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Research

Phenology in freshwaters: a review and recommendations for future research

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Phenology changes are increasingly recognized as a common response of species to ongoing global change. Phenology can be influenced by environmental cues that impact the initiation or duration of life history events as well as intrinsic organismal traits that may affect how different species respond to such environmental cues. Despite the importance of phenology for biodiversity conservation as demonstrated by terrestrial and marine research, freshwater phenology is understudied. Therefore, we conducted a literature review on freshwater phenology research to summarize the spatial, taxonomic and temporal biases of studies; as well as relationships between phenology metrics, environmental cues and intrinsic species traits studied in these systems. We find that phenology research in freshwaters may be limited by a lack of long-term time-series data, especially in lotic habitats. Phenology metrics studied differed between lotic and lentic habitats, with limnological research focused on planktonic population growth whereas macroinvertebrate emergence and fish spawning seasons are the most frequently studied aspects of phenology in streams and rivers. Across habitats, temperature is the most investigated environmental cue, with additional research attention to resources and hydrology in influencing phenology events in lentic and lotic environments, respectively. Knowledge gaps in contemporary freshwater phenology research include relationships between phenology and environmental cues in tropical systems, understanding of non-salmonid fish phenology and testing hypotheses related to intrinsic traits. We recommend that future research broaden the biological, spatial and temporal scales of phenology studies in these systems, and make use of novel data sources, methods and technologies to address contemporary research gaps.

Keywords: emergence, lakes, life history, spawning, streams, traits

Introduction

Changes in the timing of seasonal life history events (i.e. phenology) are recognized as a common response of organisms to ongoing global change (Stenseth et al. 2002, Parmesan and Yohe 2003, Root et al. 2003, Visser and Both 2005, Menzel et al. 2006, Parmesan 2006). Quantifying shifts in organisms' phenology is important because these responses can scale up to impact population dynamics and demography (Miller-Rushing et al. 2010) and community structure and function (Diez et al. 2012). For

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example, phenology responses to changing environmental contexts may skew community size distributions towards smaller-bodied individuals (Lurgi et al. 2012), disrupt synchrony between species and trophic resources (e.g. trophic mismatch) (Stenseth et al. 2002, Visser and Both 2005, Kharouba et al. 2018, Renner and Zohner 2018), alter the relative strengths of competitive interactions between coexisting species (Yang and Rudolf 2010, Carter et al. 2018, Rudolf 2019), and determine range shifts via physiological limits to species redistribution (Chuine 2010, Walther 2010, Macgregor et al. 2019).

Studies of species phenology can be informed by knowledge of external abiotic and biotic cues that indicate optimal environmental conditions for fitness, reproduction and survival (Visser and Both 2005, Mcnamara et al. 2011) and intrinsic traits that may affect organismal responses to such external cues (Altermatt 2010a, Walther 2010, Chmura et al. 2019). For example, phenology changes in response to increasing temperature are documented in terrestrial ectotherms (Scranton and Amarasekare 2017, Davies 2019), endotherms (Gordo and Sanz 2006, Moyes et al. 2011) and plants (Menzel et al. 2006, Vitasse et al. 2018, Heberling et al. 2019, Piao et al. 2019). Additionally, phenological regimes may vary among species in relation to the trophic characteristics (Visser and Both 2005, Altermatt 2010a, Thackeray et al. 2010, 2016), reproductive timing (e.g. early or late season species) (Menzel et al. 2006, Sherry et al. 2007) or generation time (Macgregor et al. 2019) of the species considered. While some of these traits may indeed affect phenology and phenological shifts directly (e.g. generation time), other traits such as reproductive timing and trophic characteristics might be linked to phenology at least in part because they are correlated with differential exposure to environmental cues and/or other unmeasured traits (e.g. physiological sensitivity to environmental cues) that may affect organismal responses to these cues (Chmura et al. 2019). Therefore, to advance our understanding on how phenology might respond to global change, we will need to account for both the environmental cues and the intrinsic traits that can jointly inform our knowledge of the timing of seasonal life history events.

Quantifying how extrinsic environmental conditions and intrinsic traits may inform species phenology can also contribute to biodiversity conservation. For example, drivers of life history events can be used to understand and predict the introduction, success and expansion of invasive species in novel habitats (Chapman et al. 2014, Capellini et al. 2015), and extinction risk may be informed, in part, by reproductive and life history characteristics that affect population growth rates and ability to recover from perturbations (Purvis et al. 2000, Hutchings et al. 2013). Differential shifts in the phenology across interacting species or between species and the abiotic conditions they require may alter species demography and population dynamics, potentially affecting species persistence (Miller-Rushing et al. 2010). Therefore, knowledge of species' phenology related to extrinsic cues and intrinsic traits will play an important role in mitigating contemporary and future biodiversity loss from multiple stressors.

Despite the demonstrated importance of phenology for the maintenance and conservation of biodiversity, species phenology in freshwater systems remains relatively understudied (Thackeray et al. 2010) compared to terrestrial (Tang et al. 2016, Renner and Zohner 2018, Piao et al. 2019) and marine (Staudinger et al. 2019, Ardyna and Arrigo 2020) systems. This is surprising because freshwater systems represent an interesting context for phenology research. Freshwaters are dominated by ectothermic organisms which are more sensitive to changes in environmental temperature and, therefore, likely to experience stronger impacts to phenology from global change, compared to endotherms (Thackeray et al. 2010, Chmura et al. 2019). Organisms in freshwater food webs are generalizable into three main trophic levels (predators, herbivorous consumers and primary producers) each of which undergo seasonal life history events, which may indicate potential for trophic mismatches. Freshwater phenology may depend on environmental cues from allochthonous inputs, hydrology, riparian shading and temperature. Differences between species can be informed by intrinsic traits such as generation time, reproductive timing, thermal sensitivity or trophic level. However, we lack a consensus on prevalent cues and traits across studies and taxa. Finally, freshwaters harbor greater biodiversity per unit area, of which disproportionately more taxa are threatened, than terrestrial and marine systems (Dudgeon et al. 2006, Harrison et al. 2018) and a synthesis of phenology research is urgently needed to better understand risks posed to these organisms. These characteristics suggest that the environmental cues important for species phenology and the magnitude of global change impacts on phenology regimes in freshwaters may differ from patterns observed in other, well-studied systems and have potential to provide novel insights into our understanding of ongoing phenology shifts.

