



Concurrent warming and browning eliminate cold-water fish habitat in many temperate lakes

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Cold-water species in temperate lakes face two simultaneous climate-driven ecosystem changes: warming and browning of their waters. Browning refers to reduced transparency arising from increased dissolved organic carbon (DOC), which absorbs solar energy near the surface. It is unclear whether the net effect is mitigation or amplification of climate warming impacts on suitable oxythermal habitat (<20 °C, >5 mgO/L) for cold-loving species because browning expands the vertical distribution of both cool water and oxygen depletion. We analyzed long-term trends and high-frequency sensor data from browning lakes in New York's Adirondack region to assess the contemporary status of summertime habitat for lacustrine brook trout. Across two decades, surface temperatures increased twice as fast and bottom dissolved oxygen declined >180% faster than average trends for temperate lakes. We identify four lake categories based on oxythermal habitat metrics: constrained, squeezed, overheated, and buffered. In most of our study lakes, trout face either seasonal loss (7 of 15) or dramatic restriction (12 to 21% of the water column; 5 of 15) of suitable habitat. These sobering statistics reflect rapid upward expansion of oxygen depletion in lakes with moderate or high DOC relative to compression of heat penetration. Only in very clear lakes has browning potentially mitigated climate warming. Applying our findings to extensive survey data suggests that decades of browning have reduced oxythermal refugia in most Adirondack lakes. We conclude that joint warming and browning may preclude self-sustaining cold-water fisheries in many temperate lakes; hence, oxythermal categorization is essential to guide triage strategies and management interventions.

lakes | cold-water habitat | browning | climate change | oxythermal squeeze

Temperate lakes are home to numerous organisms that rely on year-round access to cold water (1), including salmonid fishes (trout, salmon, and whitefish) with high economic and recreational value (2). During the warm season, cold-water specialist species are largely excluded from surface waters, instead retreating downward in the water column to find suitably cool temperatures (1). These species also require high dissolved oxygen concentrations, which become depleted at the bottom of many lakes during the summer (3). Elimination of suitable oxythermal habitat (both low temperature and high oxygen), even if it occurs during only extreme years, could extirpate cold-water species from lakes due to lack of dispersal pathways for recolonization (4).

Two profound changes are underway in temperate lakes worldwide, leading to reduced availability of suitable oxythermal habitat for cold-water species. As a result of climate change, the surface of most lakes around the world is warming at least as fast as the overlying atmosphere (5). For cold-water animals, warming trends signify greater habitat restriction during the summer, potentially resulting in forced exposure to temperatures that exceed their physiological preferences, increase their metabolic rates, and may even become lethal (6). At the same time, many temperate lakes are experiencing a phenomenon called “browning,” or increased loading of dissolved organic carbon (DOC) from the surrounding landscape (7, 8). These plant-derived compounds absorb sunlight, reducing heat penetration into deep waters (9). Thus, brown lakes are warmer at the surface (10), but average temperatures throughout their volume are cooler (11). As a result, lakes that experience both warming and browning may have increased volume of thermally suitable habitat for cold-water organisms despite rapid surface warming.

Alternatively, concurrent warming and browning may limit suitable oxythermal habitat by decreasing deep-water oxygen concentrations (12, 13). Surface warming results in a longer period of seasonal thermal stratification (14). During stratification, warm surface waters overlies cool bottom waters due to differences in water density (15), and the non-linear temperature–density relationship allows climate warming to amplify the strength and seasonal duration of the boundary between layers (16). Surface waters are typically well oxygenated due to both atmospheric exchange and primary production (17), whereas

Significance

Lake surface waters are warming worldwide, and many lakes are simultaneously experiencing increasing dissolved organic carbon loading. This “browning” traps heat at the surface, expanding deep-water thermal refuges for cold-loving species. However, browning can deplete dissolved oxygen, potentially making thermal refugia uninhabitable. Our analysis reveals that late summer oxythermal habitat availability is closely correlated with dissolved organic carbon concentrations. Browning-induced deoxygenation of bottom waters outpaces expansion of cool-water habitat in most lakes, thereby squeezing cold-loving organisms between inhospitable layers. For cold-water organisms such as salmonid fishes, the oxythermal squeeze arising from warming surface waters and declining bottom-water oxygen represents an existential threat to population persistence.

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bottom waters often experience oxygen depletion during prolonged stratification due to their isolation from sources of oxygen (18, 19). Browning enhances stratification by simultaneously warming surface waters and cooling deep waters, which increases their disparity in density (20). In addition, browning provides additional organic carbon that fuels microbial respiration (20), leading to increased biological oxygen demand in the water column (21). Finally, by decreasing penetration of photosynthetically active radiation, browning shades phytoplankton and benthic algae (22). Consequently, primary production in browning lakes becomes constrained to near-surface depths where sufficient light is available (23, 24), and photosynthetic production of new dissolved oxygen well below the surface is eliminated relative to clear lakes. Therefore, DOC loading can reduce deep-water dissolved oxygen through multiple pathways (13).

For cold-water organisms, the combination of warming surface waters and declining bottom-water oxygen concentrations can lead to an oxythermal squeeze that may threaten population persistence (1). This mechanism has been implicated in mass mortality (25) and even extirpation of species from lakes in the southern portion of their ranges, particularly when eutrophication has enhanced oxygen depletion at the bottom (26, 27). Modeling studies suggest that these problems will be amplified by continued warming (28, 29). In short, the depths of a lake can only serve as a warm-season refuge for cold-water specialist species if they remain adequately oxygenated.

It is important to resolve whether browning mitigates impacts of surface warming by expanding the depth range of cold-water habitat, or instead exacerbates suitable oxythermal habitat loss by depressing deep-water dissolved oxygen. Here, we use the thousands of Adirondack lakes of New York as a representative system to study the implications of concurrent warming and browning for the amount of the water column that is habitable during the summer for brook trout (*Salvelinus fontinalis*), one of many valuable fishery species that require year-round access to cold, well-oxygenated water. These species have suffered numerous extirpations due to acid deposition, habitat degradation, and non-native predatory fishes (30–32). Overlaid upon those historical and ongoing stressors, many Adirondack lakes are undergoing pronounced long-term browning in addition to the broader trend of surface warming (33, 34). DOC concentrations and water color are closely associated in Adirondack lakes; increases in chromophoric dissolved organic matter (CDOM) are associated with DOC increases (35). We calculated trends in temperature, oxygen, and DOC using long-term records from 28 Adirondack lakes and compared rates of change to average trends reported for a broad set of temperate lakes (12). We then used high-frequency sensors in 15 lakes to quantify habitat volume suitable for brook trout across the warm season and synthesized a wide range of lake variables to categorize these lakes based on oxythermal habitat dynamics. Finally, we applied these resulting models to historical data from a survey of 1,468 Adirondack lakes in the 1980s, enabling us to predict the present-day relative abundance of lakes in each category of oxythermal habitat availability. Together, these approaches were designed to elucidate the net impact of joint browning and warming upon suitable oxythermal habitat for brook trout within a lake, and to summarize the management challenges ahead for a region where cold-water fisheries are central to cultural identity and economic prosperity.

