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CURRENT EVIDENCE

Key differences between lakes and reservoirs modify climate signals: A case for a new conceptual model

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Scientific Significance Statement

Climate change poses a significant threat to freshwater ecosystems, though the exact nature of these threats can vary by waterbody type. An existing conceptual model describes how altered fluxes of mass and energy will affect standing waterbodies, but it does not differentiate reservoirs from lakes. Here, we synthesize evidence suggesting that lakes and reservoirs differ in fundamental ways that are likely to influence their response to climate change. We then present a revised conceptual model that contrasts climate change effects on reservoirs versus lakes.

Abstract

Lakes and reservoirs are recognized as important sentinels of climate change, integrating catchment and atmospheric climate change drivers. Climate change conceptual models generally consider lakes and reservoirs together despite the possibility that these systems respond differently to climate-related drivers. Here, we synthesize differences between lake and reservoir characteristics that are likely important for predicting waterbody response to climate change. To better articulate these differences, we revised the energy mass flux framework, a conceptual model for the effects of climate change on lentic ecosystems, to explicitly consider the differential responses of lake versus reservoir ecosystems. The model predicts that catchment and management characteristics will be more important mediators of climate effects in reservoirs than in natural lakes. Given the increased reliance on reservoirs globally, we highlight current gaps in our understanding of these systems and suggest research directions to further characterize regional and continental differences among lakes and reservoirs.

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Author Contribution Statement: NMH and BRD co-led the manuscript effort and contributed equally. JRC and BRD conducted the statistical analyses. KES and JRC designed the lake pairing analysis. NMH, NRR, and KES developed the climate change conceptual model. This paper was a highly collaborative effort and all authors contributed equally to the development of the research question and study design as well as the writing of the paper.

Data Availability Statement: Data are available in the Long Term Ecological Research Network Information System repository at https://dx.doi.org/10.6073/pasta/17cb7958c74f8bfc135f3e7f04ee944e (Corman et al. 2016).

Nicole M. Hayes and Bridget R. Deemer are joint first authors.

Additional Supporting Information may be found in the online version of this article.

Climate change and freshwaters

Climate change is one of the greatest threats to aquatic ecosystems (Blenckner 2005; Hayhoe et al. 2008). The effects of climate change range from direct changes in water level (Smol and Douglas 2007) and surface-water temperature (O'Reilly et al. 2015) to indirect, complex ecological shifts that alter trophic interactions (Winder and Schindler 2004), and have been observed in many different regions (e.g., Quayle et al. 2002; Schindler and Smol 2006; Schneider and Hook 2010). At the same time, increased human demand for water-related ecosystem services has resulted in the construction and operation of over 1 million dams globally (Lehner et al. 2011). As a result, human-made lakes (i.e., reservoirs) have come to comprise anywhere between 6% and 11% of global lentic surface area (Downing et al. 2006; Lehner et al. 2011; Verpoorter et al. 2014). While the global expansion of reservoirs has increased access to drinking water, irrigation, navigation, flood control, and hydropower, it has also fundamentally changed the movement of water, sediment, nutrients, and biota through aquatic networks. Globally, reservoirs are estimated to increase the standing stock of natural river water by over 700% (Vörösmarty et al. 1997), reduce sediment flux to the ocean by over 1 billion metric tons of sediment per year (Syvitski et al. 2005), reduce phosphorus transport to the coast by approximately 12% (Maavara et al. 2015), contribute more than 30% of all lentic nitrogen and silica retention (Harrison et al. 2009, 2012), and emit methane at higher per area rates than any natural aquatic ecosystem (Deemer et al. 2016). These findings are consistent with the notion that inland waters are not "passive pipes" (Cole et al. 2007) and that the ecological role of reservoirs is unique from lakes.

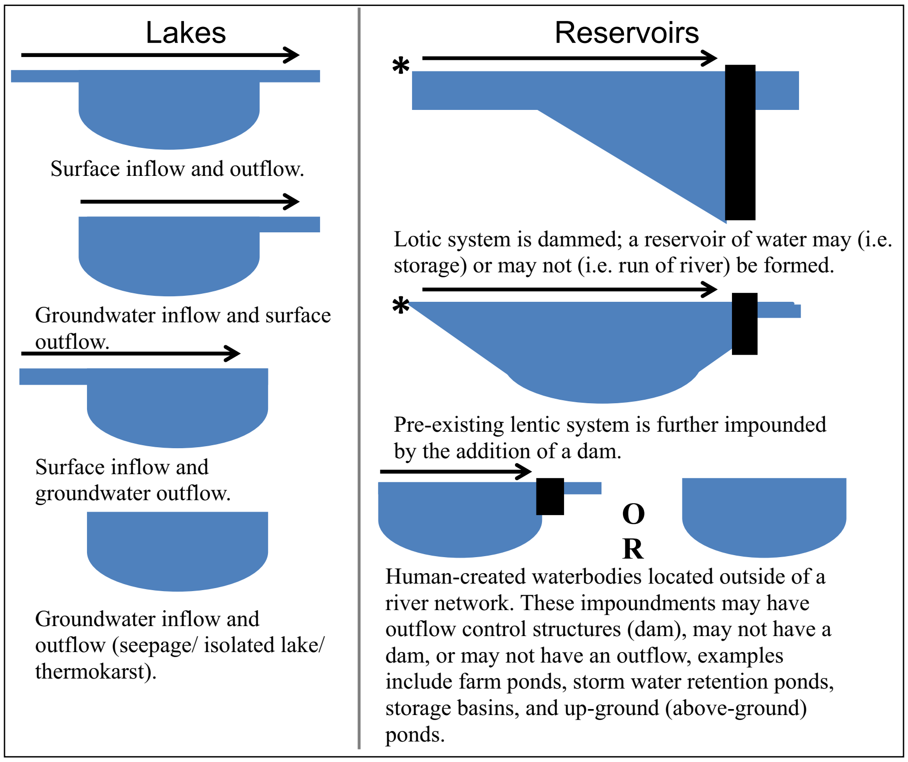
As low points on the landscape, lentic ecosystems also serve a unique role as integrators of atmospheric and catchment scale climate signals (Williamson et al. 2009). These signals, or sentinel responses, are shaped by a number of factors including large-scale geographic patterns and internal waterbody processes. Climate change conceptual frameworks have previously lumped reservoirs with natural lakes (Williamson et al. 2009) or excluded them from efforts to develop broadly applied sentinel response metrics (Adrian et al. 2009). Reservoirs and lakes are generally thought to share a number of similarities. Reservoirs are often divided into three zones for the purposes of ecological study: river, transitional, and lacustrine—with the lacustrine zone having slower water velocities and pronounced thermal stratification much like a lake ecosystem (Thornton et al. 1990). As a result, the lacustrine or lentic zone of a reservoir is thought to be similar to a lake in terms of planktic production, nutrient limitation of phytoplankton growth, and biogeochemical cycling (Wetzel 2001). Despite these similarities, reservoirs and lakes also differ in a number of ways that lead to differences in ecosystem functioning. Given the growing influence of reservoir ecosystems on the global hydrologic system (Zarfl et al. 2015), and recent evidence that reservoirs may serve ecological roles distinct from lakes even in the lacustrine zone (Beaulieu et al. 2013), we argue that these human-made systems should not be lumped with natural lakes in climate change conceptual models. An improved understanding of the interaction between reservoirs and climate may have broad scale implications for water quality from headwaters to coasts.

