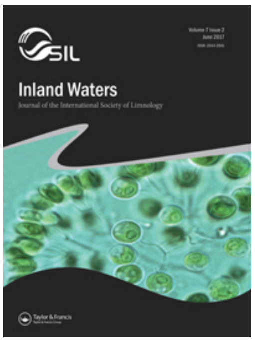

Inland Waters

ISSN: 2044-2041 (Print) 2044-205X (Online) Journal homepage: http://www.tandfonline.com/loi/tinw20

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To cite this article: Jonathan P. Doubek & Cayelan C. Carey (2017) Catchment, morphometric, and water quality characteristics differ between reservoirs and naturally formed lakes on a latitudinal gradient in the conterminous United States, Inland Waters, 7:2, 171-180, DOI: 10.1080/20442041.2017.1293317

To link to this article: https://doi.org/10.1080/20442041.2017.1293317

Published online: 04 May 2017.

INLAND WATERS, 2017
VOL. 7, NO. 2, 171–180
https://doi.org/10.1080/20442041.2017.1293317

Catchment, morphometric, and water quality characteristics differ between reservoirs and naturally formed lakes on a latitudinal gradient in the conterminous United States

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ABSTRACT

Constructed lakes and impoundments (reservoirs) likely exhibit substantial differences in their physics, chemistry, and biology from naturally formed lakes; however, because reservoirs and natural lakes generally have different latitudinal distributions, less is known about quantitative, generalized differences between the 2 waterbody types. We compared a suite of limnological variables among 1033 reservoirs and natural lakes across multiple size classes on a latitudinal gradient in the conterminous United States. In general, reservoirs had significantly greater perimeters, catchment areas, and catchment area:surface area ratios than natural lakes. Interestingly, several lakeshore land use, morphometric, and water quality response variables exhibited significant interactions between waterbody type and latitude. Southern reservoirs were deeper and had higher proportions of forested land and less agriculture and developed land use in their lakeshore than southern natural lakes, whereas northern reservoirs were shallower and had less forest and more agriculture and developed land in their lakeshore than northern natural lakes. Following the waterbody depth and land use data, natural lakes also had greater total phosphorus (TP) concentrations and shallower Secchi disk depths at lower latitudes, whereas reservoirs had greater TP concentrations and shallower Secchi disk depths at higher latitudes. Overall, natural lakes were more eutrophic than reservoirs, having greater total nitrogen and chlorophyll *a* concentrations, regardless of latitude. Our findings indicate that many physical, chemical, and lakeshore land use characteristics of reservoirs and natural lakes vary on a latitudinal gradient, which has implications for the water quality, ecology, and management of these waterbodies.

KEYWORDS
Chlorophyll *a*; impoundment; land use; latitude; nitrogen; phosphorus; water temperature

Introduction

Constructed lakes and impoundments (hereafter, reservoirs) provide critically important ecosystem services, including drinking water, fisheries, recreation, and irrigation (Rosenberg et al. 2000, Tundisi et al. 2008). In response to a growing human population and altered water availability, reservoir construction is increasing in many regions globally (Rosenberg et al. 2000, Downing et al. 2006). Despite their ubiquity and importance, however, reservoirs are generally less studied than naturally formed lakes.

Regional-scale studies indicate that reservoirs can exhibit substantial differences in their physics, chemistry, and biology from natural lakes (e.g., Jones and Bachmann 1978, Thornton et al. 1981, Whittier et al. 2002, Jones et al. 2008), but less is known about generalized differences across regions because reservoirs and natural lakes are often located in different geographic locations. For example, the conterminous United States has ~6 million enclosed inland waterbodies (Winslow et al. 2014), of which at least 2.6 million are constructed (Smith et al. 2002). In the United States, these reservoirs dominate at southern latitudes while natural lakes dominate at northern latitudes (Fig. 1; Thornton 1990). Consequently, given that approximately half of US waterbodies are reservoirs, it is important to determine if reservoir differences from natural lakes are primarily due to their latitude or if they stem from other factors, such as lakeshore land use and morphometric characteristics. Because many waterbody characteristics, including water temperature, waterbody size and shape, nutrient concentrations, phytoplankton abundance, and zooplankton community characteristics, vary on a latitudinal gradient as a result of differences in geology, glaciation history, solar radiation, temperature,

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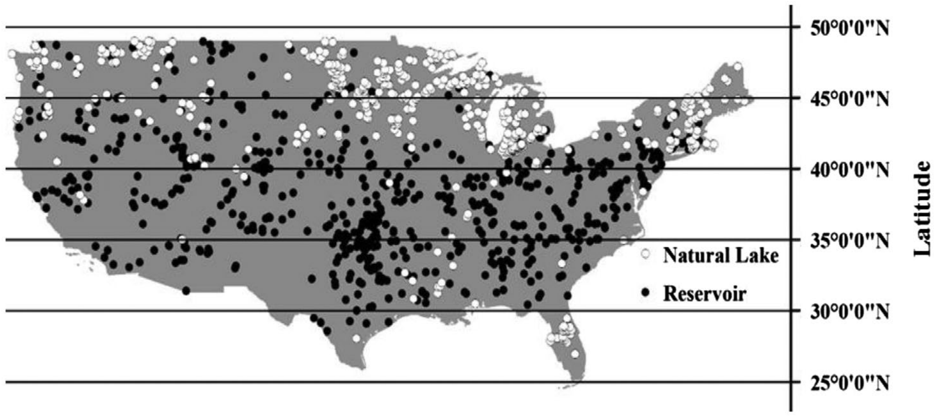