Methods

Long-Term Trends in Surface Temperature, Deep-Water Dissolved Oxygen, and DOC. We calculated long-term trends in late-summer surface-water temperature, deep-water dissolved oxygen, and surface DOC using data

from 28 lakes during the period 1994 to 2012 (drawn from ref. 36). Water color was tightly coupled to DOC concentrations but not nutrients in these lakes (*SI Appendix, Fig. S1*), indicating that DOC increases reflect lake browning. We interpolated profiles at 0.5 m intervals in the period July 15 to August 30 of each year using the `pchip` function of the R package `pracma` (37). For each profile, we identified the top and bottom of the metalimnion, a layer of rapidly declining water temperature between warm surface waters and cool deep waters, using the `meta.depths` function of the R package `rLakeAnalyzer` (38). We then took the average temperature values across depths within the warm layer overlying the metalimnion (i.e., the epilimnion), and averaged these across profiles in the defined period for each year. Most (21 of 28) lakes had a well-defined cool-water zone below the metalimnion (i.e., hypolimnion), and stratification was observed in every vertical profile. We calculated the average dissolved oxygen concentration across depths within the hypolimnion for each profile and then averaged these across all profiles for each year. Lakes had 10 to 18 y of epilimnetic temperature observations (median 15) and 11 to 18 of hypolimnetic dissolved oxygen observations (median 16). To quantify trends in late-summer surface DOC concentrations, we averaged 1 to 2 measurements per lake per year ($n = 19$ y for every lake). These and all subsequent analyses were conducted in the R statistical programming environment (39). R scripts can be accessed at <https://doi.org/10.5281/zenodo.10019433>.

We used linear mixed effects models in the R package `nlme` (40) to calculate long-term trends in surface temperature, deep-water dissolved oxygen, and surface DOC. We fitted the rate of change across all years and accounted for lake identity by fitting a random slope and intercept for each lake. We centered the year value to remove correlation between the intercept and slope (41). We confirmed homogeneity of variance and normally distributed errors prior to fitting linear trends in temperature and oxygen. For DOC, there was a clear funnel pattern in the residuals, so we removed two major outliers and $\ln$ -transformed the concentration data in order to satisfy model assumptions.

Detailed Characterization of Oxythermal Conditions. We analyzed high-frequency sensor data from 15 additional Adirondack lakes where we conduct long-term research on brook trout populations. These lakes are surrounded by heavily forested watersheds with minimal land cover modification and range widely in surface area (from 5.37 to 333.78 ha) and maximum depth (4.5 to 57.9 m; *SI Appendix, Table S1*). They are generally dimictic, but three lakes (Panther, Lower Sylvan, and Rock Lake) are considered polymictic because winds break down stratification periodically during the warm season. High DOC is associated with wetland extent in the surrounding watershed (*SI Appendix, Table S1*). All study lakes supported populations of brook trout, and natural recruitment occurs in all but two of them. Populations are supplemented by stocking in seven of the intensively studied lakes, while the other eight have not been stocked with brook trout for at least a decade (Little Moose, First Bisby, Panther, Rock Lake, East, Wilmurt, Honnedaga, and Lower Sylvan). Two larger lakes (Little Moose and First Bisby) have introduced populations of smallmouth bass that appear to constrain brook trout population size (42).

We characterized the vertical distribution of temperature and oxygen from June 16 to October 15 of 2021 using a chain of high-frequency temperature and dissolved oxygen loggers in each lake [*SI Appendix, Table S2*; (43)]. We supplemented these with occasional vertical profiles at 0.5 m intervals using a YSI 550a probe or a YSI EXO2 multiparameter sonde. Additional details of field sampling are provided in *SI Appendix*.

We combined the high-frequency sensor and profile data using a series of smoothing and interpolation procedures to produce a grid of temperature and dissolved oxygen data at 6-h time intervals and 0.1 m depth intervals from the surface to the bottom for each lake. Individual temperature and dissolved oxygen profiles were interpolated at 0.1 m depth intervals using the `pchip` function of the R package `pracma` (37). Additional information about interpolation procedures is provided in *SI Appendix*.

Using the gridded dissolved oxygen and temperature data, we assigned each depth/time combination to one of three habitat conditions: suitable, stressful, and unsuitable. We considered any point with dissolved oxygen >5 mg/L and temperature <20 °C to be suitable based on studies of brook trout tolerances for dissolved oxygen (44–46) and temperature (47–52). Temperatures between 20 and 23 °C were considered stressful, and either temperatures ≥ 23 °C or oxygen concentrations ≤ 5 mg/L were considered unsuitable. We based the 23 °C

threshold on the absence of brook trout from streams where average temperatures exceeded 23 °C for a week or more (48). These thresholds match habitat selection data from tagged brook trout in two of the study lakes, which demonstrate strong (>93%) and near complete (>98%) avoidance of the large proportion of available habitat where the water temperatures exceed 20 and 23 °C, respectively (*SI Appendix, Fig. S2*).

Based on the temperature and oxygen thresholds discussed above, we calculated a suite of metrics to describe the oxythermal habitat conditions for trout in each intensively monitored lake (*SI Appendix, Table S3*). We calculated two metrics meant to represent the oxythermal squeeze, which we consider the point at which organisms experience the greatest joint constriction of suitable temperatures and oxygen concentrations. Minimum proportion suitable (MPS) is the minimum proportion of the water column in the suitable category during the warm season. Minimum volume suitable (MVS) is the corresponding proportion of the total lake volume that is suitable. We consider MPS and MVS to be measures of potential for brook trout to avoid acute exposure to stressful habitat. We also calculated two metrics quantifying chronic exposure to suboptimal habitat. Consecutive days stressful (CDS) is the minimum number of consecutive days that the entire water column is stressful without an intervening period of relief. Total days stressful (TDS) is the total number of days the entire water column is stressful. In some lakes, even though there may always be suitable habitat available during the warm season, most of the water column may be in the stressful or unsuitable category. We calculated a metric intended to capture the total amount of the water column that is inhospitable during the high-stress months of July and August. We modeled this after Nürnberg's anoxic factor, the number of days in a period where a sediment area equivalent to the surface area of a lake is anoxic (53). We call this metric seasonal percentage inhospitable (SPI). Formulas for the MPS, MVS, and SPI metrics are presented in *SI Appendix*.

