



Indicators of the effects of climate change on freshwater ecosystems

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Abstract

Freshwater ecosystems, including lakes, streams, and wetlands, are responsive to climate change and other natural and anthropogenic stresses. These ecosystems are frequently hydrologically and ecologically connected with one another and their surrounding landscapes, thereby integrating changes throughout their watersheds. The responses of any given freshwater ecosystem to climate change depend on the magnitude of climate forcing, interactions with other anthropogenic and natural changes, and the characteristics of the ecosystem itself. Therefore, the magnitude and manner in which freshwater ecosystems respond to climate change are difficult to predict *a priori*. We present a conceptual model to elucidate how freshwater ecosystems are altered by climate change. We identify eleven indicators that describe the response of freshwater ecosystems to climate change, discuss their potential value and limitations, and describe supporting measurements. Indicators are organized in three interrelated categories: hydrologic, water quality, and ecosystem structure and function. The indicators are supported by data sets with a wide range of temporal and spatial coverage, and they inform important scientific and management needs. Together, these indicators improve the understanding and management of the effects of climate change on freshwater ecosystems.

Keywords Climate change · Freshwater · Indicators · Water quality

1 Introduction

Freshwater ecosystems provide critical ecosystem goods and services to society, support a disproportionate concentration of the planet's biodiversity, and are threatened by climate change (USGCRP 2018; Dudgeon 2019). Climate change impacts include rising temperatures, changing precipitation patterns, changing wind speeds, and increasing

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extreme events, such as heat waves, droughts, floods, and storm surges (IPCC 2021). Climate-related impacts often occur simultaneously with other anthropogenic environmental changes, such as land-use changes. Thus, it is often difficult to attribute ecological changes to climate change alone. However, some characteristics of freshwater ecosystems are particularly sensitive to climate change impacts, and when sufficient data exist, they can serve as effective indicators of climate change effects.

Here, we present a suite of indicators that provide valuable information on the effects of climate change on freshwater ecosystems. We evaluate indicators by their sensitivity to climate forcing; the number, spatial extent, and duration of associated measurements; and their association with critical ecosystem goods and services, such as the provisioning of plentiful and clean water (Dale and Beyeler 2001; USGCRP 2018). The selected indicators serve as baseline inputs for the National Climate Indicator System (NCIS), a component of the US National Climate Assessment. In the US, an NCIS was implemented as part of the US National Climate Assessment (NCA) (Kenney et al. 2020) to document the current state of climate change impacts in the USA and support sound decision-making. Our selection of indicators of the effects of climate change on freshwater ecosystems builds on previous NCAs, other reviews and publications on freshwater climate indicators (e.g., Adrian et al. 2009; Hering et al. 2010), and existing indicator compilations, such as the US Environmental Protection Agency's (EPA) climate change indicators in the USA (Kurtz et al. 2001).

2 Indicator selection process

The freshwater ecosystem types considered here include lakes, ponds, and reservoirs; rivers and streams; and wetlands. No explicit distinction is made between natural and built systems (such as reservoirs, impoundments, and canals) or among ecosystems that vary in size (e.g., lakes vs. ponds or streams vs. rivers). Given that freshwater ecosystems vary in so many attributes, such as the rate and timing of water flow, permanence, depth, and surrounding vegetation, a challenge was to identify key indicators of the effects of climate change that apply across freshwater ecosystems. Indicators were selected to improve the ability to assess climate change effects on (1) the amount of freshwater available for aquatic habitat and human use, (2) the integrity and quality of freshwater ecosystems, and (3) biological conditions that help support goods and services.

Our conceptual model informs the selection of such indicators (Fig. 1). Climate change impacts on freshwater ecosystems can occur gradually, such as slow increases in surface water temperatures over time, or rapidly and abruptly through increasing frequency of extreme events, such as heat waves, forest fires, droughts, or floods. The latter can produce rapid and substantial changes in both water quantity and quality (e.g., Williamson et al. 2016; Gómez-Gener et al. 2020). Concurrently, non-climate-related factors can also influence freshwater ecosystems, including watershed land use/land cover, atmospheric deposition, surficial geology and soils, topography, the cryosphere, and ground water. Societal factors, such as decisions regarding built infrastructure and water withdrawals, also influence water quantity, quality, and ecosystem responses to climate change. These non-climate and societal factors can also interact with climate, acting as indirect pathways for climate impacts on freshwater ecosystems. Together, climate and non-climate factors, including extreme events, interact to affect long-term trends and abrupt changes in freshwater ecosystems.