Given the importance of conserving freshwater systems and their potential to provide unique insights into impacts of shifts in species phenology on biodiversity, we contend that there is an urgent need to synthesize and summarize existing freshwater phenology research as a first step toward identifying current research biases and potential knowledge gaps. Synthesizing freshwater phenology may also help identify whether phenology responses to global change observed in terrestrial and marine communities are generalizable across other systems and may therefore be informative to make robust assessments about threats to biodiversity, globally. Here, we conducted a systematic literature review to summarize the: 1) spatial, taxonomic and temporal scopes, 2) phenological metrics, 3) environmental cues; and 4) intrinsic species traits investigated in freshwater phenological research. Our synthesis aims to provide a research agenda to advance the understanding of species phenology in freshwater ecosystems and the implications of global change on biodiversity persistence via its effects on phenology.

Literature review

We conducted a systematic review of species phenology research in freshwater systems by conducting Web of Science and Google Scholar searches for published papers using the query: ((stream* OR river* OR lake* OR freshwater* OR lotic OR lentic OR aquatic OR creek*) AND (phenology)). These search terms were decided after exploring alternative keyword combinations because we found them to identify a large number of potentially relevant studies, while minimizing the number of studies beyond the scope of our review. We exported all returned articles from Web of Science and the first 150 articles from the Google Scholar search (sorted by relevance; titles of articles ranked above 150 indicated that they were of no or minimal relevance), which resulted in 2409 candidate articles for our literature review.

We initially inspected the title and abstract of each of these studies, and papers identified as potentially relevant to our review were read in full. Specifically, we included primary literature that analyzed temporal variation in seasonal life history or life cycle events (i.e. phenology) of freshwater organisms using field, laboratory or model-based methods. We omitted studies that quantified seasonal changes in community composition without associated life history events, those which measured solely abiotic ecosystem phenology (e.g. lake stratification, hydrologic events), or those from estuaries because environmental cues in brackish systems may differ from freshwaters. We included anadromous and amphidromous fish taxa in our review as these species provide resources for freshwater environments (Samways et al. 2018). After filtering the original list of 2409 articles, we identified 419 studies that met the above criteria for inclusion in our literature review (Supporting information).

For each study included in our review, we recorded information on the spatial, taxonomic and temporal scope, as well as the phenological metrics, environmental cues, intrinsic species traits and biotic interactions investigated by the study (Supporting information). For spatial variables, we recorded the country, geographic coordinates and habitat (lotic [flowing water; streams, rivers, creeks] or lentic [non-flowing water; lakes, ponds]) of the study. For wetland studies, we classified habitats according to descriptions of individual study sites sampled within the system. In cases where coordinates were not provided, we approximated locations when possible based on named features (e.g. National Park, research station or named waterbody) to visualize the distribution of phenological studies. For temporal variables, we recorded the start year, end year, length of study (number of years from first sample to the last sample in the dataset) and the temporal grain of the analysis on an annual scale as: daily, weekly, monthly or seasonal (sampling occurred during certain months of the year).

To characterize the organisms investigated, we recorded the identities of taxa as well as the total number of taxa examined in each study. For groups of organisms where species-level identifications were less frequently reported (e.g. phytoplankton and zooplankton), the number of taxa often reflected broader taxonomic resolution (e.g. genera, diatoms or copepods) rather than the number of species. We recorded the group(s) of taxa studied as: amphibians/aquatic reptiles, crustaceans/mollusks (excluding zooplankton), fish, macroinvertebrates, primary producers (majority phytoplankton and diatoms, with fewer observations from macrophytes), vertebrates other than fish (e.g. waterfowl, beavers) or zooplankton. For studies of fish phenology, we also recorded whether the study focused on salmonids (family Salmonidae) or non-salmonids. Additionally, we recorded whether a biotic interaction was hypothesized or tested, and if so, classified this interaction as trophic (e.g. predation, parasitism), competition, mutualism, commensalism, ammensalism or an interaction between aquatic and terrestrial organisms (e.g. trophic interactions between aquatic and terrestrial organisms).

Next, we characterized the phenological metrics measured into functional categories based on a priori knowledge of freshwater seasonal life history events across freshwater taxa: egg/hatching characteristics (e.g. time to hatch, date of hatching), emergence, juvenile recruitment, metamorphosis, migrations, primary production/growing season or reproductive season (Supporting information). Although these metrics may have submetrics (e.g. date of start, date of peak, duration of event), we focused on these broader functional categories to investigate general links between phenological metrics and their potential environmental drivers investigated in the literature.

We recorded environmental cues, defined as extrinsic variables that can drive life history or life cycle events (Chmura et al. 2019), that were found to be associated with a given phenological metric investigated by each study. We classified environmental cues into the following groups: biotic, temperature, hydrology, elevation, latitude, photoperiod, resources (food, nutrients), precipitation or none (Supporting information).

For each study, we recorded intrinsic traits reported to describe differences in species phenology via differential exposure to environmental cues or correlation with underlying mechanisms that affect sensitivity to environmental cues (Chmura et al. 2019). We classified intrinsic characteristics as: generation time (including voltinism), trophic level (functional feeding guilds), migratory status, thermal sensitivity, ecological specialization, habitat use, other or none (Supporting information). Contrary to environmental cues, we found that few studies examined hypothesized relationships between intrinsic traits and species phenology. For example, studies might provide information on the thermal sensitivities of taxa without using statistical tests to test the hypothesis that species with higher thermal maxima have different seasonal timing of life history events than those with low thermal maxima. Therefore, we recorded traits used to describe differences in species phenology, even when they were not assessed using statistical tests. This allowed us to identify intrinsic traits that may be associated with mechanisms by which species differ in phenology that should be investigated by future studies.

In the following section, we summarize the findings of our literature review, with particular attention to identifying general patterns in: 1) spatial and taxonomic gaps in research efforts, 2) relationships between phenology events and environmental cues, 3) intrinsic traits that may can describe differences in phenology across species; and 4) biotic interactions that may be affected by asynchronous phenology between co-occurring species.