Key differences between lakes and reservoirs

Teasing apart the ecologically relevant differences between reservoirs and natural lakes can be a daunting task given the background variability in lentic ecosystem types. For example, one of the most common lake typological divisions is based on water source (i.e., relative contribution of groundwater versus surface water), of which reservoirs are a single lake type (Hutchinson 1957; Wetzel 2001; Figs. 1, 2). While natural lakes are generally subdivided based on hydrology (i.e., seepage, glacial, oxbow, intermittent, etc.), reservoirs are often categorized based on their size or their designed purpose (i.e., their primary reason for being constructed; Thornton et al. 1990; Poff and Hart 2002). Currently, the most common classification scheme for reservoirs divides these ecosystems into two groups: storage and run-of-river (Poff and Hart 2002). Storage reservoirs typically store large volumes of water and have large hydraulic heads, long hydraulic residence times, and allow for relatively fine-tuned control over the rate at which water is released from the dam. Run-of-river reservoirs, on the other hand, typically store less water and have relatively small hydraulic heads, short hydraulic residence times, and little or no control over the rate that water is released from the dam (Poff and Hart 2002). In many ways, these categories represent two extremes on a spectrum of reservoirs with larger "lacustrine" zones that are more like lakes (storage) to reservoirs with larger "river" zones that are more like rivers (run-of-river). To foster a more detailed discussion of reservoir type, we have depicted reservoir types based on position within river network (Fig. 1). While reservoirs created by damming a pre-existing lake are likely to share characteristics with the storage reservoir category, reservoirs created by damming a pre-existing river can resemble either a storage or a run-of-river system. In addition, reservoirs created to store water outside of a river network (e.g., farm ponds, pump storage systems, etc.) may function quite differently than those receiving surface water inputs via stream or river inlets.

In this article, we define reservoirs broadly as any human-made lake, whether it be embedded within a river network or not (Fig. 1). However, for the purpose of our analysis, we restricted our comparison to *reservoirs within river networks* (Fig. 1). This selection was made to harmonize our reservoir comparison with the types of reservoirs considered in the

What are reservoirs and lakes?
Reservoirs are defined as an intermediary between lakes and rivers, but several other characteristics, including outlet control, origin, and placement in a river network, more specifically define these systems. Similarly, lakes vary with regards to water source. Black bars indicate a dam and stars indicate reservoir types considered in this study.



Reservoir Definition: Broadly, we define reservoirs as human made lakes-- whether they be embedded in a river network or not. Still, data availability limited the types of reservoirs considered in this study. The synthesis and conceptual model developed here applies to reservoirs >0.04 km^2 that are located within a river system (indicated by the stars). Excluded reservoir systems include artificially constructed lakes and ponds placed outside of river networks (which may or may not include a dammed outflow).

Lake Definition: We broadly define lakes as naturally occurring low points in the landscape that contain standing water, predominantly in the form of open water habitat, year round. Still, data availability limited the types of lakes considered in this study. The synthesis and conceptual model developed here applies to lakes >0.04 km^2.

Fig. 1. Schematic and definition of lake and reservoir types included in this study.

Environmental Protection Agency's National Lake Assessment (NLA) and other surveys in our literature analysis (Thornton et al. 1980; Harrison et al. 2009; Powers et al. 2015). Site selection in the NLA was limited to lakes and reservoirs greater than 0.04 km^2 in size. Smaller systems, which are also often located outside of river networks (i.e., farm ponds and stormwater retention ponds), are ecologically important (Downing et al. 2009; Holgerson and Raymond 2016), however, we do not have the data necessary to consider them in our conceptual model. Despite the diverse array of lake and reservoir types, we argue that broad differences between reservoirs and natural lakes can be distinguished at the landscape scale given the unique human-made and human-operated aspects of reservoir ecosystems.

In order to assess the differences between lakes and reservoirs, we synthesize evidence from the literature and quantify evidence using a dataset from the 2007 NLA (Supporting Information Material; U.S. Environmental Protection Agency 2007; U.S. Environmental Protection Agency 2009; Corman et al. 2016). We focus our comparison of lakes and reservoirs on characteristics that have the potential to affect ecosystem response to climate change. These physical and chemical attributes are separated into four basic categories: (1)

Alternative reservoir definitions:
Environmental Protection Agency National Lakes Assessment (EPA NLA): Reservoirs include any open waters resulting from impoundment created after European settlement (e.g. post-1900).
Global Reservoirs and Dam Database (GRanD): Lakes that are explicitly classified as manmade, however there are some caveats. Some reservoirs do not have dams, for example when water is stored in natural or artificial depressions. Not all dams create reservoirs, for example run-of-river hydropower stations may not impound water and thus may not form reservoirs.
Hutchinson (1957): Lake "type 73, dams built by man, e.g., Lake Mead." This falls under the broader category, "Lakes Produced by the Complex Behavior of Higher Organisms" and is not to be confused with Type 72, "beaver dams" or Type 74, "excavations by man, as the abandoned diamond mines at Kimberley, South Africa.".
International Commission on Large Dams (ICOLD): An artificial, human-made lake, basin or tank in which a large quantity of water can be stored.
Thornton: No explicit definition provided, however reservoirs are described as having a lotic, transitional, and lentic zone, supporting the notion that a reservoir is a limnological intermediate between a lake and a river.
United States Bureau of Reclamation: (1) An artificially impounded body of water to store, regulate, or control water. (2) Body of water, such as a natural or constructed lake, in which water is collected and stored for use.
United States Geological Survey (USGS): A pond, lake, or basin, either natural or artificial, for the storage, regulation, and control of water.
Wetzel (2001): Impounded waters resulting from construction of a dam across a river.