Finally, we calculated two established metrics used to quantify oxythermal conditions. T_{D05} is the minimum temperature in the water column where dissolved oxygen exceeds a concentration of 5 mg/L (1). We calculated T_{D05} for each time step, and used the peak value over the monitoring period for each lake. If dissolved oxygen for a given time point was never ≤ 5 mg/L, we used the minimum temperature in the water column, indicating that organisms could access this temperature. Cumulative oxythermal stress dosage (COSD) incorporates both duration and degree of exceedance of the temperature threshold (29). T_{D05} for each day is used to calculate the degrees of exceedance (°C) of the threshold, and these daily exceedance values are summed across the study period. We calculated this metric twice: once for a 20 °C threshold (COSD₂₀) and once for a 23 °C threshold (COSD₂₃).

This suite of oxythermal habitat metrics for each lake provides a quantitative counterpart to our suitable-stressful-unsuitable ratings. Initial inspection of these metrics suggested that lakes could be grouped into qualitative categories based on similarity of oxythermal habitat dynamics.

Principal Component Analysis of Associated Oxythermal Habitat Availability across Lakes. To elucidate patterns of oxythermal habitat conditions that integrate across stress metrics and associated lake characteristics, we conducted a principal component analysis (54). We included all nine calculated oxythermal habitat metrics for the 15 lakes (*SI Appendix, Table S4*), as well as lake surface area and maximum depth. In addition, we expected DOC to play a special role in engendering oxythermal stress, so we included both DOC concentrations and the proportion of the riparian zone classified as wetland cover (within 100 m of shore, which often serves as a potent source of DOC) (20). We scaled all variables to have unit variance. We retained principal components having eigenvalues greater than one and prior to the "elbow" in a scree plot. PCA was performed using the R function `prcomp` and results were plotted using the `fviz.pca` biplot function of the `factoextra` package (55). The results of the PCA were used to evaluate whether there are discrete syndromes of oxythermal habitat conditions and lake characteristics and to confirm our qualitative categorization of lakes in terms of the continuous availability of suitable oxythermal habitat for brook trout throughout the warm season.

Relationship between DOC and Oxythermal Habitat Boundaries. To evaluate how browning may affect oxythermal habitat conditions, we compared the depth boundaries of high-temperature and low-oxygen conditions to DOC concentrations across our 15 intensively monitored Adirondack lakes. For temperature, we focused on the maximum depth where temperatures reached ≥ 20

°C during our monitoring period. Browning should extend suitably cold temperatures (Z_{temp20}) toward the surface (9), but light absorption and associated heat trapping should plateau at high DOC concentrations (DOC; 56). Thus, we estimated the parameters (a and r) of a negative exponential model,

$$Z_{temp20} = a * e^{(r * DOC)}.$$

For dissolved oxygen, we used linear regression to quantify how the minimum depth where concentrations were ≤ 5 mg/L (Z_{oxy5}) scaled with DOC. This analysis excluded polymictic lakes where dissolved oxygen is periodically reset, as well as very deep lakes (>30 m) having little hypoxia.

To examine whether our findings apply to other temperate geographic locations, we explored the relationship between DOC and dissolved oxygen/temperature in lakes from the NTL-LTER site in northern Wisconsin and the Poconos region of Pennsylvania. We selected these locations because these lakes have a history of limnological studies that provide extensive data (13, 57), and because they are in protected watersheds where confounding from agricultural and urban nutrient runoff is likely to be minimal. The available temperature and oxygen data are from periodic profiles rather than submerged, high-frequency sensors and have already been interpolated at 0.1-m intervals (available at ref. 58). We used the most recent five years of record for these lakes, which was available from six lakes in Wisconsin and two in Pennsylvania. We calculated the depth boundaries of warm temperatures and low oxygen during the August profile as described earlier, and averaged across the five-year record. For DOC, we averaged surface concentrations during July and August for the same period.

Estimating the Frequency of Oxythermal Habitat Categories across Adirondack Lakes. To achieve a more comprehensive regional perspective, we applied our findings on browning rates and oxythermal habitat boundaries to a database of 1,468 Adirondack lakes surveyed between 1984 and 1987 (Adirondack Lakes Survey Corporation: <https://www.adirondacklakessurvey.org>). First, we assigned each lake to one of four lake categories that emerged from our analysis (see below and *Results*). For lakes having DOC data ($n = 1,467$), we approximated modern-day concentrations by augmenting 1980s concentrations by four times the average decadal rate of increase quantified from the 28 lakes for which long-term DOC trends were available. Then, we applied our fitted equations from the 15 intensively monitored lakes to estimate the present-day depth boundaries of high-temperature and low-oxygen conditions. All lakes whose depth exceeds 30 m were categorized as buffered because cold-water species are unlikely to be limited in their access to suitable oxythermal habitat. We categorized lakes where the maximum depth ≥ 20 °C exceeded the maximum lake depth as overheated (see descriptions below). Lakes where the depth difference between 20 °C and 5 mg/L dissolved oxygen boundaries was ≤ 0.2 m were categorized as squeezed. All other lakes were considered constrained because they sustain a limited layer of cold, oxygenated water throughout the warm season. We also calculated the percentage of constrained lakes that had low DOC concentrations (< 5 mg/L), since the effects of further browning are especially nonlinear in relatively clear lakes. Applying the same categorization process to oxythermal habitat availability estimated from 1980s DOC concentrations enabled us to evaluate the proportion of Adirondack lakes that have changed category due to browning alone.

Results

There was a significant long-term increase in surface water temperatures across the 28 Adirondack lakes studied from 1994 to 2012 ($P < 0.001$). Temperatures warmed at 1.26 °C decade⁻¹ (95% CI 0.95 to 1.56 °C decade⁻¹). There was a significant long-term decline in deep-water dissolved oxygen ($P = 0.001$). Oxygen declined at a rate of 0.85 mg/L decade⁻¹ but CIs were large (95% CI 0.34 to 1.35 mg/L decade⁻¹).

These 28 lakes experienced significant browning as well ($P < 0.001$). DOC increased on average 1.11 mg/L across lakes over the period 1994 to 2012 or 0.58 mg/L decade⁻¹. Fitting lake-specific deviations from the overall rate of change demonstrated that all but one lake exhibited increasing DOC, and several increased far more rapidly than the norm (*SI Appendix, Fig. S3*).