Summary of contemporary phenology research

Spatial, taxonomic and temporal distribution of studies

Studies included in our review encompassed 57 countries across six continents and exhibited a geographic bias towards Europe and North America (Fig. 1). European research showed a greater emphasis on limnological studies, whereas North American studies skewed more towards lotic habitats (Fig. 1). By comparison, there were fewer studies on freshwater phenology in Africa, Central and Southeastern Asia, Oceania and South America.

Research efforts showed a bias towards temperate habitats for all taxa (Fig. 2). Fish phenology research extended to higher latitudes than other taxonomic groups (Fig. 2a), which may reflect a focus on cold-water salmonids in contemporary fisheries research (Myers et al. 2017). Long-term trends in annual salmonid spawning and smolting migrations were particularly well-studied in high latitude European countries and Alaska (Mundy and Evenson 2011, Kovach et al. 2015, Haraldstad et al. 2017, Campbell et al. 2019, Sparks et al. 2019). Research efforts on primary producers and zooplankton showed clusters in Europe, indicating a preponderance of long-term plankton monitoring programs in European lakes (Blenckner et al. 2007).

Different taxonomic groups dominated research efforts between habitats. Phenology research in lentic systems focused on primary producers and zooplankton, whereas fishes and macroinvertebrates were the research foci in lotic habitats (Fig. 3). Among fish studies in both lentic and lotic habitats, roughly half (47.0%) examined salmonid phenology. The disproportionate research towards this family likely reflects the economic importance of salmonid fisheries (Criddle and Shimizu 2014).

Lotic studies characterized the phenology of more taxa per study (median = 2, interquartile range [IQR] = 1–14 taxa per study), compared to lentic studies (median = 2, IQR = 1–8) (Fig. 4). However, we note that the taxonomic resolution presented in lentic studies is often coarser than species level; therefore, our estimates likely underestimate the number of species measured in lentic systems. Regardless, the relatively high biodiversity considered per study in both lotic and lentic systems indicates that the potential for future analyses to use data in the existing literature to study community-level patterns in phenology, i.e. the timing of events across many, possibly interacting, species.

Studies in lentic habitats characterized phenology over longer time periods (median = 3, IQR = 1–18 years) than studies in lotic habitats (median = 2, IQR = 1–8.6) (Fig. 4). Regarding the temporal grain of analysis, seasonal or monthly sampling regimes were the most frequently reported sampling regimes for all taxa (97.9%:amphibians, 93.8%:

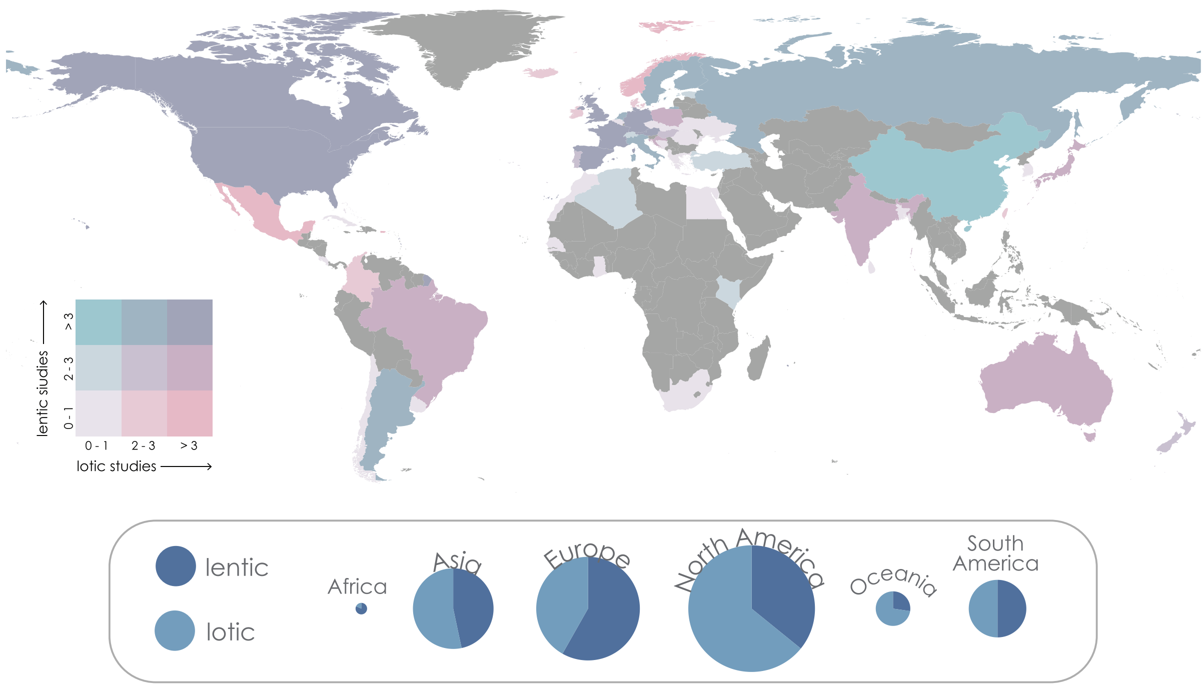

Figure 1. Map of the distribution of contemporary freshwater phenology research. The bivariate color scale illustrates the number of lotic and lentic studies in each county (countries lacking a study are colored grey). The pie charts below the map show the number of lotic and lentic studies, pooled by continents. The size of the pie charts indicates the absolute ranking (1–6) of total studies by continent.