Fig. 2. Selected alternative definitions of reservoirs.

catchment characteristics, (2) waterbody characteristics, (3) management, and (4) geographic distribution (Table 1). We use categories 1–3 to link our synthesis and NLA analysis to a modified E*m* flux conceptual model (*see* description below). Management (category 3) includes human decision-making at both the planning (hereafter referred to as "design") and post-construction (hereafter referred to as "management") stages. At the design stage, water managers strategically place dams to meet human need, usually by damming a pre-existing river or lake. Dam placement ultimately determines the catchment and waterbody characteristics discussed above as well as the regional positioning and watershed land use context, which we do not specifically address in our analysis. In the management post construction stage, reservoirs can be managed via specific decisions regarding dam withdrawal and water level management regimes, but are also subject to within-waterbody management techniques that overlap with strategies employed in natural lakes (Table 2). For the purposes of this study, we focus on within-waterbody management of lakes and reservoirs and we do not assess watershed land use management. We also do not specifically address category 4 in our analysis, as the broad-scale differences in the geographic distribution of lakes and reservoirs are addressed elsewhere in the literature (e.g., Lehner and Döll 2004 and Fig. 3) and can hinder our ability to characterize and quantify the mechanistic differences between lakes and reservoirs in a single region. We expect that many of the differences in lake and reservoir catchment management are confounded with differences in geographic distribution and we note that differences in the management of lake and reservoir catchments within the same region are not well quantified.

We identified studies that quantify key differences between lake and reservoir catchment, waterbody, and/or management characteristics (Table 1). Based on these studies and the proposed differences described in a seminal work on Reservoir Limnology (Thornton et al. 1990), we designed a targeted analysis of a subset of NLA lakes and reservoirs. We paired lake and reservoir systems based on their geographic proximity and tested for significant differences in catchment and waterbody characteristics by system type (*see* Supporting Information Material for more detail). We discuss our findings in the subsections that follow and then place the key differences we identified in the context of a new conceptual framework for climate change in lake versus reservoir ecosystems.

Differences in catchment characteristics

The literature synthesis and NLA analysis both suggest that catchment properties differ for lakes and reservoirs (Fig. 4; Table 1). The ratio of catchment area to surface area (CA : SA) was 3–4 times greater in reservoirs than lakes in a U.S. dataset (Thornton et al. 1980) and in a global database (Harrison et al. 2009). Within the subsetted NLA database, median CA and CA : SA were substantially larger in reservoirs compared to lakes (6.5 and 3 times larger respectively, Fig. 4, Supporting Information Material Table S1). Thornton et al. (1990) also proposed that reservoirs would be located lower in the landscape (Table 1). While explicit testing for differences in landscape position based on waterbody

Table 1. Summary of probable differences between lakes and reservoirs, adapted from Thornton et al. (1990), with new citations in italics.

Property	Natural lakes	Reservoirs	Evidence of differences	Citation
(1) Catchment characteristics				
Catchment area (CA): surface area (SA)	CA>SA	CA>>>SA	Reservoirs have larger CA and CA:SA	Thornton et al. (1980), *Harrison et al. (2009), This study*
Landscape position	Natural placement; fed by lower order streams; diffuse inputs	Lower in the catchment; fed by higher order streams; surface water dominated	Higher mass throughput and transfer to reservoir beds versus lake-beds from: (1) higher nitrogen and silica retention in reservoirs than lakes, and (2) high carbon burial and sedimentation rates in reservoirs	Canfield and Bachman (1981), *Syvitski et al. (2005), Harrison et al. (2009), Tranvik et al. (2009), Harrison et al. (2012), Clow et al. (2015)*
Reservoir morphometry	Circular basin; less complex perimeter	Longer, narrower basin; more complex perimeter	Reservoirs have greater perimeter areas than lakes	*This study*
(2) Waterbody characteristics				
Secchi depth	Generally deeper	Generally more shallow	Secchi depth shallower in reservoirs compared to lakes	Thornton et al. (1980), *This study*
Temperature	Somewhat lower	Somewhat higher	Similar surface waters; bottom waters are warmer in reservoirs than lakes	*This study*
(3) Management				
Waterbody management	Less managed	More managed	*See* Table 2, however management is likely geographically specific and is thus an area for future study. Smaller winter drawdowns and lower estimates of overall management stress in lakes versus reservoirs and greater water level instability in reservoirs.	*Keto et al. (2008), Kolding and van Zwieten (2012), This study (in italics)*
Catchment management	Watersheds both developed and undeveloped	Watersheds more developed	Higher P and N load in reservoirs from greater human activity in the catchment and higher shoreline development	Thornton et al. (1980)
(4) Geographic distribution				
Broad-scale distribution	Predominantly glaciated regions	Predominantly non glaciated regions	Greater fraction of lakes found in the boreal region and greater fraction of reservoirs found in the north temperate region	*Lehner and Döll (2004)*
Regional distribution (and function)	Dictated by geomorphology	Influenced by regional demand for dam-related ecosystem services	Primary designed purpose of dams varies by geographic region, with possible implications for morphometry and watershed placement (e.g., run of river versus storage dams)	*Poff and Hart (2002)*

Table 2. Common types of aquatic ecosystem management and implications for energy and mass processing.

