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SPECIAL ISSUE-LETTER

Climate-influenced phenology of larval fish transport in a large lake

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Scientific Significance Statement

In large lakes, for example, Lake Michigan, larval fish dynamics are directly influenced by climate-driven physical transport processes that advect mostly passive larvae through heterogeneous habitats. Under changing climatic conditions, hatch times may not coincide with phenologies of favorable transport and prey availability. However, these potential mismatches have not been studied in large lakes. Historic and future simulations of larval transport indicate strong intra- and inter-annual variability, with advection to generally less suitable offshore habitats increasing seasonally (from spring to summer) and occurring earlier in warm years. While earlier offshore transport in future years might be offset by changes in hatch timing, mismatches in emergence of larval fish and their zooplanktonic prey may limit future recruitment potential.

Abstract

Elucidating physical transport phenologies in large lakes can aid understanding of larval recruitment dynamics. Here, we integrate a series of climate, hydrodynamic, biogeochemical, and Lagrangian particle dispersion models to: (1) simulate hatch and transport of fish larvae throughout an illustrative large lake, (2) evaluate patterns of historic and potential future climate-induced larval transport, and (3) consider consequences for overlap with suitable

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temperatures and prey. Simulations demonstrate that relative offshore transport increases seasonally, with shifts toward offshore transport occurring earlier during relatively warm historic and future simulations. Intra- and interannual trends in transport were robust to assumed pelagic larval duration and precise location and timing of hatching. Larvae retained nearshore generally encountered more favorable temperatures and zooplankton densities compared to larvae transported offshore. Larval exploitation of nearshore resources under climate change may depend on a concomitant shift to earlier spawning and hatch times in advance of earlier offshore transport.

For over a century, researchers have examined variability of larval fish growth, survival, and ultimately recruitment by considering the intricate link between hatch timing and environmental suitability during the pelagic larval duration (PLD; Hjort 1914). Hjort postulated two hypotheses relating PLD experiences and annual survivorship: (1) the "Critical Period" hypothesis, illustrating the importance of phenological synchrony between larval first feeding and the density and availability of appropriately sized prey (later expanded as the "Match – Mismatch" hypothesis [Cushing 1969, 1990] to contextualize spatiotemporal synchrony between larvae and their zooplanktonic prey), and (2) the Aberrant Drift hypothesis, outlining implications of interannual variability in physical transport patterns. Although relatively unexplored as a mechanism of recruitment variation in freshwater systems (potentially due to generally greater larval survival and shorter PLD in freshwater than marine systems; Houde 1994), physical transport processes in large lakes may strongly influence early life success, especially for larvae that are relatively small at hatch. Physical transport effects in large lakes may be more similar to marine systems than small freshwater systems, with currents frequently surpassing larval swimming capabilities and freshwater larvae potentially being passively transported long distances (Dettmers et al. 2005; Höök et al. 2006; Beletsky et al. 2007; Ludsin et al. 2014; Fraker et al. 2015; Rowe et al. 2022; Schraidt et al. 2023).

Climate-driven shifts in the phenology of aquatic ecosystems can affect the annual recruitment of fish in multiple ways, including through shifts in the timing of spawning and physical processes (e.g., thermal stratification) that together can influence larval hatch and subsequent early life transport and experiences. Immutable factors such as photoperiod may limit reproductive and hatch phenology plasticity in temperate species (Conover 1992; Gortázar et al. 2007) and contribute to spatiotemporal mismatches between larval occurrence and favorable (i.e., conditions enhancing larval growth and survival) physical transport processes, thermal environments, and zooplanktonic prey. Ambient water temperatures have direct and synergistic impacts on larval fish phenology, behavior, and physiology (Pörtner and Peck 2010; Pankhurst and Munday 2011) that may introduce variability in hatch timing, consumption, and growth. Similarly, spatiotemporal patchiness in size, production, and distribution of zooplanktonic prey (Folt and Burns 1999; Simoncelli et al. 2019), together with variation in larval emergence, transport, and abiotic conditions, may further contribute to mismatches that exacerbate differences in larval growth and survival. A better understanding of the relationship between large lake physical transport phenology and early life experiences can help clarify the role of transport in structuring recruitment, and aid projection of future recruitment potential under changing climatic conditions (Eppehimer et al. 2019).

In large lake ecosystems, the transport or retention of larval fish into favorable habitats is largely a function of physical processes acting on fish larvae immediately after hatching. Larval fish emerging from shallow, nearshore spawning habitats experience physical transport processes within the coastal boundary layer that are primarily wind-driven and modified by spatiotemporal density stratification and the Coriolis force (Rao and Schwab 2007). Prior to spring–summer stratification, relatively strong alongshore currents form due to the action of wind stress on the shallow water column and the steering effect of the shoreline, resulting in limited offshore transport (Rowe et al. 2022). In addition, a coastal thermal bar (i.e., a frontal zone at the confluence of warmer nearshore water and colder offshore water) can further concentrate lake warming and nutrient influx from tributary discharge to nearshore waters (Huang 1972; Moll et al. 1993; Auer and Gatzke 2004; Wang et al. 2012) while also retaining spring-spawned larvae, such as alewife (*Alosa pseudoharengus*) and yellow perch (*Perca flavescens*), until the onset of summer stratification. Following summer stratification, however, offshore transport is enhanced. Moreover, with vertical stratification, coastal upwelling and downwelling (vertical displacement of the thermocline) respond to variable mid-latitude winds, with associated offshore or onshore movement of surface water, respectively, due to Ekman transport (Beletsky et al. 1997). As a result, interannual differences in warming of large lakes may contribute to variable but somewhat predictable offshore larval transport, derived from climate-induced shifts in the timing of stratification.

