between 1982 and 2019 (Fig. 3c). The resulting four-decade time series, the longest phenological record for macrophytes, revealed an overall earlier timing of maximum SAV biomass of 6 d decade^{-1} with a median peak occurring around 30 August in the 1980s and 06 August in the 2010s. This shift coincides with increasing mean summer air temperature (0.6°C decade^{-1}), supporting the typical directionality of change for plants subjected to warming climate (Thackeray

et al. 2016). Variability in the window of peak biomass is also increasing, with a standard deviation of 7 d in the 1980s to 20 d in the 2010s. This variability could be caused by higher nutrient loads to LSP from increased agriculture development in the flood plain (Goyette et al. 2016). Eutrophication of LSP has been associated with both SAV decline and changing species composition, particularly due to decreasing abundance of *Vallisneria americana* in years with high water levels (Giacomazzo et al. 2020). This species inhabits deep-water habitats in LSP and is likely more vulnerable to light availability through interannual variation in water levels. Thus, the overall phenological changes appear to be a combined influence of eutrophication and different climate drivers. Regardless, the sharp shift in peak SAV biomass over the last decades challenges the typical annual one-point sampling scheme for capturing changing consequences on ecosystem functioning.

Our second example comes from the long-term monitoring of Lake Müggelsee, a temperate and polymictic lake (area: 7.5 km^2, mean depth: 4.9 m) in Berlin, Germany (Fig. 3d–f). This lake underwent strong changes in SAV abundance and diversity during the last century (Hilt et al. 2013) where changes in periphyton shading are assumed to play a major role in delaying recolonization by SAV (Roberts et al. 2003). Since 2000, periphyton biomass has regularly been sampled between April and August from plastic strips deployed in the lake (Roberts et al. 2003). Over this 20-yr period (Fig. 3d–f), early summer (June–July) water temperature increased by 1°C decade^{-1} simultaneously with a decrease in the minimum summer periphyton biomass (marginally significant $p = 0.06$) and a significantly earlier day of minimum periphyton biomass (-13 d decade^{-1}), going from a median of 26 June before 2012 to 07 June after. This earlier occurrence of periphyton biomass minimum is similar to the earlier spring clear-water phases observed in temperate lakes (Matsuzaki et al. 2021), which is assumed to be caused by earlier zooplankton grazing. Whether periphyton phenological shifts could trigger shift between alternative equilibria in shallow lakes, however, remains to be investigated.

Similar seasonal shifts of BPP associated to climate warming were found in two experiments conducted in 1000-liter indoor temperature-controlled macrocosms (Limnotrons). The phenological response of SAV (*Myriophyllum spicatum*; Fig. 3g–i) and periphyton (Fig. 3g,j,k) to warming was followed in two subsequent years, one simulating the dominance of phytoplankton (2014) and the second the dominance of SAV (2015). In each year, a control treatment with typical temperate shallow water temperature was compared to a warm treatment ($+4$°C, Fig. 3g, $n = 4$ per treatment). For SAV, warming prolonged the growing season, maintaining high biomass throughout the fall (Fig. 3h). This resulted in increasing carbon turnover due to both enhanced sedimentation and decomposition (Velthuis et al. 2018). Phenological changes were also observed at the beginning of the season where *Myriophyllum* plants reached the

Fig. 3. Observations of potential impacts of warming on the phenology of SAV and periphyton. Top panels report biomass and phenological change of SAV in fluvial Lake Saint-Pierre (**a–c**) and periphyton in Lake Müggelsee (**d–f**). Bottom panels show experimental evidence of the impact of warming on SAV and periphyton. In (**g**) temperature are those of the SAV-dominated experiment. Error bars are standard errors and trend lines are significant ($p < 0.01$) ordinary least square regressions, except for (**c**) given heteroscedasticity across years a generalized least square regression with a power of the covariate variance structure was fitted using the nlme package in R (Pinheiro et al. 2020; R Core Team 2020). Absence of autocorrelation was assessed by looking at residuals. DM, dry mass; PVI, percent volume inhabited; limno., limnotron, Chl *a*, chlorophyll *a*. For data, see Botrel et al. (2023*b*).

water surface 17 d earlier in the warm treatment, a difference of $-4\,\mathrm{d^\circ C^{-1}}$ (Fig. 3i). Periphyton phenology was also significantly affected by warming with peak biomass occurring ~ 2 weeks

earlier in both warm treatments (Fig. 3j,k). This earlier occurrence, again of $-4\,\mathrm{d^\circ C^{-1}}$, is similar to reports for terrestrial plants and algae taxa (Thackeray et al. 2016). Interestingly,

when phytoplankton was dominant, periphyton showed faster growth in the warm treatment toward the end of May (Fig. 3j). The higher growth was catalyzed by increase nutrient concentrations due to an earlier parasite-driven termination of the spring phytoplankton bloom in the warm treatment (Kazanjian et al. 2018; Frenken et al. 2020). This seasonal change in nutrients was not recorded during SAV dominance when control and warm treatments had similar nutrient concentrations, suggesting a strong impact of SAV on nutrient dynamics (Fig. 3j). This potential role of SAV in nutrient retention and in alleviating cascading impacts on periphyton phenology deserves further investigation.