Implementation of an indicator system to understand the effects of climate change on freshwater ecosystems—or any ecosystem for that matter—depends on several key

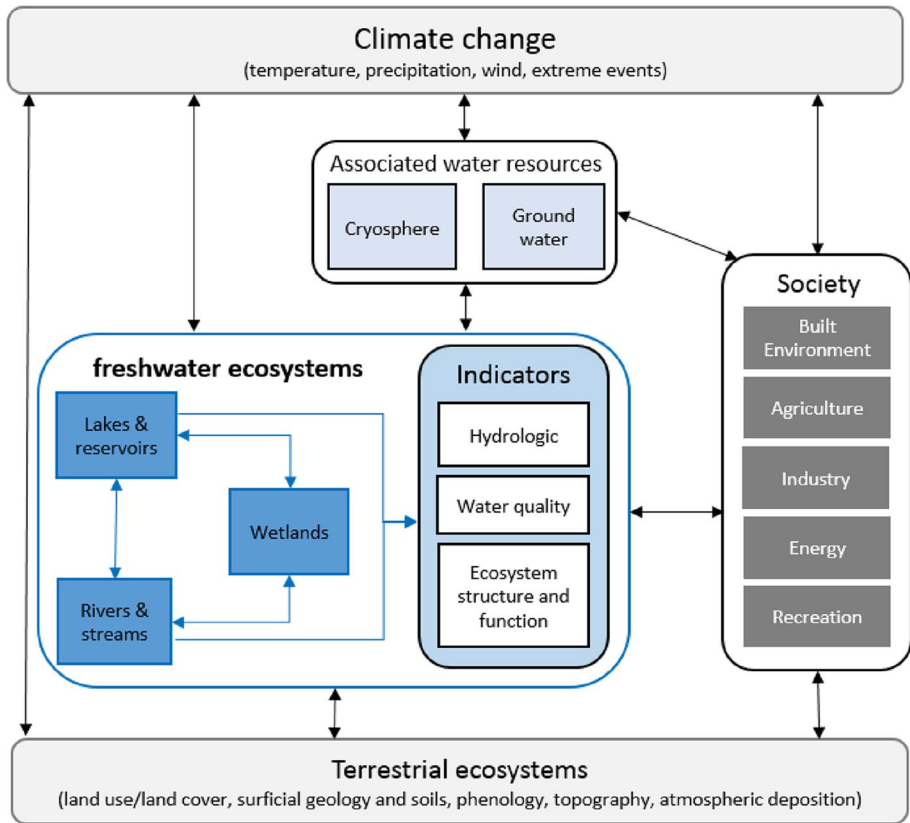


Fig. 1 Conceptual model highlighting how freshwater ecosystems are impacted by climate change. Indicators of the effects of climate change are organized into three categories: hydrologic, water quality, and ecosystem structure and function indicators. Climate-driven changes in these indicators, in turn, have implications for various sectors of society. Note all effects have associated feedbacks represented by the double-ended arrows

components. First, sufficient data must exist over broad spatial and temporal scales. Second, data must be accessible—both for historical trend analysis as well as for use in calibration and validation in forecasting future changes. Finally, the indicator must be able to distinguish signals associated with climate change from the effects of other factors, or the interactions between climate and other stressors must be well understood. Monitoring data can help distinguish the relative contributions of climate versus other drivers on each indicator.

The data collected for each indicator builds the body of evidence for causal linkages between climate drivers and freshwater ecosystem indicator responses (Table 1). Note that Table 1 shows predicted responses to a specific directional trend in a climate driver and it does not show possible interactions among climate drivers and subsequent ecosystem responses. Actual ecosystem responses can be sensitive to multiple aspects of climate (e.g., temperature and precipitation) simultaneously. Air temperatures are increasing in nearly all regions, but trends in precipitation and wind speeds vary both within and across regions. Hence the directional change in some freshwater indicators

Table 1 Indicators of the effects of climate change on freshwater ecosystems. Directional effects of changes in climate characteristics (i.e., air temperature, precipitation, and wind) are indicated by symbols, – for decreases and + for increases. The number of symbols indicates the magnitude of the effect, where substantial effects have three symbols (– – – or + + +), moderate effects two (– – or + +), or minimal effects one (– or +), though these can vary with system hydrology, land use, and land cover. The columns of “lakes,” “streams,” and “wetlands” indicate the number of monitoring sites with 10 or more years of continuous (for streamflow) or discrete observations (all other indicators) available through the USGS and EPA Water Quality Portal (see also Fig. 2). NA not applicable, DOC dissolved organic carbon, Chl *a* chlorophyll *a*, HABs harmful algal blooms. Streamflow represents the number of gages active during the period 1889–2019 is considered an indicator of the effects of climate change on freshwater ecosystems and water cycle and is detailed elsewhere (Peters-Lidard et al. 2021). Stream water temperature data include groundwater sites

Indicator category	Indicator	Warmer air tem- perature	Increased pre- cipitation	Stronger winds	Lakes	Streams	Wetlands
Hydrology	Streamflow	–	+ + +	–	NA	14,262	NA
	Lake level	– –	+ + +	–	^a	NA	NA
	Wetlands extent	– –	+ + +	–	NA	NA	^a
Water quality	Water temperature	+ + +	– –	–	5480	29,944	101
	DOC	+	+ + +	+	923	5055	48
	Chl <i>a</i> and HABs	+	+ + +	+	5512	3303	21
	Water clarity	+ / –	– – –	–	7759	2166	19
	Dissolved oxygen	– – –	– –	+	4564	17,205	100
Ecosystem structure and function	Diatom assemblage composition	^b	^b	^b	^a	^a	^a
	Invertebrate assemblage composition	^b	^b	^b	^a	^a	^a
	Phenology	^b	^b	^b	^a	^a	^a

^aSources other than the Water Quality Portal or USGS NWIS house most data for this indicator. See text for more information

^bEcosystem structure and function indicators exhibit responses to climate change that are difficult to describe using “–” or “+” responses

will correspondingly vary by region, and there can be heterogeneous responses even within regions.