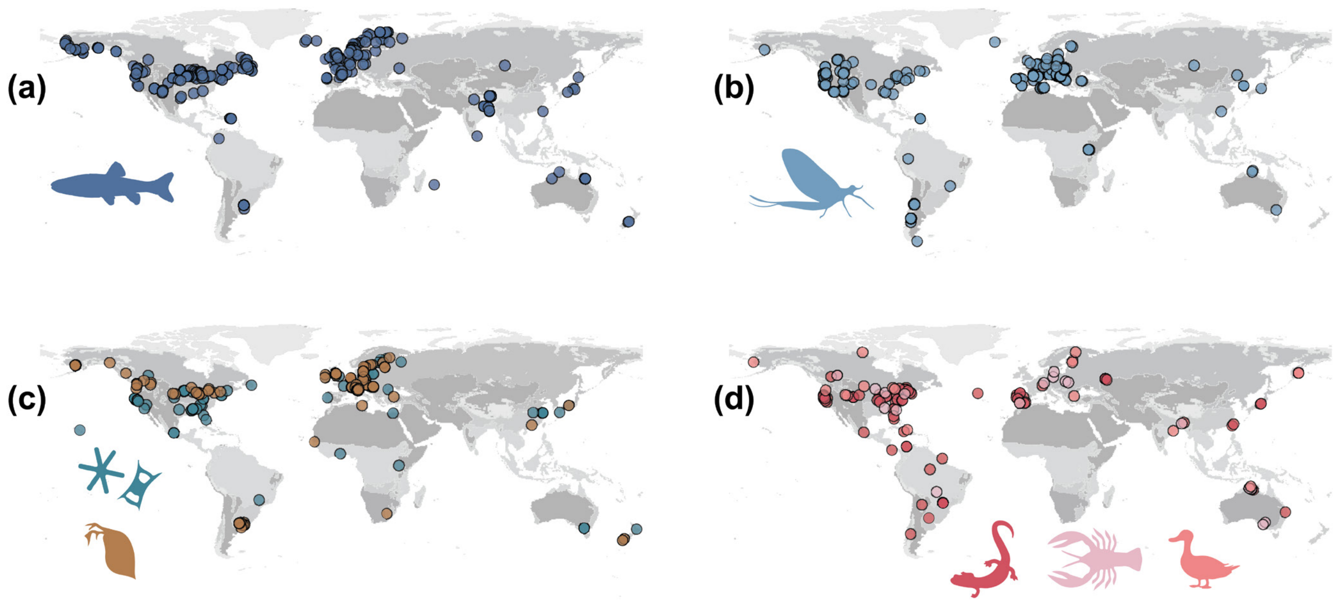

Figure 2. Locations of studies with known geographic coordinates, separated by taxa class studied as: (a) fish, (b) macroinvertebrates, (c) primary producers (green) and zooplankton (brown) and (d) (colors indicated by icons from left to right) amphibians, crustaceans and mollusks, and vertebrates other than fishes. Shaded grey polygons are Köppen–Geiger climate regions from Beck et al. (2018).

crustaceans/mollusks, 96.6%: fishes, 88.9%: macroinvertebrates, 100.0%: other vertebrates, 82.8%: primary producers, 84.1%: zooplankton, of studies) (Supporting information). The incidence of daily or weekly sampling regimes was highest in studies focusing on primary producers (mostly comprising lentic phytoplankton and diatoms; 17.3% of studies), macroinvertebrates (11.1%), and zooplankton (15.8%) although it was always less frequently employed than seasonal or monthly sampling. These results suggest some, albeit limited, correspondence between fine temporal grain sampling approaches and phenology research on taxa with faster life histories.

Phenology metrics

In lentic habitats, the population growth and production season for planktonic organisms and primary producers was the most-studied phenology metric (Fig. 5a), which may reflect the tendency for lentic research in lake habitats to emphasize bottom–up effects as the processes at lower trophic levels are recognized as important structuring force in these food webs. Contrary to the majority of lotic systems, autochthonous production provides the resource base for lentic food webs (Galloway et al. 2014, Lau et al. 2014). Phytoplankton and diatoms are trophic resources for zooplanktonic grazers, which

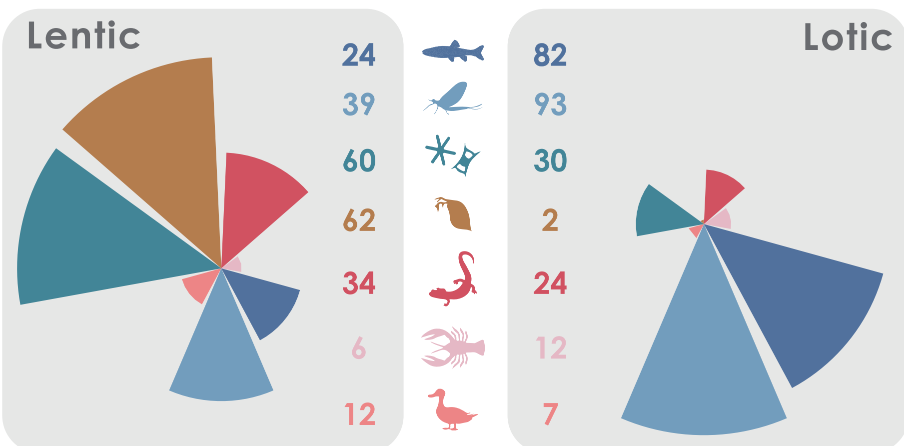

Figure 3. The number of studies with reported measures of phenology for each group of taxa in lentic (left) and lotic (right) habitats. Bar chart colors indicate taxa as (from top to bottom in icon legend): fish, macroinvertebrates, primary producers, zooplankton, amphibians, crustaceans and mollusks, and vertebrates other than fishes. The number of studies within each habitat that studied taxa groups is provided next to the legend icon.

