

Multidecadal trends in ultraviolet radiation, temperature, and dissolved oxygen have altered vertical habitat availability for *Daphnia* in temperate Lake Giles, USA

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Abstract

1. Long-term browning has resulted in increases in dissolved organic carbon and reduced water clarity that have altered the vertical physical structure of many lake ecosystems. The primary responses include reduced ultraviolet (UV) penetration, warming surface waters, and decreased deepwater dissolved oxygen concentrations that interactively alter vertical habitat suitability for zooplankton.
2. Over 3 decades, *Daphnia* populations have decreased in abundance and shallowed in their vertical distribution in temperate Lake Giles (Pennsylvania, USA). Using 3 decades of corresponding long-term vertical profile data of UV radiation, water temperature, and dissolved oxygen, we modelled both the suitable vertical habitat and thermally optimal habitat for *Daphnia* to understand the potential role of habitat availability for their population dynamics.
3. The vertical extent of suitable habitat increased over time primarily due to strong decreases in UV penetration. In contrast, thermally optimal habitat decreased due to strong increases in vertical thermal gradients that were especially strong in late summer.
4. The vertical distribution of *Daphnia* became shallower over this time period and may be a response to lower UV exposure near the surface, but continued warming of surface waters and decreasing deepwater dissolved oxygen concentrations are likely to lead to a vertical *habitat squeeze*.
5. The biological implications of long-term browning require more attention due to the complex and important implications for population dynamics, species interactions, and food web structure in lakes.

KEYWORDS

habitat model, lake browning, ultraviolet radiation, vertical structure, zooplankton ecology

1 | INTRODUCTION

Habitat selection is a function of a wide range of abiotic and biotic variables determined by species' life history traits, including climate, landscape variability, food availability, competition, and predation (MacArthur & Levins, 1964; Rosenzweig, 1981). Climate change and other anthropogenic stressors strongly influence the abiotic conditions in habitats of many species, often leading to changes in species ranges and/or community composition (Walther, 2010). One prevalent example affecting the physical, chemical, and biological structure in freshwater ecosystems is long-term browning. Browning is a result of increased dissolved organic carbon and leads to reduced water clarity and altered vertical distribution of light and heat (Pilla et al., 2018; Williamson et al., 2015). This alteration of the vertical light and heat environment leads to reduced penetration of photosynthetically active radiation (PAR) as well as shorter ultraviolet (UV) penetration (Williamson et al., 2015). In response, surface waters can warm rapidly (Pilla et al., 2018; Williamson et al., 2015), a pattern that is prevalent in lakes throughout the world via various mechanisms including browning (Kraemer et al., 2015; O'Reilly et al., 2015; Pilla et al., 2020). This increase in surface water temperatures with a consequent increase in strength of stratification (Pilla et al., 2018) can lead to lower dissolved oxygen availability in deeper waters (Knoll et al., 2018; Williamson et al., 2015). These trends of decreasing dissolved oxygen are geographically widespread across many temperate lakes (Jane et al., 2021), with an increasing frequency and volume of critically low dissolved oxygen conditions that are important for respiring organisms (Brothers et al., 2014; Jankowski et al., 2006). These combined effects of browning are important factors for habitat availability and suitability for freshwater organisms that are subject to rapidly changing conditions in their environment. Changes in the size or location of available habitat may lead to increased overlap with prey or predators, inferior food resources, or occupancy of habitats with physiologically sub-optimal conditions, all of which have implications for fitness including survival, growth, and reproduction. The changes in habitat availability and the response of planktonic species also influence food web interactions and overall ecosystem structure and function.

For planktonic species in lakes, strong changes to abiotic conditions in their habitat require a rapid response in temporal or spatial habitat selection (Kraemer et al., 2021). *Daphnia* have been widely studied and are exceptional indicator species for understanding the potential zooplankton responses to environmental change. Across all types of freshwater ecosystems in the world, *Daphnia* are common and abundant zooplankton grazers that serve as a key intermediate trophic level in aquatic food webs. The general ecology, life history, and habitat of *Daphnia* have been very well studied, making *Daphnia* an exemplary model organism for ecological and evolutionary studies (Lampert, 2011). Past studies have indicated the importance of three major abiotic variables that also strongly respond to browning for *Daphnia* survival, growth, and reproduction that ultimately determine their fundamental niche or suitable habitat: UV radiation (Leech & Williamson, 2000; Williamson et al., 1994;