These four examples consistently showed that warming temperatures are related to earlier timing in BPP phenology. The magnitude of the shifts was surprisingly similar at $-4 \, \mathrm{d}°\mathrm{C}^{-1}$ for experimental work, and -6 to -13 d per decade for the time series. For macrophytes, shifts were observed using multiple life cycle events, including timing of peak biomass, growing season duration, and reproductive traits (number of plants reaching the surface being a proxy of flowering time), confirming multiple ways in which phenological change could be tracked. Although we found a clear response to temperature change, results suggest a broader consideration of the influence of multiple drivers and interspecific interactions in the future. In the fluvial lake study, increased variability in the window of peak macrophyte biomass and the decrease in overall biomass were linked to eutrophication and a greater range in water level fluctuations. The examples from Lake Müggelsee and the Limnotron experiment suggest that the interactions among periphyton and macrophytes should be investigated to better understand changing phenology of both groups.

Consequences of changing BPP phenology?

Although evidence that BPP phenology is sensitive to human pressures remains rare, there is even less information on the consequences of BPP phenological changes on ecosystem functioning. We can, however, reasonably hypothesize that seasonal shifts can affect a suite of functions sustained by BPP as well as their synchrony with other biological and physical events. *Mismatches in species responses* to various drivers could modify time lags between BPP seasonal events with those of its consumers and organisms that use BPP structures as a habitat, potentially interrupting or modifying energy flows across trophic levels (Dell et al. 2014). Across trophic levels, grazers are apparently sensitive to warming similarly to primary producers (Thackeray et al. 2016). For benthic habitats, however, this sensitivity may be muted depending on cascading effects of trophic structure. This is supported by a warming mesocosm experiment where the shift in peak abundance of a dominant grazer, a snail, displayed a similar climate sensitivity as periphyton ($-4.8 \, \mathrm{d}°\mathrm{C}^{-1}$), but peaks were only observed in the absence of predators (Cheng et al. 2023). Conversely, spring peak periphyton biomass was only observed

when snail grazing pressure was released in the presence of fish. *Priming effects* have been observed when higher ecosystem processing rates throughout a season were sustained by earlier onset and higher biomass accumulation of BPP. For example, a freezing stochastic weather event resulted in forest canopy loss, increased light availability and a higher macroalgae spring bloom biomass in a stream (Mulholland et al. 2009). This sustained greater nitrate uptake and herbivore growth rates throughout the summer compared to previous years. Changing phenology can also be seen as a *shift in time of functional effect trait distribution*, that is, the species attributes that impact ecosystem functioning (Lavorel and Garnier 2002). For example, Asaeda et al. (2010) showed that the phenology of *Sparganium erectum* affects the hydraulics, sedimentation, and nutrient cycling in rivers. This species is characterized by submerged growth form in winter, then emerges in late spring and the shoots finally collapse in the fall. Compared to the other phases, emergence had lower sedimentation rates and favored downstream exports of the accumulated sediments. A change in this species phenology in relation to riverine inputs might thus modify sediment load and nutrient delivery downstream. As illustrated by these examples, future research on consequences of phenological changes should investigate how species interactions will shift with warming and how effect traits vary with life cycle events and in relation to environmental conditions.