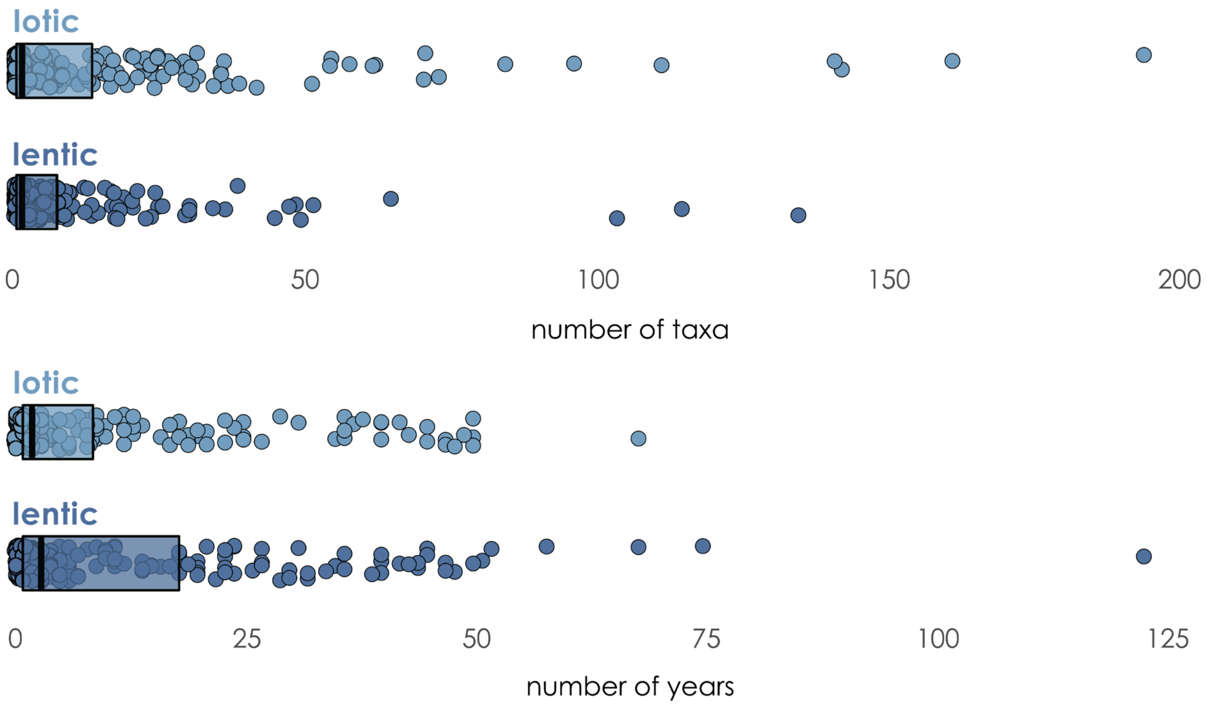

Figure 4. The number of taxa (top) and study length (bottom) reported in studies of lotic (light blue) and lentic (dark blue) phenology. Points show values for individual studies and cross bars show median and interquartile ranges for each habitat.

are, in turn, prey for insects and larval fish (Ohlberger et al. 2014). Therefore, shifts in production regimes in these systems may impact trophic interactions at higher trophic levels. Additionally, understanding the drivers of seasonal dynamics of cyanobacteria blooms in lentic systems is also important due to the risks posed to public health and economies by these events (Coffer et al. 2020).

In lotic systems, the phenology metrics that received the most research attention were emergence and reproductive seasons (Fig. 5b). Macroinvertebrate emergence is important because the flux of adult insects provides trophic resources for terrestrial consumers, and changes in emergence phenology may impact the strength of aquatic–terrestrial linkages (Larsen et al. 2016). Emergence phenology is also important for resource fluxes in instream environments where allochthonous leaf litter input composes the base of food webs and macroinvertebrate detritivores control seasonal breakdown rates of organic matter (Benstead and Huryn 2011). The timing of migratory and reproductive events of fish and other vertebrates is important to the functioning of lotic systems because the structuring role that adults and juveniles play as predators (Giam and Olden 2016), and the carcasses of semelparous salmonid species can shape the activity and phenology of terrestrial scavengers which depend on these anadromous trophic resources (Lisi and Schindler 2011, Deacy et al. 2019, Rubenstein et al. 2019).

Environmental cues

Across all metrics and habitats considered, the most studied environmental cue for phenology was temperature (Fig. 5). A research foci on temperature-based cues for freshwater phenology likely reflects the temperature-dependence of growth, performance and metabolism in ectotherms (Gillooly et al. 2001, 2002, Huey and Berrigan 2001). In addition, temperature determines the birth rate, mortality rate and development time in ectotherm populations, affecting the timing and duration of phenological events (Scranton and Amarasekare 2017). These results indicate that ongoing and future climate warming may have strong impacts on timing of phenology events in freshwater systems. Increasing temperatures have advanced or delayed emergence dates in macroinvertebrates (Hassall et al. 2007, Anderson et al. 2019, Baranov et al. 2020), migration and spawning events in fishes (Kovach et al. 2016, Lynch et al. 2016, Austin et al. 2019), production blooms in phytoplankton (Elliott 2012a, Winder and Sommer 2012, Walters et al. 2013) and population growth peaks in zooplankton (Wojtal-Frankiewicz 2012). However, fewer studies have investigated the potential implications of these phenology shifts for community size structure, biomass production or ecosystem functioning.

In lentic habitats, secondary to temperature, resources were important environmental cues for phenology events and particularly the timing of the production and growing seasons for planktonic organisms (Fig. 5a). Phytoplankton peaks may occur earlier and have a higher magnitude with increasing nutrients compared to scenarios of nutrient limitation (Elliott et al. 2006, Thackeray et al. 2008, Elliott 2012b). The phenology of zooplankton may respond to shifts in phytoplankton trophic resources by matching trends in producer peaks, or they may become decoupled from their prey (de Senerpont Domis et al. 2007, Winder et al. 2009, Nicolle et al. 2012). Therefore, changes in the trophic state