Figure 1. Geographical location of the natural lakes (white circles; $n = 441$) and reservoirs (black circles; $n = 592$) sampled as part of the 2007 US EPA National Lakes Assessment (NLA) and included in our analyses. Latitude was included as a covariate in all regression analyses because of the higher frequency of reservoirs at lower latitudes than natural lakes.

precipitation, and historical land use (e.g., Vincent et al. 1986, Lewis 1996, Stomp et al. 2011, Abell et al. 2012, Beaver et al. 2014b, Winslow et al. 2014), extrapolating studies across the United States may be challenging. Therefore, quantifying these waterbody type differences while explicitly controlling for the effects of latitude is necessary.

Reservoirs likely exhibit many catchment, morphometric, and physical differences from natural lakes. Because many reservoirs are created from impounding rivers, reservoirs are generally expected to have greater catchment areas, catchment area:surface area ratios, and perimeters than natural lakes (Thornton et al. 1981, Kimmel et al. 1990, Whittier et al. 2002, Knoll et al. 2015). Additionally, reservoirs are generally noted to be warmer than natural lakes in the United States because of their geographical differences (Thornton 1990, Wetzel 1990), and reservoirs can have more variable thermal stratification than natural lakes because of active management, such as hydropower production or dam withdrawals at multiple depths (Ford 1990, Harris and Baxter 1996, Han 2000). Because these catchment and waterbody characteristics can potentially influence water quality and ecosystem processing (e.g., Jones et al. 2004, 2008, Bremigan et al. 2008), it is important to examine if these catchment and physical waterbody differences still exist after accounting for waterbody geographical differences.

Previous waterbody type comparisons have found conflicting or no evidence as to whether reservoirs or natural lakes are more eutrophic in the United States (e.g., Jones and Bachmann 1978, Canfield and Bachmann 1981, Wetzel 1990, 2001, Whittier et al. 2002, Cooke et al. 2005, US EPA 2009). Whether reservoirs or natural lakes have higher concentrations of total nitrogen (TN), total phosphorus (TP), and, subsequently, chlorophyll *a* (Chl-*a*) concentrations (e.g., Jones and Bachmann 1976, Jones and Knowlton 2005, Beaulieu et al. 2013, Beaver et al. 2014a, Rigosi et al. 2014, Yuan and Pollard 2014, Yuan et al. 2014) may depend on which waterbody has greater lakeshore anthropogenic land use (Carpenter et al. 1998, Hall et al. 1999, Arbuckle and Downing 2001, Fraterrigo and Downing 2008, Gémesi et al. 2011, Knoll et al. 2003, 2015) or catchment and waterbody morphometric differences (e.g., Prepas et al. 2001, Jones et al. 2004, 2008, Bremigan et al. 2008). Two previous studies that compared the trophic status of natural lakes and reservoirs at the conterminous US scale found contrasting results. One study found that reservoirs were less eutrophic than natural lakes in terms of TP, but because latitude or region was not taken into account in that study (Canfield and Bachmann 1981), the generalizability of this result remains unknown. The US Environmental Protection Agency (US EPA 2009) found no differences in trophic status (TN and TP) between natural lakes and reservoirs in their 2007 National Lakes Assessment (NLA). The US EPA (2009) examined differences among waterbodies at the conterminous US scale but did not report analyses that specifically accounted for geographic region or latitude. As a result, there is currently contrasting evidence on baseline differences that may exist between reservoirs and natural lakes, which warrants further evaluation.

Here, we used data collected from the US EPA's 2007 NLA to expand on previous studies and quantify and contrast multiple physical, lakeshore land use, and water quality characteristics between natural lakes and reservoirs in the conterminous United States while accounting for latitude. Because the NLA used a randomized stratified design that randomly selected waterbodies within multiple size classes, we were able to compare and generalize waterbody and water quality characteristics across natural lakes and reservoirs of different sizes. The overarching goal of this study was to examine if generalizable, baseline differences exist in catchment, morphometric, and water quality characteristics between natural lakes and reservoirs after accounting for latitude, which has implications for their ecology and management.

Methods

EPA National Lakes Assessment sampling

As part of the EPA NLA, >1000 waterbodies in the conterminous United States were sampled once or twice during spring or summer 2007. Waterbodies with at least 1 m depth and a minimum surface area of 0.04 km^2 were chosen in a randomized stratified design based on size classes (termed probabilistic waterbodies; US EPA 2009, Peck et al. 2013). Natural lakes and reservoirs were sampled across 5 designated surface area size classes: 0.04–0.1, >0.1–0.2, >0.2–0.5, >0.5–1, and >1 km^2. Our goal was to compare natural lakes and reservoirs across these different size classes, not just small waterbodies, which numerically dominate the US waterbody population. Thus, our comparisons were not weighted to represent the entire waterbody population of the US, but rather be representative of the entire range of waterbody sizes across the conterminous US. The NLA weights were calculated solely from waterbody surface areas (Peck et al. 2013) and do not reflect any other waterbody characteristics (e.g., nutrient concentrations, catchment characteristics, and land use). Some lake characteristics, but certainly not all, scale by surface area, and therefore weighting would disproportionally emphasize the characteristics associated with the small waterbodies in the NLA. Consequently, because this study focused on a suite of limnological characteristics beyond surface area, we conducted our analyses across the size classes in the NLA without weighting. The EPA classified the waterbodies as either natural lakes ($n = 441$) or reservoirs ($n = 592$), defined as naturally formed or constructed, respectively.