Toward an understanding of the causes and impacts of BPP phenological changes
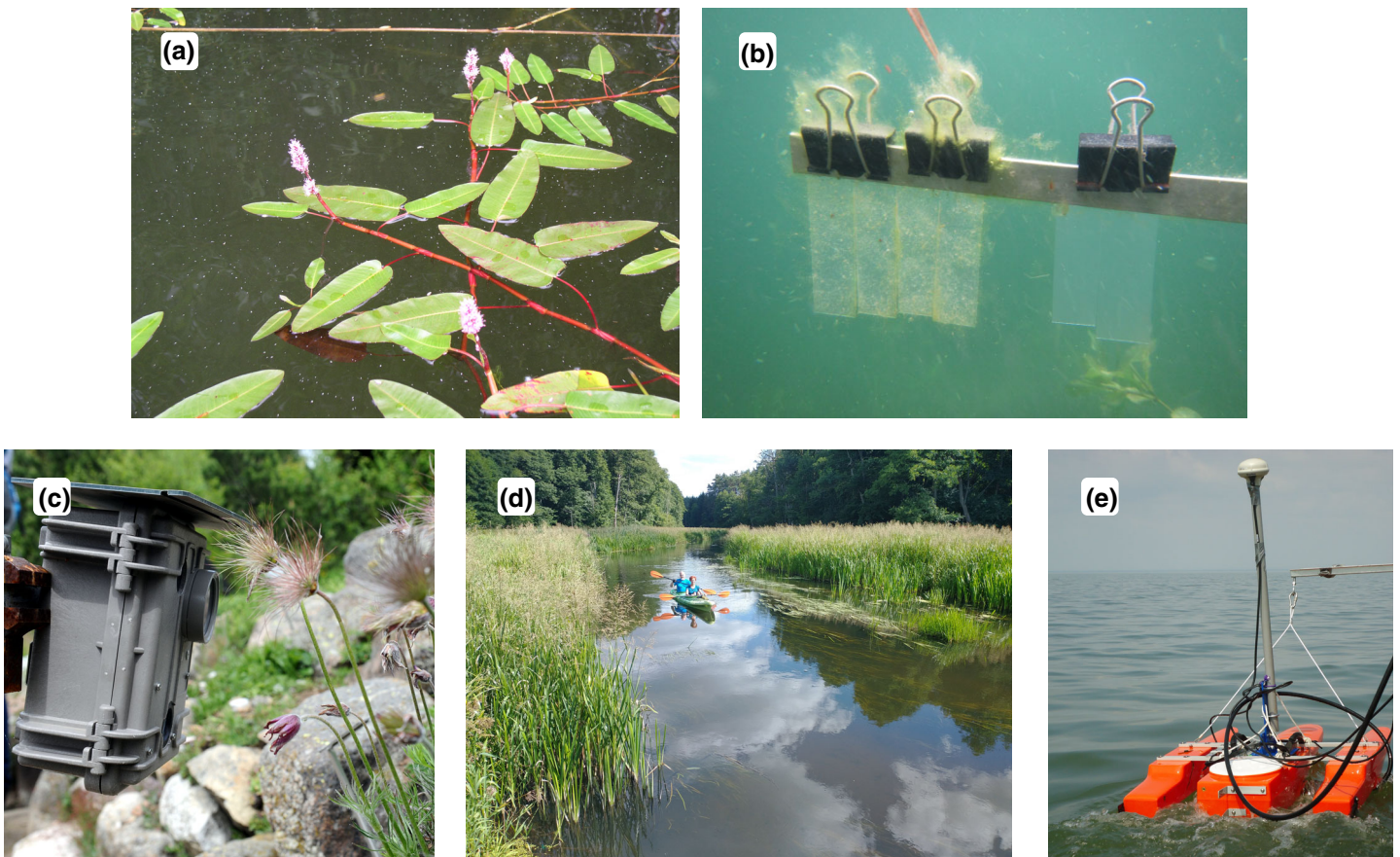
Our study underscores the importance of better understanding the cause, manner (direction and magnitude) and consequences of changing BPP phenology, and several different research directions are suggested. First, we recommend that a standardized approach to monitor BPP phenological response be established. At present, diverse variables are reported as phenological responses (Table 1), but comparable metrics and easily measurable organismal traits or life cycle events should be chosen in future studies to allow comparison across multiple sites. The phenological response variables should also be relevant for ecosystem functioning. As ecological processes tend to scale with size (Brown et al. 2004), BPP biomass, areal cover or proxy of these should be considered for this purpose. Response variables should also align with the emerging trait database effort, at least for aquatic macrophytes (Iversen et al. 2022). More effort should also be devoted to delineating phenological events that can be tracked in time as this is currently rarely done. Understanding impacts will also require a better comprehension of the relation between BPP phenology and ecosystem functioning. Here, the deployment of in situ sensors could help determine whether environmental conditions, BPP phenology, and ecosystem functioning are synchronous or not. Experimental research on the impact of individual and interactive drivers on BPP phenology should

additionally be conducted to increase our understanding of the consequences of changes on these critical habitats.