Type of management	Purpose of management	Energy (E) and/or mass (*m*) implications	Citation
Selective withdrawal (predominantly reservoirs)	In reservoirs with outlet gates at multiple heights, selective hypolimnetic withdrawal can control downstream temperatures and/or improve water quality within the reservoir.	E: Enhances "net energy" per water volume by preferentially spilling colder water, may also lead to de-stratification.	Nürnberg (2007)
	Density flow releases shunt runoff plumes downstream to avoid reservoir sedimentation and reduce particulate associated pollutants. Increasing flow velocity through bottom outlets can also flush deposited sediments out of the reservoir by scouring the bed.	*m*: Can reduce the effect of the catchment on mass inputs via shunting of turbidity flows out the dam.	Huang et al. (2014), Tiğrek and Aras (2012)
Pool drawdowns (predominantly reservoirs)	Water level drawdowns can create flood storage, control for nuisance macrophytes, generate hydropower (e.g., hydropower peaking), and/or meet demands for consumptive water uses.	E: May either enhance or destabilize stratification regime. *m*: May lead to shifts in water column chemistry, species composition and community metabolism.	Blenckner (2005), Moreno-Ostos et al. (2008), Baldwin et al. (2008), Bell et al. (2008), Zohary and Ostrovsky (2011), Valdespino-Castillo et al. (2014)
Temperature curtains	Engineered curtains can control inflow or outflow ecosystem hydrology.	E: Can enhance "net energy" per water volume by preferentially spilling colder water. Can change stratification dynamics by preventing plunging inflows.	Vermeyen (2000)
Aeration and oxygenation systems	Air bubblers and oxygen diffusers can oxygenate bottom waters.	E: Can weaken stratification. *m*: Can stir up sediments and change mass processing by changing redox status of bottom waters.	Beutel and Horne (2014), Beutel et al. (1999)
Chemical treatments	Aluminum sulfate additions can strip phosphorus from the water column and increase water clarity.	E: Possible change to stratification regime due to increased waterbody clarity. *m*: May alter the effects of mass inputs via artificial flocculation and precipitation of nutrients and via unintentional effects on benthic communities and biogeochemical cycles.	Kennedy and Cooke (1982), Nogaro et al. (2013)
	Metals, photosensitizers, and herbicides can eliminate cyanobacterial blooms.	*m*: May change the biotic pool (including toxic effects on nontarget species).	Jančula and Maršálek (2011)
Sediment dredging (predominantly reservoirs)	Dredging may clear navigation channels, improve water quality, reduce eutrophication, and/or enhance bottom water oxygen saturation.	E: Greater volumes of water preserve the energy (and mass) effects for a longer duration. *m*: Takes away the "mass legacy" and changes nature of waterbody filter	Sahoo and Schladow (2008); Blenckner (2005)
Eco-technology (biomanipulation)	Removal of benthivorous/cyprinid fish can increase water clarity and decrease Chl *a*.	E: Possible change to stratification regime due to increased waterbody clarity. *m*: Takes away a portion of the biotic pool.	Meijer et al. (1999), Søndergaard et al. (2007)
Coverings	Light limiting coverings can reduce evaporation and algal growth.	E: Block solar heating and evaporative cooling, limit water column turbulence. *m*: Reduce autochthonous production.	Álvarez et al. (2006), Maestre-Valero et al. (2011)

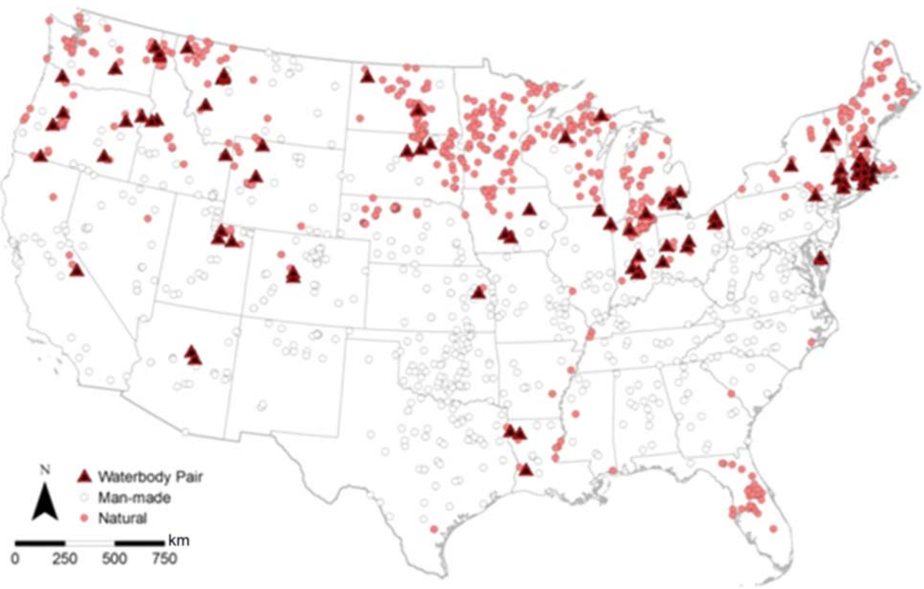


Fig. 3. Regional distribution of lakes (light red) and reservoirs (white) in the NLA in 2007. Lake and reservoir pairs selected for analysis in this study are shown as red triangles.

elevation did not reveal ecologically significant differences between lakes and reservoir pairs in the NLA (Supporting Information Material Table S1), greater CA : SA for reservoirs suggests they are indeed located lower in the landscape (Soranno et al. 1999). Given that waterbodies with lower landscape position have higher material inputs from the watershed (Soranno et al. 1999; Kratz et al. 1997), we hypothesize that reservoirs generally receive higher mass inputs than natural lakes. Although we did not find any studies that directly compared material inputs in lakes versus reservoirs, several global and national-scale studies report that reservoirs tend to have greater retention of watershed material than natural lakes (Harrison et al. 2009; Harrison et al. 2012; Clow et al. 2015). Finally, Thornton et al. (1990) predicted that reservoirs would differ in their morphometry; lakes would be more circular while reservoirs would be long and narrow with complex perimeters. Our analysis of the NLA paired lake-reservoir dataset supported this prediction with a median reservoir perimeter two times greater than the median lake perimeter (Fig. 4, Supporting Information Material Table S1).

Differences in waterbody characteristics

Reservoirs also differ from lakes with respect to within waterbody characteristics (Fig. 4; Table 1). For example, Secchi depths were found to be shallower in reservoirs than lakes in a U.S. dataset (Thornton et al. 1980) as well as in our analysis of the subsetted NLA dataset (Fig. 4; Table 1 and Supporting Information Material Table S1). Greater CA : SA and associated nutrient and sediment inputs likely lead to higher production and suspended sediments in reservoirs, decreasing water clarity (Supporting Information Material

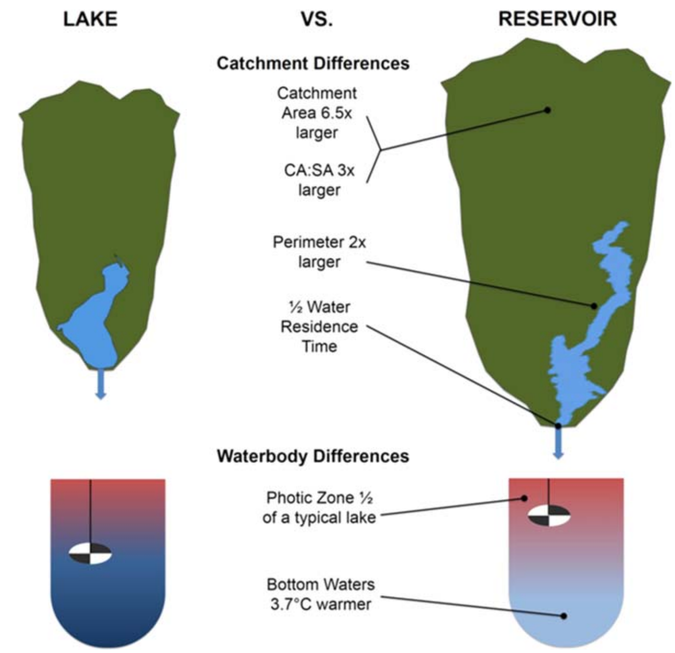


Fig. 4. Generalized watershed and waterbody schematics for a lake versus a reservoir. Differences are summarized from the literature synthesis and NLA analysis.