Most data (existing discrete samples, but not necessarily continuous observations) supporting each indicator are available through the USGS and EPA Water Quality Portal (WQP; <https://www.waterqualitydata.us/>; Fig. 2; Read et al. 2017). This portal houses data from the EPA's STorage and RETrieval and Water Quality eXchange (STORET and WQX; <https://www.epa.gov/waterdata/storage-and-retrieval-and-water-quality-exchange>) database, USGS NWIS, the USGS BioData database (<https://aquatic.bioda.ta.usgs.gov>), and the US Department of Agriculture's (USDA) data delivery application (STEWARDS; https://data.nal.usda.gov/dataset/stewards-data-delivery-application-usdaars-conservation-effects-assessment-project_146). In addition to Federal data, the STORET database also contains a substantial amount of Tribal, State, and academic data from hundreds of different monitoring agencies and groups, and in many cases,

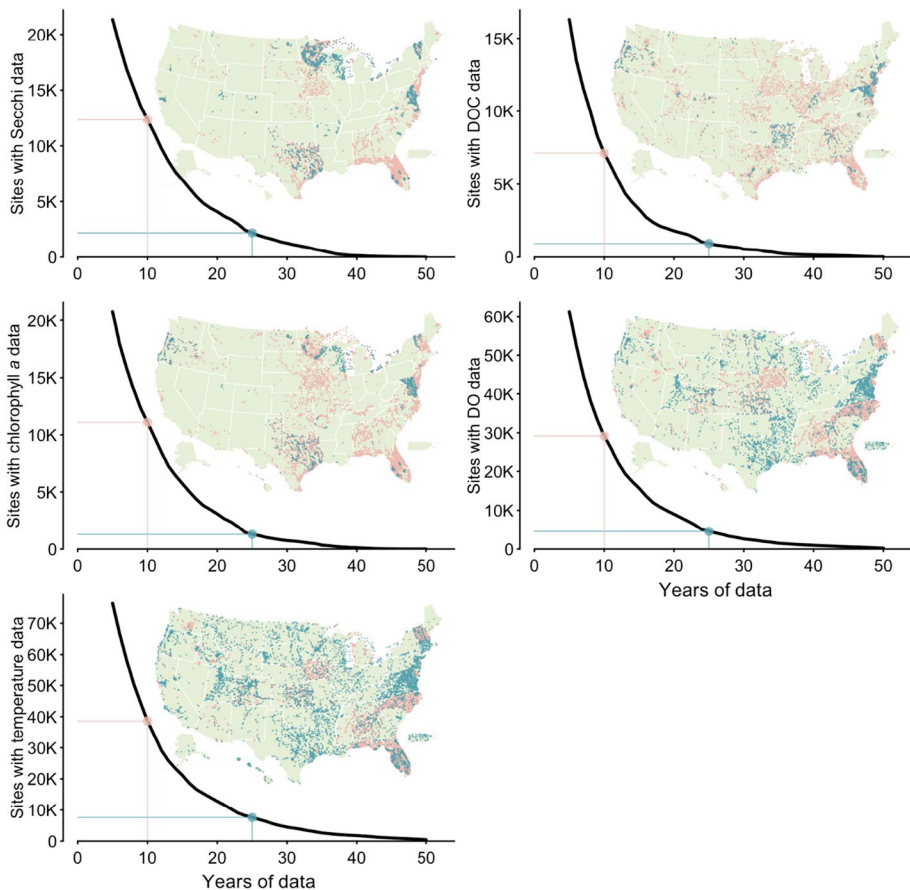


Fig. 2 Data availability (K, thousands of sites) and geographic coverage through the USGS and EPA Water Quality Portal (<https://www.waterqualitydata.us/>). Orange and blue lines and mapped locations indicate sites with at least 10 and 25 years of data, respectively as of August 2021. See text for more details on data availability, including data availability from other sources

substantial data also exist outside of these centralized repositories. Specific data sets supporting each indicator are described in more detail below.

3 Hydrology indicators

Hydrologic characteristics, such as streamflow, lake level, and wetland extent, define the spatial extent, depth, and flow of freshwater ecosystems. These indicators are directly affected by climate change, including changes in precipitation and evaporation, with the latter strongly dependent on temperature (USGCRP 2018). Streamflow and other hydrologic characteristics, such as the amount of heavy precipitation and the percent of precipitation falling as rain versus snow influence freshwater ecosystems and are used as indicators of the effects of climate change on the water cycle (Peters-Lidard et al. 2021). Ecologically, drought and reductions in stream baseflows stress organisms, including fishes (Rolls et al. 2012) and invertebrates (Herbst et al. 2019), can increase concentrations of nutrients and other solutes (Olson 2019; Gómez-Gener et al. 2020).