Zagarese et al., 1994), water temperature (Moore et al., 1996; Orcutt & Porter, 1983; Pangle & Peacor, 2010; Stich & Lampert, 1984; Williamson et al., 2002), and dissolved oxygen (Hanazato & Dodson, 1995). In lakes, these three abiotic variables exhibit strong vertical gradients in the water column and interact to determine where *Daphnia* can survive. *Daphnia* are one of the most sensitive zooplankton to UV radiation (Leech & Williamson, 2000), where high exposure to UV radiation near the lake surface can result in DNA damage as well as decreases in growth and survival (Williamson et al., 1994; Zagarese et al., 1994). *Daphnia*'s thermally optimal conditions allow for the highest growth and reproduction rates (Orcutt & Porter, 1983; Williamson et al., 2002), that in turn correspond to peak *Daphnia* abundances within a similar temperature range across latitudes (Gillooly & Dodson, 2000). While water temperatures between c. 5°C up to 25°C are generally positively linked to survival, growth, and reproduction (Moore et al., 1996; Orcutt & Porter, 1983; Pangle & Peacor, 2010; Stich & Lampert, 1984), the most optimal temperatures are around 13–18°C. Water temperatures that are at or above 25°C quickly begin to impart sublethal or lethal effects (Orcutt & Porter, 1983; Williamson et al., 2002). Finally, dissolved oxygen availability is a key factor that may limit the vertical extent of the suitable habitat available of *Daphnia*, and can reach critically low hypoxic (<3 mg/L) to anoxic (<0.5 mg/L) levels in deep waters during the summer stratified period. Some zooplankton taxa can temporarily tolerate low levels of oxygen (c. 1 mg/L) for several hours during the day (Williamson & Magnien, 1982; Woodmansee & Grantham, 1961; Wright & Shapiro, 1990), and use low oxygen strata as a refuge from fish predators that are less tolerant of hypoxia (Tessier & Welser, 1991; Wright & Shapiro, 1990). However, such low oxygen conditions can also create a sub-optimal habitat that reduces growth, size, and reproduction, even if mortality is low (Hanazato & Dodson, 1995). The vertical gradients of these three abiotic factors combined contribute to suitable habitat for *Daphnia* in lake ecosystems (Figure 1). These variables are not static over seasonal or decadal time frames as they are responsive to weather patterns, climate change, and anthropogenic stressors, such as browning, that directly and indirectly alter aquatic conditions, leading to changes in suitable and optimal habitat for *Daphnia* vertically in the water column of lakes.

In Lake Giles (Pennsylvania, USA), these three abiotic variables that are key for *Daphnia* habitat have changed rapidly over the past 3 decades due to long-term lake browning (Knoll et al., 2018; Pilla et al., 2018; Williamson et al., 2015). These historical physical changes in lakes have been well documented, but efforts to assess the biological relevance of browning-induced changes in UV radiation, water temperature, and dissolved oxygen availability for key zooplankton species such as *Daphnia* are scarce (Williamson et al., 2020). Here, we use 3 decades of empirical data from the open-water season in Lake Giles to assess the trends in and variables associated with *Daphnia* abundance and their vertical habitat availability during summer stratification when these variables are most influential. We addressed the following research questions: (1) How have *Daphnia* abundance and vertical distribution changed

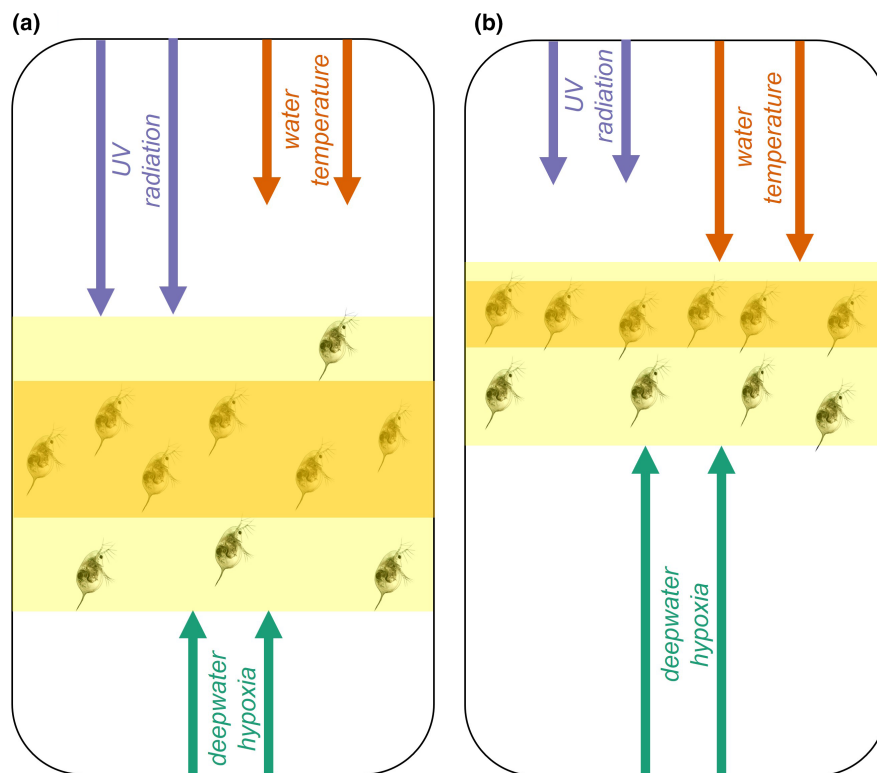


FIGURE 1 Conceptual diagram of the three abiotic variables of interest that can define the boundaries of vertical suitable habitat for *Daphnia*. Abiotic constraints include UV radiation in the surface waters (purple), warm temperatures in the surface waters (orange), and deepwater hypoxia at depth (green). The vertical span between these three limiting variables constitutes the theoretically suitable habitat (light yellow) based on these abiotic factors. The thermally optimal habitat is represented by dark gold bands, which may or may not fall within the suitable habitat. (a) In clear lakes, especially during spring to early summer, UV radiation in the surface waters is of relatively greater importance in setting upper habitat boundaries compared to warm water temperature, and deepwater hypoxia is of less importance in setting the bottom boundaries. (b) In low transparency lakes, or lakes in mid- to late-summer, warm surface water temperatures have relatively greater importance than UV radiation in creating upper habitat boundaries, and deepwater hypoxia is more important in creating the lower habitat boundary.

over time in Lake Giles during the summer? (2) How has the vertical extent of suitable habitat changed over time in Lake Giles during the summer, and which abiotic variables have been the most important limiting factor for *Daphnia* habitat? (3) How has the thermally optimal habitat for *Daphnia* changed in Lake Giles over time during the summer season compared to the suitable habitat? Such biological responses to browning are very understudied, despite the growing knowledge of physical responses. Extending our knowledge to the interactive implications for *Daphnia* and their habitat may provide a future outlook for their population dynamics and potential trophic interactions, given their ubiquitous global distribution.