We argue that a great deal of understanding will arise from improved basic monitoring of BPP. Despite BPP spatial patchiness, tracking BPP phenology might be easier than for pelagic phytoplankton because of their sessile nature, slower turnover rates, and visibility with the naked eye. Monitoring simple BPP features and phenological events such as plant height, flowering, emergence, and senescence can be done at convenient and accessible sites (Fig. 4). For example, surface flowering, similar to Japan's cherry blossoms, can be followed by properly placed automated time-lapse cameras, such as those of the global PhenoCam Network (Brown et al. 2016) or even by community science programs. Phenocams can also be used to measure changes in color, a proxy of maturation and biomass, such as the green-excess index that has been applied to track emergent macrophytes (Andresen et al. 2018). A snorkeling program for periphyton already exists for lakes in Québec, Canada, similar to a SAV kayaking program in the Hudson River that can be adapted to phenological phenomena.

Moving phenocams placed on aquatic animals may also provide recurrent visits to otherwise unattainable places, like for seagrass research powered by sharks (Gallagher et al. 2022).

In addition, BPP phenology can be monitored through repeated measurements of areal cover and density using recent technological advances. Frequent satellite images provide the first example of long-term macrophyte phenologies (Hou et al. 2019). Space born and airborne hyperspectral sensors as well as topobathymetric LiDAR (light detection and ranging) can even detect different macrophyte growth forms, including SAV near the water surface. However, these optical techniques are poorly suited in turbid conditions where signals can be detected at 2 m depth at best (Rowan and Kalacska 2021). For submerged growth forms, acoustic techniques are thus best suited in deeper zones and can even be applied to benthic mat-forming filamentous algae (Depew et al. 2009; Botrel et al. 2023a). Increasing the frequency of SAV sonar surveys could be done by using unmanned autonomous boats or through community science programs using fishing sonar data processed on cloud-based platforms

Fig. 4. BPP phenology can be monitored by following biological events such as (**a**) aquatic vegetation flowering or (**b**) biomass accrual such as periphyton on artificial substrates. These can be visually tracked using (**c**) time-laps cameras or (**d**) community science programs, and by using remote sensing techniques including (**e**) hydroacoustics. Photograph credits: (**a**) and (**b**) Sabine Hilt, (**c**) Jaqen attributed under a CC BY-SA 4.0 license, (**d**) MOs810 attributed under a CC BY-SA 4.0 license, (**e**) Morgan Botrel.

(Helminen et al. 2019; Goulon et al. 2021). Insights on SAV phenology could also be gained by better exploiting gauging station networks (as fluvial lake example; Fig. 3c). For periphyton, fluoroprobes and hand-held spectrometers could measure change in pigments rapidly (Ghunowa et al. 2019). As each technique has its strengths and weaknesses, multiple techniques will likely be required to have a better understanding of BPP phenology. Research of the synergistic and complimentary use of multiple techniques, by developing intercalibrations (Botrel et al. 2023*a*), for example, should also be expanded. In conclusion, BPP are highly responsive to phenological changes in inland waters. Seasonal tracking of life cycle events is feasible and broadly applicable using automated techniques or community science initiatives. We recommend that BPP be included into monitoring programs as sensitive indicators of global change and that a more concerted effort is made to better understand the impact of BPP phenological shifts on ecosystem functioning.

References

Andresen, C., C. Tweedie, and V. Lougheed. 2018. Climate and nutrient effects on Arctic wetland plant phenology observed from phenocams. Remote Sens. Environ. **205**: 46–55. doi:10.1016/j.rse.2017.11.013

Asaeda, T., L. Rajapakse, and M. Kanoh. 2010. Fine sediment retention as affected by annual shoot collapse: *Sparganium erectum* as an ecosystem engineer in a lowland stream. River Res. Appl. **26**: 1153–1169. doi:10.1002/rra.1322

Bernhardt, E. S., and others. 2022. Light and flow regimes regulate the metabolism of rivers. Proc. Natl. Acad. Sci. USA **119**: e2121976119. doi:10.1073/pnas.2121976119

Biggs, B. J. F. 1996. Chapter 2: Pattern in benthic algae in streams, p. 31–56. *In Algal ecology*. Academic Press. doi:10.1016/B978-012668450-6/50031-X

Birk, S., and others. 2012. Three hundred ways to assess Europe's surface waters: An almost complete overview of biological methods to implement the Water Framework Directive. Ecol. Indic. **18**: 31–41. doi:10.1016/j.ecolind.2011.10.009

Botrel, M., C. Hudon, J. B. Heffernan, P. M. Biron, and R. Maranger. 2022. Climate-driven variations in nitrogen retention from a riverine submerged aquatic vegetation meadow. Water Resour. Res. **58**: e2022WR032678. doi:10.1029/2022WR032678

Botrel, M., and R. Maranger. 2023. Global historical trends and drivers of submerged aquatic vegetation quantities in lakes. Glob. Chang. Biol. **29**: 2493–2509. doi:10.1111/gcb.16619