Intensive monitoring of 15 lakes revealed four qualitative categories of oxythermal habitat availability during the height of the warm season, which we call “buffered”, “constrained”, “squeezed”, and “overheated” (Figs. 1 and 2). Buffered lakes were deep (>30 m) with large surface areas, and they maintain large volumes of suitable habitat (high MPS and MVS) throughout the study period with little to no hypoxia (Fig. 2 and *SI Appendix, Table S4*). T_{DO5} was always well below the preferred temperature of brook trout, and seasonal percentage inhospitable (SPI) was low. Constrained lakes always maintained cool oxygenated habitat, but this was restricted to a relatively narrow band between warm surface waters and hypoxic deep waters (Fig. 1*A* and *SI Appendix, Table S4*). Constrained lakes, although never forcing organisms into stressful conditions, had a relatively small minimum proportion of the water column (12 to 21%) within the stress-free oxythermal range (low MPS). The proportion of volume (MVS) that met brook trout needs in constrained lakes was as low as 6%, but T_{DO5} was usually close to their preferred temperature. However, SPI in these lakes could be high, ranging from 63.25% up to 89.49%. Squeezed lakes had little to no habitat falling into suitable temperature and oxygen ranges at the seasonal oxythermal bottleneck, primarily due to deoxygenation of bottom waters. These lakes usually had at least one period when warm surface temperatures intersected hypoxic deep waters (Fig. 1*B* and *SI Appendix, Table S4*). All but one squeezed lake had MPS of 0, with one being at 0.01, representing a minimum absolute volume of 7,533.5 m³. Except for one lake, these lakes had periods where cold-water specialist species were forced into stressful conditions. All squeezed lakes had high T_{DO5} , the lowest being just under the 20 °C stressful threshold (19.84 °C) while the highest was 25.62 °C. The latter lake had the highest COSD₂₀ value of all lakes (291.53 °C). Overheated lakes experienced little to no anoxia due to periodic mixing that reset oxygen, yet unlike squeezed lakes, they had long durations of time where the entire water column was thermally stressful. In these lakes, brook trout would have to endure between 10 and 30 successive days without relief from heat stress, and up to 46 stressful days per year (Fig. 1*C* and *SI Appendix, Table S4*). For all of these lakes, T_{DO5} was high (22.03 to 23.91 °C), and seasonal percentage of inhospitable habitat (SPI) was close to 100% (91.71 to 98.51%).

PCA of our nine oxythermal habitat availability metrics supports the qualitative delineation of four lake categories (Fig. 3). We

retained three principal components, together explaining 91.3% of variance (PC1-59.5%; PC2-18.2%; PC3-13.6%; *SI Appendix, Table S5*). PC1 strongly contrasted buffered lakes (First Bisby, Little Moose, and Honnedaga) against overheated lakes (Panther, Lower Sylvan, and Rock Lake) and was positively associated with maximum depth and suitable oxythermal habitat availability at the most stressful time of the year such that buffered lakes showed high MPS and MVS (Fig. 3 and *SI Appendix, Table S5*). The result was a large minimum absolute volume of cool oxygenated habitat. In contrast, overheated lakes were associated with long durations and large amounts of stressful conditions (high MDS, TDS, SPI, and T_{DO5}). While Pico was also in this category, it separated from these lakes along PC3, which was associated with DOC and COSD₂₃. For PC2, negative associations with TDS and COSD₂₀ were responsible for the highest loadings.

Across our intensively monitored Adirondack lakes, DOC concentrations were a strong predictor of the maximum depth ≥ 20 °C ($P < 0.001$ for both coefficient and exponent; Fig. 4*A*), and the exponential model explained most of the variance across lakes ($R^2 = 0.84$). The final fitted equation was:

$$Z_{\text{temp}20} = 10.49 * e^{(-0.16 * \text{DOC})}$$

As expected, the effect of DOC on the warm-water boundary was steep at low concentrations but then plateaued at higher DOC. In low-DOC lakes, this thermal stress depth was 6.2 m on average, while it was reduced to roughly 2 m in the highest-DOC lake.

The minimum depth of dissolved oxygen ≤ 5 mg/L was strongly negatively related to DOC concentrations (slope = -0.75; $P < 0.001$; $R^2 = 0.85$). In lakes with high DOC, this boundary depth was close to the surface (~1 m), while it extended to 7.4 m in low-DOC lakes (Fig. 4*B*).

Profiles of water temperature and dissolved oxygen in lakes of Wisconsin and Pennsylvania showed comparable dependence of warm-temperature and low-oxygen boundaries upon DOC concentrations as we observed in our intensively monitored Adirondack lakes (Fig. 4*A* and *B*). Indeed, even the differences in the functional form of the relationships were similar across lake districts. Two Wisconsin lakes had higher DOC concentrations (14.3 and 20.5 mg/L) than our intensively monitored Adirondack lakes, leading to August hypoxia extending very near the surface

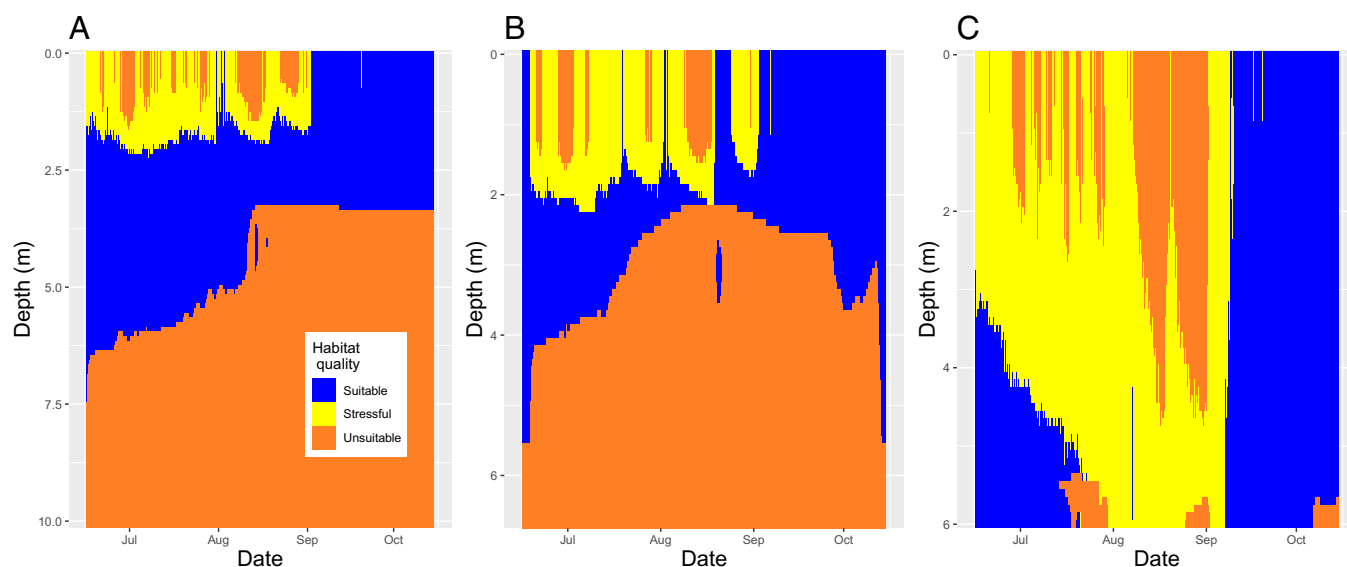


Fig. 1. Examples of three out of the four cold-water habitat categories: (A) constrained, (B) squeezed, and (C) overheated. Buffered lakes are not shown.