3.1 Lake level

The surface level of lakes integrates the response of lake ecosystems to major climate forcings and other sources of inputs and outflows, including withdrawals for human use. Changes in water level in large lakes equate to substantial changes in stored volume, surface extent, and aquatic habitat. Low lake levels can affect a variety of ecosystem characteristics; for example, by reducing fisheries habitat and altering the cycling and availability of toxins such as mercury (Watras et al. 2020). At a continental scale, variations in lake levels are linked with broad-scale spatial patterns in precipitation, evaporation, runoff, and water use, and thereby are linked with atmospheric and oceanic circulation patterns (USGCRP 2018). Since 1992, 58% of the variation in the water levels of 200 globally-distributed large lakes has been attributed to climate drivers (Kraemer et al. 2020).

Water level data products are available from the US Department of Agriculture (USDA), National Aeronautics and Space Administration (NASA), Global Reservoirs and Lakes Monitor (G-REALM; https://ipad.fas.usda.gov/cropeplorer/global_reservoir/). These products provide a time-series of water level variations for the world's largest lakes and reservoirs ($\geq 100 \text{ km}^2$) since 1992. The US National Oceanographic and Atmospheric Administration (NOAA) also monitors lake levels in the Laurentian Great Lakes (<https://www.coast.noaa.gov/llv/>). Volume scales with surface extent, and thus the Reservoir and Lake Surface Area Timeseries (ReaLSAT), which contains surface extent estimates for 669,107 lakes and reservoirs $0.1\text{--}100 \text{ km}^2$ in area, 1984–2015, can also inform volumetric changes and variability (Khandelwal et al. 2022).

3.2 Wetland extent

The total area and types of wetlands regulate the ecosystem goods and services provided. Wetlands protect the downstream landscape from floods and storm surges, regulate aspects of water quality, increase carbon sequestration, and support fisheries, waterfowl migrations, and rare and endangered species populations (Zedler and Kercher 2005). Reductions in precipitation and increases in temperature can convert open-water emergent marshes to a drier wetland type with widespread consequences for associated biota, reduced wetland

connectivity to lakes and rivers, and reduced carbon fluxes (Johnson et al. 2010; Olefeldt et al. 2013; Cohen et al. 2016). There is generally a paucity of long-term and spatially extensive data from which to develop climate change indicators in wetlands, but wetland extent is the exception.

Changes in the extent of regional wetland complexes, such as the Prairie Pothole Region wetlands, may be an especially good indicator of climate change effects on wetlands (Niemuth et al. 2010). Hydrologic modeling suggests that warming will lead to substantial shortening of the flooded state of these wetlands (Johnson et al. 2010). However, precipitation is also important. For example, from 1997 to 2009 these wetlands experienced longer hydroperiods because of exceptionally wet conditions (Dahl 2014), which underscores the difficulty of predicting ecosystem responses and discriminating natural decadal-scale variability from unidirectional effects of other aspects of climate change.

Wetland extent and type in the conterminous US are available from several sources. First, data have been reported on a semi-regular schedule since the 1950s by the US Fish and Wildlife Service (FWS), and National Wetland Status and Trends reports. In addition, some state and regional wetland area assessments are available online (www.fws.gov/Wetlands/Status-and-Trends/index.html). Finally, the National Wetland Condition Assessment, conducted every 5 years beginning in 2011, also provides some data on the extent. This survey of ~1000 sites was the first widespread ecosystem assessment of wetland condition in the USA at a continental scale (Kentula and Paulsen 2019). However, this dataset has limited temporal coverage to date and hence a limited ability to detect climate change effects.

4 Water quality indicators

Water quality describes the physical, chemical, or biological characteristics of the water in an aquatic ecosystem relevant to human uses. Water quality indicators considered herein are water temperature, salinity, dissolved organic carbon, chlorophyll *a* and harmful algal blooms, water clarity, and dissolved oxygen.

4.1 Water temperature

Water temperature responds to climate change through changes in air temperature, solar radiation, evaporative losses, and surface and subsurface hydrologic and material exchanges. Freshwater ecosystem temperatures vary substantially both spatially and temporally (Hill et al. 2014; O'Reilly et al. 2015). Increasing temperature can directly affect dissolved oxygen levels (Jane et al. 2021), and the temperature dependence of biological processes means that warming can also affect several ecological properties, including the likelihood of harmful algal blooms (Mantzouki et al. 2018), species distributions (Comte and Olden 2017), food web structure (Gilman et al. 2010; Rohr et al. 2011; Dobrowski et al. 2013), and ecosystem structure and function.

Three of the more notable changes in the thermal properties of freshwater ecosystems in response to climate warming are increases in water temperature, increases in thermal stratification, and decreases in the duration of seasonal ice cover (Winder and Schindler 2004; Kaushal et al. 2010; O'Reilly et al. 2015; Sharma et al. 2019; Pilla et al. 2020; Woolway et al. 2020; Jane et al. 2021). Water temperatures are also influenced by precipitation and associated terrestrial inputs of nutrients, sediments, and organic matter that can reduce

water clarity and thus increase heat absorption in lake surface waters, often leading to less pronounced warming, or even cooling, of deeper waters (Rose et al. 2016).