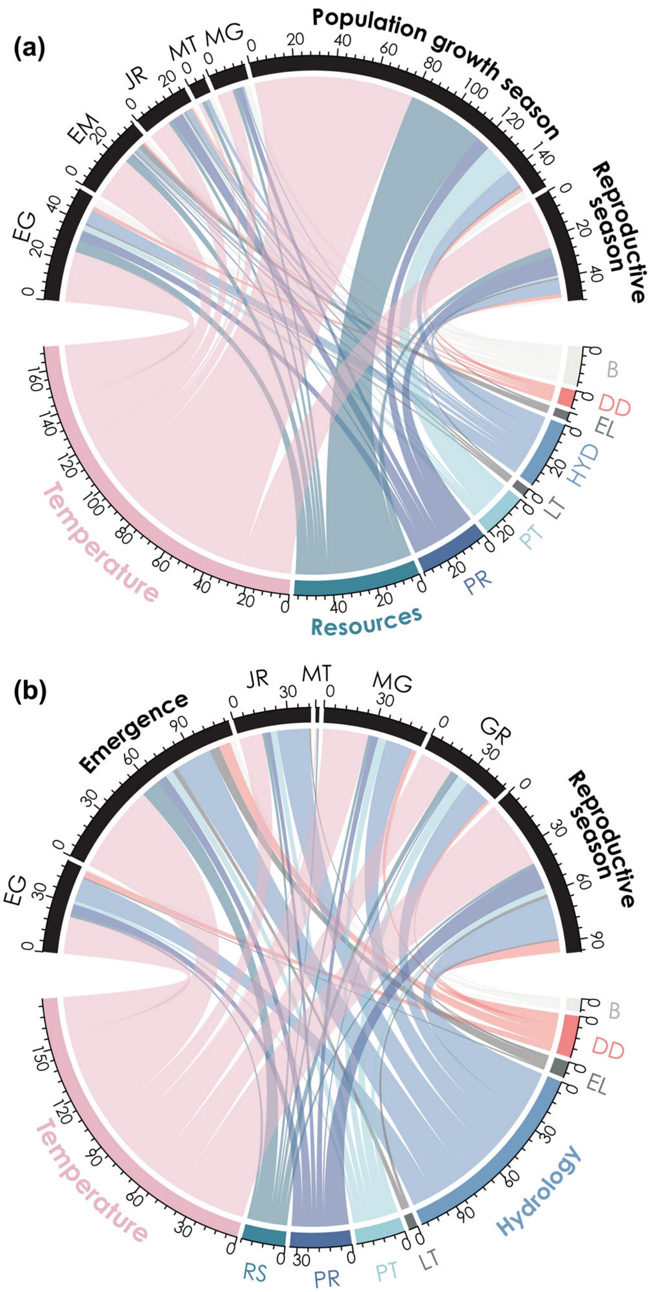

Figure 5. Diagrams showing relationships between environmental cues and phenology metrics in lentic (a) and lotic (b) habitats. Numbers on the edges indicate the number of studies examining phenology metrics (upper half circle) and environmental cues (lower half circle, coded by color). The thickness of lines connecting cues and phenology metrics indicates the number of studies reporting a relationship between the variable pairs, with thicker lines showing greater research attention towards the relationship. Abbreviations for phenology metrics are egg/hatching (EG), emergence (EM), juvenile recruitment (JR), metamorphosis (MT), migration (MG) and population growth/production season (GR). Abbreviations for environmental cues are resources (RS), precipitation (PR), photoperiod (PT), latitude (LT), hydrology (HYD), elevation (EL), degree days (DD) and biotic factors (B). Studies that did not investigate an environmental cue–phenology metric relationship are omitted from the figure.

of lentic habitats are likely to interact with temperature to influence planktonic phenology, as well as the phenology of abiotic lake processes, such as the timing and duration of the clear water phase (de Senerpont Domis et al. 2007, Elliott 2012b, McMeans et al. 2019).

In lotic habitats, in addition to temperature, hydrology cued phenology events (Fig. 5b). The role of hydroclimatic cues for fish phenology has been recognized by Flitcroft et al. (2016) who proposed a framework that accounts for discharge and temperature to characterize seasonal migratory and spawning events, and Heim et al. (2019) who suggested streamflow impacts on phenology be examined based on the seasonal availability of temporary habitats that are important for growth, spawning and refuge. For many fish species, spawning peaks may occur during or shortly following high flows (Smith 1991, Gorman and Stone 1999, Krabbenhoft et al. 2014, Catalano 2015, Valdez et al. 2019) which make available habitat and resources critical for survival and rearing of eggs and juveniles (e.g. inundation of floodplain habitats) (Peterson and VanderKooy 1995, Turner et al. 2010). However, some opportunistic species may spawn during low flows due to increased water temperature, stable environment and protection from piscivores (King et al. 2020).

For macroinvertebrates, low flow events can cue emergence to terrestrial stages by indicating declining optimal habitat for aquatic larvae (Giberson and Garnett 1996, Harper and Peckarsky 2006, Castro-Rebolledo and Donato-Rondon 2015) or increasing availability of suitable sites for oviposition (Peckarsky et al. 2000). Alterations to the natural flow regime from anthropogenic modifications can decrease habitat availability for fishes that require specific substrates for spawning or juvenile rearing (Peterson and VanderKooy 1995, Meneks et al. 2003), and create ecological traps for aquatic larvae of rheophilic macroinvertebrate species when adults oviposit near modified habitats (Hardersen 2008). Climate change-induced alterations to the duration, magnitude and timing of streamflow events may cause macroinvertebrates to emerge earlier, at smaller sizes and less fecund (Harper and Peckarsky 2006), or reduce temporal partitioning between spawning fish species (Krabbenhoft et al. 2014).

Intrinsic traits

Most studies failed to provide intrinsic traits that may be associated with mechanisms that explain patterns of phenology across species (Supporting information). Of those that did, reproductive timing was the most investigated trait. With respect to hydrologic cues, summer spawning fishes advanced phenology with earlier flows whereas spring spawning species did not (Krabbenhoft et al. 2014). However, with respect to temperature cues, spring spawners advanced timing with warming while summer spawners did not shift (Lyons et al. 2015). In macroinvertebrates, species with spring emergence periods showed greater phenology advances in response to increasing temperature compared to summer-emerging species (Hassall et al. 2007). In phytoplankton, community advances in annual blooming events can be attributed to disproportionate gains in abundance of early season taxa, relative to late season taxa (Elliott et al. 2006, Walters et al. 2013).

Generation time may also describe variation in phenology regimes across species. Planktonic organisms with shorter life cycles synchronously advanced production peaks, whereas those with longer life cycles become asynchronous (Adrian et al. 2006). Voltinism (i.e. number of generations per year) is a trait that is often reported for invertebrates but the potential effect of this trait on species-specific phenology is rarely tested in aquatic invertebrates, in contrast to terrestrial invertebrates (Macgregor et al. 2019). Exemplar questions on patterns of species phenology as related to voltinism include: 1) are taxa with longer (uni- or semivoltine) or shorter generation time (multivoltine) more likely to shift the timing of emergence or production peaks in response to environmental cues; and 2) which taxa can shift their life cycles (e.g. facultative voltinism) in response to changes in various environmental cues (Jönsson et al. 2009, Altermatt 2010b)?

Another intrinsic trait that may warrant further investigation in describing phenology across species, and specifically patterns related to temperature cues, is thermal sensitivity. With increasing temperatures, cold-water spawning fishes may delay spawning events, while cool and warm water species advance spawning seasons (Shuter et al. 2012). Zooplankton taxa with broader thermal ranges may be less responsive to increasing temperatures, whereas thermophilic species can increase the magnitude of their annual population growth peaks (Gerten and Adrian 2002).

