

1 **The Regional and Global Significance of Nitrogen Removal in Lakes**
2 **and Reservoirs**

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44 **Abstract**

45 Human activities have greatly increased the transport of biologically available N through
46 watersheds to potentially sensitive coastal ecosystems. Lentic water bodies (lakes and
47 reservoirs) have the potential to act as important sinks for this reactive N as it is
48 transported across the landscape because they offer ideal conditions for N burial in
49 sediments or permanent loss via denitrification. However, the patterns and controls on
50 lentic N removal have not been explored in great detail at large regional to global scales.
51 In this paper we describe, evaluate, and apply a new, spatially explicit, annual-scale,
52 global model of lentic N removal called NiRReLa (**N**itrogen **R**etention in **R**eservoirs and
53 **L**akes). The NiRReLa model incorporates small lakes and reservoirs that have been
54 included in previous global analyses, and also allows for separate treatment and analysis
55 of reservoirs and natural lakes. Model runs for the mid-1990s indicate that lentic systems
56 are indeed important sinks for N and are conservatively estimated to remove 19.7 Tg N
57 yr⁻¹ from watersheds globally. Small lakes (< 50 km²) were critical in the analysis,
58 retaining almost half (9.3 Tg N yr⁻¹) of the global total. In model runs, capacity of lakes
59 and reservoirs to remove watershed N varied substantially (0-100%) both as a function of
60 climate and the density of lentic systems. Although reservoirs occupy just 6% of the
61 global lentic surface area, we estimate they retain approximately 33% of the total N
62 removed by lentic systems, due to a combination of higher drainage ratios (catchment
63 surface area : lake or reservoir surface area), higher apparent settling velocities for N, and
64 greater N loading rates in reservoirs than in lakes. Finally, a sensitivity analysis of
65 NiRReLa suggests that, on-average, N removal within lentic systems will respond more
66 strongly to changes in land use and N loading than to changes in climate at the global
67 scale.

68 **Introduction**

69 Human activities such as fertilizer manufacturing, fossil fuel combustion, and
70 cultivation of legume crops have more than doubled rates of reactive (non-N₂) N input to
71 terrestrial ecosystems (Vitousek et al. 1997; Galloway et al., 2004). A substantial portion
72 of this excess reactive N is exported from terrestrial ecosystems to aquatic ecosystems
73 (Galloway et al. 2003; Green et al. 2004; Seitzinger et al. 2006; Seitzinger and Harrison,
74 In Press), and a suite of environmental impacts have been attributed to N loading in
75 coastal waters, including eutrophication, hypoxia leading to fish kills, and biodiversity
76 loss, among others (Howarth et al. 1996; Vitousek et al. 1997; Carpenter et al. 1998).

77 The network of streams, lakes, and reservoirs that deliver N to coastal systems are
78 not simple conduits, but rather play an important role in processing this excess N. A
79 well-developed body of research has demonstrated that fluvial freshwater systems are
80 important in mediating N export from watersheds (e.g. Alexander et al., 2000; Peterson et
81 al., 2001; Seitzinger et al., 2002; Wollheim et al., 2006; Mulholland et al., 2008).

82 However, comparatively little work has been done to evaluate the regional and global
83 importance of lakes and reservoirs to the downstream transport of N. Once reactive N
84 enters surface waters it has multiple potential fates, including permanent loss via
85 denitrification, sediment burial, and temporary storage in biomass (Saunders and Kalff
86 2001). A number of system-specific and regional studies have shown that denitrification
87 and N burial in freshwater aquatic systems (treated collectively hereafter as *N removal*:
88 N_{in} minus N_{out}) can constitute an important sink for N within watersheds (Table 1).

89 Indeed aquatic ecosystems are potential hot-spots for N loss given that denitrification is
90 favored in sediments and hypoxic or anoxic bottom waters, particularly in systems with

91 abundant organic carbon (C) and nitrate (Piña-Ochoa and Alvarez-Cobelas 2006;
92 Seitzinger et al., 2006).

93 Due to their relatively long water residence time (compared with streams and
94 rivers), and the resulting opportunity for enhanced particle settling and nutrient
95 processing, lakes have long been recognized as systems where extensive denitrification
96 and N burial can occur (Wetzel 2001). Hence, the presence of lakes or creation of
97 impoundments and their placement in the landscape could play an important role in
98 determining the biosphere's response to anthropogenically enhanced N loading not only
99 at the watershed but at larger regional and global scales. Improved understanding of the
100 role that lentic systems play in watershed N removal could contribute to the development
101 of future N management strategies by elucidating how changing N sources, climate, and
102 the placement of lakes and reservoirs within watersheds are likely to interact to affect N
103 transport to downstream fresh and coastal waters.