Botrel, M., C. Hudon, P. M. Biron, and R. Maranger. 2023*a*. Combining quadrat, rake, and echosounding to estimate submerged aquatic vegetation biomass at the ecosystem scale. Limnol. Oceanogr. Methods **21**: 192–208. doi:10.1002/lom3.10539

Botrel, M., R. Maranger, M. M. Alirangues Nuñez, G. Kazanjian, S. Kosten, M. Velthuis, and S. Hilt. 2023*b*. Data on phenological changes of benthic primary producers from Lake Saint-Pierre (1982–2019), Lake Müggelsee (2000–2021), Limnotron warming experiments and a literature synthesis (Version 2) [Dataset]. Zenodo. doi:10.5281/zenodo.8408821

Brahney, J., M. Bothwell, L. Capito, C. Gray, S. Null, B. Menounos, and P. Curtis. 2021. Glacier recession alters stream water quality characteristics facilitating bloom formation in the benthic diatom *Didymosphenia geminata*. Sci. Total Environ. **764**: 142856. doi:10.1016/j.scitotenv.2020.142856

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology **85**: 1771–1789. doi:10.1890/03-9000

Brown, T. B., and others. 2016. Using phenocams to monitor our changing Earth: Toward a global phenocam network. Front. Ecol. Environ. **14**: 84–93. doi:10.1002/fee.1222

Calero, S., D. Joye, A. Rey-Boissezon, and M. Rodrigo. 2017. Time and heat for sexual reproduction: Comparing the phenology of *Chara hispida* of two populations at different latitudes. Aquat. Bot. **136**: 71–81. doi:10.1016/j.aquabot.2016.09.011

Calero, S., L. Morellato, and M. Rodrigo. 2018. Persistence of submerged macrophytes in a drying world: Unravelling the timing and the environmental drivers to produce drought-resistant propagules. Aquat. Conserv. Mar. Freshw. Ecosyst. **28**: 894–909. doi:10.1002/aqc.2879

Calero, S., and M. Rodrigo. 2019. Reproductive phenology of submerged macrophytes: A tracker of year-to-year environmental variations. J. Veg. Sci. **30**: 1217–1227. doi:10.1111/jvs.12801

Cheng, H., M. Feng, P. Zhang, H. Zhang, H. Wang, J. Xu, and M. Zhang. 2023. Effects of warming on aquatic snails and periphyton in freshwater ecosystems with and without predation by common carp. Water **15**: Article 1. doi:10.3390/w15010153

Chmura, D., and T. Molenda. 2012. Influence of thermally polluted water on the growth of helophytes in the vicinity of a colliery waste tip. Water Air Soil Pollut. **223**: 5877–5884. doi:10.1007/s11270-012-1323-1

Dell, A. I., S. Pawar, and V. M. Savage. 2014. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. J. Anim. Ecol. **83**: 70–84. doi:10.1111/1365-2656.12081

Depew, D. C., A. W. Stevens, R. E. H. Smith, and R. E. Hecky. 2009. Detection and characterization of benthic filamentous algal stands (*Cladophora* sp.) on rocky substrata using a high-frequency echosounder. Limnol. Oceanogr. Methods **7**: 693–705. doi:10.4319/lom.2009.7.693

Fernandez-Zamudio, R., P. Garcia-Murillo, and C. Diaz-Paniagua. 2018. Effect of the filling season on aquatic plants in Mediterranean temporary ponds. J. Plant Ecol. **11**: 502–510. doi:10.1093/jpe/rtx026

Figuerola, J., L. Santamaria, A. Green, I. Luque, R. Alvarez, and I. Charalambidou. 2005. Endozoochorous dispersal of aquatic plants: Does seed gut passage affect plant performance? Am. J. Bot. **92**: 696–699. doi:10.3732/ajb.92.4.696

Franceschini, M., A. de Neiff, and M. Galassi. 2010. Is the biomass of water hyacinth lost through herbivory in native areas important? Aquat. Bot. **92**: 250–256. doi:10.1016/j.aquabot.2010.01.005

Frenken, T., and others. 2020. Warming advances virus population dynamics in a temperate freshwater plankton community. Limnol. Oceanogr. Lett. **5**: 295–304. doi:10.1002/lol2.10160

Gallagher, A. J., and others. 2022. Tiger sharks support the characterization of the world's largest seagrass ecosystem. Nat. Commun. **13**: Article 1. doi:10.1038/s41467-022-33926-1