Researchers followed standardized protocols at each waterbody to sample physical, chemical, and biological conditions. Integrated samples were collected from 2 m depth to the surface for water chemistry analyses and for Chl-*a* concentrations. Phytoplankton genera biovolumes were also enumerated for each lake; however, because some biovolume data were missing, we did not examine waterbody type differences of phytoplankton groups in this study. Some waterbodies in the NLA were resampled later in the season or had replicate samples taken. We only analyzed data collected from the first visit and first replicate to maintain consistency across waterbodies. All data from the EPA NLA survey and comprehensive field and laboratory methods are publicly available (http://water.epa.gov/type/lakes/lakessurvey_index.cfm).

Statistical analyses

We assessed many catchment, lakeshore land use, waterbody morphometric, and water quality variables between natural lakes and reservoirs. Our response variables were waterbody maximum depth; waterbody surface area; waterbody perimeter; watershed basin area around the waterbody (hereafter referred to as catchment area); catchment area:surface area; elevation; surface water temperature (temperature at 0 m); mean water column temperature; surface water temperature minus the water temperature just above the sediments from NLA profile data (hereafter, termed water column temperature differential); surface dissolved oxygen (DO) concentration (DO percent saturation was not provided); mean water column DO; Secchi disk depth; turbidity; water color; proportion of forested, wetland, pasture, crop, agriculture, developed, and anthropogenic (the sum of agriculture and developed) lakeshore land use, where lakeshore land use was defined as land use within a 200 m buffer around each waterbody, as quantified by the National Land Cover Dataset (NLCD) and reported by the EPA; nutrient concentrations of TN, TP, TN:TP molar ratio, total organic carbon (TOC), dissolved organic carbon (DOC), and total silica; and Chl-*a* concentrations. In lieu of having the bathymetry or wind speed data needed to calculate some water column stratification metrics (Read et al. 2011), we used the water column temperature differential as a proxy for the strength of thermal stratification of a waterbody (i.e., the lower the temperature differential, the weaker the stratification; Wetzel 2001). We compared only the proportion of land use categories (e.g., forested, agriculture) in the 200 m buffer around each lake (standardized by the size of the lake to enable comparison among waterbodies) to account for land use in closest proximity to each waterbody (e.g., Tufford et al. 1998, Tran et al. 2010, Howell et al. 2012). No information on the number of inflows, outflows, or landscape position was provided for each waterbody, so we were unable to directly assess hydrological regimes for the waterbodies.

We analyzed the effects of waterbody type (reservoirs or natural lakes), latitude, and their interaction on our response variables using multiple linear regression models with waterbody type as an indicator variable (Kutner et al. 2005), coded 0 for natural lakes and 1 for reservoirs. Our primary multiple linear regression model for each analysis was:

$$Y = B_0 + B_1X_{waterbody\_type} + B_2X_{latitude} + B_3X_{waterbody\_type\times latitude} + \varepsilon,$$

where Y represents the response variable of interest; B_0 is the intercept term; B_1, B_2, and B_3 are model parameters for the waterbody type term, latitude term, and their interaction, respectively; and ε is a stochastic error term. To meet the assumptions of normality and equal variances, waterbody maximum depth, surface area, waterbody perimeter, catchment area, catchment area:surface area, elevation, Secchi disk depth, turbidity, water color, TN, TP, molar TN:TP ratios, TOC, DOC, total silica, and Chl-*a* were ln-transformed. The land use categories expressed as proportions were logit-transformed prior to analyses (Warton and Hui 2011). If the proportions had zero values, the minimum observed value was added as a constant prior to logit-transformation so those data could be included (Warton and Hui 2011), which did not change the significance of the predictor variables. The *P*-values for statistical tests were considered significant at $\alpha \leq 0.05$, and all analyses were performed in JMP Pro 12 (SAS Institute, Cary, NC, USA).

Results

Across the conterminous US, we observed many significant differences in catchment, lakeshore land use, waterbody morphometry, and water quality characteristics between reservoirs and natural lakes when controlling for the effect of latitude (Table 1 and 2), indicating that reservoirs and natural lakes have baseline differences separate from the latitude-driven effects. If the interaction between waterbody type and latitude was significant in addition to the individual waterbody type effect, the waterbody type effect was interpreted in the context of latitude.

Reservoirs had significantly greater waterbody perimeters, catchment areas, and catchment area:surface area ratios and were higher in elevation than natural lakes (Table 1 and 2; Fig. 2a and 2b; all $F_{1,1029} \geq 18.40$, $P < 0.0001$); however, the differences in elevation between waterbody types started to converge with increased latitude, resulting in a significant interaction between waterbody type and latitude for elevation ($F_{1,1029}$ = 14.12, P = 0.0002). Reservoirs had, on average, 2 times larger waterbody perimeters (41 ± 7 vs. 18 ± 8 km, 1 SE), 12 times larger catchment areas (5000 ± 1300 vs. 400 ± 1600 km^2), and 7 times larger catchment area:surface area ratios (530 ± 130 vs. 72 ± 160) compared to natural lakes. Although

Table 1. Multiple linear regression model statistics and results for the effects of waterbody type as an indicator variable (with natural lakes coded as 0 and reservoirs coded as 1; positive indicates greater values in reservoirs), latitude, and the interaction of waterbody type and latitude on physical, lakeshore land use, and water quality response variables. The parameter values and their standard error (SE) are given for the waterbody type, latitude, and interaction terms in the regression model. The lakeshore land use data were calculated for a 200 m buffer around the perimeter of each waterbody. Statistically significant results are highlighted in bold, and *n* is the sample size of waterbodies in each analysis.