Water temperature data for the past several decades are available for thousands of streams, rivers, and lakes (but few wetlands) across the USA. The USGS continuously monitors water temperature at ~1200 river and lake sites. The USGS Spatial Hydro-Ecological Decision System (SHEDS; <http://db.ecosheds.org/>) also provides measurements on > 7000 sites and > 18,000 time-series. In total, there are over 35,000 freshwater ecosystem sites with at least 10 years of data, and over 7000 sites with over 25 years of data (Fig. 2; Read et al. 2017)), but only a minority of sites has been designated as suitable for climate-related monitoring (Lins 2012) because other factors often influencing stream temperatures (Poole and Berman 2001; Caissie 2006). Additional lake temperature data are available through publications by the Global Lake Temperature Collaboration (<http://www.laketemperature.org/>) (O'Reilly et al. 2015; Sharma et al. 2016) and the Environmental Data Initiative (EDI; <https://environmentaldatainitiative.org/>), including datasets published therein (e.g., Pilla et al. 2021; Stetler et al. 2021).

Ice cover records for some freshwater ecosystems go back centuries (Magnuson et al. 2000; Sharma et al. 2016, 2019), and records for over 800 lakes are available through the National Snow and Ice Data Center (<http://nsidc.org/>), with many trends published (Magnuson et al. 2000; Benson et al. 2012). Ice cover is also measured through repeated aerial photographs and satellite imagery (e.g., Duguay et al. 2003; Surdu et al. 2014).

4.2 Dissolved organic carbon

Dissolved organic carbon (DOC) is a heterogeneous mix of compounds derived from the incomplete decomposition of organic matter that often gives waterbodies a yellow to brown hue. Wetlands are the dominant source of DOC to other freshwater ecosystems (Gergel et al. 1999), so changes in wetland hydrology will have strong effects on wetland DOC export to downstream aquatic ecosystems. DOC has multiple roles in aquatic ecosystems, including regulating the fate of contaminants such as heavy metals and pesticides, solar UV disinfection of parasites and pathogens, and microbial community respiration. DOC also controls dissolved oxygen supply and renewal and contributes to the production of carcinogenic disinfection byproducts during water treatment (Solomon et al. 2015; Williamson et al. 2017; Kritzberg 2017).

DOC levels in freshwater ecosystems are characterized by measuring DOC quantity (concentration) and quality (typically dissolved absorbance, otherwise referred to as color), and they have been shown to respond to both precipitation and temperature. The ratio of color to quantity, referred to as DOC-specific absorbance, has likewise been documented to be responsive to increasing temperature and precipitation (Williamson et al. 2014; Glaser et al. 2016). Concentrations of DOC have been increasing in many inland waters in the Northeast USA and in many parts of Northern Europe since about 1990 and have been attributed to climate change, reductions in acid deposition, and land use change (Monteith et al. 2007; Weyhenmeyer and Karlsson 2009; Meyer-Jacob et al. 2019).

There are over 7000 freshwater ecosystem sites with at least 10 years of DOC measurements, and about 500 sites with at least 25 years of measurements (Fig. 2). DOC data are also collected as part of the US EPA National Aquatic Resource Surveys of lakes and streams. In general, long-term DOC data are not as available as other standard water quality data, but a strong surge in interest in the role of DOC in freshwater ecosystems has led to a widespread increase in data in recent years.

4.3 Chlorophyll *a* and harmful algal blooms

Chlorophyll *a* is a pigment found in all photosynthetic green plants and algae, which form the base of most freshwater food webs. Chlorophyll *a* concentrations are used as a surrogate of primary producer biomass. Freshwater ecosystems with high chlorophyll *a* concentrations often have a green color to them. High algal biomass can contribute to oxygen depletion in waterbodies and subsequent hypoxic and anoxic conditions when algae die, sink, and decompose.

High nutrient and chlorophyll *a* concentrations are often associated with harmful algal blooms, in which cyanobacteria can produce toxins that are harmful to people and wildlife. Harmful algal blooms tend to occur at higher water temperature and when the water column exhibits greater thermal stratification (O'Neil et al. 2012), and temperature is one of the most important factors affecting the occurrence and concentrations of toxins (Mantzouki et al. 2018). There is some evidence that harmful algal blooms are increasing in frequency, magnitude, and duration globally (Huisman et al. 2018; Ho et al. 2019). However, climate-induced increases in thermal stratification may also reduce chlorophyll *a* and algal biomass of large lakes by inhibiting the input of nutrients to surface waters. In a study of 188 globally distributed lakes, warming was associated with chlorophyll increases in lakes with high baseline chlorophyll, whereas it was associated with chlorophyll decreases in lakes with low baseline chlorophyll (Kraemer et al. 2017).

Chlorophyll *a* concentrations and harmful algal blooms in freshwater ecosystems also are responsive to changes in nutrients, especially phosphorus and nitrogen (Carlson 1977; Nürnberg 1996; Elser et al. 2007). Increases in precipitation can increase nutrient inputs, especially in agricultural and urbanized watersheds, whereas droughts may decrease watershed nutrient inputs substantially (Rose et al. 2017). However, drought can increase the loading of nutrients from lake sediments when it is associated with prolonged anoxia. Attributing changes in chlorophyll *a* and harmful algal blooms to climate change must account for nutrient trends and the possibility of non-climate factors, such as land use, changes driving changes in nutrient concentrations.