Ghunowa, K., A. S. Medeiros, and R. Bello. 2019. Hyperspectral analysis of algal biomass in northern lakes, Churchill, MB, Canada. Arct. Sci. **5**: 240–256. doi:10.1139/as-2018-0030

Giacomazzo, M., A. Bertolo, P. Brodeur, P. Massicotte, J.-O. Goyette, and P. Magnan. 2020. Linking fisheries to land use: How anthropogenic inputs from the watershed shape fish habitat quality. Sci. Total Environ. **717**: 135377. doi:10.1016/j.scitotenv.2019.135377

Giorgi, A., C. Feijoó, and G. Tell. 2005. Primary producers in a Pampean stream: Temporal variation and structuring role. Biodivers. Conserv. **14**: 1699–1718. doi:10.1007/s10531-004-0694-z

Glisson, W., and D. Larkin. 2021. Hybrid watermilfoil (*Myriophyllum spicatum × Myriophyllum sibiricum*) exhibits traits associated with greater invasiveness than its introduced and native parental taxa. Biol. Invasions **23**: 2417–2433. doi:10.1007/s10530-021-02514-7

Glisson, W., R. Muthukrishnan, C. Wagner, and D. Larkin. 2022. Invasive *Nitellopsis obtusa* (starry stonewort) has distinct late-season phenology compared to native and other invasive macrophytes in Minnesota, USA. Aquat. Bot. **176**: 103452. doi:10.1016/j.aquabot.2021.103452

Goulon, C., O. Le Meaux, R. Vincent-Falquet, and J. Guillard. 2021. Hydroacoustic autonomous boat for remote fish detection in LakE (HARLE), an unmanned autonomous surface vehicle to monitor fish populations in lakes. Limnol. Oceanogr. Methods **19**: 280–292. doi:10.1002/lom3.10422

Goyette, J.-O., E. M. Bennett, R. W. Howarth, and R. Maranger. 2016. Changes in anthropogenic nitrogen and phosphorus inputs to the St. Lawrence sub-basin over 110 years and impacts on riverine export. Global Biogeochem. Cycles **30**: 1000–1014. doi:10.1002/2016GB005384

Gronchi, E., D. Straile, S. Diehl, K. D. Jöhnk, and F. Peeters. 2023. Impact of climate warming on phenological asynchrony of plankton dynamics across Europe. Ecol. Lett. **26**: 717–728. doi:10.1111/ele.14190

Han, X., L. Feng, C. Hu, and X. Chen. 2018. Wetland changes of China's largest freshwater lake and their linkage with the Three Gorges Dam. Remote Sens. Environ. **204**: 799–811. doi:10.1016/j.rse.2017.09.023

Handley, R., and A. Davy. 2005. Temperature effects on seed maturity and dormancy cycles in an aquatic annual, *Najas marina*, at the edge of its range. J. Ecol. **93**: 1185–1193. doi:10.1111/j.1365-2745.2005.01062.x

Helminen, J., T. Linnansaari, M. Bruce, R. Dolson-Edge, and R. A. Curry. 2019. Accuracy and precision of low-cost echosounder and automated data processing software for habitat mapping in a large river. Diversity **11**: Article 7. doi:10.3390/d11070116

Hilt, S., J. Köhler, R. Adrian, M. T. Monaghan, and C. D. Sayer. 2013. Clear, crashing, turbid and back—Long-term changes in macrophyte assemblages in a shallow lake. Freshw. Biol. **58**: 2027–2036. doi:10.1111/fwb.12188

Hilt, S., S. Brothers, E. Jeppesen, A. J. Veraart, and S. Kosten. 2017. Translating regime shifts in shallow lakes into changes in ecosystem functions and services. Bioscience **67**: 928–936. doi:10.1093/biosci/bix106

Hoffmann, M., U. Raeder, and A. Melzer. 2014. Influence of the gender on growth and phenology of the dioecious macrophyte *Najas marina* ssp intermedia. Hydrobiologia **727**: 167–176. doi:10.1007/s10750-013-1795-z

Hou, X., L. Feng, X. Chen, and Y. Zhang. 2018. Dynamics of the wetland vegetation in large lakes of the Yangtze Plain in response to both fertilizer consumption and climatic changes. ISPRS J. Photogram. Remote Sens. **141**: 148–160. doi:10.1016/j.isprsjprs.2018.04.015

Hou, X., X. Chen, W. Liu, L. Feng, and T. Ali. 2019. Changes in the wetland vegetation growth patterns in large lakes on the Yangtze Plain. Int. J. Remote Sens. **40**: 4290–4301. doi:10.1080/01431161.2018.1562583