2 | METHODS

2.1 | Study sites and long-term data

Lake Giles is located at 428m above sea level on the Pocono Plateau in northeastern Pennsylvania, USA. Lake Giles is an oligotrophic lake with a maximum depth of 25m and surface area of 0.48km². Lake Giles is a dimictic lake and typically stratifies in April or May

until October to December when autumn mixing occurs, and we focus this study specifically on the summer stratified months of May through August when data have been most consistently collected over time. For the past 3 decades, Lake Giles has experienced long-term lake browning leading to rapid increases in dissolved organic carbon and decreased PAR and UV radiation penetration (Williamson et al., 2015). Several recent studies have analysed the patterns in long-term browning and the consequences for thermal structure (Pilla et al., 2018), deepwater dissolved oxygen (Knoll et al., 2018), and zooplankton communities (Williamson et al., 2015, 2020). Long-term vertical profile data of UV radiation, water temperature, and dissolved oxygen have been taken approximately one or two times per month during the open water season from 1993 to 2020 (Williamson, 2020). Monthly daytime abundance data of *Daphnia catawba*, the dominant *Daphnia* species in Lake Giles, were collected from 1990 through 2018 using a bongo-style net with 48- or 202- μ m mesh at the deepest point in the lake, and counted in a Bogorov chamber. Zooplankton tows were collected separately from the epilimnion and the metalimnion plus hypolimnion using the net's closing feature. We note that the resulting *Daphnia* abundance as measured and reported here only captures daytime abundance in

the pelagic zone, which may be influenced by the variables under investigation here, but also may be influenced by increased horizontal migration patterns to littoral areas. The proportion of *Daphnia* in the epilimnion was calculated by dividing the proportion collected in the epilimnion by the proportion of the depth of the water column that comprised the epilimnion, defined as the mixed layer with $<1^{\circ}\text{C}$ change per metre. Additional details of zooplankton sampling and counting can be found in Williamson et al. (2015, 2020). We extended these previous studies to assess the sub-seasonal changes in *Daphnia* abundance and vertical distribution in the water column, and explicitly link the physical structural changes in UV penetration, surface water temperature, and dissolved oxygen availability to these patterns and to habitat suitability for *Daphnia* at both long-term and sub-seasonal time scales.

2.2 | Vertical habitat model design

We defined three habitat metrics: suitable habitat, thermally optimal habitat, and overlap between the thermally optimal habitat and the suitable habitat. Suitable vertical habitat available for adult *Daphnia* was modelled as the depth range between the limiting factors of UV radiation and warm water temperature in the surface and deepwater hypoxia (or lake bottom) in deep waters (Figure 1). We used vertical profiles of UV radiation, water temperature, and dissolved oxygen to model these habitat metrics. Vertical UV radiation at 320nm data were used to calculate the 1% depth of subsurface exposure, which was considered to be the maximum UV radiation exposure tolerable for adult *Daphnia* habitat (Cooke et al., 2008; Fischer et al., 2006). Vertical water temperature profiles taken at 1-m intervals were linearly interpolated to 0.01-m intervals. The depth at which 25°C was reached was used as the maximum thermal limit in surface waters (Orcutt & Porter, 1983; Williamson et al., 2002), if it occurred. Vertical dissolved oxygen profiles were similarly linearly interpolated from 1- to 0.01-m intervals, and the depth at which 3 mg/L was reached was used as a limit for deep waters (Wright & Shapiro, 1990), if it occurred. If deepwater dissolved oxygen never reached ≤ 3 mg/L, the lake bottom of 25m was considered to be the limiting boundary. For each sampling date from 1993 to 2020 with vertical profiles of UV radiation, water temperature, and dissolved oxygen, the suitable habitat was calculated as the depth span below the 1% UV depth, below the 25°C depth (if reached, otherwise 0 m), and above the 3 mg/L depth (if reached, otherwise lake bottom; Figure 1).

Thermally optimal habitat for adult *Daphnia* was determined as the shallowest and deepest depth within the $13\text{--}18^{\circ}\text{C}$ temperature range (Orcutt & Porter, 1983; Williamson et al., 2002), which corresponds to the peak in *Daphnia* abundance that occurs slightly later in the spring when water temperatures reach $15\text{--}20^{\circ}\text{C}$ (Gillooly & Dodson, 2000). Dates with water temperature data that never exceeded 18°C were considered to have thermally optimal habitat to 0 m, and dates with temperatures that never reach below 13°C were considered to have thermally optimal habitat through the lake bottom. The overlap between the thermally optimal habitat and the

suitable habitat was calculated as the proportion of the thermally optimal habitat that was within the suitable habitat.