There are over 10,000 freshwater ecosystem sites with at least 10 years of chlorophyll *a* data (Fig. 2). However, only about 1000 sites have at least 25 years of data, and notably few occur in the Western USA. Some data are available on lake chlorophyll *a* and cyanotoxin concentrations from the US EPA's National Lakes Assessment (USEPA 2009). Additionally, Filazzola et al. (2020) compiled a dataset of 228,168 chlorophyll measurements from 11,959 lakes around the world, including data from the LAGOS (LAke multi-scaled GeOSpatial and temporal database; Soranno et al. 2015), which includes observations throughout the Midwest and Northeast USA. Measurements of harmful algal blooms are less common than chlorophyll *a* measurements, and uniform standards defining blooms are generally lacking.

4.4 Water clarity

Water clarity is one of the most universal metrics of water quality due in large part to the ease of measurement (e.g., with Secchi disks) and the association of clear water with both health and aesthetics. Water clarity regulates key aspects of aquatic ecosystems including the water temperature, the thermal structure, and the compensation depth, which is defined as the depth at which daily photosynthesis is equal to autotrophic respiration. Low water

clarity can contribute to hypoxia and anoxia at deeper depths (Jane et al. 2021). Both long-term decreases and increases in water clarity have been reported and have been associated with changes in precipitation and land use practices (e.g., Lottig et al. 2014). In addition to climate change, other factors, such as changes in land use/land cover and the presence of invasive mussel species, can affect water clarity (Bunnell et al. 2021).

The US Figure contains data from over 12,000 sites that have over 10 years of water clarity measurements, and over 2000 sites with at least 25 years of measurements (Fig. 2). Long-term clarity trends in thousands of lakes have been published (Lottig et al. 2014) and are available through citizen science programs such as the Secchi Dip-In (<http://www.secchidipin.org/>). These in situ records have been matched with satellite reflectance measurements, providing over 250,000 paired observations, thereby enabling the estimation of water clarity at thousands more waterbodies (Ross et al. 2019). State and tribal water management agencies also collect water clarity data for many lakes and streams.

4.5 Dissolved oxygen

Dissolved oxygen regulates many aspects of aquatic ecosystems, and low dissolved oxygen can be lethal to many aquatic organisms. Analysis of long-term dissolved oxygen records indicates that both surface- and deep-waters in lakes have lost oxygen since 1980 at rates 2–9 times faster than the oceans (Schmidtke et al. 2017; Jane et al. 2021). As the water warms, oxygen solubility declines, and solubility loss explains most of the observed long-term decline in lake surface dissolved oxygen concentrations (Jane et al. 2021). In contrast, deep-water DO declines in lakes have been associated with stronger thermal stratification and water clarity losses. Warmer surface waters and longer periods of seasonal stratification reduce dissolved oxygen concentrations by enabling more time for oxygen consumption and drawdown to occur and increasing the resistance to renewal from the atmosphere (North et al. 2014; Sahoo et al. 2016). Freshwater ecosystems with high algal productivity also often have low dissolved oxygen in deep waters. As algal cells sink and decompose, oxygen is drawn down, leading to low deep-water dissolved oxygen concentrations. In turn, when dissolved oxygen is depleted, sediments can release phosphorus (Knoll et al. 2018), which can further stimulate high algal growth and generally unfavorable water quality conditions (Mallin et al. 2006; Jeppesen et al. 2010).

There are about 30,000 freshwater ecosystem sites, predominantly streams, with at least 10 years of dissolved oxygen measurements, and approximately 4000 sites with at least 25 years of measurements (Fig. 2). Long-term (at least 15 years of observations) lake dissolved oxygen measurements have been compiled for over 400 lakes around the world and are publicly available in EDI (Stetler et al. 2021; Jane et al. 2021).

5 Ecosystem structure and function indicators

Ecosystem structure and function indicators are composites of multiple ecological attributes (e.g., species) that, when combined, provide an integrative assessment of ecological status and integrity. The climate preferences and distributions of a range of many aquatic organisms are well-documented, and many long-term monitoring programs have been conducted in the last half-century (Noss 1990; Rohr et al. 2007). These data sets enable biodiversity metrics to serve as indicators of the effects of climate change on freshwater ecosystems.

5.1 Phenology

Climate change alters seasonal dynamics of organism behavior and associated events, and climate change-induced phenological shifts are well-documented for many species (e.g., While and Uller 2014; Thackeray et al. 2016; Cohen et al. 2018). Phenological changes can affect the fitness of organisms by altering the synchrony between predators and their prey or food resources and between hosts and parasites (Winder and Schindler 2004; Mas-Coma et al. 2009). In many regions, seasonal stages or phases are shifting earlier for spring events and later for autumn events. Freshwater phytoplankton is among the most sensitive taxa to phenological changes associated with both warming temperatures and changing precipitation (Thackeray et al. 2016). In wetlands, the flowering and greening of wetland plants and the calling and breeding of frogs are highly sensitive to cumulative temperature (degree days) and thus are useful phenological indicators (Cohen et al. 2018). However, to our knowledge, large-scale, repeated measurements of phenology have not been collected for US wetland plants, despite the fact that it can be monitored at a variety of scales using aerial photographs, and LIDAR could be used to monitor emergent vegetation (e.g., Salas 2021).