Response variable	n_{lakes}	$n_{reservoirs}$	Intercept parameter ± SE	Waterbody type value ± SE	Waterbody type *P*	Latitude value ± SE	Latitude *P*	Interaction value ± SE	Interaction *P*
Physical variables									
ln(maximum depth)	441	591	1.04 ± 0.28	0.06 ± 0.03	0.08	0.02 ± 0.01	**0.01**	−0.02 ± 0.01	**0.02**
ln(surface area)	441	592	1.32 ± 0.56	0.06 ± 0.07	0.39	−0.03 ± 0.01	**0.02**	0.01 ± 0.01	0.51
ln(waterbody perimeter)	441	592	3.15 ± 0.40	0.21 ± 0.05	**<0.0001**	−0.03 ± 0.01	**0.003**	−0.005 ± 0.01	0.64
ln(catchment area)	441	592	4.40 ± 0.78	0.65 ± 0.10	**<0.0001**	−0.02 ± 0.02	0.27	−0.005 ± 0.02	0.80
ln(catchment area:surface area)	441	592	3.08 ± 0.48	0.59 ± 0.06	**<0.0001**	0.01 ± 0.01	0.34	−0.01 ± 0.01	0.25
ln(elevation)	441	592	−0.15 ± 0.39	0.42 ± 0.05	**<0.0001**	0.14 ± 0.01	**<0.0001**	−0.04 ± 0.01	**0.0002**
Surface temperature	439	586	43.83 ± 1.01	−0.32 ± 0.13	**0.01**	−0.48 ± 0.02	**<0.0001**	−0.04 ± 0.02	0.12
Mean water temperature	439	586	43.03 ± 1.34	−0.05 ± 0.16	0.77	−0.53 ± 0.03	**<0.0001**	0.01 ± 0.03	0.67
Water column temperature differential	439	586	2.57 ± 1.87	−0.40 ± 0.23	0.08	0.08 ± 0.05	0.07	−0.11 ± 0.05	**0.02**
ln(Secchi disk depth)	408	571	−1.70 ± 0.31	−0.01 ± 0.04	0.88	0.05 ± 0.01	**<0.0001**	−0.02 ± 0.01	**0.03**
ln(turbidity)	441	592	3.24 ± 0.40	0.08 ± 0.05	0.11	−0.04 ± 0.01	**<0.0001**	0.02 ± 0.01	0.06
ln(water color)	441	592	3.11 ± 0.26	−0.10 ± 0.03	**0.003**	−0.02 ± 0.01	**0.01**	0.01 ± 0.01	0.18
Land use									
logit(% forested)	441	592	−0.39 ± 1.01	−0.06 ± 0.12	0.63	−0.05 ± 0.02	0.06	−0.14 ± 0.02	**<0.0001**
logit(% wetland)	441	592	−0.76 ± 0.82	−1.07 ± 0.10	**<0.0001**	−0.06 ± 0.02	**0.003**	0.10 ± 0.02	**<0.0001**
logit(% pasture)	441	592	−4.07 ± 0.90	0.32 ± 0.11	**0.004**	−0.04 ± 0.02	0.07	−0.01 ± 0.02	0.59
logit(% crop)	441	592	−6.07 ± 0.91	−0.24 ± 0.11	**0.03**	0.01 ± 0.02	0.71	0.06 ± 0.02	**0.005**
logit(% agriculture)	441	592	−2.92 ± 0.98	0.12 ± 0.12	0.33	−0.04 ± 0.02	0.13	0.03 ± 0.02	0.17
logit(% developed)	441	592	0.70 ± 0.69	−0.33 ± 0.08	**0.0001**	−0.09 ± 0.02	**<0.0001**	0.03 ± 0.02	**0.04**
logit(% agriculture + developed)	441	592	0.90 ± 0.70	−0.22 ± 0.09	**0.01**	−0.07 ± 0.02	**<0.0001**	0.05 ± 0.02	**0.007**
Chemical variables									
Surface DO	435	547	5.37 ± 0.66	−0.004 ± 0.08	0.96	0.07 ± 0.02	**<0.0001**	0.01 ± 0.02	0.44
Mean DO	435	547	2.13 ± 0.63	0.04 ± 0.08	0.57	0.10 ± 0.02	**<0.0001**	0.05 ± 0.02	**0.001**
ln(TN)	441	592	6.81 ± 0.31	−0.16 ± 0.04	**<0.0001**	−0.01 ± 0.01	0.31	0.01 ± 0.01	0.14
ln(TP)	441	592	4.07 ± 0.46	0.09 ± 0.06	0.12	−0.01 ± 0.01	0.20	0.02 ± 0.01	**0.03**
ln(TN:TP)	441	592	3.53 ± 0.27	−0.25 ± 0.03	**<0.0001**	0.01 ± 0.01	0.31	−0.01 ± 0.01	**0.05**
ln(TOC)	441	592	1.99 ± 0.25	−0.22 ± 0.03	**<0.0001**	−0.003 ± 0.01	0.57	−0.001 ± 0.01	0.86
ln(DOC)	441	592	1.77 ± 0.24	−0.21 ± 0.03	**<0.0001**	−0.0001 ± 0.01	0.99	−0.002 ± 0.01	0.68
ln(total silica)	441	592	0.97 ± 0.39	0.09 ± 0.05	0.08	0.01 ± 0.01	0.23	−0.02 ± 0.01	**0.04**
ln(Chl-*a*)	439	589	5.64 ± 0.43	−0.15 ± 0.05	**0.006**	−0.08 ± 0.01	**<0.0001**	0.02 ± 0.01	0.06