2.3 | Data analyses

Non-parametric Mann–Kendall trend tests from the *Kendall* package in R (McLeod, 2011) were used to assess the long-term changes in *Daphnia* abundance, proportion of *Daphnia* in the epilimnion, suitable vertical habitat, thermally optimal habitat, and habitat overlap across the months of May, June, July, and August. To control for differences in sampling frequency over time, one sampling date nearest the 15th of each month was used to represent vertical habitat availability for each month and year. A non-parametric Friedman's rank sum test blocked by year was used to assess differences across months for the same five variables, given the repeated time series measurements. If statistically significant, it was followed by a post hoc pairwise Wilcoxon rank sum test blocked by year. The relative importance of each of the three limiting abiotic variables on suitable habitat was calculated as the proportion of samples per year where each variable was the most severely limiting factor in the surface (UV radiation and water temperature) or in deep waters (deepwater hypoxia). Non-parametric Mann–Kendall trend tests were used to assess the long-term changes in the relative importance of each limiting variable. All analyses were conducted in R version 4.0.2 (R Core Team, 2021). Figures were created using the *ggplot2* (Wickham, 2016), *ggpattern* (Mike, 2021), and *ggpubr* (Kassambara, 2020) packages in R.

3 | RESULTS

3.1 | Long-term trends in abundance and habitat

Total *Daphnia* abundance generally decreased over the 3 decades of the time series (Figure 2a). The decrease in abundance was especially strong in May ($\tau = -0.429$, $p = 0.029$) and August ($\tau = -0.357$, $p = 0.035$; Figure S1). Long-term trends in vertical distribution of *Daphnia* as measured by proportion of the population in the epilimnion were more variable but generally increased (Figure 2b), primarily associated with strong increases in the proportion of *Daphnia* population in the epilimnion in May ($\tau = 0.474$, $p = 0.031$; Figure S1). *Daphnia* vertical distribution became distinctly shallower over time in May.

Suitable vertical available habitat for *Daphnia* generally increased over the 3 decades of this study (Figure 3, Figure 4a). This increasing pattern was especially notable in May ($\tau = 0.636$, $p = 0.008$) and June ($\tau = 0.537$, $p = 0.001$; Figure S2a) due to long-term decreases in UV radiation paired with generally mild surface water temperatures and high deepwater dissolved oxygen in early summer (Figure 3). The relative importance of the three abiotic variables on the span of the suitable vertical habitat changed over time (Figure 5). UV radiation significantly decreased in importance ($\tau = -0.489$, $p = 0.005$),

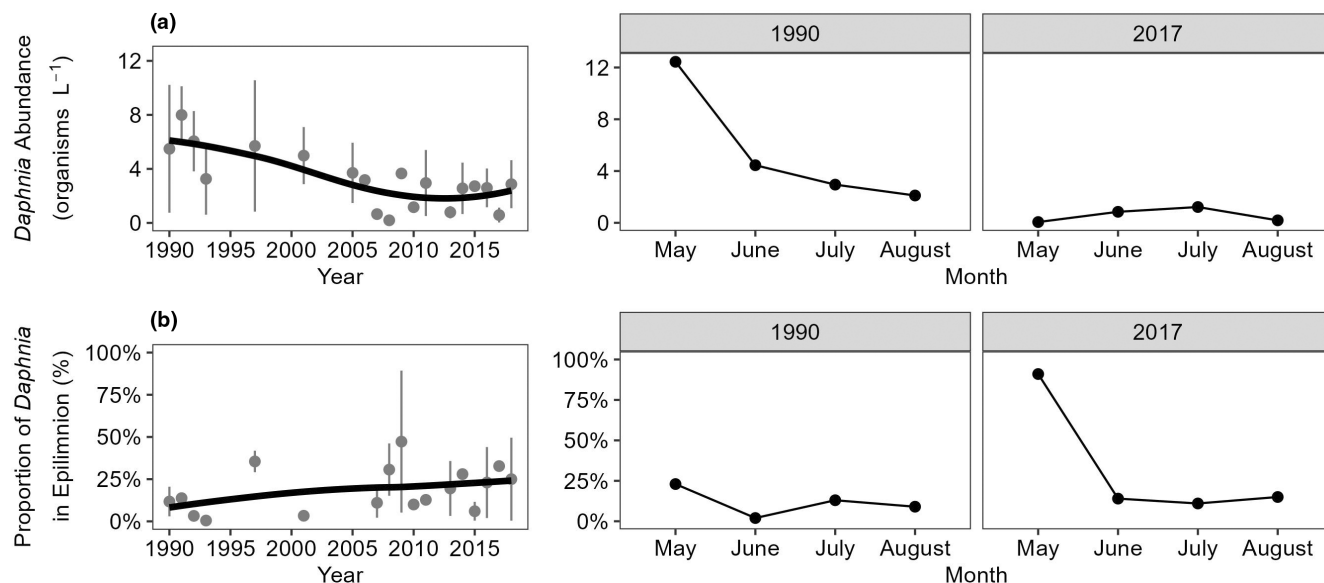


FIGURE 2 Long-term summertime trends in (a) *Daphnia* total water column abundance and (b) vertical distribution of *Daphnia* as measured by proportion of the population in the epilimnion. Each data point is the summertime average from May to August with $\pm 1SD$. Panels to the right in each row highlight the phenological trends during the summer for two example years, for one early year (1990) and one recent year (2017). Trend lines in (a) and (b) are LOESS smoothed curves. Trends for each month for each variable can be found in [Figure S1](#).