Table S1). Additionally, residence times were shorter in reservoirs as compared to lakes (approximately half as long, Supporting Information Material Table S1, Fig. 4). We also found that surface-water temperatures were similar in NLA lakes and reservoirs; however, bottom water temperatures were warmer in reservoirs (Supporting Information Material Table S1, Fig. 4). While differences in bottom water temperatures could result from differences in flushing rates and associated stratification regimes, these differences have not been fully explored in the literature. Future research efforts should focus on determining differences in lake and reservoir waterbody characteristics but also identifying the mechanisms driving these differences and the implications for ecosystem processes.

Differences in within-system management

Within-system management can alter the hydrology, chemistry, biology, and/or light regime of the waterbody to improve water quality, fish production, or other characteristics necessary for human uses (e.g., recreation, hydropower generation, flood control, erosion reduction, water supply, navigation, etc.). We identified eight common lake and reservoir management strategies of broadscale ecological significance (Table 2). Three of the strategies (pool drawdown, selective withdrawal, and sediment dredging) are common in reservoirs whereas the other five (temperature curtains, aeration/oxygenation systems, biomanipulation, chemical treatments, and covering) can be employed in either system type. While not an exhaustive list, these management techniques highlight the extent to which human activities may mask or amplify climate signals. For example, within-system management strategies can interfere with biological life cycles (e.g., fish stranding mortality associated with hydropower peaking, Bell et al. 2008; and elimination of cyanobacteria blooms via chemical treatments, Jančula and Maršálek 2011), seasonal hydrologic dynamics (e.g., via pool drawdowns, Zohary and Ostrovsky 2011; and via the reduced evaporation associated with coverings, Álvarez et al. 2006), and water column chemistry (reduced water column phosphorus concentrations associated with alum treatments, Kennedy and Cooke 1982; Nogaro et al. 2013; and higher concentrations of reduced solutes associated with pool drawdown, Baldwin et al. 2008; Zohary and Ostrovsky 2011; Harrison et al. 2017).

Based on our synthesis of available literature, we expect reservoirs to experience more within-system management than natural lakes for two main reasons. First, dams are constructed with some human use in mind and are thus likely to experience altered hydrology, biology, chemistry, and/or light regimes in support of these intended uses. Second, an outlet structure is a characteristic component of many reservoir ecosystems that can exert significant control on waterbody conditions. While lakes can have managed outflow structures (i.e., temperature curtains, Vermeyen 2000; and water withdrawal pumps), many reservoirs necessitate a water outlet that prevents over-filling. In fact, reservoirs were excluded from one recent study of lake sentinel responses due to their "anthropogenically controlled" hydrology alone (Adrian et al. 2009). Still, large-scale information about lake and reservoir management regimes is quite limited. For example, the NLA category for management contains qualitative information about perceived management stress where available, but is often left blank (U.S. Environmental Protection Agency 2009). Of the management pressure that was noted in the NLA paired dataset, reservoirs experienced approximately double the management stress of natural lakes (mean lake management stressor score of 2.2 for natural lakes and 4.2 for reservoirs out of a total possible score of 5). NLA-based visual estimates also suggest that reservoirs experience water level fluctuations of significantly higher amplitude than those in natural lakes (mean of 4 m and 0.7 m of fluctuation in reservoirs and lakes, respectively). Quantifying the relative importance of different management strategies in lakes as compared to reservoirs is beyond the scope of this synthesis but is an important area for future work that may also complement efforts to better classify reservoir systems.

Existing conceptual models for climate change effects in lentic ecosystems

Several models have been developed to predict the effects of climate change on lake ecosystems (e.g., Blenckner 2005; Leavitt et al. 2009) and these models are often uniformly applied to both lakes and reservoirs. There is a general notion that lakes and reservoirs act similarly as regulators (Tranvik et al. 2009), integrators, and sentinels of climate change (Williamson et al. 2009); however, studies that explicitly compare the sensitivity of lakes versus reservoirs to climate change are rare (e.g., Nowlin et al. 2004; Beaulieu et al. 2013). This lack of comparative information limits the inclusion of reservoirs into conceptual models. Yet, incorporating basic differences between reservoirs and lakes in terms of catchment, waterbody, and management characteristics help make existing frameworks more useful for predicting climate change effects.

The Energy (E) mass (*m*) flux framework proposed by Leavitt et al. (2009) may be particularly useful in distinguishing the effects of climate change on reservoirs as compared to lakes. In this framework, the effects of climate change on lentic ecosystems are modeled via a consideration of the transfer of both E (irradiance, heat, kinetic E of wind) and *m* (water, solutes, particles) through landscape and "lake" filters. We refer to the lake filter as the "waterbody" filter so as to facilitate discussion of both lakes and reservoirs. These filters function to transform E and *m* inputs and can thus influence the way that climate drivers influence ecosystems. The capacity for human-mediated processing of E and *m* in these systems is an important topic for research and is particularly relevant for reservoir ecosystems (which by definition are human-designed and human-managed). While Leavitt and colleagues emphasize the important role of human disturbance in mediating the landscape filter (e.g., with respect to land use), they do not explicitly consider aquatic ecosystem management. In the sections that follow, we discuss