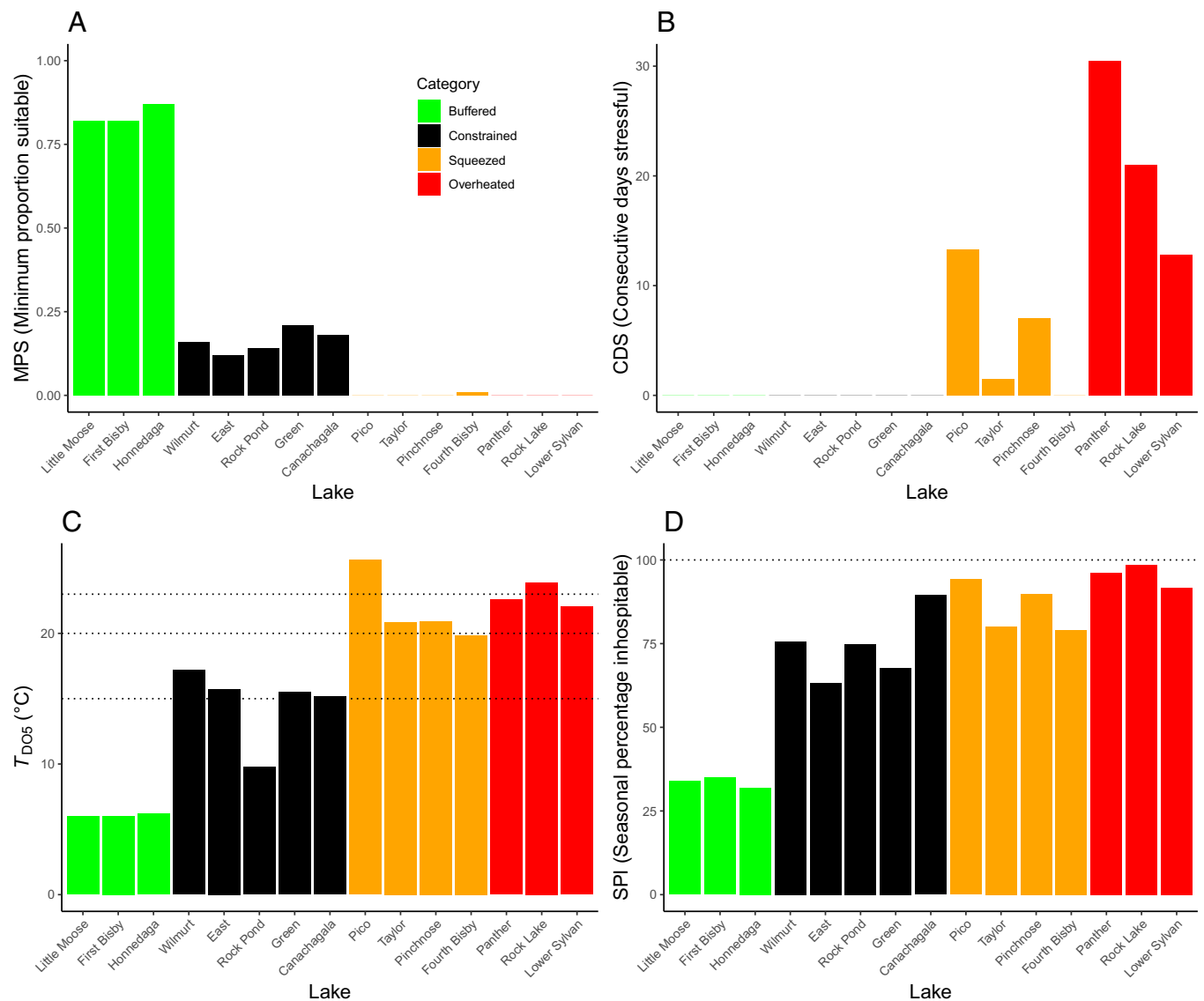


Fig. 2. Plots of select cold-water habitat metrics color coded by lake category (buffered, constrained, squeezed, and overheated): (A) minimum proportion suitable (MPS), (B) consecutive days stressful (CDS), (C) T_{DO5} with dotted horizontal lines at 15, 20, and 23 °C, and (D) seasonal percentage inhospitable (SPI) with the dotted line at 100%.

(1.2 and 0.9 m). Conversely, several Wisconsin lakes had lower DOC concentrations than any of our focal lakes, and their low-oxygen boundaries were correspondingly deep (up to 18.5 m); although they were also deeper than most Adirondack lakes (~20 m; Fig. 4C). Similarly, the downward penetration of temperatures ≥ 20 °C closely followed the negative exponential pattern observed in our intensively monitored Adirondack lakes (Fig. 4A), yielding stressful thermal conditions much deeper in low-DOC lakes (up to 10.0 m) than high-DOC lakes (as little as 0.9 m).

Only six of 1,468 lakes surveyed in the 1980s exceeded 30 m in depth (Fig. 4C). DOC concentrations were available from 1,467 of these lakes (Fig. 4D). Applying our fitted equations to estimate modern-day DOC in these lakes suggests that no more than 1.45 m of the water column would retain suitable oxythermal habitat for brook trout (mean max depth = 6.5 m). Categorizing each of these lakes by using its estimated DOC concentration and maximum depth to predict oxythermal habitat constraints during the warm season suggests that Adirondack lakes in general are far less likely to be buffered than our 15 intensively monitored lakes (0.4% vs. 20.0%; Fig. 4E). The proportions of overheated (21.7%

vs. 20%) and squeezed (25.8% vs. 26.7%) lakes are similar between these two sets of lakes, but far more fall into the constrained category in the broad survey (52.1% vs. 33.3%). Only 71 of the 764 lakes in the constrained category are estimated to have low contemporary DOC concentrations (4.8% of 1,467 lakes). Comparing lake oxythermal categorizations based on 1980s measurements vs. present-day estimates suggests a large number of lakes have moved from overheated (35.7% vs. 21.7%) to squeezed (15.0% vs. 25.8%; *SI Appendix, Table S6*) in recent decades. Although the number of lakes in the constrained category changed only slightly overall (48.9% vs. 52.1%), browning has reduced low-DOC constrained lakes from 23.4% to only 4.8% of surveyed lakes (*SI Appendix, Table S6*).