Climate drivers of phenology vary by latitude. In a meta-analysis of hundreds of published studies on diverse taxa, researchers found that temperature was the primary driver of phenological changes at mid-latitudes, whereas both temperature and precipitation were important drivers at low latitudes. These drivers correspond to the dominant factors regulating seasonality across latitudes (Cohen et al. 2018). Additionally, aquatic organisms, such as frogs, toads, and salamanders, have exhibited a more pronounced shift toward earlier breeding dates at high latitudes than at low latitudes (While and Uller 2014). Various other factors can mediate the sensitivity of organisms to climate-associated phenological changes. For example, nutrient concentrations and enrichment can regulate the sensitivity of phytoplankton phenology to climate-induced changes in water temperature and stratification (Thackeray et al. 2008; Feuchtmayr et al. 2012).

Substantial efforts have been made to generate phenological datasets that contain many taxonomic classes, and many datasets have been released with scientific publications (e.g., Brown et al. 2016). The US National Phenology Network maintains data on phenological data on many different species and ecosystems (Schwartz et al. 2012). However, limited data from many geographically under-sampled regions and species means that phenological changes may be underestimated, and freshwater organisms have been under-represented in some studies (e.g., Cohen et al. 2018).

5.2 Diatoms

Diatoms are a class of algae that form microscopic cell walls containing silica. These cell walls are frequently preserved in sediments after organisms die, creating a fossil record in the sediments. The records preserve changes in diatom assemblages (i.e., increases in the relative abundances of some taxa, declines in others) associated with climate change over centennial to millennial time scales. The primary link between diatom ecology and climate is via wind and stratification. For example, different diatom species have different mixing depth optima. Therefore, the change in abundance of different diatom species in sediment records can be used to estimate mixing depths or track changes in mixing depths resulting from changes in wind speed (Saros et al.

2012, 2016). However, other factors such as pH, Si, and salinity can also affect diatom species assemblages and must be considered when interpreting paleolimnological records.

Coupling lake-specific information with diatom fossil records enables a long-term perspective of climate-driven changes in ecosystem structure. In some regions, warming has led to shallower lake mixing, particularly where wind speeds have declined or water clarity has decreased, leading to an increase in diatom species that have shallower mixing depth optima (Saros et al. 2012; Brown et al. 2017). In other areas, warming has led to deeper lake mixing, particularly where wind speeds have increased, leading to an increase in diatom species that have deeper mixing depth optima (Saros et al. 2012, 2016).

The primary data source for diatom records in the USA is the Diatom Paleolimnology Data Cooperative, (<https://diatom.ansp.org/dpdc/>; Sullivan and Charles 1994). This cooperative contains data for dozens of lake sites, with diatom records spanning hundreds to thousands of years. However, the need to continually harmonize taxonomy represents an important challenge with respect to the integration and comparison of data collected by different organizations and individuals (Lee et al. 2019; Alers-García et al. 2021). Other data sources include the Diatoms of North America database as a source of at least taxonomic information: <https://diatoms.org>. Additionally, the US EPA National Lakes Assessment surveys collect diatom data.

5.3 Invertebrates

Invertebrates are key consumers in aquatic ecosystems that can both contribute to and provide useful metrics of water quality. Macroinvertebrate assemblages are frequently measured to monitor stream, river, and lake health. Thermal preferences for benthic macroinvertebrates, which are the primary food sources of many economically important fishes, are relatively well established (U.S. Environmental Protection Agency 2016), and the spatial distribution of macroinvertebrates also is well documented in many regions. Multispecies distribution models and other statistical techniques can help understand and quantify macroinvertebrate biodiversity shifts and regional sensitivity to climate warming and streamflow change (Chinnayakanahalli et al. 2011; Domisch et al. 2013; Butman et al. 2016; Hawkins and Yuan 2016; Pyne and Poff 2017; Mustonen et al. 2018).

In the USA, the National Water Quality Assessment (NAWQA; <https://water.usgs.gov/nawqa/>) program had standardized monitoring of water quality and macroinvertebrate assemblages in stream and river networks in over 40 watersheds from 1991 to 2019, and the US EPA through the National Aquatic Resource Survey program has conducted nationwide surveys of river and lake macroinvertebrates every 5 years, beginning in 2004 and lakes beginning in 2007 (USEPA 2009; U.S. Environmental Protection Agency 2016). Additionally, the US EPA maintains a repository of state river bioassessment surveys since 2000 in a central database (STORET; http://www.epa.gov/STORET/dw_home.html), although states may use different sampling protocols and are not necessarily taxonomically consistent. The USGS BioData program (MacCoy 2011) also contains macroinvertebrate data as well as data for algae, fish, and supporting habitat data from rivers and streams. Standardized measurements of macroinvertebrate biodiversity are also available from other regions, including > 600 reference streams and rivers sampled between 1978 and 2002 in the UK (<https://www.ceh.ac.uk/services/rivpacs-reference-database>).