Table 2. All response variables compared between natural lakes and reservoirs, with each variable's untransformed mean values, with standard errors (SE). Significant waterbody type effect or the interaction between waterbody type and latitude effect denoted by * = $P \leq 0.05$, ** = $P < 0.01$, or *** = $P < 0.001$.

Variable	Waterbody effect?	Interaction effect?	Natural lakes mean ± SE	Reservoirs mean ± SE
Physical variables				
Maximum depth		*	8.9 ± 0.6 m	9.1 ± 0.5 m
Surface area			21.4 ± 4.7 km²	12.0 ± 3.9 km²
Waterbody perimeter	***		17.5 ± 8.1 km	40.9 ± 6.6 km
Catchment area	***		413 ± 1560 km²	4950 ± 1280 km²
Catchment area:surface area	***		71.5 ± 159	527 ± 131
Elevation	***	***	478 ± 37.7 m	768 ± 31.0 m
Surface temperature	**		24.7 ± 0.2 °C	24.1 ± 0.2 °C
Mean water column temperature			21.6 ± 0.3 °C	21.5 ± 0.2 °C
Water column temperature differential		*	6.3 ± 0.4 °C	5.5 ± 0.3 °C
Secchi disk depth		*	2.2 ± 0.1 m	1.9 ± 0.1 m
Turbidity			13.4 ± 2.0 NTU	15.4 ± 1.6 NTU
Water color	**		19.6 ± 0.9 PCU	14.8 ± 0.7 PCU
Land use				
Forested		***	28.1 ± 1.7%	32.8 ± 1.4%
Wetland	***	***	23.9 ± 0.9%	9.3 ± 0.7%
Pasture	**		4.7 ± 0.7%	6.8 ± 0.6%
Crop	*	**	8.7 ± 0.7%	5.2 ± 0.6%
Agriculture			13.4 ± 1.1%	12.0 ± 0.9%
Developed	***	*	18.6 ± 1.1%	12.9 ± 0.9%
Agriculture + developed	*	**	32.0 ± 1.5%	24.9 ± 1.2%
Chemical variables				
Surface DO			8.4 ± 0.1 mg/L	8.4 ± 0.1 mg/L
Mean DO		**	6.2 ± 0.1 mg/L	6.2 ± 0.1 mg/L
TN	***		1560 ± 115 µg/L	904 ± 94.3 µg/L
TP		*	108 ± 15.1 µg/L	122 ± 12.4 µg/L
TN:TP molar ratio	***	*	88.7 ± 7.4	59.3 ± 6.1
TOC	***		13.4 ± 1.0 mg/L	7.0 ± 0.8 mg/L
DOC	***		11.6 ± 0.9 mg/L	6.4 ± 0.7 mg/L
Total silica		*	8.8 ± 0.6 mg/L	8.4 ± 0.5 mg/L
Chl-*a*	**		42.8 ± 3.9 µg/L	24.2 ± 3.2 µg/L

there was no significant waterbody type effect for maximum depth ($P = 0.08$), there was a significant interaction effect of latitude and waterbody type with depth ($F_{1,1028} = 5.77$; $P = 0.02$). Reservoirs were deeper at latitudes lower than 44°N, and natural lakes were deeper at higher latitudes. There were no significant main waterbody or interaction effects for waterbody surface area ($P > 0.38$).

As expected, surface and mean water column temperatures across both types of waterbodies significantly decreased with increasing latitude (Table 1; $F_{1,1021} \geq 265.14$, $P < 0.0001$), and surface and mean DO concentrations increased with increasing latitude ($F_{1,978} \geq 23.09$, $P < 0.0001$). Natural lakes (24.7 ± 0.2 °C) had significantly greater surface temperatures than reservoirs (24.1 ± 0.2 °C; $F_{1,1021} = 6.68$, $P = 0.01$) across all latitudes, but there was no difference in mean water column temperatures between waterbody types ($P = 0.77$). There were no significant differences in surface and mean DO concentrations between waterbodies ($P > 0.56$); however, there was a significant waterbody and latitude interaction effect for mean DO concentrations ($F_{1,978} = 10.39$, $P = 0.001$). Reservoirs had greater mean DO concentrations at latitudes higher than 40°N, and natural lakes had greater mean DO concentrations at lower latitudes. There was also a significant waterbody and latitude interaction effect for the water column temperature differential, a proxy for thermal stratification (Fig. 2c; $F_{1,1021} = 5.79$, $P = 0.02$). Reservoirs had a lower water column temperature differential than natural lakes at latitudes higher than 36°N, and natural lakes had a lower water column temperature differential at lower latitudes.