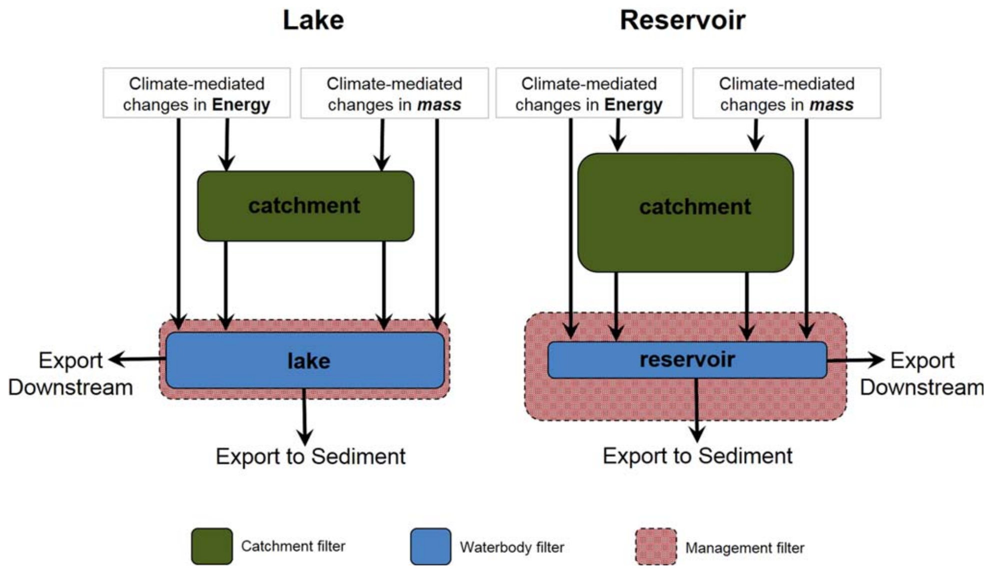


Fig. 5. A conceptual model of climate related effects on lake ecosystems (left) and reservoirs (right). This model builds on the Energy-mass (E*m*) flux framework proposed by Leavitt et al. (2009) and includes the four pathways by which climate drivers (factors that cause changes in an ecosystem; shown in black) enter environmental filters and move between the filters. Filters are environmental features that transduce and transform Energy (E) and mass (*m*). The catchment and waterbody act as filters (Blenckner 2005; green and blue boxes respectively) in this model as does the new management filter proposed as a result of this study (red boxes). The relative size of the catchment and waterbody filters represents the magnitude of the transduction and transformation based on the differences identified between lake and reservoir ecosystems in the NLA data analysis. Because differences in lake and reservoir management were not tested directly in this study, we show the management filter with a dashed border and suggest that it should be the focus of future research. Ultimately, the catchment, waterbody, and management filters interact to determine the relative proportion of the climate signal exported to the sediments or to downstream river networks and estuaries.

how reservoir design and aquatic management strategies alter the way in which E and *m* fluxes are transformed within the catchment and the resulting effects on abiotic and biotic variables within the waterbody. We predict that these differences will alter the magnitude and fraction of E and *m* exported to lentic sediments versus downstream river networks and coastal environments.

A new model for climate change in reservoirs and lakes

Conceptual ecosystem model

We constructed a conceptual model that incorporates key differences between lakes and reservoirs (Figs. 4, 5) to visualize variability in the export of climate-mediated changes in E and *m* to the sediment or downstream river networks. Our model builds on previous models proposed by Blenckner (2005) and Leavitt et al. (2009) and considers the pathways by which E and *m* are transformed by environmental filters. Our model incorporates three environmental filters: catchment, waterbody, and management. Filter size represents the magnitude of E or *m* transformed within each filter. Although previous versions of the model consider an atmospheric filter (Leavitt et al. 2009), our sample design does not allow for comparisons beyond the regional level. The catchment filter (or landscape filter; Blenckner 2005) alters the properties and magnitudes of E and *m* flux into waterbodies. Our waterbody filter affects the magnitude of E and *m* fluxes exported to sediments or downstream river networks, which varies considerably from previous models.

The arrows in our conceptual diagram represent direct and indirect transfer of E and *m* to waterbodies (Fig. 5). Direct inputs of E to the waterbody filter include solar irradiance, heat, and wind while indirect E pathways, those that move through the catchment filter first, influence catchment characteristics such as soil and vegetation development and subsequent terrestrial subsidies to lakes (Leavitt et al. 2009). Mass directly enters the waterbody via precipitation, particles, and solutes (e.g., wet and dry deposition) and indirectly via run-off of water and associated dissolved and particulate matter from the catchment. These indirect pathways are subject to environmental filtering and thus the properties of E and *m* that pass through the environmental filters are altered (Leavitt et al. 2009). Quantifying the extent to which filters alter the magnitude of each pathway is beyond the scope of this study, thus each line carries the same thickness (Fig. 5).

E*m* flux in lakes and reservoirs

Our conceptual model proposes a larger catchment filter for reservoirs than lakes (Table 1; Fig. 5). The larger catchment filter for reservoirs represents their propensity to drain larger catchments, their more complex shorelines, and their higher influx: content ratio (Fig. 4). With larger CA : SAs and larger perimeters, reservoirs are expected to experience a greater interaction with the catchment and thus increased catchment-mediated influx of E and *m*. These higher catchment-mediated influxes do not appear to be received by larger waterbodies as we found no evidence that reservoirs are larger than natural lakes (Supporting Information Material Table S1). Thus, larger inputs of *m* relative to content (e.g., greater inputs of water from inflow relative to reservoir water content) lead to shorter residence times and higher influx to content ratios in reservoirs. Mean residence time exerts an important control on processing time within the water column (Soranno et al. 1999), thus while it is a function of catchment characteristics, we discuss it in terms of the waterbody filter.

Key differences between lake and reservoir waterbody characteristics highlight the importance of the waterbody filter in processing E and *m* from the catchment in ways that will affect export to sediment or downstream ecosystems (Table 1; Fig. 4). Differences in water clarity can alter water chemistry and lead to changes in the productivity and diversity of lake ecosystems (Berger et al. 2006). Thermal regime can also affect the extent to which a waterbody reflects climate forcing. A study of three medium-sized German lakes with different mixing regimes and thermal structures found very different thermal responses to the North Atlantic Oscillation (NAO) among lakes, wherein the NAO signal was most persistent in the deep, dimictic system with stable summer stratification (Gerten and Adrian 2001). Additionally, shorter residence times may reduce E and *m* processing time. For example, Brooks et al. (2014) concluded that waterbody residence time was negatively correlated with nitrogen, phosphorus, and chlorophyll *a* concentrations, suggesting increased *m* processing in systems with longer residence times. We propose a smaller waterbody filter for reservoirs given their shorter residence times; however, more work is needed to tease apart the role of the differences we report between lakes and reservoirs and the resulting effects on E and *m* processing and export from the waterbody filter.