Biotic interactions

Relatively few studies investigated phenology with regard to biotic interactions associated with these events (67 of 419 studies; Supporting information). Of these 67 studies, the most frequently examined interactions were trophic interactions (50 studies). In lentic habitats, ongoing global change may cause temporal mismatches between phytoplankton and zooplankton phenology and this asynchrony could alter bottom–up resource flow to higher trophic levels (de Senerpont Domis et al. 2007, Seebens et al. 2009, Donnelly et al. 2011, Winder and Sommer 2012). Trophic mismatches may also occur in top–down predation effects of lentic fishes and predaceous invertebrates on zooplankton (Schindler et al. 2005, Wagner and Benndorf 2007, Brodersen et al. 2011, Wagner et al. 2013), but some limnological studies found fish phenology was able to track shifts in prey resources (Jolley et al. 2010, Hovel et al. 2019). In lotic systems, changes in the timing of anadromous salmon carcasses and emerged aquatic insect pulses can cause trophic mismatches with terrestrial consumers (Lisi and Schindler 2011, Larsen et al. 2016, Deacy et al. 2019, Rubenstein et al. 2019), whereas fishes were found to track emerged insect resource pulses (Bell et al. 2017, Hansen et al. 2020). These contrasting results indicate that more research is needed to understand the ecological contexts under which trophic mismatches will occur in freshwater systems.

Following trophic interactions, competition and terrestrial–aquatic linkages were the most investigated biotic interactions (12 and 6 studies, respectively; Supporting information). Competitive interactions associated with phenology are likely to be particularly important when phenology events are timed to lessen competition for food resources. For example, shifts in the timing of lotic larval fish appearance and lentic zooplankton peaks may increase temporal overlap between species and competition for limited resources (Adrian et al. 1999, Duffy 2010, Turner et al. 2010). Research on the phenology of terrestrial–aquatic interactions has focused on the timing of marine subsidies of salmonid carcasses on terrestrial consumers (Lisi and Schindler 2011, Deacy et al. 2016, 2019, Rubenstein et al. 2019), whereas timing in subsidies of emergent aquatic insects on riparian consumers are relatively unstudied (Larsen et al. 2016). Another biotic interaction that may warrant investigation is the interaction between nest building and nest associate fish species as shifts in the phenology of either species could alter synchronous spawning with its mutualistic partner (Kim and Kanno 2020). Our review indicates that the implications of potential shifts in these positive interactions is largely unknown.

Knowledge gaps and future directions

Spatial, taxonomic and temporal biases

Our review identified several spatial, taxonomic and temporal knowledge gaps in contemporary freshwater phenology research. Phenology studies skew towards Northern Hemisphere temperate ecosystems and the lack of tropical studies can bias our knowledge of environmental cues. For example, the prevalence of temperature-dependent phenological regimes may be biased by the disproportionate representation of temperate systems where seasonal variation in temperature plays a structuring role in biological communities. It remains to be seen whether lower seasonal temperature variation in tropical environments means that other environmental cues are better indicators of organisms' phenology (Chambers et al. 2013). For example, Castro-Rebolledo and Donato-Rondon (2015) suggest that hydrology may be the primary cue for macroinvertebrate emergence in tropical environments, and future research should continue to clarify the environmental drivers of freshwater phenology in tropical systems.

Although salmonid species are of economic and ecological importance, we suggest that future freshwater fish phenology research efforts should emphasize phenology of non-salmonid species and could incorporate an existing life history strategy framework into fish phenology research (Mims et al. 2010, Mims and Olden 2012, 2013). For example, understanding whether periodic strategists (long-lived, large bodied, high fecundity) respond to different environmental cues than opportunistic (short-lived, small bodied, low fecundity) strategists (Chevalier et al. 2014) could be useful to generalize which species may be more sensitive to shifts in phenology.

A limitation of contemporary phenology research in lotic habitats is a lack of long-term datasets. Research shows that shorter time series may be insufficient to detect trends in phenology, therefore limit the potential to monitor ongoing phenology shifts in these environments (Olsen et al. 2020). To address this research gap, studies could conduct contemporary surveys at sites with records of past phenology measurements or employ space-for-time substitution approaches (Blois et al. 2013). In addition, long-term stream monitoring programs such as the National Rivers and Streams Assessment (NRSA; <www.epa.gov/national-aquatic-resource-surveys/nrsa>) and National Ecological Observatory Network (NEON; <www.neonscience.org/>) in the US, and Office Français de la Biodiversité (OFB) freshwater fish monitoring program (<www.naiades.eaufrance.fr/>) in France, should consider characterizing species phenology in a small subset of their monitoring sites, for example, in locations expected to experience the greatest changes in climate and other environmental cues such as flow.

Environmental cues and intrinsic traits

Temperature was the most frequently examined environmental cue, but future research should also investigate how climate change may interact with multiple global change stressors to influence phenology. The effects of nutrient loading and increasing temperatures may synergistically affect the timing of lentic phytoplankton production (Elliott et al. 2006, Elliott 2012b), land use and cover change may exacerbate temperature-driven phenology shifts in macroinvertebrate emergence (Villalobos-Jiménez and Hassall 2017, Anderson et al. 2019), and hydroclimatic stressors may synergistically impact fish migration, recruitment and spawning (Ayllón et al. 2019). Future research should continue to quantify how temperature and other environmental cues influence phenology of different species and how additional stressors can amplify or mitigate these effects.

Alterations to the streamflow regime from climate change or fragmentation may also impact species phenology in lotic systems (Krabbenhoft et al. 2014, Flitcroft et al. 2016). Changes in the duration, magnitude or timing of high and low flow events can reduce reproductive success owed to mortality of eggs or juveniles via scouring or desiccation. Although flow requirements for emergence and spawning are less well-studied than thermal requirements, the recent availability of hydrologic time-series data (Ruhi et al. 2018a, Global Runoff Data Centre 2020) and advances in time-series analytic methods such as multivariate autoregressive state-space (MARSS) models (Holmes et al. 2012) and wavelet mean field (Sheppard et al. 2016) present opportunities to investigate relationships between flow and species phenology. For example, Ruhi et al. (2018b) used MARSS models to show associations between dam hydropeaking intensity and the abundance of macroinvertebrate taxa with particular trait states at downstream reaches, and similar techniques could be applied to examine temporal emergence patterns. Of particular interest for future research could be investigating potential impacts of streamflow alterations on larval fish and juvenile recruitment phenology. The timing of these events is often associated with access to temporary habitats and resources created by flow events that benefit the growth and survival of juveniles (Peterson and VanderKooy 1995, Rodger et al. 2016). Therefore, flow regime changes and associated impacts on larval abundances or biomass may alter freshwater fish community structure and function, as has been shown for coastal and marine systems (Asch 2015, Auth et al. 2018).