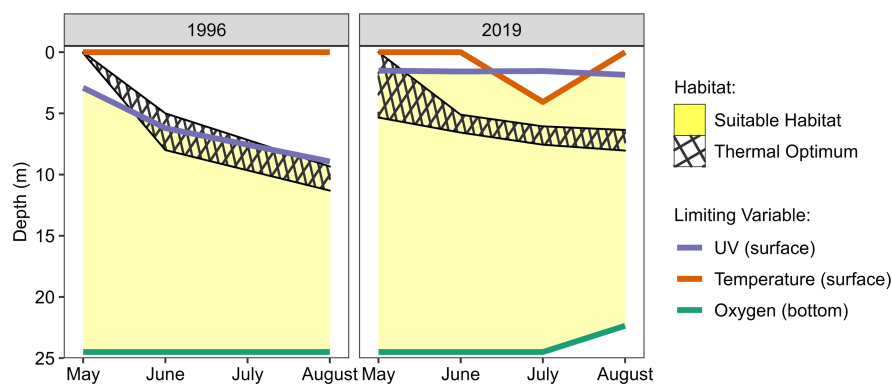


FIGURE 3 Summertime patterns in habitat availability for two example years, for one early year (1996) and one recent year (2019). Suitable habitat is limited above by UV radiation (purple) or water temperature (orange) in the surface and by deepwater hypoxia (green) or by the lake bottom at depth. Light yellow area highlights the suitable habitat throughout the summer for each representative year, and crosshatched area indicates the thermally optimal habitat.

while both water temperature ($r = 0.489$, $p = 0.005$) and deepwater hypoxia ($r = 0.381$, $p = 0.018$) increased in importance ([Figure 5](#)).

In contrast to suitable habitat, thermally optimal habitat generally decreased over time ([Figure 3](#), [Figure 4b](#)). Thermally optimal habitat decreased significantly in June ($r = -0.491$, $p = 0.003$), July ($r = -0.394$, $p = 0.032$), and August ($r = -0.406$, $p = 0.026$; [Figure S2b](#)). The overlap between the thermally optimal habitat and the suitable habitat increased over time ([Figure 4c](#)), particularly in June ($r = 0.590$, $p = 0.001$) and July ($r = 0.477$, $p = 0.026$; [Figure S2c](#)).

3.2 | Monthly summertime patterns

Daphnia abundance was significantly higher in May and June compared to July and August ($p < 0.001$), consistent with the early

summer *Daphnia* peaks typical in Lake Giles ([Figure 2a](#)). However, there was a less pronounced early summer *Daphnia* peak in recent years ([Figure 2a](#); [Figure S1](#)). Vertical distribution, measured as proportion of *Daphnia* in the epilimnion, showed no significant differences across these months ($p = 0.160$; [Figure 2b](#), [Figure S1](#)).

Suitable habitat on average was greatest in May and lowest in August ($p = 0.018$; [Figure 3](#), [Figure S2a](#)). In August, both surface water temperatures and deepwater dissolved oxygen reached their critical limits (25°C and 3 mg/L , respectively) more frequently in the last decade of this study compared to the first 2 decades, largely offsetting the increase in habitat from reduced UV radiation ([Figure 3](#)). Thermally optimal habitat was similar across all 4 summer months ($p = 0.086$; [Figure S2b](#)). However, the overlap between thermally optimal habitat and suitable habitat was significantly lower on average in May compared to the other 3 months ($p < 0.001$; [Figure S2c](#)),

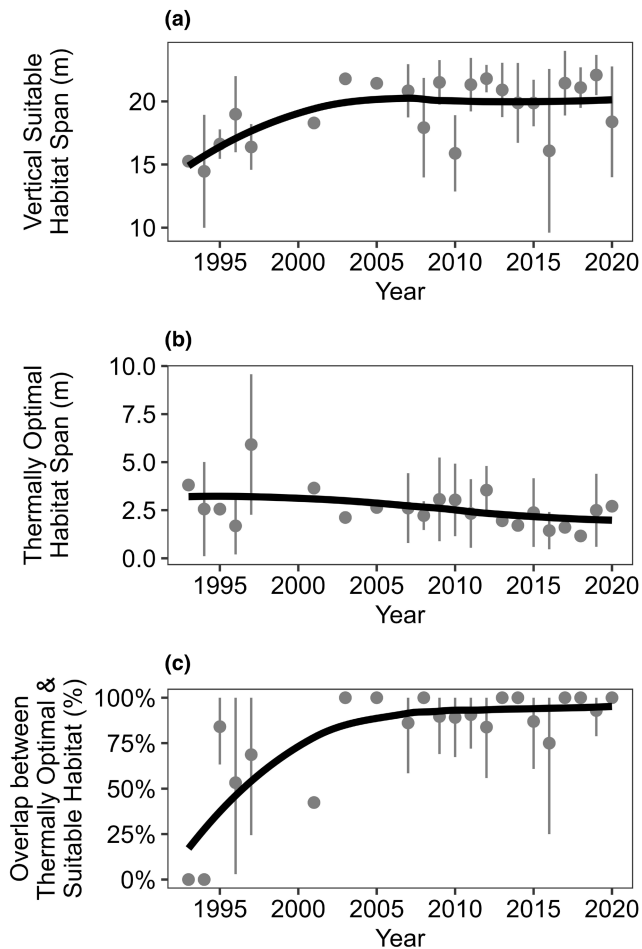


FIGURE 4 Long-term summertime average trends in (a) suitable habitat span, (b) thermally optimal habitat span, and (c) overlap between the thermally optimal habitat and suitable habitat. Each data point is the summertime average of monthly data from May to August with $\pm 1SD$. For (a) and (b), y-axis represents the vertical extent of the habitat metric (i.e., summertime average = 15 m of suitable habitat in 1993) with the variability from the months of May to August represented in the standard deviation. Trend lines are LOESS smoothed curves. Trends for each month for each variable can be found in Figure S2.

indicating a greater cost of occupying the thermally optimal habitat in May compared to later in the summer.