Herein, we use Lake Michigan, USA (surface area = 57,753 km^2, volume = 4918 km^3) as an illustrative case study within the Laurentian Great Lakes. In spring and early summer, relatively warm nearshore waters receive tributary nutrients that promote relatively high phytoplankton and zooplankton production. Multi-decadal declines in offshore productivity toward oligotrophication (attributed to decreased nutrient loading and increasing dreissenid mussel filtration; Hecky et al. 2004), coupled with increases in nearshore productivity (Stadig et al. 2019; Pothoven and Vanderploeg 2020), have enhanced the production gradient between nearshore and offshore waters. Differences in phytoplankton and zooplankton production may exacerbate phenological asynchrony between larvae and favorable conditions, due to the timing of larval emergence and physical transport processes. By integrating a suite of previously published climate, hydrodynamic, biogeochemical, and Lagrangian particle dispersion (LPD) models (Supporting Information Fig. S1), we investigated: (a) consequences of climate-induced shifts in transport phenology on historic patterns of larval offshore advection, and (b) the likelihood of future matches with favorable thermal conditions and zooplanktonic prey. Effects of interannual thermal conditions on the seasonality of larval transport in Lake Michigan were evaluated by comparing historic warm and cool years that coincided with strong and weak fish recruitment trends, respectively, and future simulations. We expected offshore transport to increase throughout the season and for the probability of offshore transport to occur earlier in warm years. In general, we expected that larvae retained nearshore would experience more favorable thermal conditions and greater zooplankton densities.

Methods

Integrated modeling framework

To simulate fine-scale coupling of physical-ecological processes and their direct influence on early life experiences of potentially passive fish larvae, we integrated a series of previously published models, validated to Lake Michigan. Models used two-way coupling of a regional climate model with a three-dimensional (3D) Great Lakes—Atmosphere Regional Model (GLARM, Xue et al. 2017, 2022), a 3D biophysical model consisting of a Finite Volume Community Ocean Model (Chen et al. 2003) and a nutrient-phytoplankton-zooplankton-detritus (NPZD) model with an added fifth compartment to represent benthic filter feeder (i.e., dreissenid mussel) biomass (Rowe et al. 2017). Outputs from these models were used to drive a LPD model to simulate the influence of physical processes on the transport and early life experiences of fish larvae emerging from relatively shallow nearshore hatch sites (Table 1).

Hydrodynamic modeling of historic years was forced by interpolated meteorological observations from stations around Lake Michigan, following methods outlined in Rowe et al. (2017). Future climate and hydrodynamic conditions were projected by GLARM-V2 (version 2; Xue et al. 2022) to simulate climate-hydrodynamic interactions within a 3D, unstructured grid (5795 nodes, 10,678 cells, and 20 vertical sigma layers following lake bathymetric depth) to simulate water currents and temperatures within Lake Michigan. A NPZD biophysical model (Rowe et al. 2017) simulated phosphorus-limited lower trophic-level dynamics as influenced by physical, biogeochemical, and ecological processes (e.g., tributary phosphorus inputs, dreissenid mussel filter feeding, zooplankton grazing effects, etc.). The combined effect of the two models (GLARM and NPZD) guided a LPD model that included floating, sinking, and swimming velocities in the random-walk vertical turbulence module (Rowe et al. 2016) to expand model utility to predict larval fish physical transport in Lake Michigan (Rowe et al. 2022; Schraidt et al. 2023). Collectively, the integrated models have demonstrated reasonable skill simulating historic water temperatures, wind, upwelling, nutrient availability, primary production, zooplankton biomass, and the physical transport of larval fish in Lake Michigan (*see* Supporting Information "Biophysical model description and validation" section).

To explore potential consequences of shifting phenology, we aimed to evaluate transport and environmental experiences among larvae hatched over a range of potential dates; thereby avoiding explicit a priori assumptions related to precise spawn timing and duration, which vary dramatically within and among years (Table 1; Supporting Information Table S1). Simulation of larval transport and environmental experiences consisted of modeling 139 potential hatch (release) days, spanning from 15 March to 31 July. At the start of each release day, larvae ($n = 42{,}185$) emerged uniformly from all nearshore cells in Lake Michigan (bathymetric depths <10 m; Fig. 1a) facilitating the assessment of regional physical transport processes. The number of larvae emerging from each hatch cell (range = 1–49 larvae hatch cell^{-1}) was proportional to cell area, which varied owing to irregular shoreline features and nearshore bathymetry. Larvae were initially randomly distributed vertically throughout the water column, and their vertical position was then simulated using random-walk turbulent dispersion such that larvae remained in the surface mixed layer. While larvae may display positive or negative vertical swimming, for yellow perch in Lake Michigan, transport models assuming neutrally buoyant larvae outperformed models assuming active positive vertical movement (Schraidt et al. 2023). Rather than assume a single fixed PLD, which varies largely within and among species (e.g., Table 1), we consider a range of potential PLDs (assuming larvae were passively susceptible to transport for 10, 20, 30, 40, or 50 d). From emergence through the end of the assumed PLD, individual larvae were tracked throughout Lake Michigan. Sub-hourly experiences of larvae were summarized as each individual's mean daily experiences, including: (a) 3D position and positional bathymetry (i.e., bathymetric depth of lake at an individual's horizontal position), (b) temperature (°C), and (c) zooplankton biomass (mg carbon L^{-1}) of the occupied 3D cell. This approach permitted post-hoc comparison of simulated larval transport and early life experiences across various PLDs.