We observed systematic differences in reservoir versus natural lake lakeshore land use that varied on a latitudinal gradient. Natural lakes (19 ± 1%, 1 SE) had greater developed lakeshore land use than reservoirs (13 ± 1%) at all latitudes (Table 1 and 2; $F_{1,1029} = 14.89$, $P = 0.0001$), but this difference converged at higher latitudes ($F_{1,1029} = 4.09$, $P = 0.04$). Crop and agriculture + developed lakeshore land use were also significantly greater in natural lakes than in reservoirs ($F_{1,1029} \geq 4.50$, $P \leq 0.03$); however, there were also significant interactions between waterbody type and latitude (Fig. 2d; $P \leq 0.008$). Natural lakes had greater crop and agriculture + developed land use at latitudes lower than 45°N, whereas reservoirs exhibited greater proportions of these 2 land use types at higher latitudes. Reservoirs had significantly greater pasture lakeshore land use at all latitudes ($F_{1,1029} = 8.15$, $P = 0.004$), and there were no significant waterbody or interaction effects for total agriculture ($P > 0.17$). Following those results, we observed an opposite interaction for forested land use (Fig. 2e; $F_{1,1029} = 31.75$, $P < 0.0001$), with reservoirs being more forested in lower latitudes (<40°N), and natural lakes were more forested at higher latitudes. Natural lakes had significantly greater wetland lakeshore land use (24 ± 1%) than reservoirs (9 ± 1%) at all latitudes ($F_{1,1029} = 111.17$, $P < 0.0001$), and the differences between waterbody types converged at higher latitudes ($F_{1,1029} = 24.25$, $P < 0.0001$).

Across the conterminous US, we observed that natural lakes were generally more eutrophic than reservoirs. On average, natural lakes had almost 2 times larger concentrations of TN (Table 1 and 2, Fig. 3a; $F_{1,1029} = 16.92$, $P < 0.0001$). Although there was no significant waterbody effect for TP (Fig. 3b; $P = 0.12$), we observed a significant interaction effect; natural lakes had higher TP concentrations at lower latitudes (<37°N) and lower TP concentrations than reservoirs at higher latitudes ($F_{1,1029} = 4.75$, $P = 0.03$). Because the difference in TN concentrations between the 2 waterbody types was greater than that of TP, reservoirs had significantly lower mean TN:TP molar ratios (59 ± 6, 1 SE) than natural lakes (89 ± 7; Fig. 3c; $F_{1,1029} = 54.09$, $P < 0.0001$), with a convergence of TN:TP ratios at lower latitudes ($F_{1,1029} = 3.97$, $P = 0.05$). Natural lakes also had significantly greater concentrations of TOC (13 ± 1 mg/L) and DOC (12 ± 1 mg/L) than reservoirs (7 ± 1 and 6 ± 1 mg/L, respectively; $F_{1,1029} \geq 51.08$, $P <$ 0.0001). Although there was no waterbody effect on silica concentrations ($P = 0.08$), reservoirs had greater silica concentrations at latitudes lower than 45°N, and natural lakes had greater silica concentrations at higher latitudes ($F_{1,1029} = 4.35$, $P = 0.04$).

Following the land use and nutrient data, natural lakes had almost double the concentration of Chl-*a* (43 ± 4 μg/L) than reservoirs (24 ± 3 μg/L) across all latitudes (Table 1 and 2, Fig. 3d; $F_{1,1024} = 7.72$, $P = 0.006$). Natural lakes (20 ± 1 PCU) also had greater water color than reservoirs (15 ± 1 PCU; $F_{1,1029} = 9.06$, $P = 0.003$). Likewise, reservoirs had deeper Secchi disk depths at lower latitudes (<40°N), and natural lakes had deeper Secchi disk depths at higher latitudes ($F_{1,975} = 4.47$, $P = 0.03$). There were no significant waterbody or interaction effects for turbidity ($P > 0.06$).