Hutchinson, J. 2019. Ex situ phenology of *Zizania texana*, an endangered aquatic macrophyte, under different water velocities. Aquat. Bot. **153**: 88–94. doi:10.1016/j.aquabot.2018.12.004

Iversen, L. L., J. G. Girón, and Y. Pan. 2022. Towards linking freshwater plants and ecosystems via functional biogeography. Aquat. Bot. **176**: 103454. doi:10.1016/j.aquabot.2021.103454

Janssen, A. B. G., S. Hilt, S. Kosten, J. J. M. de Klein, H. W. Paerl, and D. B. Van de Waal. 2021. Shifting states, shifting services: Linking regime shifts to changes in ecosystem services of shallow lakes. Freshw. Biol. **66**: 1–12. doi:10.1111/fwb.13582

Kazanjian, G., and others. 2018. Impacts of warming on top-down and bottom-up controls of periphyton production. Sci. Rep. **8**: 9901. doi:10.1038/s41598-018-26348-x

Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the holy grail. Funct. Ecol. **16**: 545–556. doi:10.1046/j.1365-2435.2002.00664.x

Luo, J., R. Pu, H. Duan, R. Ma, Z. Mao, Y. Zeng, L. Huang, and Q. Xiao. 2020. Evaluating the influences of harvesting activity and eutrophication on loss of aquatic vegetations in Taihu Lake, China. Int. J. Appl. Earth Observ. Geoinform. **87**: 102038. doi:10.1016/j.jag.2019.102038

Mahato, M., and D. Johnson. 1991. Invasion of the Bays Mountain Lake dragonfly assemblage by *Dromogomphus spinosus* (odonata, gomphidae). J. N. Am. Benthol. Soc. **10**: 165–176. doi:10.2307/1467576

Matsuzaki, S.-I. S., R. C. Lathrop, S. R. Carpenter, J. R. Walsh, M. J. Vander Zanden, M. R. Gahler, and E. H. Stanley. 2021. Climate and food web effects on the spring clear-water phase in two north-temperate eutrophic lakes. Limnol. Oceanogr. **66**: 30–46. doi:10.1002/lno.11584

Michelutti, N., M. Douglas, D. Antoniades, I. Lehnherr, V. St Louis, K. St Pierre, D. Muir, G. Brunskill, and J. Smol. 2020. Contrasting the ecological effects of decreasing ice cover versus accelerated glacial melt on the High Arctic's largest lake. Proc. R Soc. B Biol. Sci. **287**: 20201185. doi:10.1098/rspb.2020.1185

Mulholland, P., B. Roberts, W. Hill, and J. Smith. 2009. Stream ecosystem responses to the 2007 spring freeze in the southeastern United States: Unexpected effects of climate change. Glob. Chang. Biol. **15**: 1767–1776. doi:10.1111/j.1365-2486.2009.01864.x

Phillips, G., N. Willby, and B. Moss. 2016. Submerged macrophyte decline in shallow lakes: What have we learnt in the last forty years? Aquat. Bot. **135**: 37–45. doi:10.1016/j.aquabot.2016.04.004

Pinero-Rodriguez, M., I. Gomez-Mestre, and C. Diaz-Paniagua. 2021. Herbivory by spadefoot toad tadpoles and reduced water level affect submerged plants in temporary ponds. Inland Waters **11**: 457–466. doi:10.1080/20442041.2021.1933855

Pinheiro, B., Bates, D., DebRoy, S., & Sarkar, D. (2020). Linear and nonlinear mixed effect models [R package version 3.1-144]. Available from https://CRAN.R-project.org/package=nlme

Power, M. 1992. Hydrologic and trophic controls of seasonal algal blooms in Northern California rivers. Arch. Hydrobiol. **125**: 385–410. doi:10.1127/archiv-hydrobiol/125/1992/385

R Core Team. (2020). *R: A language and environment for statistical computing [Logiciel]*. R Foundation for Statistical Computing. Available from https://www.R-project.org/

Roberts, B., P. Mulholland, and W. Hill. 2007. Multiple scales of temporal variability in ecosystem metabolism rates: Results from 2 years of continuous monitoring in a forested headwater stream. Ecosystems **10**: 588–606. doi:10.1007/s10021-007-9059-2

Roberts, E., J. Kroker, S. Körner, and A. Nicklisch. 2003. The role of periphyton during the re-colonization of a shallow lake with submerged macrophytes. Hydrobiologia **506**: 525–530. doi:10.1023/B:HYDR.0000008560.73832.1c

Rowan, G. S. L., and M. Kalacska. 2021. A review of remote sensing of submerged aquatic vegetation for non-specialists. Remote Sens. (Basel) **13**: Article 4. doi:10.3390/rs13040623