Analysis

Insights into larval fish transport phenology were gained through retrospective simulations of historic warm and cool years, followed by simulation of potential future conditions (Gardner et al. 2024). Results were contextualized through comparison of alewife and yellow perch early life-histories which display high vulnerability to physical transport

Table 1. Reproductive and early life history characteristics of referenced model species.

Life stage characteristics	Alewife, *Alosa pseudoharengus*	Yellow Perch, *Perca flavescens*
Adult spawning		
Timing*	Early June to Early August†,‡,§	Early May to Late June†,‖
Temperature (°C)	10–27†	7.2–13†,¶
Habitat(s)	Tributaries, Drowned River Mouth Lakes, coastal and nearshore zones	Drowned River Mouth Lakes, coastal and nearshore zones
Depth	Pelagic	Benthopelagic
Fecundity	10,000–22,407†	3035–157,594†
Egg		
Diameter (mm)	0.95–1.27†	2.3–3.5†
Duration (days)*	2–15#	6–27†
Buoyancy	Semi-buoyant†	Semi-demersal to skein†
Larval		
Mean hatch length (mm)	3.5†; 3.8**	5.8†
Yolk-sac duration (days)*	2–5†,**	4‖
Metabolic optimum temperature (°C)	24–26††	29–32‡‡
Growth rate (mm d^{-1})	0.5‡; 0.62**; 0.8–0.9§§,‖‖	0.11–0.52##
PLD timing	June to August‡,§§,‖‖	Late May to August¶¶,##
PLD*	15–50**	30–60¶¶,##,¶

*Temperature dependent (e.g., exhibits general trend of occurring earlier or contracting in warmer years).
†Auer (1982).
‡Eppehimer et al. (2019).
§Weber et al. 2015;
‖Mansueti (1964).
¶Whiteside et al. (1985).
#Edsall (1970).
**Heinrich (1981).
††Stewart and Binkowski (1986).
‡‡Post (1990).
§§Höök et al. (2007).
‖‖Starzynski and Lauer (2015).
¶¶Dettmers et al. (2005).
##Weber et al. (2011).

processes throughout a relatively long PLD (Table 1). Annual mean lake surface temperatures were compared to fishery-independent derived annual indices of year-class strength for alewife (Warren et al. in press) and yellow perch (Makauskas and Clapp 2018). From this comparison, eight historic simulation years were selected: 4 yr (i.e., 1998, 2005, 2010, 2016) displayed both strong year-class strength and warm spring–summer water temperatures, while another 4 yr (i.e., 1996, 2001, 2014, and 2015) displayed weak–year class strength and cool water temperatures (*see* Supporting Information). Simulations of potential future larval transport were completed using GLARM climate projections for the mid-century (2040–2050) in the Representative Concentration Pathway 8.5 climate-warming scenario (*see* Supporting Information). Although regarded as a somewhat extreme representation of mid-century conditions (Hausfather and Peters 2020; Burgess et al. 2023), exploring pronounced differences between historic and mid-century climate outcomes should provide valuable insights into evolving patterns of climate-induced larval transport. From this exercise, three potential future simulation years were selected from mid-century representing a range of spring–summer thermal profiles: cool (2041), moderate (2044) and warm (2047; Supporting Information Fig. S3).

Summary analysis of historic and future simulations consisted of first assigning larvae to one of five distinct hatch regions in Lake Michigan (Fig. 1a; Stadig et al. 2019). The number of larvae released each day from each region varied by shore length: 12,278 larvae emerged from Green Bay, 4875 in the northwest, 13,723 in the northeast, 6334 in the southwest, and 4975 in the southeast. To highlight regional differences in areas assumed to contribute large numbers of recruits (Supporting Information Table S1), many of our results compare transport and early life experiences of larvae hatched in southwest vs. southeast regions. Relative offshore transport of