104 In recent years, a number of local and regional field-based and modeling studies
105 have investigated the controls on N removal within lakes and reservoirs. In general, N
106 removal in lentic systems (kg N yr^{-1}) has been observed to correlate positively with N
107 loading rates, and water residence time, and negatively with lake mean depth (Kelly et
108 al., 1987; Dillon and Molot 1990; Molot and Dillon 1993; Windolf et al., 1996; Saunders
109 and Kalff 2001).

110 Based on these relations, a number of models have been developed to predict
111 lentic N removal at regional and, in one case, global scales (although the focus has been
112 primarily on flowing waters and large lakes; Alexander et al., 2002; Seitzinger et al.,
113 2002; Seitzinger et al., 2006). These models suggest that lakes and reservoirs can be

114 important in determining the fate of N at regional scales, but that the importance of lakes
115 can vary widely depending on the basin in question. For example Alexander et al. (2002)
116 found that in New Zealand's Waikato Basin lakes and reservoirs were among the most
117 statistically significant variables in a model predicting N transport, retaining 39-76% of N
118 inputs to surface waters in the Waikato Basin and its sub-watersheds. Several lakes were
119 estimated to retain over 50% of the N entering them with a maximum removal of 87% of
120 N input. Conversely, Seitzinger et al. (2002) estimated that reservoirs account for very
121 little N removal in watersheds of the Northeastern US.

122 Our goal was to develop a global-scale model that could account for such regional
123 differences in lentic N removal, using relations that have been developed through
124 observations of individual lakes and reservoirs. Previous attempts to scale up analyses of
125 individual lentic systems in a spatially explicit manner to quantify regional- and global-
126 scale patterns of lake and reservoir N removal have been limited to the large river basin
127 scale and have not included the smallest lakes and reservoirs on the landscape (0.001-0.1
128 km²; Seitzinger et al., 2006). In this paper, we describe, apply and evaluate a new,
129 spatially explicit, annual-scale, global model of N removal in lakes and reservoirs called
130 the **Nitrogen Retention in Reservoirs and Lakes (NiRReLa)** model. The NiRReLa model
131 moves beyond previous studies in several respects. First, the model is calibrated using a
132 truly global dataset of N removal, comprised of information from 115 lakes and
133 reservoirs, substantially more than any similar previous study. Furthermore, NiRReLa is
134 the first attempt to incorporate small (down to 0.001 km² surface area) lakes and
135 reservoirs into a global analysis of lentic N removal in a spatially explicit manner, and
136 has a higher spatial resolution (half degree: ~2,500 km² at the equator) than any previous

137 global models of lentic N removal. NiRReLa also allows model users to estimate the
138 relative importance of lakes versus reservoirs on the landscape with respect to N removal,
139 an analysis that has not previously been possible.

140

141 **Methods**

142 **The NiRReLa Model Structure and Calibration**

143 *Model Structure*

144 The NiRReLa model was formulated to estimate annual lentic N removal
145 globally, in a spatially distributed fashion. In the NiRReLa model, N removal (N_{rem} ; kg
146 N yr⁻¹) for lakes and reservoirs is calculated as:

$$147 \quad N_{rem} = R \times N_{in} \quad (1)$$

148 where N_{in} is an estimate of N input to lake and reservoir surface waters, taken from
149 Bouwman et al. (2005) and R is an estimate of the fraction of N retained within lakes and
150 reservoirs. R is calculated in a manner similar to Wollheim et al. (2006) and Alexander et
151 al. (2002), as:

$$152 \quad R = 1 - \exp\left(\frac{-V_f}{H_l}\right) \quad (2)$$

153 where V_f is the apparent settling velocity for N (m yr⁻¹) by lake or reservoir sediments,
154 and H_l is the hydraulic load (m yr⁻¹) for a given lake, reservoir, or a series of tightly
155 coupled reservoirs. V_f is essentially a piston velocity for N removal in lentic systems and
156 accounts both for N removed via denitrification and for N removed via burial in
157 sediments. Based on evaluation of existing studies (described below; Table 2), separate
158 V_f values were assigned for lakes and reservoirs. H_l (m yr⁻¹) was calculated as:

159
$$H_l = \frac{1000 \times Q}{A} \quad (3)$$

160 where Q is water input to lakes and reservoirs ($\text{km}^3 \text{ yr}^{-1}$) and A (km^2) is either surface area
161 of individual lakes (for large lake analysis) or cumulative surface area of lakes in a given
162 half-degree grid cell (for small lake analysis). H_l can be calculated either according to
163 Eq. 3 or Eq. 5.