4 | DISCUSSION

While *Daphnia* abundance has decreased over time in Lake Giles, the vertical distribution of *Daphnia* especially in early summer has become somewhat shallower. Long-term decreases in UV exposure (Williamson et al., 2015) combined with warming surface waters (Pilla et al., 2018) may play an important role in optimising habitat nearer the surface in May (Leech et al., 2005; Williamson et al., 2020), when water temperatures do not reach the critical 25°C threshold. However, in mid to late summer, surface water temperatures become too high, which restricts the surface habitat for *Daphnia*,

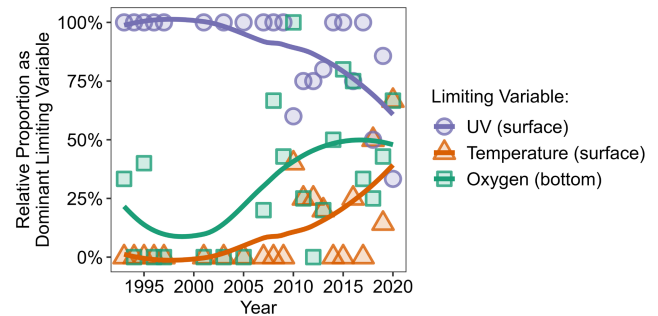


FIGURE 5 Relative frequency that each abiotic variable was the dominant limiting variable of *Daphnia* suitable habitat availability over time in the surface and in the bottom. Surface constraints were UV as the depth of 1% UV penetration at 320nm (purple) or temperature as the 25°C isotherm (orange), and bottom constraints were oxygen as the 3 mg/L isocline indicating deepwater hypoxia (green) or lake bottom (not shown). UV radiation has significantly decreased as a dominant limiting factor, while surface water temperature and deepwater hypoxia have significantly increased in importance. Trend lines are LOESS smoothed curves.

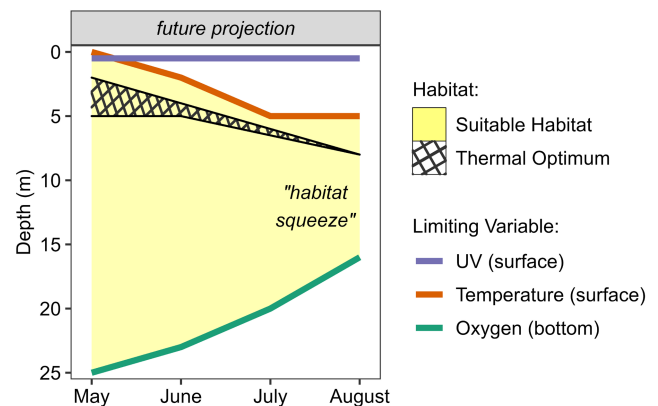


FIGURE 6 Conceptualised future projection of summertime patterns in habitat availability with continued rates of browning for an additional 3 decades (i.e., by c. 2050). Suitable habitat will rarely be limited at the surface by UV radiation (purple), but frequently limited by warm surface water temperatures (orange) for several meters in the surface. Worsening deepwater hypoxia (green) will become increasingly limiting in deeper waters, especially as the summer develops to July and August. As with Figure 3, light yellow area highlights the projected suitable habitat, and crosshatched area indicates the projected thermally optimal habitat.

despite beneficial long-term decreases in UV exposure. Alongside surface water warming, sharp increases in the vertical thermal gradient during the peak stratified period in Lake Giles (Pilla et al., 2018) have led to a decrease or thinning of the thermally optimal habitat in June through August. Several studies have reported trends of longer and stronger summer stratification in lakes (Austin & Colman, 2007; Ayala et al., 2020; Fang & Stefan, 2009; Stetler et al., 2020; Woolway et al., 2017, 2019), and we expect that Lake Giles has experienced a similar response of earlier onset of stratification, later autumn mixing, and consequently longer stratified periods, despite the lack of consistent long-term data outside the summer stratified period.

Hence, the onset of both surface water temperatures $>25^{\circ}\text{C}$ and deepwater dissolved oxygen levels $<3\text{ mg/L}$ is likely to become earlier in the year, with potential implications for *Daphnia* spring bloom timing and corresponding food availability. The increased vertical thermal gradients (Pilla et al., 2018) are also likely to continue to reduce the thermally optimal habitat span, which may effectively disappear in the future (Figure 6), potentially leading to only sub-optimal habitat for *Daphnia* and thereby reduced growth, survival, or reproduction.