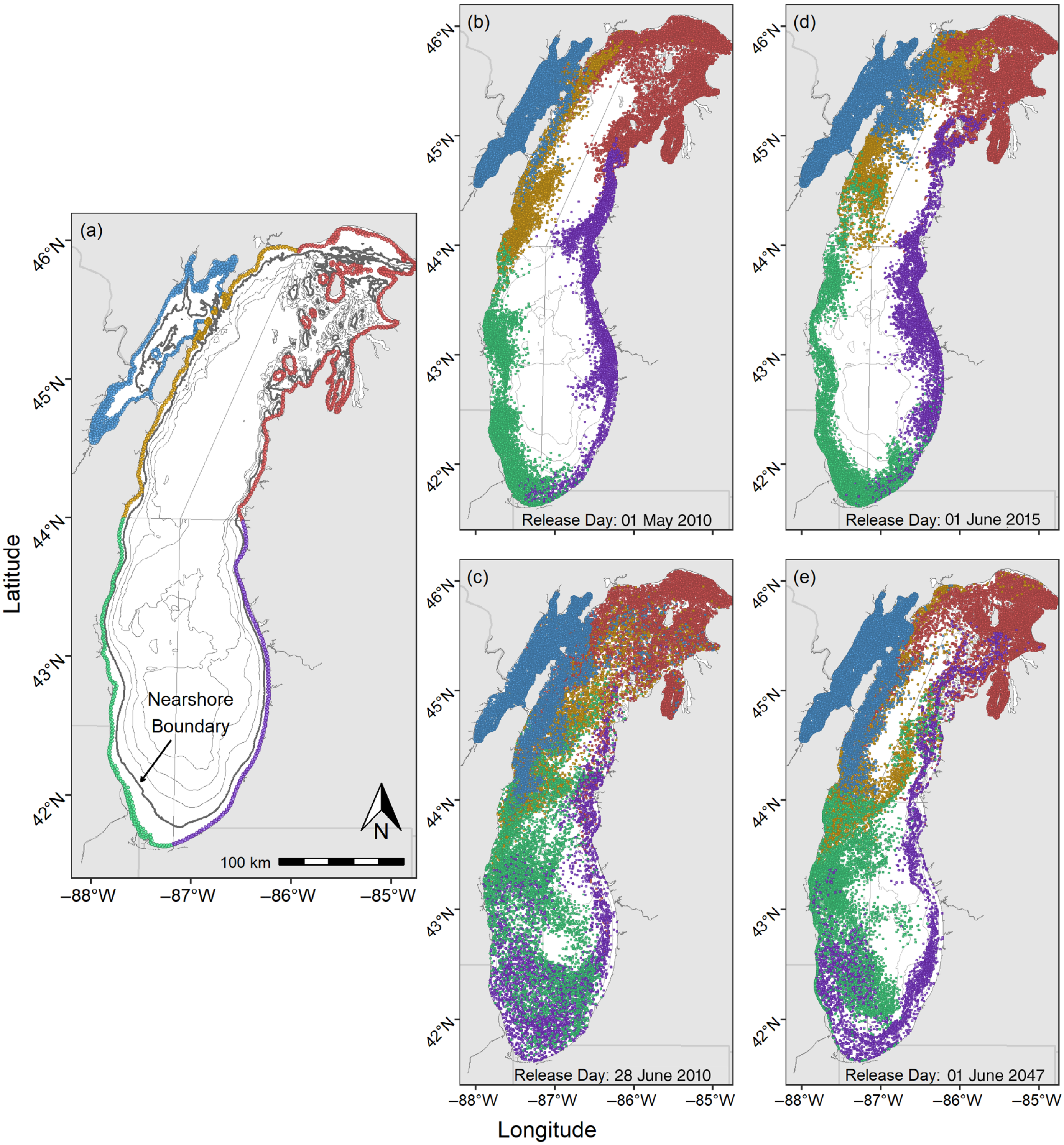

Fig. 1. (**a**) Locations of larval emergence from daily nearshore hatch locations throughout Lake Michigan, where different colors indicate the five distinct regions. Black isobath indicates the extent of the nearshore boundary used in this study (25 m), with subsequent light gray isobaths indicating 50-, 75-, and 100-m depths. Seasonal effects of physical transport processes are demonstrated by visual comparison of location (50-d post-release) of larvae released on (**b**) 01 May 2010 (DOY 122) and (**c**) 28 June 2010 (DOY 180). Interannual effect of thermal conditions (warm vs. cool) on larval transport highlighted by location (50-d post-release) of larvae released 01 June (DOY 153) in (**d**) 2015 (cool year), and (**e**) 2047 (warm year). Final locations represent climate-driven physical transport processes experienced by individuals throughout the 50-d simulation.