In addition to the catchment and waterbody filter, we propose a management filter that mediates functioning of the waterbody filter as well as E and *m* flux leaving the lake (Fig. 5). This was motivated by the literature review (described above, Table 2) wherein we identified eight common lake and reservoir management strategies that are likely to have direct effects on E and/or *m* fluxes. As discussed above, we expect management differences to be particularly pronounced in reservoirs given the presence of outlet control features on many dams and the fact that reservoirs were designed for human use (Table 2). Thus, we propose a larger management filter for reservoirs than for lakes (Fig. 5). These management strategies can have important consequences for both E and *m* fluxes (Table 2) although quantifying the magnitude of these effects is beyond the scope of this synthesis. Still, several recent studies have highlighted the capacity for within-system management to alter whole-ecosystem ecology. For example, hypolimnetic oxygenation was found to alter the fraction of *m* that was exported to sediments versus potentially transported downstream in a temperate reservoir (Gerling et al. 2016) and shade coverings were found to affect ecosystem E distribution (i.e., stratification) and reduce water column turbidity and dissolved oxygen (Maestre-Valero et al. 2011). Given the ubiquity of outlet control features on dams and the variety of effects that outlet control can have on E and *m* fluxes (Table 2), future research should focus on the propensity for outlet management techniques to either buffer or intensify climate signals (Fig. 6).

Summary of Research Recommendations:

1. Determine the extent to and mechanisms by which catchment properties and/or morphological factors alter the magnitude of E and *m* processing in lakes as compared to reservoirs.
2. Quantify the relative importance of different management strategies in buffering or intensifying climate change signals.
3. Describe connections between expected shifts in E and *m* processing and implications for ecosystem processes (e.g. carbon burial, biomass production, nutrient transformations, etc.).
4. Directly compare effects of climate change on lake as compared to reservoir limnological properties through field observations, experiments, or using compiled datasets.
5. Test conceptual model proposed here in tropical regions.
6. Improve the global mapping of reservoir systems. Quantify and map the global coverage of various reservoir (and lake) types and examine the potential role of typology in defining differences between systems (e.g. for small ponds).

Fig. 6. Recommended directions for future research.

Model limitations

The model we present identifies mechanistic differences in how lakes and reservoirs process climate change by focusing on geographically paired lakes, which allows for comparison of lakes and reservoirs experiencing similar climate forcing. However, this approach cannot be used to identify differences in climate forcing between lakes and reservoirs at a broader scale. In the United States, reservoirs have a more southern distribution than lakes (Fig. 3) and this pattern of regional distribution will determine the type of climate forcing these ecosystems experience. For example, the southwestern United States has experienced recent regional tendencies toward more severe droughts (Kunkel et al. 2008), likely leading to decreased indirect *m* inputs and increased direct E inputs compared to the more northerly distributed lakes. These differences in the distribution of lakes and reservoirs and the geographic difference in climate change will lead to differences in E and *m* exposure between lakes and reservoirs. Despite the geographic limitations, our model provides evidence for key differences in how geographically co-located reservoirs and lakes respond to climate change.

In addition, we simplify what constitutes the catchment itself. The filtering effect of the catchment varies based on land use (Blenckner 2005), for example, climate drove differential effects in nutrient loading between forested and agricultural watersheds (Hayes et al. 2015). Although there were no significant differences in land use in the subset of the NLA analyzed in this study (Supporting Information Material Table S2), observations from a global dataset of 115 lakes and reservoirs suggest that reservoir catchments are more human-dominated (higher nitrogen loading rates in reservoirs than lakes, Harrison et al. 2009). Future research should focus on how catchment land use affects the transport and transformation of E and *m* in lakes versus reservoirs.

Broadscale implications of the model

The E*m* flux framework predicts that the effect of a climate driver is determined by the ratio of input to content, suggesting that reservoirs, with higher input to content ratios, will be more affected by catchment mediated E and *m* inputs. Previous work has established the importance of *m* inputs to ecosystem climate sensitivity (Vogt et al. 2011) and has documented greater inputs of *m* (including sediment, nutrients, and water) in waterbodies with larger catchments (Soranno, et al. 1999). Recent work finds that reservoirs retain larger quantities of carbon, nitrogen, silica, and phosphorus than lakes (e.g., Harrison et al. 2009; Harrison et al. 2012; Clow et al. 2015; Maavara et al. 2015) and many models of lake and reservoir *m* retention find that *m* export is positively related to *m* loading (Saunders and Kalff 2001; Harrison et al. 2009). Thus, we suggest that reservoirs may be especially sensitive to climate drivers that increase *m* flux, such as storm events.

While our conceptual diagram suggests higher indirect E and *m* loading to reservoirs than lakes, it is less clear how different ecosystem parameters such as residence time and waterbody morphology interact with *m* loading to determine the *fraction* of inflow *m* that is buried (either as biomass or particulate matter) versus exported from the waterbody. For example, we suggest that low residence times in reservoirs may result in less processing time for E and *m* within the waterbody (e.g., lower fraction of E and *m* converted to biomass and exported to sediment), despite relatively large *m* burial on a total mass basis (due to the high magnitude of *m* loading and the potentially greater interface between sediments and water as a result of increased perimeter). In addition to residence time, other ecosystem characteristics (e.g., depth and temperature at sediment water interface) can also affect *m* processing rates. In a study of global nitrogen retention in lakes and reservoirs, reservoirs had higher settling velocities (function of residence time, depth, and fraction of *m* retained) than lakes (Harrison et al. 2009) indicating that a higher fraction of *m* is exported to sediments in reservoirs than in lakes. The fraction of inflowing *m* that is exported to sediments can also vary based on the type of *m* in question. For example, a regional analysis of river networks in agricultural basins found consistent N retention, but variable P retention behind dams (Powers et al. 2015). More work is needed to tease apart the role of E and *m* type, inflow rate, residence time, and other morphological factors in determining the efficiency of E and *m* processing in the waterbody filter (e.g., how E and *m* are either exported downstream or to sediments).

The waterbody filter has important implications not just for lake and reservoir ecology, but also for downstream and coastal ecosystems. Processing within waterbodies affects both the relative fraction and absolute magnitude of E and *m* exported downstream (as compared to sediments). While reservoirs are known to retain high fractions of *m* (e.g., bioavailable elements and sediment), the effect of climate drivers on the transport of *m* through the waterbody can fundamentally alter downstream and coastal ecosystems.