Trends in suitable habitat showed general increases over the past 3 decades, suggesting suitable habitat is not a primary cause of the decreasing abundance of *Daphnia*. Increases in suitable habitat were strongly associated with long-term decreases in UV penetration due to lake browning (Williamson et al., 2015), which became a less important limiting factor of suitable habitat over time. As long-term browning has resulted in rapid decreases in UV penetration (Williamson et al., 2015), the in-lake exposure to UV has also decreased. This decrease in UV exposure can benefit UV-sensitive organisms like *Daphnia* (Leech et al., 2005) by reducing DNA damage and mortality (Williamson et al., 1994; Zagarese et al., 1994). However, moderate levels or short-term UV exposure can be beneficial for *Daphnia*, as it can reduce pathogens and parasites (Overholt et al., 2012; Shaw et al., 2020), indicating there may be an optimal UV exposure for *Daphnia*, as is the case for temperature. In contrast, surface water temperature and deepwater dissolved oxygen have become increasingly important for suitable habitat, with occurrences of extremely warm surface temperatures (Pilla et al., 2018) or hypoxic to anoxic deepwater conditions (Knoll et al., 2018) only in recent years. On short-term time frames (i.e., hours), some *Daphnia* can tolerate these increasingly common low deepwater oxygen conditions as a refuge from predation (Tessier & Welser, 1991; Wright & Shapiro, 1990); however, as the vertical extent of these hypoxic and especially anoxic zones increases to shallower depths in the water column, trade-offs between predation refuges, thermal optima, and UV exposure will become very important for *Daphnia*. Other zooplankton or fish taxa that are less tolerant of low oxygen conditions are likely to experience more rapid and serious trade-offs with their habitat selection. These more recent patterns have led to habitat restrictions at both the surface and bottom of the lake that will probably remain important interactive factors influencing vertical habitat availability in the future. As surface water temperatures are expected to continue to warm (O'Reilly et al., 2015; Pilla et al., 2020; Woolway et al., 2020) and deepwater dissolved oxygen concentrations are expected to continue to decline (Jane et al., 2021), suitable habitat may soon decrease, resulting in a future *habitat squeeze* (Craig et al., 2015) for *Daphnia* (Figure 6).

In contrast to suitable habitat, the span of the thermally optimal habitat decreased over time while its overlap with the suitable habitat generally increased. This smaller zone for *Daphnia* to optimise thermal conditions may play a role in the general decrease in *Daphnia* abundance. If inhabiting a smaller thermally optimal zone, *Daphnia* may be forced into higher population densities that could lead to increased intra-specific competition for resources such as

algal food sources, or to a trade-off between thermally optimal conditions and lower population densities. However, the increase in overlap between thermally optimal and suitable habitat suggests that there are fewer trade-offs for *Daphnia* habitat selection between thermally optimal conditions and tolerable levels of UV exposure and dissolved oxygen. For example, during May in the early years of this study, there was no thermally optimal habitat available within the available suitable habitat, which probably forced *Daphnia* into a significant trade-off between selecting a habitat with optimal thermal conditions or one with tolerable UV exposure, but not both. Previous work has shown that *Daphnia* are highly sensitive to UV radiation and avoid high UV exposure during the daytime (Leech et al., 2005). This habitat preference probably forced *Daphnia* into sub-optimal thermal conditions in May, especially in early years when optimal thermal conditions occurred only in areas with very high UV exposure. As this overlap increased both seasonally as the summer develops and over long-term time scales, these potential trade-offs have decreased, allowing *Daphnia* to simultaneously optimise thermal conditions that also have tolerable UV and dissolved oxygen conditions. However, given that sampling was limited only to the daytime, *Daphnia* vertical migration may have mitigated some of these potential trade-offs due to their avoidance of UV and visual predation during the day (Williamson et al., 2011).

One key component that complicates this analysis is the diel vertical migration capabilities of *Daphnia* that are a central part of their diel habitat selection. In many deep lakes, *Daphnia* migrate downward during the daytime to avoid UV exposure and visual predators prevalent near the surface; at night time when these pressures are relieved, they migrate upwards in search of more optimal food availability and thermal conditions (Williamson et al., 2011). Because *Daphnia* were only sampled during the daytime in this study, the assessment of habitat suitability is also limited to daytime, when *Daphnia* are expected to be deeper in the water column. Generally, only a minority of *Daphnia* were present in the epilimnion during the daytime samples throughout this study, as expected. Even though *Daphnia* are not likely to occupy surface waters during the day, the very deep UV penetration in Lake Giles in the 1990s may have forced them into even deeper strata of the lake with cooler temperatures during the daytime. The extreme decreases in UV penetration may have become negligibly important over time in influencing the habitat availability of *Daphnia*, as they are unlikely to inhabit surface waters during the daytime due to their diel migration patterns. At nighttime, UV pressures are relieved, suggesting a greater importance of temperature and dissolved oxygen, plus other biotic variables, as the most key in determining habitat availability and selection. Similarly, our sampling limitations may have underestimated the total daytime *Daphnia* abundance over time if the zooplankters increased their horizontal migration patterns over time, more commonly moving out of the deep pelagic zone on a diel or longer-term basis. The reduction in *Daphnia* abundance in the deep pelagic zone during the day may be due to a true decrease in individuals in Lake Giles, but may also reflect their habitat selection in a horizontal, rather than vertical, direction. For example, shallower littoral areas

can be a predation refuge for zooplankton (Burks et al., 2001) because macrophytes protect them from visual predators and shoreline trees reduce incoming UV. The littoral area may also provide greater food availability (Lauster et al., 2006) and generally have lower variability in abiotic conditions such as temperature and dissolved oxygen (Burks et al., 2002). Hence, we can be confident that the trends in the relative vertical distribution of *Daphnia* are not influenced by raw abundance, but it is possible that reduced *Daphnia* abundance could be linked to using daytime (as opposed to nighttime) sampling. However, the complex interactions amongst the abiotic variables tested here (i.e., the changes in vertical gradients), as well as additional abiotic and biotic variables that influence *Daphnia* populations, are important to consider in understanding the consequences of long-term browning for whole lake ecosystems.