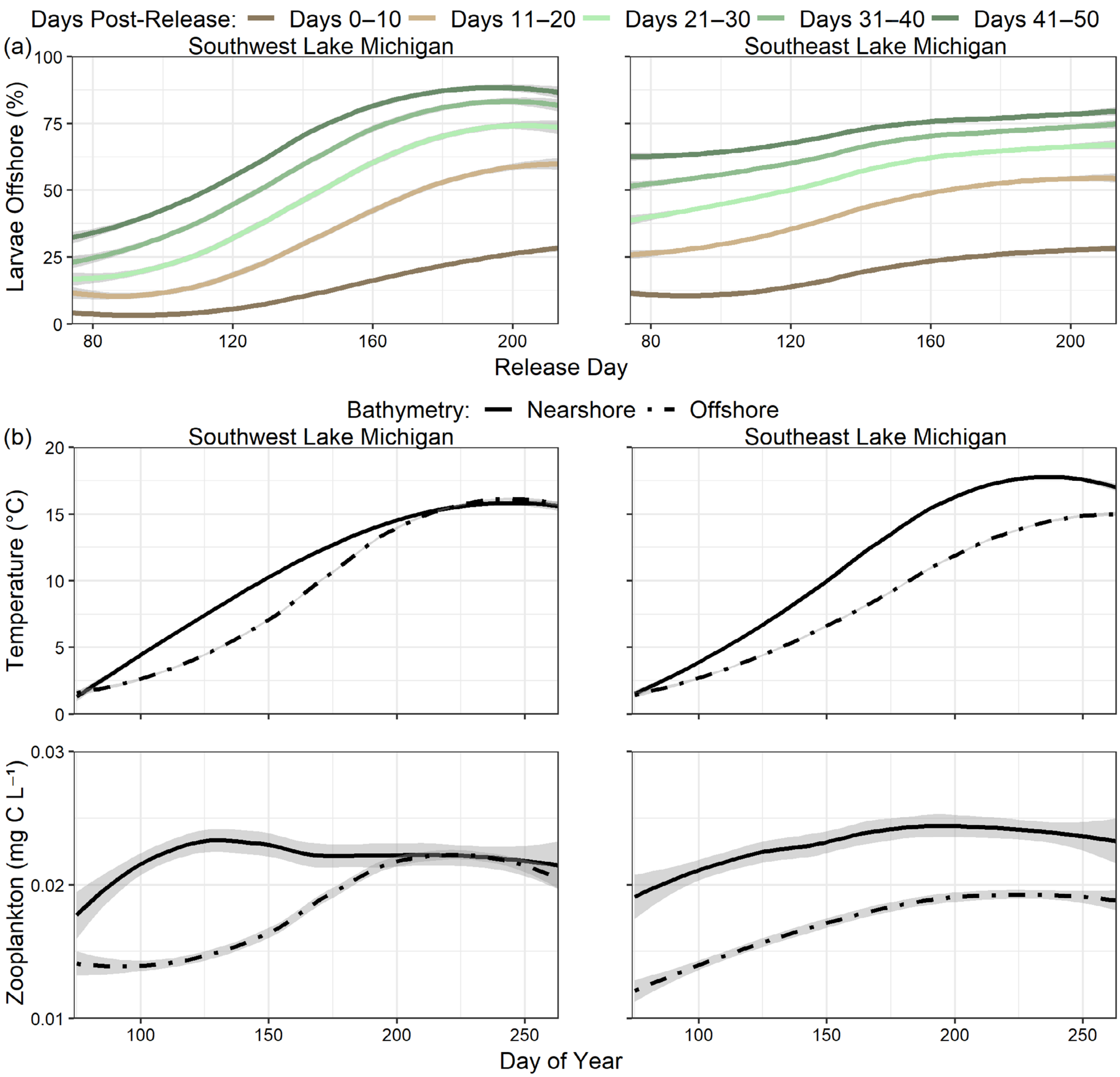

Fig. 2. Local polynomial regression fit and 95% confidence bands drawn to display trends in: (**a**) average proportion of larvae from southwest (left) and southeast (right) daily cohorts ($n = 42{,}185$ per release day) advected offshore (> 25 m) across eight historic simulation years, grouped by release date, and (**b**) mean daily temperature (°C) and zooplankton biomass (mg C L^{-1}) encountered by nearshore vs offshore larvae during specific simulation days. Note that larvae hatching (released) later are more likely to be advected offshore, and offshore larvae seemingly experience date-specific relatively low temperatures and zooplankton densities.

daily larval cohorts was assessed by classifying individual positional bathymetry as located in either nearshore (< 25-m isobath) or offshore (> 25-m isobath) waters (Warren et al. 2018), and summarizing encountered environmental conditions (temperature and zooplankton biomasses). Inter- and intra-annual comparisons were standardized by days post-release (e.g., Days 0–10, 11–20, etc.) and years were grouped by climate scenarios (i.e., historic warm, cool, and future). Simulations were analyzed using Python (version 3.9.12) and R (version 4.2.2). Trends in larval fish offshore transport, experienced temperature, and encountered zooplankton biomass were fit using nonparametric local polynomial regression (loess; $\alpha = 1$, $\lambda = 2$; Jacoby 2000).

Results

Averaged across historic simulations, the proportion of larval fish advected offshore (>25-m isobath) increased seasonally with release day (compare Figs. 1b and 1c, 2a). This pattern occurred throughout Lake Michigan's five regions irrespective of the assumed PLD (Supporting Information Fig. S4a). Along Lake Michigan's southwestern shoreline, larval fish experienced the greatest seasonal difference in the mean number of fish transported offshore by the end of a 20-d PLD, ranging on average across the 8 historic years from 9.9% to 63.9% for 22 March (day of year [DOY] 81) and 11 July (DOY 192) cohorts, respectively (Fig. 2a). In both