164

165 *Model Calibration*

166 The NiRReLa calibration dataset includes N removal data for 115 lakes and
167 reservoirs (80 lakes and 35 reservoirs) from a range of sources. This dataset includes
168 lakes from a broad range of size classes, and regions (Table 1). To avoid the potentially
169 confounding influence of seasonal N uptake and storage, we limited our dataset to lakes
170 and reservoirs for which at least a complete year of data during the ice-free period was
171 available.

172 The fraction of N removed by lakes and reservoirs (R_{cal} ; unit-less) was estimated
173 as in Dillon and Molot (1990), as

174
$$R_{cal} = \frac{N_{in} - N_{out}}{N_{in}} \quad (4)$$

175 where N_{in} is the mass of N estimated to enter a lake or reservoir annually (kg N yr^{-1}) and
176 N_{out} is the mass of N (kg N yr^{-1}) estimated to exit a lake or reservoir annually via surface
177 water outlet(s).

178 For each lake and reservoir in our calibration dataset, an apparent settling velocity
179 for N (V_{f-cal}) and hydraulic load (H_{l-cal}) were estimated. Hydraulic load (H_{l-cal}) was
180 estimated as in Wollheim et al. (2006) as:

181
$$H_{l-cal} = \frac{z}{T} \quad (5)$$

182 where z is lake or reservoir average depth (m) and T is water residence time (yr:
183 calculated as lake volume/water discharge). V_{f-cal} was estimated as:

184
$$V_{f-cal} = -H_{l-cal} \times \ln(1 - R_{cal}) \quad (6)$$

185 where H_{l-cal} is hydraulic load and R_{cal} is an estimate of the fraction of N retained within
186 lakes and reservoirs (Eq. 4).

187 We also collected ancillary information for each system, including name, location
188 (latitude and longitude), and surface area (Table 1). Lakes or reservoirs were considered
189 to be tropical if they were located between the equator and 22.5° N or S, temperate if they
190 fell between 22.5° and 55° N or S and boreal if they were above 55° N or S.

191 In the NiRReLa model development process, we tested whether there were any
192 significant relations between lake or reservoir characteristics and apparent settling
193 velocity (V_f) for N. We tested for relations using simple and multiple regression
194 approaches as well as one-way ANOVAs. There were no significant correlations between
195 V_f and system size, N concentrations (either as Total N or NO_3^-) or distance from the
196 equator ($p > 0.05$ in all cases). Therefore, these factors were not included in the NiRReLa
197 model. However, V_f was significantly higher (by 1-Way ANOVA; Table 2) in reservoirs
198 than in lakes (Table 2), both for the entire dataset and for subsets of the dataset divided
199 into tropical, temperate, and boreal categories. In order to satisfy the assumptions of
200 equal variances and normal distribution of the residuals of the ANOVA test, V_f data were
201 log transformed. Based on this analysis, we incorporated the difference between lakes
202 and reservoirs into the NiRReLa model by assigning reservoirs a higher V_f than lakes.

203 The values assigned were calculated as the median V_f values in the calibration dataset
204 (4.6 m yr⁻¹ and 9.1 m yr⁻¹ for lakes and reservoirs, respectively).

205

206 **Global Application of NiRReLa**

207 *Spatial Data*

208 A number of spatial datasets were used in the global application of the NiRReLa
209 model. These datasets all had a spatial resolution of 0.5° × 0.5° (approximately 50 km² ×
210 50 km² at the equator) and were selected to represent conditions in 1995. Water runoff
211 (m yr⁻¹), water discharge (km³ yr⁻¹), and basin delineations for large rivers were taken
212 from Fekete et al. (1999). Estimates of N loading to surface waters were from Bouwman
213 et al. (2005) and a low estimate of N loading was derived from output of the **Nutrient**
214 **Export from Watersheds – Dissolved Inorganic Nitrogen (NEWS-DIN)** model (Dumont
215 et al., 2005). Bouwman et al. (2005) estimate TN inputs to surface waters as a function
216 of N loaded to the landscape (fertilizer N, manure N, atmospheric N deposition, N
217 fixation, and point-source N inputs) and N removed from the landscape (N removal via
218 crop harvest and export) coupled to a hydrologic model of N transport to surface waters.
219 Lake locations and attributes were taken from Lehner and Döll (2004), currently the most
220 comprehensive, global survey of lentic water bodies, containing 243,071 lakes and 822
221 reservoirs globally.