This study also highlights the important role of management, especially in reservoir systems. Under a changing climate, waterbody management may be re-assessed to address any of the following broad categories: (1) management to support designed purpose, (2) management for climate adaptation, or (3) management for climate change mitigation. Management for the designed purpose may require modification to comply with the Endangered Species Act or to accommodate other socio-ecological considerations that were not apparent when the dam was constructed. In the case of management for climate adaptation, reservoir management may be modified compensate for a changing climate (Eum and Simnovic 2010). Reservoirs, especially those with highly disturbed catchments, are extremely likely to require management to adapt to the effects of climate change including higher peak flows and improved water conservation under drought (Palmer et al. 2008). Finally, the capacity for reservoir management to either mitigate or enhance greenhouse gas emissions is a topic of current research given the important role of reservoirs in contributing to anthropogenic CH_4 emissions (Deemer et al. 2016). In the Pacific Northwest U.S.A., a study of six reservoirs found that water level drawdowns were associated with significantly higher methane emissions (Harrison et al. 2017), suggesting that water level management may affect the contribution of these systems toward radiative forcing in the atmosphere. Catchment management may also affect CH_4 emissions from lakes and reservoirs by altering lentic nutrient loading and associated primary production. High rates of primary production have been linked to high lake and reservoir CH_4 emissions in mesocosm (Davidson et al. 2015), regional (West et al. 2015), and global studies (Deemer et al. 2016). Given the significant global push to construct new dams (Zarfl et al. 2015), the propensity for reservoir design (e.g., landscape placement) to determine adaptive and mitigative capacity is an important area for future work.

Latitude matters: addressing the temperate lake bias

The conceptual model presented here does not consider differences in the geographic distribution of lakes and reservoirs, but instead describes the mechanistic differences expected between a lake and reservoir found in the same region. In addition, the evidence we used to formulate our conceptual model is based largely on north temperate and boreal systems. This is a common bias as global analyses of lakes and reservoirs generally have disproportionately less data from tropical systems than temperate and boreal systems (three tropical systems of 27 in Harrison et al. 2012, and 28 tropical systems of 115 in Harrison et al. 2009). Similarly, the reservoir pairs from the U.S. NLA dataset used to supplement this synthesis are temperate biased; only three of 66 lake-reservoir pairs are located below 35° north latitude (Fig. 3). While the majority of global lakes are situated at northern latitudes (Verpoorter et al. 2014), the same is not true for reservoirs, which are disproportionately located at lower latitudes (Lehner and Döll 2004). Future studies that compare lakes and reservoirs in tropical regions are needed to better verify the validity of the conceptual model proposed here for tropical systems. With increasing dam construction in tropical areas (Zarfl et al. 2015), this dearth of data for tropical and subtropical reservoirs becomes increasingly urgent to correct.

Reservoirs at lower latitudes may differ in fundamental ways from those at higher latitudes. Tropical lakes and reservoirs generally experience larger water level fluctuations than in temperate zones (Kolding and van Zwieten 2012), such that hydrology-driven changes in E and *m* processing may be amplified in these systems. Tropical lakes and reservoirs are known to experience higher sediment loading than their temperate and boreal counterparts, a pattern that has been largely attributed to tropical watershed deforestation (Syvitski et al. 2005 and citations therein). While analysis of the paired NLA dataset did not find significant land use differences between lakes and reservoirs (Supporting Information Material Table. S2), other studies suggest that reservoirs may be located in more developed watersheds (e.g., higher shoreline development indices, Thornton et al. 1980). In the tropics, deforestation constitutes a large portion of watershed "development." Reservoir management for fish production may also be disproportionately important in tropical systems. Since most freshwater fish production comes from the tropics, management of these systems often includes introduction of new species adapted to the reservoir environment, stocking, and management of fishing effort (van Zwieten et al. 2011). Our proposed conceptual model is thus likely to differ for tropical ecosystems; however, more research is needed to formulate specific hypotheses about differential fates of E and *m* in these systems (Fig. 6).

Important typological considerations when comparing lakes and reservoirs

This synthesis focuses on reservoirs that are formed by damming pre-existing lakes and rivers, and compares these human-created ecosystems to natural lakes > 0.04 km^2 in size. Still, there are other types of artificial and natural lakes that deserve further attention (Fig. 1). For example, small ponds (< 0.01 km^2), both natural and human made are estimated to represent upward of 20% of global lake and reservoir surface area (Verpoorter et al. 2014; Holgerson and Raymond 2016) and can be disproportionately active with respect to ecosystem functioning such as having higher per-area greenhouse gas emissions (Holgerson and Raymond 2016) and rates of sediment deposition (Downing et al. 2008) than larger lentic systems do. Still, these smaller systems are often ignored in ecological studies (Downing 2010), making it difficult to include them in a synthesis such as this one. One might not expect the same dichotomies between natural and human-made ponds as the ones we report here for larger systems. For example, human-made farm ponds and stormwater retention ponds may not necessarily have higher catchment areas and CA : SAs than natural ponds. Future effort should be made to quantify and map the global coverage of various reservoir (and lake) types and to examine the potential role of typology in defining differences between systems (e.g., for small ponds, Fig. 6).

Similarly, the comparisons between lakes and reservoirs made here are subject to other biases in how lakes and reservoirs are surveyed and studied. For example, the NLA does not include some less common lake types (e.g., saline lakes, etc.) nor do they consider mine ponds, or cooling ponds. The NLA sites are also selected based on the National Hydrography Dataset which may not accurately represent the full suite of reservoir types. While the papers synthesized here do not generally focus on or discuss detailed system typology, it is likely that they only represent a subset of system types. Some less studied natural lake types may also have properties analogous to human made reservoirs (i.e., lakes formed behind travertine dams, beaver ponds, and floodplain lakes) and these comparisons could be instructive to study in the future.

Conclusions

Here, we identify fundamental differences between lake and reservoir systems likely to yield different responses to climate forcing. The analysis and synthesis presented above support the notions that reservoirs receive more catchment-mediated E and *m* inputs per unit volume than lakes and that E and *m* is likely to be processed differently within the waterbody of a reservoir than of a lake. We stress the important role that the catchment and management filters may play in determining the ultimate fate of E and *m* in reservoirs and, consequently, the extent to which reservoirs are functioning as sentinels or buffers of climate change drivers. While this synthesis focuses on temperate lakes and reservoirs > 0.04 km^2, we stress the need to consider both latitude and typology in future efforts to compare lake and reservoir climate change responses. Given the rapid response of lentic ecosystems to current climate forcing and the continued global construction of reservoirs, an improved understanding of how reservoirs are mediating climate effects has important implications for lake and reservoir ecology as well as downstream ecosystems.

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