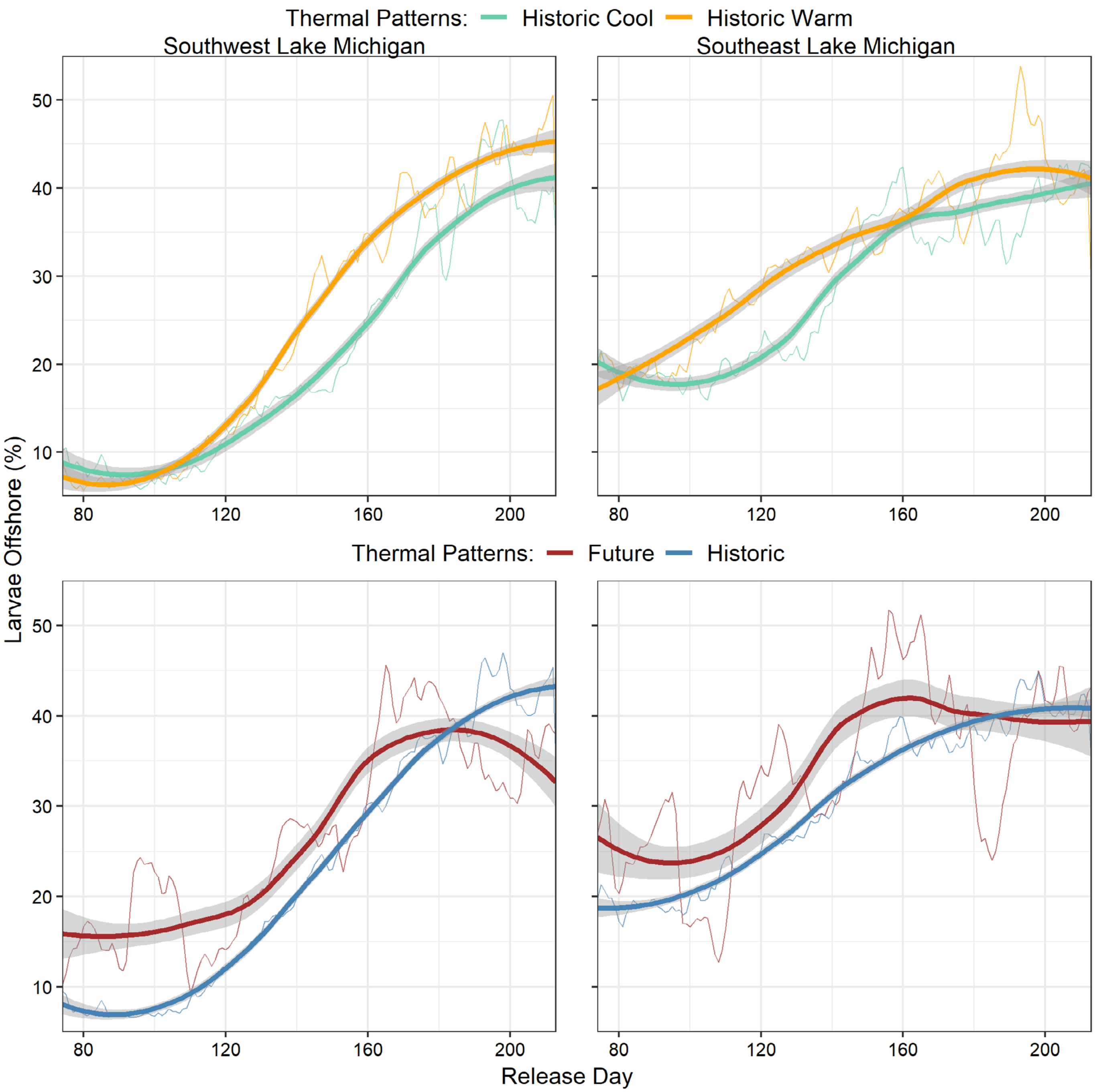

Fig. 3. Average proportion of larvae from daily cohorts ($n = 42{,}185$ per release day) advected offshore (> 25 m) in historic (cool and warm) and future simulation years during the first 20-d post-hatch. Local polynomial regression and 95% confidence band (bold lines) represents the best fit of averaged historic and future years (thin background lines).

nearshore and offshore habitats, water temperature and encountered zooplankton biomass experienced by larvae increased during spring and summer, but generally remained lower for larvae in offshore regions compared to nearshore, especially in the southeast (Fig. 2b; Supporting Information Fig. S4b). This same pattern generally held in the southwest through mid-July, but by late-July larvae in nearshore and offshore environments encountered comparable water temperatures and zooplankton biomasses (*see* Supporting Information “Discussion of peculiarities” section).

The phenology of larval transport in Lake Michigan was heavily influenced by spring–summer thermal conditions.