Discussion

We find that the benefits of browning for brook trout and other cold-water species from reduced penetration of surface warming are generally outweighed by losses of suitable oxythermal habitat due to enhanced deep-water oxygen depletion. In lakes with low DOC,

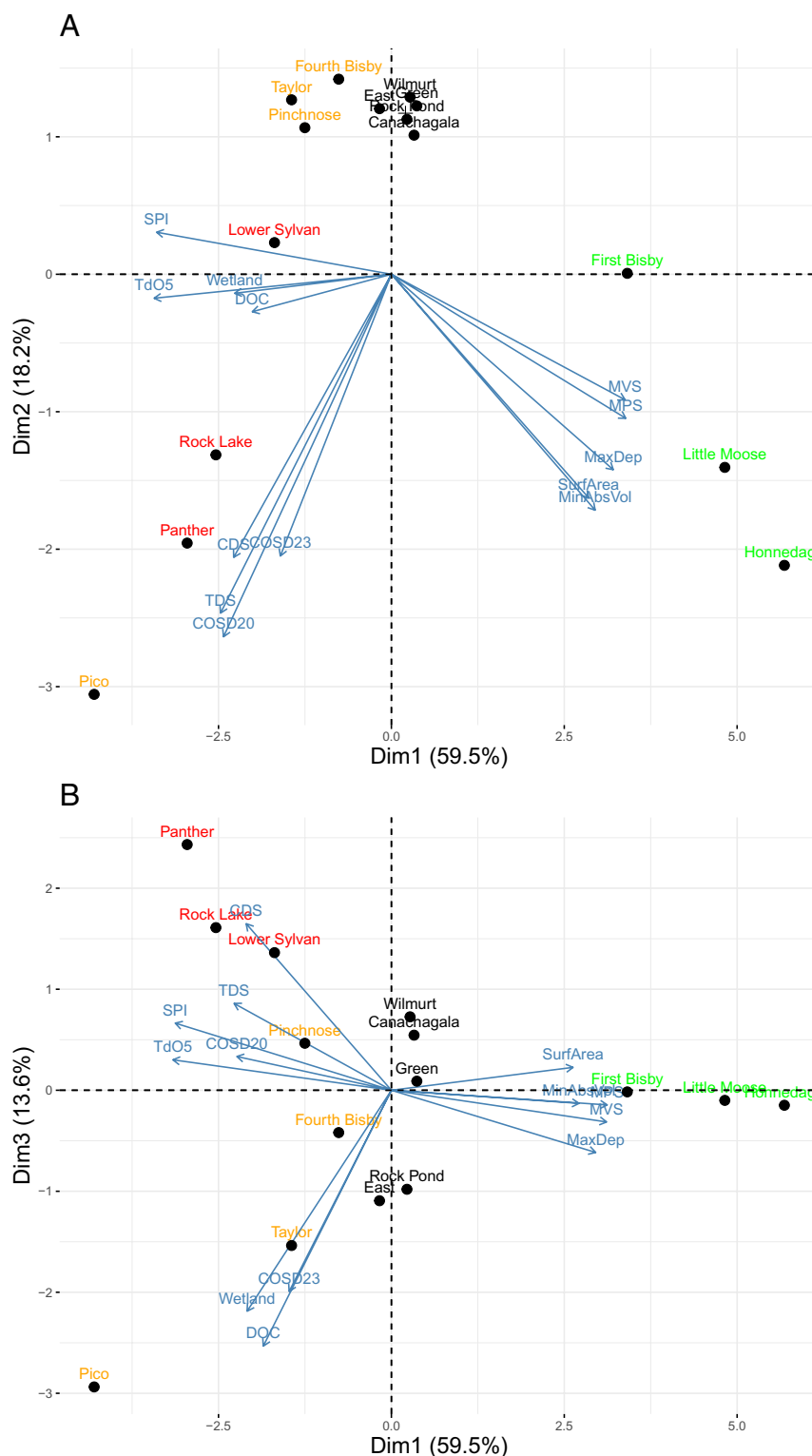


Fig. 3. Results of principal component analysis of lake attributes, depicting (A) principal components one and two (B) principal components one and three. Each point represents one of the 15 lakes. Lake names are color coded according to oxythermal habitat category: buffered, green; overheated, red; squeezed, orange; and constrained, black. Axes represent the individual principal components with percentage of variance explained in parentheses. The length of blue vectors corresponds to the relative correlation of individual variables to the corresponding principal component. SPI, seasonal percentage inhospitable; TdO5, T_{DO5} ; MVS, minimum volume suitable (percentage); MPS, minimum proportion suitable; TDS, total days stressful; CDS, consecutive days stressful; COSD20, cumulative oxythermal stress dosage (20 °C threshold); COSD23, cumulative oxythermal stress dosage (23 °C threshold); Wetland, percentage of wetlands in surrounding watershed; DOC, DOC concentration; MaxDep, maximum lake depth; SurfArea, lake surface area; MinAbsVol, minimum volume of suitable habitat during the season.

browning may help mitigate against climate warming because expansion of cool-water volumes outpaces expansion of hypoxic volumes. However, at even moderate DOC concentrations, the increase in

hypoxia begins to exceed thermal benefits, especially in shallow lakes. Thus, combined warming and browning is certain to have already severely reduced the oxythermal habitat available to cold-dwelling