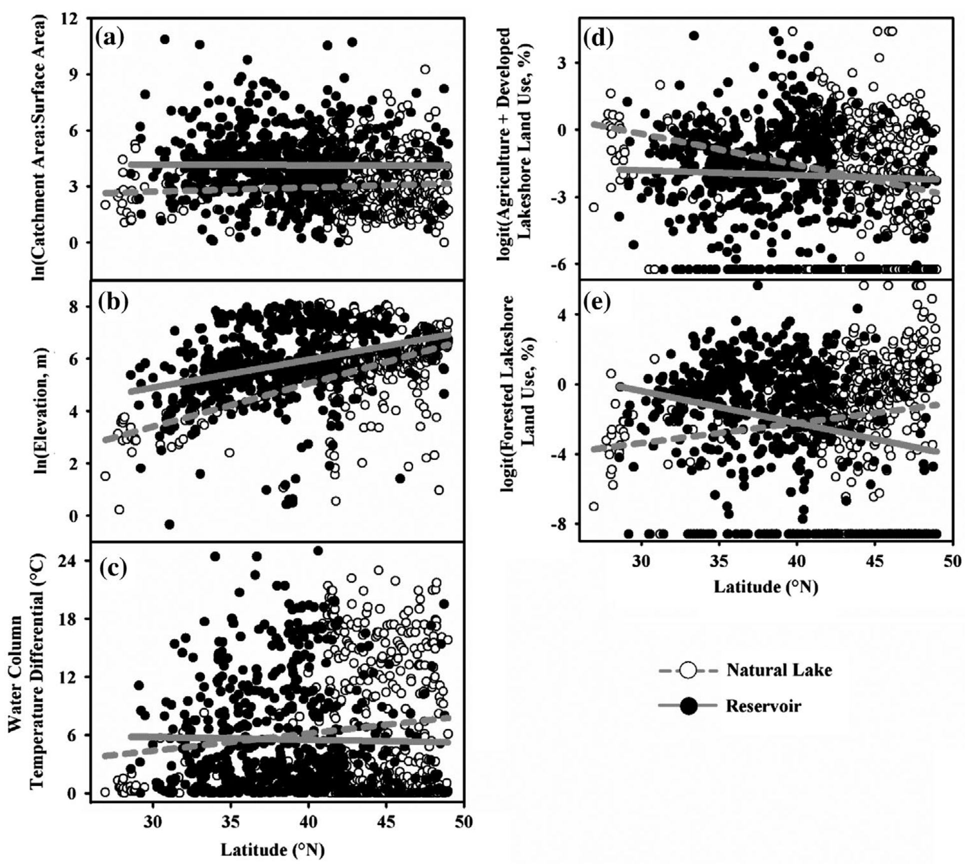

Figure 2. Conterminous US relationships of latitude and (a) catchment area:surface area, (b) elevation, (c) water column temperature differential, (d) the proportion of agriculture + developed lakeshore land use, and (e) the proportion of forested lakeshore land use of natural lakes (dotted grey line, white circles) and reservoirs (solid grey line, black circles).

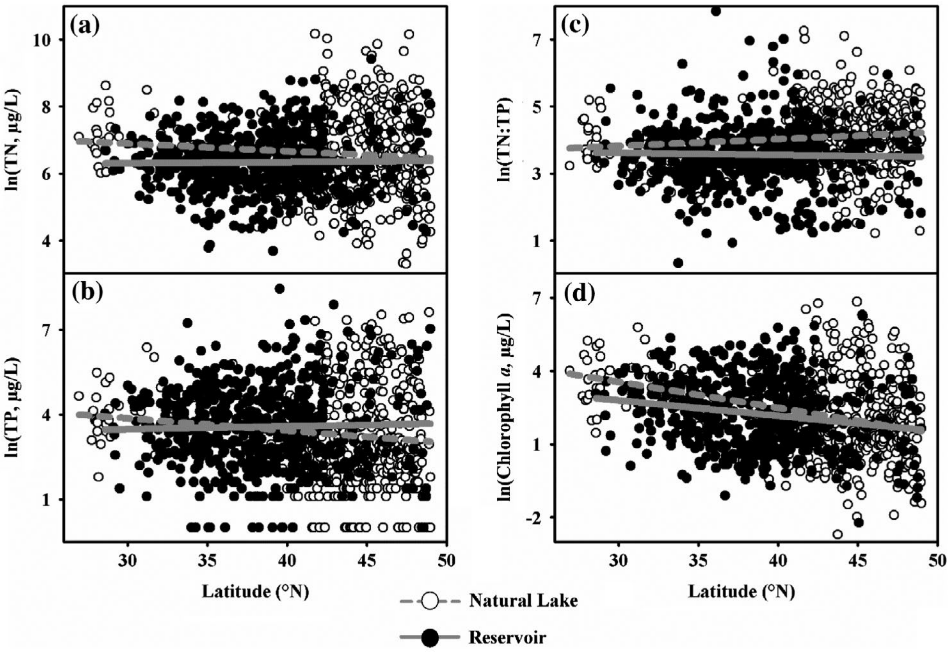

Figure 3. Conterminous US relationships of latitude and (a) total nitrogen (TN), (b) total phosphorus (TP), (c) molar TN:TP ratio, and (d) chlorophyll *a* of natural lakes (dotted grey line, white circles) and reservoirs (solid grey line, black circles).

Discussion

This study expands our current knowledge of reservoir and natural lake comparisons by examining a suite of limnological variables across waterbodies of different size classes while accounting for latitude. Previous comparisons of reservoirs and natural lakes were conducted either at local to regional levels (e.g., Jones and Bachmann 1978, Whittier et al. 2002), were qualitative (e.g., Wetzel 1990, 2001, Cooke et al. 2005), or did not specifically account for geographic differences of waterbodies in analyses at the conterminous US scale (e.g., Canfield and Bachmann 1981, US EPA 2009). Because of the large geographical differences between reservoirs and natural lakes in the US (Canfield and Bachmann 1981, Thornton 1990; Fig. 1), accounting for latitude is important to statistically quantify waterbody type differences because many physical and water quality parameters vary on a latitudinal gradient as a result of baseline differences in multiple factors, such as solar radiation, temperature, and geology (Vincent et al. 1986, Lewis 1996, Abell et al. 2012, Winslow et al. 2014). Although some parameters did not vary with latitude (e.g., some catchment characteristics, TN, and Chl-*a* concentrations), several differences between the waterbody types were dependent on local land use and other geographic factors that vary regionally across the US. Consequently, our results emphasize the importance of accounting for latitude in waterbody type comparisons.