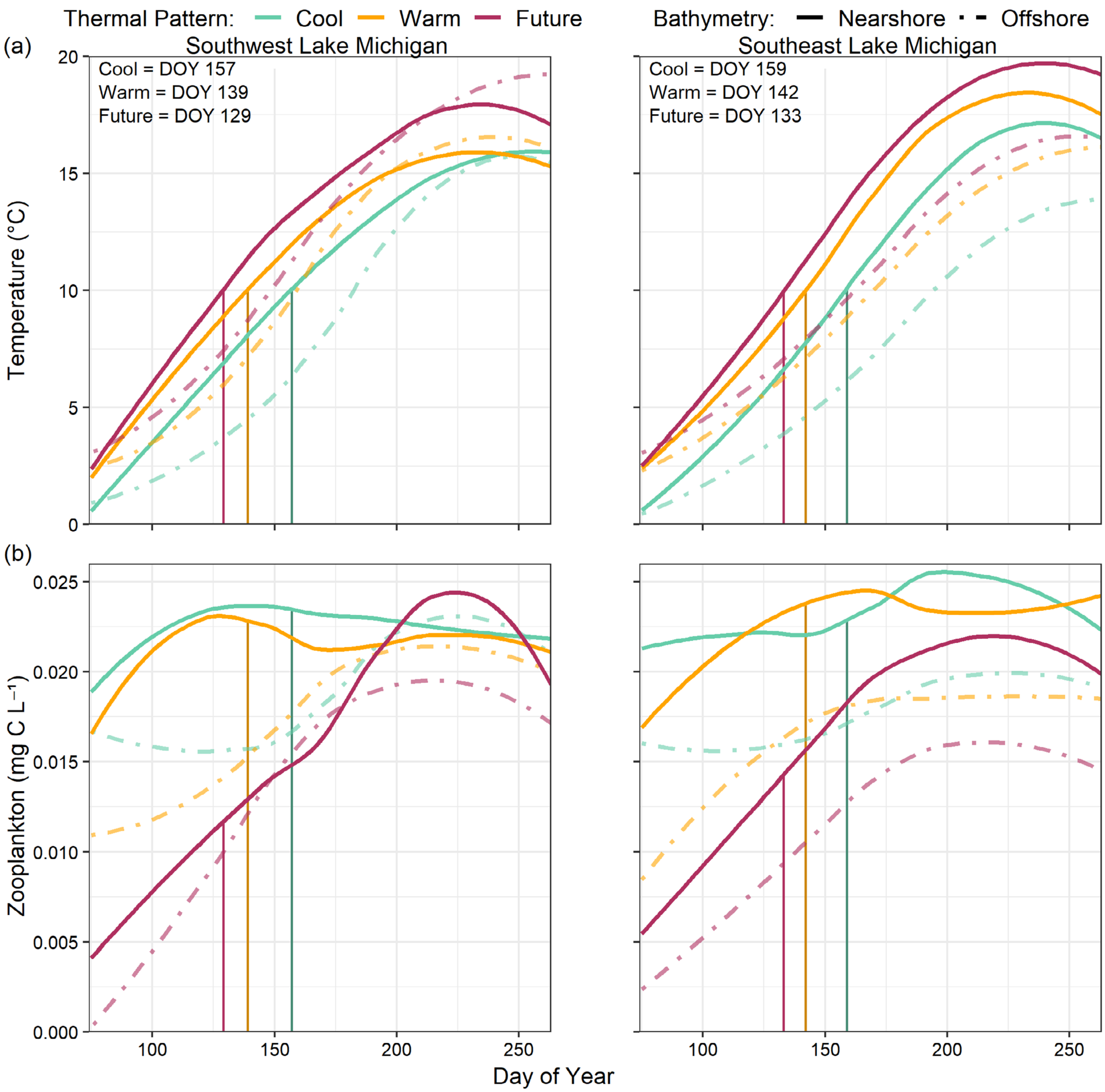

Fig. 4. Fit of local polynomial regression to (**a**) daily temperature (°C) and (**b**) zooplankton biomass (mg C L^{-1}) encountered by larvae in nearshore (< 25 m, solid) and offshore (> 25 m, dashed) waters, grouped by release average thermal pattern exhibited by the simulation year (i.e., cool: 1996, 2001, 2014, and 2015; warm: 1998, 2005, 2010, and 2016; and future: 2041, 2044, and 2047). Vertical lines and corresponding text (top left) represent a theoretical larval emergence date when water temperature exceeds 10°C.

Despite transport being largely wind-driven, observed wind patterns (direction and magnitude) were highly variable within and among years, and lacked trends consistent with simulated transport patterns (Supporting Information Figs. S5, S6). Instead, thermal conditions greatly mediated offshore transport, with increased relative offshore advection often occurring weeks earlier in warm years than in cooler years (Fig. 3; Supporting Information Fig. S7; compare Fig. 1d and 1e). Differences in the timing of offshore advection between historically warm vs. cool years were most notable along Lake Michigan's southwestern shoreline from late spring to late summer. With extensive warming throughout the simulated hatch window, future years were characterized by a greater proportion of larvae transported offshore during early spring.

Across historic and future years, larvae generally experienced warmer temperatures in nearshore waters than in offshore waters (mean difference = 0.8–2.8°C, respectively, in southwest and southeast; Fig. 4a; Supporting Information Fig. S8). Similarly, larvae retained in nearshore habitats generally encountered higher zooplankton biomasses than larvae in offshore habitats (17.6–30.1% reduction in mean encountered zooplankton biomass offshore in southwest and southeast, respectively; Fig. 4b; Supporting Information Fig. S8). Zooplankton biomass encountered nearshore by larvae in future years was simulated to be much lower than historic years (29.6–31.0% reduction in mean zooplankton biomass encountered nearshore in southwest and southeast, respectively), as was future offshore zooplankton biomass (26.5–37.8% reduction in mean zooplankton biomass encountered offshore in southwest and southeast, respectively). Earlier warming of nearshore waters in future simulation years was generally accompanied by decreased production of zooplankton biomass. Lower zooplankton biomass in future years, coupled with potential earlier offshore advection, suggests that future larval recruitment dynamics may be characterized by more frequent spatiotemporal mismatches in the emergence of larvae and their zooplanktonic prey.