Biotic factors also play an important and dynamic role in *Daphnia* habitat selection and population abundance, and their pressures vary at diel, seasonal, and decadal time scales. One of the many biotic factors that influence *Daphnia* abundance, distribution, and habitat availability is visual predation, which is dependent on light availability (Weidel et al., 2017). In Lake Giles, two metrics of vertical light availability, 10% and 1% PAR penetration depths, have indicated a large decrease in visible light at depth for visual predators as the 10% and 1% light penetration depths have decreased by 7.8 and 6.9 m, respectively, since the early 1990s (Williamson, 2020; Williamson et al., 2020). This decrease in visible light at depth has potentially reduced the area for visual predators such as fish to effectively prey upon *Daphnia*, leading to a potential increase in *Daphnia*'s refuge from visual predation. However, in Lake Giles, young-of-year fish populations have generally increased during browning, thought to be largely driven by decreases in UV exposure and recovering pH (Williamson et al., 2015, 2020). These young-of-year fish that prey on *Daphnia* are almost always found in warm surface waters where visible light is high, and rarely found in cooler, deeper waters (Williamson et al., 2020), suggesting that the vertical distribution of increasing abundance of young-of-year fish is more strongly associated with vertical gradients in temperature than trends in light availability. Hence, the increase in predator abundance alone may be an important influence on *Daphnia* abundance, even though the refuge from visual predation may have increased due to long-term lake browning. Similarly, changes in abundance or distribution of other tactile predators of *Daphnia* may influence their habitat selection. For example, the cyclopoid copepod *Cyclops scutifer* is an invertebrate predator of *Daphnia* that prefers cooler waters (Elgmork, 1967; Johnson et al., 2007). *Cyclops scutifer* abundance has increased in Lake Giles (Williamson et al., 2020) as a result of the increased volume of cooler deep waters (Pilla et al., 2018) that has expanded their habitat. The increase in the abundance of these predators and the potential for predator-prey habitat overlap in deeper waters certainly plays an important, but largely unstudied, role in *Daphnia* habitat selection and optimisation.

Changes in vertical light availability also influence the vertical distribution of phytoplankton, which is a critical food source for *Daphnia*. For example, *Daphnia* have a population boom following

the spring bloom in phytoplankton during May to June, with the high grazing rates on phytoplankton leading to a *clear water phase* (Sommer et al., 2012). This occurs in Lake Giles, as evidenced here by the greater *Daphnia* abundance in May and June compared to the later in the summer. While this seasonal pattern in *Daphnia* abundance is primarily a response to algal food resources early in the summer, previous studies have found no connection between the long-term decrease in *Daphnia* abundance and algal resources due to the lack of change in chlorophyll-*a* concentrations in Lake Giles over time (Williamson et al., 2020). Later in the summer, *Daphnia* populations are regulated by increased predation by fish (Luecke et al., 1990; Sommer et al., 2012), which are increasing in Lake Giles (Williamson et al., 2015). As with vertical distribution of *Daphnia* and their vertical habitat availability, the vertical distribution of algal food resources is likely to be responsive to long-term browning in Lake Giles. The depth of the chlorophyll maximum (a proxy for algal biomass peak) is related to penetration of PAR and to thermocline depth (Leach et al., 2018), both of which becoming shallower in Lake Giles (Pilla et al., 2018; Williamson et al., 2015). As PAR penetration and thermocline depths become shallower due to browning, the algal peak would be expected to become shallower over time as well, and as a primary food resource, may play a role in the shallower vertical distribution of *Daphnia* (Williamson et al., 1996). Furthermore, long-term browning has the potential to alter phytoplankton community composition (i.e., from diatom to cyanobacteria dominated) and corresponding food quality for zooplankton grazers such as *Daphnia* (Senar et al., 2021); however, the long-term monitoring at Lake Giles does not include such measurements to assess the role of browning on algal food quality. These interactions between abiotic and biotic variables in browning Lake Giles suggest complex drivers of suitable vs. optimal habitat and the associated trade-offs for *Daphnia* populations.

Daphnia abundance, vertical distribution, and suitable habitat are responsive to both abiotic and biotic interactions at seasonal to long-term time scales. While critical thresholds in water temperature and deepwater dissolved oxygen for *Daphnia* survival have only been reached in the past 10 years in Lake Giles, global studies of long-term trends suggest continued warming of surface waters (O'Reilly et al., 2015; Pilla et al., 2020; Woolway et al., 2020) and decreased deepwater dissolved oxygen levels (Jane et al., 2021) that may lead to a future oxy-thermal *habitat squeeze* (Craig et al., 2015) for *Daphnia* (Figure 6). Similar implications for thermally optimal habitat are likely as vertical thermal gradients become stronger (Pilla et al., 2018), possibly leaving little to no zone within the thermally optimal temperature range for *Daphnia*. In such cases, *Daphnia* will be forced into sub-optimal conditions of one or more abiotic variables that can influence their growth, reproduction, or survival. In addition, biotic factors that are also influenced by reduced light penetration will influence *Daphnia* habitat selection and associated trade-offs, potentially leading to reduced visual predation despite greater predator abundance and changes in vertical distribution of algal food resources.

Understanding these factors influencing *Daphnia* habitat selection will have important implications for zooplankton population dynamics that ultimately influence lake food web dynamics, ecosystem function, and important ecosystem services including fisheries and water quality.

AUTHOR CONTRIBUTIONS

R.M.P. conceived the idea for the manuscript, compiled the data, conducted analysis, and wrote the manuscript. C.E.W. contributed comments, wrote text, and edited all drafts.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The datasets for limnological and zooplankton variables analysed in this study are freely available at the Environmental Data Initiative (Williamson, 2020). [10.6073/pasta/b1754d3a6b09df0f83976458ceb4b107](https://doi.org/10.6073/pasta/b1754d3a6b09df0f83976458ceb4b107).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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