222 Though the general approach to estimating N removal within all lakes and
223 reservoirs was similar across all system sizes, the availability of data required that N
224 removal in large and small reservoirs be estimated somewhat differently. For example,
225 information about watershed surface area was not readily available for small lakes and

226 reservoirs, but this information was available for large lakes and reservoirs (Lehner and
227 Döll 2004). In order to accommodate these differences in data availability for model
228 calculations, lakes were divided into two size classes (large and small) where lakes and
229 reservoirs with surface areas greater than 50 km² are referred to as “large” and those
230 between 0.001-50 km² are referred to as “small”. One-tenth of a hectare (0.001 km²) was
231 considered to be the smallest surface area for a perennial water body, as in Downing et al.
232 (2006). Distribution of small lakes is described below.

233

234 *NiRReLa and Small Lakes and Reservoirs*

235 Small lakes and reservoirs are extremely numerous and constitute a substantial portion of
236 the total surface area of lakes and reservoirs globally (approximately 31% for lakes < 0.1
237 km² according to Downing et al., 2006). Small lentic systems are important sites for
238 biogeochemical processing (Wetzel 2001), but they are currently not included in any
239 global models of N transport. As such, we deemed it important to include these small
240 systems in NiRReLa. This presented a challenge, however, because currently there is no
241 global database that includes water bodies smaller than 0.1 km². To overcome this
242 limitation in the available global data, we assumed that the spatial distribution of the
243 smallest lakes (<0.1 km²) would scale in a linear fashion with the distribution of slightly
244 larger (0.1-50 km²) lakes. We then calculated the total global number and surface area of
245 small lakes and reservoirs, assuming Pareto-type distributions for both lake and reservoir
246 number and lake and reservoir surface area, as in Downing et al. (2006). The number,
247 average surface area, and cumulative surface area of lakes and reservoirs within given
248 size ranges were determined as in Downing et al. (2006), using identical coefficients.

249 Lakes and reservoirs were assumed to have a Pareto-type size distribution, as
250 demonstrated by a recent analysis (Downing et al., 2006), and the shape of this
251 distribution was determined by a coefficient c , describing the relative abundance of large
252 versus small lakes.

253 Total global small lake and reservoir surface areas were then distributed on the
254 global landscape. Small lake surface areas (A_{sm}) were distributed in direct proportion to
255 the distribution of smaller lakes (0.1-50 km²) in Lehner and Döll (2004) lakes database
256 as:

$$257 \quad A_{sm} = A_{sm-tot} \frac{A_{GLWD2-cell}}{A_{GLWD2-tot}} \quad (7)$$

258 where A_{sm} is the total surface area of lakes 0.001 – 50 km² in each cell, A_{sm-tot} is the
259 calculated global total surface area of lakes with individual surface areas between 0.001
260 and 50 km², $A_{GLWD2-cell}$ is the lake surface area of 0.1-50 km² lakes in a given cell as
261 reported in Lehner and Döll (2004), and $A_{GLWD2-tot}$ is the global total lake surface area of
262 0.1-50 km² lakes as reported in Lehner and Döll (2004). Due to a general lack of data on
263 global spatial distribution of small reservoirs, these systems were distributed uniformly
264 across all grid cells between 55°N and 55°S. A_{sm-tot} was 2.55×10^6 km² for lakes and
265 9.83×10^4 km² for reservoirs. For comparison, the total small lake and reservoir surface
266 area values in Lehner and Döll (2004) were 3.7×10^5 and 2.8×10^3 , respectively,
267 highlighting the importance of including the smallest lakes and reservoirs.