Scheffer, M., S. H. Hosper, M.-L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. Trends Ecol. Evol. **8**: 275–279. doi:10.1016/0169-5347(93)90254-M

Schneider, S. 2007. Macrophyte trophic indicator values from a European perspective. Limnologica **37**: 281–289. doi:10.1016/j.limno.2007.05.001

Simao, C., F. Alves, A. de Barros, P. Simao, A. Pott, and C. Aoki. 2021. Reproductive phenology of aquatic macrophytes in the Cerrado-Pantanal ecotone. Acta Bot. Bras. **35**: 92–103. doi:10.1590/0102-33062020abb0364

Tabosa, A. B., L. Q. Matias, and F. R. Martins. 2012. Live fast and die young: The aquatic macrophyte dynamics in a temporary pool in the Brazilian semiarid region. Aquat. Bot. **102**: 71–78. doi:10.1016/j.aquabot.2012.05.004

Thackeray, S. J., and others. 2016. Phenological sensitivity to climate across taxa and trophic levels. Nature **535**: 241–245. doi:10.1038/nature18608

Torso, K., B. Scofield, and D. Chess. 2020. Variations in aquatic macrophyte phenology across three temperate lakes in the Coeur d'Alene Basin. Aquat. Bot. **162**: 103209. doi:10.1016/j.aquabot.2020.103209

Toth, V. 2018. Monitoring spatial variability and temporal dynamics of phragmites using unmanned aerial vehicles. Front. Plant Sci. **9**. doi:10.3389/fpls.2018.00728

Toth, V., P. Villa, M. Pinardi, and M. Bresciani. 2019. Aspects of invasiveness of Ludwigia and Nelumbo in shallow temperate fluvial lakes. Front. Plant Sci. **10**. doi:10.3389/fpls.2019.00647

Turnage, G., J. Madsen, and R. Wersal. 2018. Phenology of curlyleaf pondweed (*Potamogeton crispus* L.) in the southeastern United States: A two-year mesocosm study. J. Aquat. Plant Manage. **56**: 35–38.

Vadeboncoeur, Y., and others. 2021. Blue waters, green bottoms: Benthic filamentous algal blooms are an emerging threat to clear lakes worldwide. Bioscience **71**: 1011–1027. doi:10.1093/biosci/biab049

Van Onsem, S., and L. Triest. 2021. Trading offspring for survival: High duckweed cover decreases reproductive potential and stimulates elongation in the submerged macrophyte *Chara globularis* Thuillier. Hydrobiologia **848**: 2667–2680. doi:10.1007/s10750-021-04577-y

Vander Zanden, M. J., and Y. Vadeboncoeur. 2020. Putting the lake back together 20 years later: What in the benthos have we learned about habitat linkages in lakes? Inland Waters **10**: 305–321. doi:10.1080/20442041.2020.1712953

Velthuis, M., S. Kosten, R. Aben, G. Kazanjian, S. Hilt, E. T. H. M. Peeters, E. van Donk, and E. S. Bakker. 2018. Warming enhances sedimentation and decomposition of organic carbon in shallow macrophyte-dominated systems with zero net effect on carbon burial. Glob. Chang. Biol. **24**: 5231–5242. doi:10.1111/gcb.14387

Villa, P., M. Bresciani, R. Bolpagni, F. Braga, D. Bellingeri, and C. Giardino. 2020. Impact of upstream landslide on perialpine lake ecosystem: An assessment using multi-temporal satellite data. Sci. Total Environ. **720**: 137627. doi:10.1016/j.scitotenv.2020.137627

Wetzel, R. G. 2001*a*. Chapter 18. Land-water interfaces: Larger plants, p. 527–575. *In Limnology: Lake and river ecosystems*. Academic Press.

Wetzel, R. G. 2001*b*. Chapter 19 : Land-water interfaces: Attached microorganisms, littoral algae and zooplankton, p. 577–623. *In Limnology: Lake and river ecosystems*. Academic Press.

Woolway, R. I., B. M. Kraemer, J. D. Lenters, C. J. Merchant, C. M. O'Reilly, and S. Sharma. 2020. Global lake responses to climate change. Nat. Rev. Earth Environ. **1**: 388–403. doi:10.1038/s43017-020-0067-5

Yang, Z., A. Davy, X. Liu, S. Yuan, and H. Wang. 2020. Responses of an emergent macrophyte, Zizania latifolia, to water-level changes in lakes with contrasting hydrological management. Ecol. Eng. **151**: 105814. doi:10.1016/j.ecoleng.2020.105814