As observed in previous waterbody type comparisons (Wetzel 1990, 2001, Knoll et al. 2015), reservoirs exhibited much greater catchment areas, catchment area:surface area ratios, and perimeters than natural lakes, likely a result of their formation from impounding lotic systems (Thornton et al. 1981). After accounting for latitude, natural lakes had greater surface water temperatures than reservoirs, despite no overall significant waterbody effect of surface area and maximum depth, which are generally important factors determining water temperature (Gorham 1964, Gorham and Boyce 1989). This waterbody temperature difference was only observed for surface water temperature, not mean water column temperature, suggesting that natural lakes may have warmer surface water because of their significantly greater developed lakeshore land use. Increasing impervious surface area along lakeshores is often associated with warmer surface temperatures in waterbodies (Thompson et al. 2008a, 2008b, Doubek et al. 2015).

Overall, our analysis supports observations from previous studies (Jones and Bachmann 1978, Canfield and Bachmann 1981) that natural lakes were generally more eutrophic than reservoirs, as defined here by significantly higher TN, TN:TP ratios, and Chl-*a* concentrations, which may be due to several reasons. First, reservoirs generally had lower agriculture + developed lakeshore land use and higher forested lakeshore land use than natural lakes, especially at lower latitudes. Human-dominated lakeshore land use corresponds to increased nutrient and phytoplankton concentrations (Jones and Bachmann 1976, Carpenter et al. 1998, Arbuckle and Downing 2001, Hall et al. 1999, Jones and Knowlton 2005, Schindler 2006, Fraterrigo and Downing 2008, Gémesi et al. 2011), and the difference in lakeshore land use is likely a key reason why natural lakes were more eutrophic than reservoirs. Natural lakes also had greater TOC, DOC, and water color at all latitudes, which is also likely related to lakeshore land use. In addition to higher overall anthropogenic lakeshore land use types, natural lakes also had more than twice the wetland lakeshore land use, on average, than reservoirs (e.g., Dillon and Molot 1997, Halsey et al. 1997, Prepas et al. 2001). Second, as noted earlier, natural lakes had overall greater surface water temperatures than reservoirs, which may stimulate increased Chl-*a* and phytoplankton concentrations (e.g., Paerl and Huisman 2008, Beaulieu et al. 2013, Paerl and Otten 2013, Rigosi et al. 2014). Third, waterbody management may possibly influence whether natural lakes or reservoirs are more eutrophic. For example, reservoirs actively managed for drinking water may be more likely to receive alum, oxygenation, or other treatments that decrease nutrient and phytoplankton concentrations (e.g., McGinnis and Little 2002, Cooke et al. 2005, Gerling et al. 2014), although the NLA dataset did not identify which waterbodies were receiving water quality management. Southern reservoirs had greater forested land use than natural lakes, which may be indicative of more intense management for services such as drinking water, but this remains unknown from this dataset. Fourth, we found that reservoirs were located at higher elevations, on average, than natural lakes, which indicates they may be more isolated and receive less upstream drainage and runoff than natural lakes at a lower landscape position (Kratz et al. 1997), despite having greater catchment areas. Fifth, reservoirs are generally much younger than natural lakes and therefore may have had less time than glacially formed lakes to accumulate sediments and nutrients. More research is needed to determine which of these hypotheses, or others, are the most important drivers of the difference in nutrient and Chl-*a* concentrations between waterbody types.

Northern reservoirs were less thermally stratified than northern natural lakes, as indicated by significantly lower water column temperature differentials, but southern (<36°N) reservoirs were more thermally stratified than southern natural lakes. Although there was no overall significant difference of maximum depth between waterbodies that could influence these temperature differences (Gorham 1964, Gorham and Boyce 1989), maximum depth also exhibited a significant interaction between latitude and waterbody type. Southern reservoirs were deeper than southern natural lakes, and northern reservoirs were shallower than northern natural lakes; therefore, latitudinal depth differences may be one reason why there was a significant interaction of the water column temperature differential between waterbodies at different latitudes. In addition, reservoirs tend to experience more variable stratification and epilimnetic–hypolimnetic water column mixing than natural lakes because of water withdrawals at different dam outflow depths (Ford 1990, Harris and Baxter 1996, Han 2000), which may also account for some this interaction.

We observed that many of our response variables varied on a latitudinal gradient or exhibited significant latitudinal interaction effects, as have many other studies (e.g., Vincent et al. 1986, Lewis 1996, Stomp et al. 2011, Abell et al. 2012, Beaver et al. 2014b, Winslow et al. 2014), and thus it was important to include latitude in our analyses, as advocated by Canfield and Bachmann (1981). Notably, although natural lakes were overall more eutrophic than reservoirs, this waterbody difference converged at higher latitudes (>45°N), likely related to lakeshore land use and maximum depth differences. These latitudinal differences emphasize the importance of local land use and other geographic factors that vary regionally in the US. Overall, these differences between reservoirs and natural lakes may have implications for the ecology and management of freshwater ecosystem services they provide (Bartram and Chorus 1999, Falconer 1999, Hudnell 2010). Because both reservoirs and natural lakes are increasingly experiencing anthropogenic stress, identifying baseline differences between the 2 types of ecosystems is a first step in predicting how these waterbodies may respond to future change.

Acknowledgements

We thank J.R. Jones, A.B. Gerling, K.D. Hamre, B.L. Brown, 2 anonymous reviewers, and colleagues from the Global Lake Ecological Observatory Network (GLEON) for helpful feedback and comments on this manuscript

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was financially supported by the US National Science Foundation (DEB-1601061, ICER-1517823), Virginia Tech's Department of Biological Sciences, Fralin Life Sciences Institute, Global Change Center, the Interfaces of Global Change program, and the Institute for Critical Technology and Applied Science.

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