268 The fraction of N removed by small lakes and reservoirs (R_{sm}) was calculated as
269 in Eq. 2 (See Wollheim et al., 2006 and Alexander et al., 2002), and N removal in small
270 lakes and reservoirs was calculated as the product of R_{sm} and N load. Hydraulic load for
271 small lakes and reservoirs (H_{l-sm}) was calculated as in Eq. 3. For small lakes and

272 reservoirs, Q is total discharge ($\text{km}^3 \text{ yr}^{-1}$) generated within each half-degree cell and A is
273 the cumulative surface area of small ($<50 \text{ km}^2$) lakes or reservoirs in a given half-degree
274 cell. Water and N leaving terrestrial systems within each half-degree grid cell were
275 assumed to enter a composite lake or reservoir made up of all small lakes or all small
276 reservoirs before entering large lakes or reservoirs.

277 In NiRReLa, water and N are partitioned between small lakes and reservoirs in
278 proportion to the relative surface areas of lakes and reservoirs within a given half-degree
279 cell. For example, if 25% of the total lake and reservoir surface area within a cell is
280 attributed to reservoirs, and the remainder is allocated to lakes, NiRReLa routes 25% of
281 the water and N to reservoirs and the remainder to lakes.

282

283 *NiRReLa and Large Lakes and Reservoirs*

284 The spatial distribution of large lakes and reservoirs was taken from the global
285 database of Lehner and Döll (2004), which contains 3067 of the largest lakes (area ≥ 50
286 km^2) and 654 of the largest reservoirs globally (storage capacity $\geq 0.5 \text{ km}^3$). Lakes in
287 Lehner and Döll (2004) $<50 \text{ km}^2$ (from GLWD2) are accounted for above.

288 We estimated annual N removal (kg N yr^{-1}) in these large lakes and reservoirs (N_{large})
289 according to Eqns. 1 and 2, just as for small lakes and reservoirs. However, N_{in} and H_l
290 are calculated somewhat differently for large lakes than for small lakes. For large lakes
291 and reservoirs N_{in} , the amount of N estimated to enter a given large lake or reservoir
292 annually, is calculated as:

$$293 \quad N_{in} = W \times N_{surf} \quad (8)$$

294 where W represents the size of the watershed for a given large lake or reservoir (km^2) and
295 N_{surf} is the area-weighted average rate of N loadings to surface waters ($\text{kg N km}^{-2} \text{yr}^{-1}$)
296 within the large river watershed (Fekete et al., 1999) in which a large lake is located, as
297 estimated by Bouwman et al. (2005). This approach is identical to that used by
298 Seitzinger et al. (2006). Hydraulic load for large lakes and reservoirs (H_l) was calculated
299 according to Eq. 3. Rather than being estimated at the grid-cell level as for small lakes
300 and reservoirs, numerical values for Q and A for large systems were taken directly from
301 Lehner and Döll (2004). To avoid double counting N removal by both large and small
302 lakes, we assumed that small lakes and reservoirs processed N before it reached large
303 lakes or reservoirs.

304

305 **Model Sensitivity Analysis**

306 A sensitivity analysis was performed in order to evaluate the response of
307 NiRReLa model output to changes in various input parameters, including: rates of water
308 runoff and N loading, the number, size and spatial distribution of lakes and reservoirs,
309 and V_f within lakes and reservoirs. Water runoff and N loading were both halved and
310 doubled. An additional low-end estimate of N loading was developed by taking
311 predictions of DIN export from a river DIN export model (NEWS-DIN; Dumont et al.,
312 2005) and using these estimates as inputs to the NiRReLa model. The NEWS-DIN
313 model (Dumont et al., 2005) calculates DIN export from rivers to the coastal zone, and
314 accounts for N removal within watersheds. Using NEWS-DIN model output as N input
315 to the NiRReLa model results in a conservative estimate of lake and reservoir
316 denitrification because: 1) before entering lakes and reservoirs, N exported from

317 terrestrial landscapes has already been subject to removal in rivers before entering
318 NiRReLa lakes and reservoirs, and 2) NEWS-DIN only estimates DIN, which is only a
319 fraction of N.