Another opportunity for future research is to clarify the role of intrinsic traits in describing differential patterns of phenology across species. Publicly available trait datasets exist for amphibians (Trochet et al. 2014, Oliveira et al. 2017, Mendoza-Henao et al. 2019), crayfish (Bland 2017), fishes (Frimpong and Angermeier 2009, Schmidt-Kloiber et al. 2015, Froese and Pauly 2018), macroinvertebrates (Charvet et al. 2000, Usseglio-Polatera et al. 2000, Poff et al. 2006, Vieira et al. 2006), as well as thermal tolerances (Bennett et al. 2018) and phylogenetic relationships across taxa (Chang et al. 2019).

Use of these large-scale datasets to investigate intrinsic traits that may describe differential timing or sensitivity of species phenology and whether environmental or organismal mechanisms underlie these patterns (Chmura et al. 2019).

Phenology beyond the species-level

Species' phenology shifts do not happen in isolation but within ecological networks of interacting species (Miller-Rushing et al. 2010, Walther 2010, Hua et al. 2016). However, our literature review indicates that the potential implications of asynchronous phenology for freshwater community structure and function remain relatively unexplored. We suggest that future research efforts address how asynchronous phenology can modify freshwater food webs, including trophic mismatches and interaction strengths (Thackeray 2016). For example, predictions of shifts in the phenologies of multiple interacting species based on abiotic time-series data can be used to test hypotheses regarding seasonal variation in food web metrics such as connectance, linkage diversity or chain lengths (Compson et al. 2019, Takimoto and Sato 2020). Such food web model approaches will be important to understand potential implications of changes in biodiversity for freshwater ecosystem functioning (Thompson et al. 2012).

Freshwater phenology research could also investigate patterns and distributions among multiple communities across broad spatial scales. For example, patterns indicating later phenology events with increasing altitude and latitude are known in terrestrial systems (Hopkins 1919, 1920, Vitasse et al. 2018), but spatial gradients in community phenology have received comparatively less attention in freshwaters. Frameworks that incorporate thermal mechanisms to development and physiology may be one way to examine phenological seasonality in temperate freshwaters at large spatial scales (Newbold et al. 1994). Body size mediates many ecological processes in freshwater environments

(Hildrew et al. 2007) and organisms in these systems may exhibit greater sensitivity to effects of warming on body size, compared to terrestrial taxa (Forster et al. 2012). Therefore, future research could investigate whether potential warming-induced changes in timing of phenology events are associated with impacts on body size distributions or the strength of size-structured trophic interactions.

Conservation implications of phenology

Knowledge of species' life history can inform biodiversity conservation and our literature review identified a number of applications in which phenology can benefit freshwater conservation. Phenology events can inform invasive species management to identify potential areas susceptible for expansion and methods to control the spread of established introduced species populations (Liang et al. 2005, Dexter et al. 2015, Gooding et al. 2018, Bondarev et al. 2019, O'Brien et al. 2019, Suresh et al. 2019, Giménez et al. 2020). Detailed studies on the phenology of imperiled and declining species may also assist in species recovery plans (Gorman and Stone 1999, Joshi et al. 2018, Watanabe et al. 2020). For lotic fish and invertebrates, flow requirements for emergence, spawning and larval recruitment should be used to inform management of water resources, including planning of dams which may fragment migratory patterns or timed dam releases (Gorman and Stone 1999, Valdez et al. 2019). Finally, phenology events can be used to inform species distribution models and improve assessments of potential species range shifts in response to ongoing global change (Chuine 2010, Macgregor et al. 2019).

Novel data sources and technologies

Our review identified novel data sources and technologies that can be applied to future freshwater phenology research. For example, citizen science datasets will be invaluable in filling data gaps, particularly in under sampled regions, and show particular promise for monitoring macroinvertebrate emergence at relatively large spatial scales (Hassall et al. 2007). Natural history collections and museum specimens may also provide access to data on phenology events spanning several decades and have identified phenology shifts in plants and invertebrates (Brooks et al. 2014, Meineke and Davies 2019, DeLeo et al. 2020, Olsen et al. 2020). One potential utility of these data not yet explored is whether they can be used to quantify phenology of non-salmonid freshwater fishes, for example to identify dates of presence of spawning condition individuals or arrival dates of juveniles and migrants.

Novel technologies can also help elucidate trends in phenology events. For example, meteorology radar data can be used to monitor macroinvertebrate emergence (Hansen et al. 2020), video cameras and environmental DNA can provide dates of fish spawning migration events (Kuczynski et al. 2017, Thalinger et al. 2019), and web images can be digitized to estimate phenology dates based on morphological features (e.g. presence of nuptial coloration) (Atsumi and Koizumi 2017).

Conclusion

Consistent in the above knowledge gaps is the need to adopt a more macroscale approach towards freshwater phenology research. Thus far, the body of research has been conducted at relatively small biological, spatial and temporal scales, but quantifying phenology shifts in response to global change and their implications for biodiversity and ecosystem functioning will demand broader perspectives in each of these dimensions (Thackeray 2016). Additionally, future research should investigate phenology by testing mechanistic hypotheses to assess environmental cues and intrinsic traits (Chmura et al. 2019). Analyses of phenology events across broad latitudinal and elevational gradients can be helpful to elucidate environmental and organismal mechanisms underlying variation at large spatial scales but have seldom been applied in freshwater habitats. Creative combinations and applications of emerging and existing data sources with novel methods and technologies will be necessary to expand the scope of freshwater phenology research.

Data availability statement

Data available from the Figshare Repository: <http://doi.org/10.6084/m9.figshare.13664546.v2> (Woods et al. 2021).

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Author contributions

Taylor Woods: Conceptualization (equal); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Anna Kaz**: Conceptualization (equal); Data curation (equal); Methodology (equal); Writing – review and editing (equal). **Xingli Giam**: Conceptualization (equal); Methodology (equal); Writing – review and editing (equal).

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