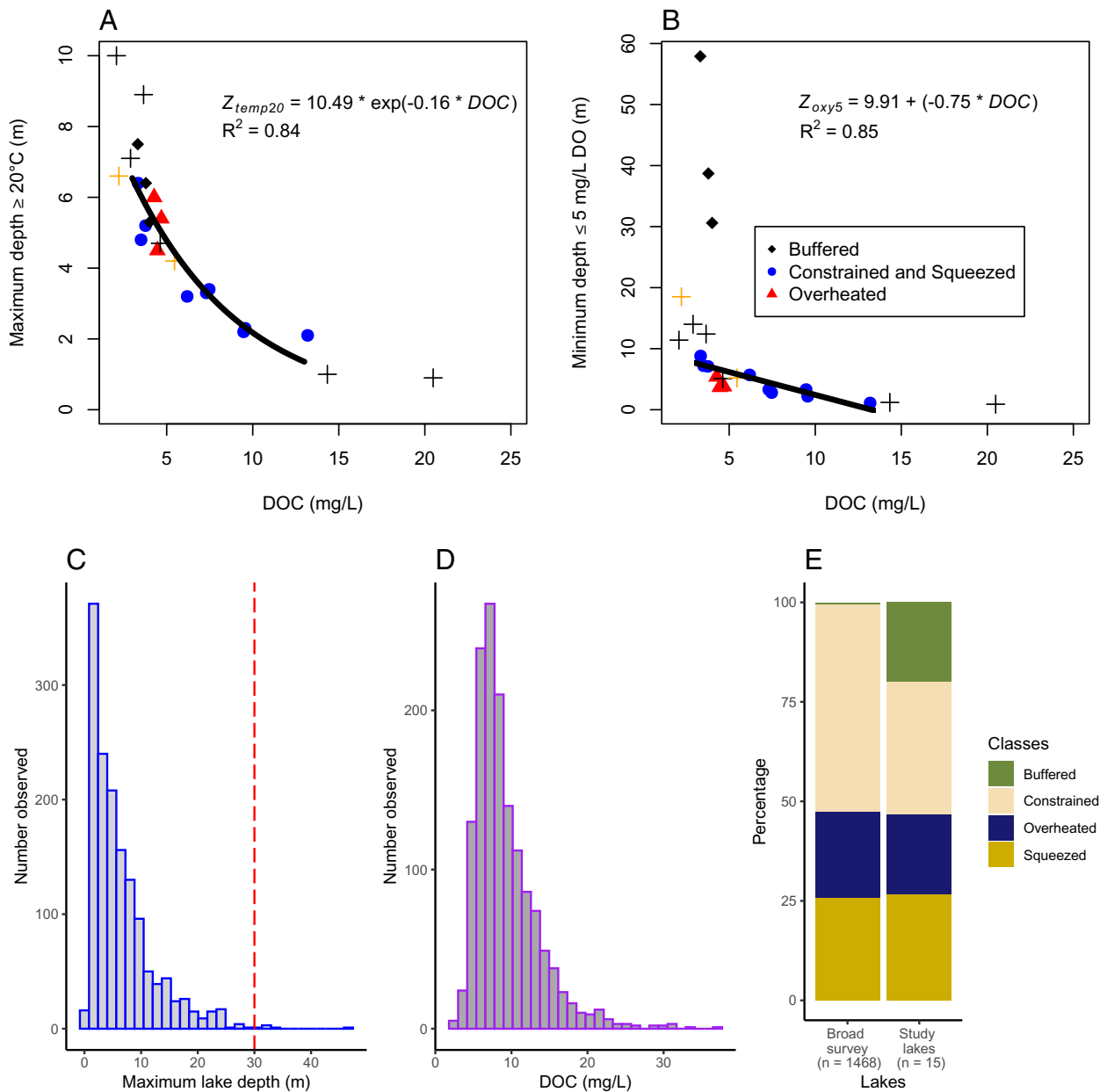


Fig. 4. Relationship between (A) the maximum depth in the water column over the season that temperatures were $\geq 20^{\circ}\text{C}$ and DOC concentration. Solid plot characters represent intensively monitored Adirondack lakes while crosses represent Wisconsin (black) and Pennsylvania (orange) lakes. The regression line is fitted to all Adirondack lakes only. (B) The shallowest depth over the season that dissolved oxygen was $\leq 5\text{ mg/L}$. The regression line is fitted only to constrained and squeezed Adirondack lakes. (C) Distribution of maximum depths in 1,468 Adirondack lakes. The dashed red line indicates 30 m where lakes are likely to be in the buffered category. (D) Distribution of DOC concentrations in 1,467 Adirondack lakes. (E) Percentages of lakes in the oxythermal habitat categories in the 1,467 lakes (ALSC) and the 15 lakes monitored with high-frequency sensors.

organisms in most Adirondack lakes. This combined threat is likely to be exacerbated in the future, and only the deepest lakes are likely to contain robust oxythermal refuges in the decades ahead.

The rates of change in surface temperature, bottom oxygen, and surface DOC of Adirondack lakes are relatively rapid and have surely caused substantial biological impacts. For example, prior work in one of our polymictic overheated lakes demonstrated a negative relationship between annual brook trout reproductive activity and both air and bottom-water temperature across an 11-y observation period. One particularly warm year resulted in the population losing an entire year class (49). Browning-induced heat trapping at the surface of Adirondack lakes has led to surface warming rates more than double the average rates reported for temperate lakes worldwide (12) and more than 180% faster declines in

deep-water dissolved oxygen. There is no reason to believe that browning has slowed since 2012 because we observe similar increases in DOC in eight of our intensively monitored lakes over the period 2002 to 2022 (*SI Appendix, Fig. S4*). Only three out of 15 of our intensively monitored lakes currently retain large amounts of cold-water habitat throughout the warm season, such that brook trout would not face oxythermal habitat challenges in the foreseeable future. Mining the extensive historical data for Adirondack lakes data suggests that future prospects of oxythermal habitat are even bleaker because deep lakes are rare and DOC concentrations in most lakes were high enough to produce a substantial net loss of suitable oxythermal habitat under observed rates of browning.

We find that rising DOC shifts the maximum depth of thermally stressful temperatures closer to the surface (Fig. 4A), in line

with observations that browning results in volumetrically cooler lakes (9). Consistent with the relationship between DOC concentration and light attenuation (59), the negative exponential relationship between DOC and the maximum depth of stressful temperatures indicates that browning of high-transparency lakes could somewhat expand oxythermal habitat, but that the beneficial effect diminishes rapidly as DOC concentrations rise. Early in the 1994 to 2012 dataset, several lakes had DOC concentrations below any observed in our contemporary intensively monitored lakes. This suggests that present-day temperature profiles of Adirondack lakes already reflect substantial heat trapping at the surface due to browning. This reduction in the volume of water in which incoming radiation is absorbed elucidates why observed long-term surface warming has been so rapid in Adirondack lakes compared to other temperate regions (12).