6 Future research needs

Substantial data exist for most of the indicators identified herein, but many gaps persist. Technologies such as high-frequency in situ autonomous environmental sensors and remote sensing can complement existing datasets and traditional sampling approaches to expand the temporal and/or spatial scale of observations. Complementing historic aquatic resource monitoring (e.g., USGS stream gage sites), new freshwater network data collections conducted at broad spatial scales (e.g., in the US National Ecological Observatory Network; Goodman et al. 2014) and citizen-scientist programs such as the Secchi Dip-In (<https://www.nalms.org/secchidipin/>) can provide data to improve understanding of climate change impacts, as well as foster greater scientific engagement and literacy (Bonney et al. 2009). However, many sensor networks and sensor technologies are relatively young. Additionally, although some remote sensing observations extend as early as the 1980s, in some cases (e.g., Sentinel series of satellites) observations have only existed since the 2010s. Another approach to deriving the greatest value from observations lies in assessing the degree to which individual observations are sentinels of broader spatial patterns and trends (Adrian et al. 2009; Williamson et al. 2009) by understanding covariance among ecological characteristics. Assessments of indicator synchrony and covariance across ecosystems could enable the selection of a reduced number of surveyed sites that are still broadly representative (Ricker and Ruggiero 1998; Murdoch et al. 2014).

Understanding the effects of climate change requires the integration of many diverse datasets. These data should be publicly accessible and of known accuracy and precision, with associated metadata and provenance documentation. Maintaining and updating environmental datasets are not trivial. Currently, there are many different data repositories, data standards, and types of data that range in quality from raw and unfiltered to highly processed and documented. This heterogeneity is due in part to the fact that there are several different types of freshwater ecosystems and many different organizations monitoring them. There is no single central federal freshwater ecosystem database in the USA, but the USGS and EPA Water Quality Portal represent an important step toward database centralization. Additional data repositories such as the Environmental Data Initiative (<https://environmentaldatainitiative.org/>) and Internet of Water (<https://internetofwater.org/>) are also increasing the availability of key indicator data. Additionally, many state and local agencies and non-profits also collect freshwater ecosystem data and maintain water quality databases. Pulling all the necessary data together from repositories and more diverse and often unstructured sources could effectively leverage substantial past data collection efforts to better understand climate impacts on freshwater ecosystems.

Wetlands stand out among freshwater ecosystems in their lack of adequate databases to examine the effects of climate change. In addition to the Wetlands Status and Trend reports; <https://www.fws.gov/wetlands/status-and-trends/>), the National Wetland Condition Assessment was conducted in 2011 and 2016, and it is planned to continue at 5-year intervals. This ecosystem assessment of ~1000 sites consists of biotic and abiotic indicators, including several discussed above for other freshwater ecosystems. Thus, in the future, much better indicators may be available for wetlands but only at a coarse frequency.

Climate change is altering the abundance, growth, recruitment, and ranges of many aquatic taxa. Freshwater fishes and amphibians are threatened, with particularly strong effects on cold-adapted species, including extirpation at their warmer range boundaries (Lynch et al. 2016; Comte and Olden 2017; Cohen et al. 2019). Species range shifts are also occurring, and species movements are often outpaced by the speed at which

isotherms are moving (Isaak and Rieman 2013; Comte and Olden 2017; Woolway and Maberly 2020). These changes can provide important indicators of the ecological and economic impacts of climate change when sufficient data are available. Some biotic characteristics can be more difficult to measure than physical or chemical characteristics, but they often provide essential information on ecological functioning and ecosystem services provisioning. Growing monitoring programs and the maturation and compilation of databases help enable a better understanding of freshwater biotic responses to climate change.

A final key challenge lies in attributing specific observed changes to climate alone. Freshwater ecosystems face multiple anthropogenic stressors concurrent with climate change. These include habitat loss, invasive species, pollution, and emerging diseases (Rohr et al. 2011). Many of these other stressors are correlated with climate change impacts in space or time. Additionally, due to the combinations of factors driving freshwater ecosystem change, many ecosystems are experiencing novel conditions. Ecological novelty may cause changes in ecosystem dynamics that may be difficult to attribute to climate change but facilitate increased extinction risks (Pandolfi et al. 2020). It is important to recognize that, even though the indicators discussed here are well documented to be sensitive to climate change, a correlation between any proposed indicator and climate change does not necessarily mean that climate change is the causal driver. There are, however, approaches to strengthen the inference that an indicator is indeed causally linked to climate change. For example, when data are available, other stressors can be included with climate in a statistical modeling framework to parse the effects of climate change from other changes. In addition, estimates of sensitivity to climate based on field observations can be validated with experimental studies. Additionally, human impacts should be assessed to characterize the degree to which a particular freshwater ecosystem is likely to be more sensitive to other environmental changes (such as changes in land use) instead of climate change. Monitoring networks that have designated reference ecosystems, where anthropogenic inputs and disturbances are minimal, are of great value in identifying climate change impacts (Stoddard et al. 2006; US EPA 2016).

We propose the inclusion of eleven indicators of the effects of climate change on freshwater ecosystems (Table 1) as input into the ongoing US National Climate Assessments. This work highlights the utility of a number of commonly measured characteristics that can provide critical information on the impacts of climate change on freshwater ecosystems. The ultimate effects of these impacts will depend in large part on the magnitude of climate change, and the future actions we take as a society to protect and conserve freshwater resources, not only from climate change but also from other interacting stressors that threaten freshwater species and the goods and services these ecosystems provide.

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