Discussion

Results simulating historic and potential future larval dispersion in Lake Michigan demonstrate strong seasonal effects on offshore transport of nearshore spawned passive fish larvae. Although the proportion of larvae transported offshore increased with DOY and days post-hatch, the timing of offshore transport occurred earlier in warm years than in cool years. These patterns remained consistent regardless of the assumed PLD, suggesting that various large lake species may be vulnerable to seasonally different offshore transport, even if only susceptible to transport for a few days post-hatch. If transport variation in large lakes contributes to recruitment variation, species emerging mid- to late-spring (e.g., yellow perch) are more likely affected by transport-induced recruitment variability than species emerging in early-summer (e.g., alewife), given that larger inter-annual differences in offshore transport occurred in late spring. At the same time, the effects of earlier offshore transport in warm years may be somewhat offset by temperature-dependent shifts in reproductive and development phenologies that result in earlier hatch dates (Kapusta and Bogacka-Kapusta 2016; McQueen and Marshall 2017; Lombardo et al. 2020). For example, assuming a fixed thermal threshold (10°C) for the appearance of spring-spawned fish larvae, emergence in future years would occur between 3 and 10 d earlier than in historically warm years, and 15 and 30 d earlier than historically cooler years (Supporting Information Fig. S8). However, warming of nearshore waters that would historically promote earlier spawning, may exceed historic photoperiod cue ranges at higher latitudes (Pankhurst and Porter 2003) resulting in an inability to adequately adjust hatch timing and more frequent mismatches with favorable physical transport processes.

Our simulations illustrated how physical transport phenologies may affect environmental conditions experienced by larval fish and how variation in spring and summer warming can affect the probability of transport. Thermal conditions and zooplankton biomass encountered by larvae generally increased with DOY, at least through Day 225 (mid-August), but were generally lower for larvae in offshore waters than was experienced in nearshore waters (*see* Supporting Information "Discussion for exceptions" section). Lake Michigan is a relatively cold system and comparison of larval alewife and yellow perch thermal thresholds supporting maximum physiologic performance (Deslauriers et al. 2017) indicate that regionally averaged ambient water temperatures were likely limiting optimal consumption and growth in both nearshore and offshore habitats throughout historic and future simulations. Thus, while larvae are unlikely to grow at their maximum rate even in nearshore zones, warmer temperatures and greater prey availability in the nearshore should allow faster growth in this zone. That said, temperature effects on larval fish may not simply act through potential consumption rates but can also affect processes such as rate of yolk-sac absorption, developmental ontogeny, and PLD (O'Connor et al. 2007; Pankhurst and Munday 2011).

Increased warming into mid-century revealed potential decreased numbers of encountered zooplankters throughout the lake. While the magnitude of this decline may reflect certain model processes and assumptions (*see* Supporting Information), mid-century thermal conditions are poised to influence lake phytoplankton dynamics, and potentially zooplankton dynamics, through two important processes. First, warm winter temperatures into the mid-century are unlikely to support strong winter stratification (Woolway et al. 2021). Given that winter stratification and subsequent spring turnover can (a) enhance phytoplankton productivity by limiting mixed-layer depth and associated light limitation (Rowe et al. 2017), and (b) increase nutrients available for algal production the following spring (Hampton et al. 2017), the loss of winter stratification could limit primary and secondary production. Second, warming spring temperatures will likely lead to an earlier onset of summer stratification (Winder and Schindler 2004; Magee and Wu 2017; Anderson et al. 2021). As algal blooms are typically associated with spring mixing and the onset of thermal stratification in deep lakes (Winder and Sommer 2012), initial blooms my precede seasonal light regimes necessary to support sizeable phytoplankton production blooms. Taken together, these potential processes that may lead to decreased phytoplankton biomass can reasonably be expected to also lead to decreased zooplankton densities (Pothoven and Vanderploeg 2022). That said, these predicted climate change influences on zooplankton densities should be studied further. Additional research into biophysical mechanisms driving model-predicted declines in zooplankton biomass and structuring larval fish transport should provide greater insight into future fish recruitment potential within large lakes.

Compared to the many physical transport processes of marine systems, larval dispersion in large lakes is largely wind-driven. Initial exploration of regional winds underpinning historic simulations of larval transport (*see* Supporting Information "Wind Analysis" section; Figs. S5, S6) lacked clear patterns of seasonality and were characterized by high within and among year variability. Seasonality of offshore larval transport was, however, strongly influenced by the timing of spring–summer stratification, demonstrated through progressively earlier offshore transport of larvae in simulated warm years. While rates of annual warming in large lakes contribute to the duration and disappearance of the thermal bar (Hamilton and MacIntyre 2023), other factors such as late winter heat content (i.e., mean lake temperature throughout upper 100 m) may better explain the phenology of stratification (Rogers 1987) influencing larval offshore transport. Future winter warming will likely result in large lakes retaining more heat, potentially leading to even earlier stratification and offshore transport of larvae than was simulated here. The plasticity of fish reproductive and hatch phenologies in response to changing climatic conditions may determine if spring-spawned larvae are able to exploit favorable nearshore resources in the future.

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