Our modeled relationships between DOC and the thickness of the refuge from stressful temperatures above and hypoxic water below suggest that there is a threshold DOC concentration where hypoxia will virtually preclude the persistence of suitable oxythermal habitat through a typical summer. Profiles from two high-DOC (>14 mg/L) lakes in Wisconsin support this inference: low dissolved oxygen concentrations rise to within a meter of the surface. It is ironic that increasing DOC concentrations often result in increased thermally habitable depth ranges for cold-water organisms (9), yet this cold water is less hospitable overall because it includes an expanding hypoxic zone (13). Thus, the net effect of browning is beneficial only under a limited set of conditions (Fig. 4B). In constrained and squeezed lakes, we observed a linear relationship between DOC and the boundary depth for hypoxia. In contrast to effects on near-surface temperatures, oxygen depletion upward from the bottom did not diminish with rising concentrations of DOC until hypoxic water nearly intersected overly warm water. These dual effects create oxythermal bottlenecks for cold-water species. Shallower lakes (5.5 to 9.1 m) with moderate to high DOC concentrations fall into the squeezed category where warm surface water intrudes into hypoxic deep water. Furthermore, our highest DOC lake was relatively deep (12.5 m, Pico) yet still experienced an overlap of warm temperatures and hypoxia that categorize it as squeezed. Our recent field surveys of trout demography as well as a century of anecdotal reports from anglers indicate that this lake has never supported brook trout except via stocking, and most stocked fish do not survive for long. These observations accord with the long duration of unsuitable conditions throughout the entire water column observed in summer 2021, as reflected by the highest COSD₂₃ value among our intensive study lakes.

Although constrained lakes currently maintain some suitable habitat through the warm period, it is not clear whether they will sustain oxythermal refugia under continued warming and browning. In lakes that currently feature low DOC, cold-water species may benefit somewhat from browning that raises suitable habitat closer to the surface, creating a buffer against expanding deep-water deoxygenation. Yet most constrained lakes no longer have low DOC, and they lack the large volume of cool, oxygenated habitat present in the hypolimnion of buffered lakes. Continued climate warming and lengthening of the stratified season will overcome any benefits of browning for protecting oxythermal refuges in most constrained lakes, where cold-water species already have very limited availability of suitable habitat.

Our calculations suggest substantial loss of constrained lakes with low DOC in the Adirondacks between the 1980s (23.4% of 1,468 lakes) and 2023 (4.8% of 1,468 lakes; *SI Appendix, Table S6*). Continued browning will result in even greater loss of low-DOC constrained lakes because overheated lakes are more likely to transition to squeezed than constrained categorization

based on our calculations. Squeezed lakes are likely to remain in that category under further browning and warming; it is highly unlikely that oxythermal habitat volume has increased in any of the lakes that were already squeezed in the 1980s because they were already experiencing substantial deep-water hypoxia. Thus, for all but the modest number of deep buffered and low-DOC constrained Adirondack lakes, we conclude that further browning generally will be deleterious to cold-water species.

The continued thinning and heating of the surface layer has implications for fish production, a substantial proportion of which is typically supported by benthic energy sources in lakes (60). Benthic productivity is typically highest in the littoral zone, the thickness of which is defined by depth of light penetration (61, 62). As lakes continue to brown, the littoral zone will become both shallower and hotter, thereby preventing trout and other cold-water fishes from accessing food resources that are fueled by benthic primary production (63). At the same time, these fishes and their prey are also excluded from detrital resources of the profundal zone by deoxygenation. Though speculative, such restrictions upon feeding opportunities can only exacerbate the impacts of the many other stressors faced by cold-water fishes in the Adirondacks (30–32).

The large, deep lakes that fall into the buffered category are special because their oxythermal habitat availability is largely unaffected by warming and browning. These lakes can have warm water at the surface but show little to no hypoxia below the thermocline. T_{DO5} in these lakes is well below the preferred temperature of brook trout, typically being around 6 °C (Fig. 2C and *SI Appendix, Table S4*). The Adirondacks have few lakes whose depth enables them to behave as buffered lakes (<1%; Fig. 4C), yet these ecosystems will necessarily play a critical role in sustaining brook trout, lake trout, round whitefish, and other cold-water species in a warmer, browner future. The scarcity of buffered lakes in the Adirondacks is likely to apply to most regions around the world because small, shallow lakes are numerically dominant (64).

Our empirical findings and lake categorizations inform the application of the resist–accept–direct (RAD) framework—which guides fishery management as ecosystem states exceed the bounds of historical norms (65, 66)—to trout and other cold-water species that face both warming and browning. Under the RAD framework, managers can take actions that actively resist directional shifts in ecosystem state, or they can accept these shifts and await system stabilization at a new, yet-unknown state, or they can direct the fishery toward a new desirable state even as ecosystem conditions are changing (66). We conclude that buffered lakes have a special role in protecting cold-water specialist species without direct population management, but that conservation efforts are still required under the resist approach. It is important that buffered lakes be inventoried and protected from species invasions, shoreline development, and other irreversible alterations. The popularity of large, clear lakes for recreation and vacation residences can foster additional stressors (67); for example, brook trout in two of three buffered lakes in our intensively monitored area are impacted by introduced populations of smallmouth bass (42). Our best hope for maintaining cold-water fisheries without intensive management is to confer the highest levels of protection upon buffered lakes, including ensuring that new predators are not introduced and that overharvest is avoided. Constrained lakes (52.1% of Adirondack lakes) may also be amenable to a resist approach, particularly those that currently have low DOC concentrations, but further investigation will be required to identify key interventions. Squeezed (25.8% of lakes) and overheated (21.7%) lakes are likely the best candidates for an accept approach. Such lakes make up 47.5% of Adirondack lakes based on the available data (Fig. 4E). Recommending a direct approach is

premature in the Adirondack region because most lakes still maintain an assemblage of native species whose oxythermal habitat needs are poorly understood.

As both warming and browning continue (68, 69), we must identify strategies that help sensitive cold-water species to persist in temperate lakes. Unfortunately, we find limited scope for browning to mitigate the effects of climate warming on brook trout habitat, and our analyses suggest a looming crisis from deoxygenation of thermal refuges. Oxythermal bottlenecks are likely to affect most Adirondack lakes in the decades ahead, and the prevalence of shallow lakes in all temperate lake districts of North America and Eurasia suggests similar vulnerability. Our oxythermal habitat categorization approach provides a system for initial triaging among lakes, and we particularly encourage precautionary measures for buffered lakes that naturally serve as oxythermal refuges for cold-water species. Constrained lakes also may serve an important role by virtue of being more common on the landscape, but they may eventually face oxythermal bottlenecks if warming and browning trends continue apace.

Data, Materials, and Software Availability. Long-term monitoring data for 28 Adirondack lakes are publicly available at <https://doi.org/10.1038/sdata.2018.59> (36). Temperature and dissolved oxygen profiles for Wisconsin and Pennsylvania lakes are publicly available at <https://doi.org/10.6073/pasta/c45f4e4826b5f615023b857dc59856f3> (58). Raw data as csv files for

high-frequency sensor data and ancillary data from 15 Adirondack lakes are available at <https://doi.org/10.6073/pasta/8ca9b5b1199e1d7922669ee6e0e2a5f8> (43). R scripts used in analyses are publicly available at <https://doi.org/10.5281/zenodo.10019433> (70).

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