320 We also evaluated NiRReLa sensitivity to the number, size and spatial distribution
321 of lakes and reservoirs in several ways. First, we ran NiRReLa without any
322 extrapolation to include the world's smallest lakes, including only lakes and reservoirs
323 reported in a spatially explicit global dataset of small (0.1-50 km²) lakes and reservoirs
324 (GLWD2; Lehner and Döll 2002). In a second approach, we only extrapolated down to
325 lakes with a surface area ≥ 0.01 km². In two additional experiments, we tested model
326 sensitivity to assumptions about distribution of N and water between lakes versus
327 reservoirs by varying distribution of N and water between small reservoirs and small
328 lakes by $\pm 20\%$ and further tested NiRReLa's sensitivity to changes in the number of
329 small lakes and the shape of the Pareto distribution by varying the Pareto exponent (c in
330 Eqns. 4, 5, and 10 in Downing et al., 2006) by ± 1 S.E.. Finally, sensitivity of NiRReLa
331 predictions to changes in V_f was also evaluated by varying V_f from the 25th percentile
332 value to the 75th percentile of all lakes and reservoirs in our calibration dataset, (2.20-7.56
333 m yr⁻¹ and 3.15-19.41 m yr⁻¹ for lakes and reservoirs, respectively).

334

335 **Results and Discussion**

336 **Apparent Settling Velocities**

337 As stated above in the section on model calibration, we did not detect any
338 significant correlations between reservoir and lake characteristics and apparent settling
339 velocities (V_f) in our global dataset. However, there was a significant difference in V_f

340 between lakes and reservoirs, with reservoirs demonstrating a higher V_f on average than
341 lakes (mean V_f for lakes and reservoirs: 6.8 and 13.6 m yr⁻¹, respectively). The model V_f
342 value for lakes is comparable to V_f values from a number of other studies (reviewed by
343 Alexander et al., 2002) and is somewhat lower than V_f observed for rivers (Howarth et al.,
344 1996; Alexander et al., Submitted, this volume). The NiRReLa V_f value for reservoirs is
345 somewhat higher than V_f values observed in lakes, and is closer to V_f values observed for
346 rivers (Wollheim et al., 2006), possibly because reservoirs function as hydrologic
347 intermediates between rivers and lakes.

348

349 **NiRReLa Model Performance**

350 It was not feasible to test the results predicted by the entire NiRReLa model at the
351 global scale since there currently is no global-scale validation data on N inputs to surface
352 waters or large basin-scale data on N removal within lakes and reservoirs. However, we
353 were able to evaluate the NiRReLa model's capacity to predict percent N removal within
354 individual lakes and reservoirs by comparing measurement-based estimates of N removal
355 in lakes and reservoirs (Eq. 4) with NiRReLa-modeled estimates of N removal (Eq. 2).

356 In this test, the NiRReLa model performed reasonably well for both lakes and reservoirs
357 (Figure 1). The root mean squared error for the NiRReLa model was 17% for both lakes
358 and reservoirs, and 95% of the predictions fell within 43% of the measured removal rates
359 for both lakes and reservoirs (41% and 44% for lakes and reservoirs, respectively).

360 Neither the slope nor the intercept of the least-squares regression between measured and
361 modeled TN removal ($r^2 = 0.54$ and $r^2 = 0.51$ for lakes and reservoirs, respectively) was
362 significantly different from unity, suggesting a lack of systematic bias to the NiRReLa

363 model. Thus, although a significant amount of variation remains unexplained, we were
364 able to use the NiRReLa model to develop the first half-degree resolution maps of lake
365 and reservoir N removal.

366

367 **N Removal by Lakes and Reservoirs at Global Scale**

368 Using the NiRReLa model, we estimate that globally, lentic aquatic systems
369 larger than 0.001 km^2 remove $19.7 \text{ Tg N yr}^{-1}$ from watershed flow paths (Table 3). This
370 amount is slightly less than one third of the 65 Tg N yr^{-1} estimated to enter surface
371 freshwaters globally (Bouwman et al., 2005), and is roughly equivalent to 7% of all land-
372 based N sources (268 Tg N yr^{-1} ; Seitzinger et al., 2006). The NiRReLa-estimated amount
373 of N removal occurring in lakes and reservoirs globally is approximately 4 times the
374 amount estimated to occur in estuaries ($\sim 5 \text{ Tg N yr}^{-1}$; Seitzinger et al., 2006), and
375 comparable to the amount of N removal estimated to occur in rivers and streams (20-35
376 Tg yr^{-1} , based on different assumptions and databases; Seitzinger and Kroeze 1998,
377 Green et al., 2004; Bouwman et al., 2005; Seitzinger et al., 2006). It should be noted that
378 these existing estimates of river and stream N removal often include reservoir N removal.
379 In fact, our analysis suggests that in many regions most of the N removal previously
380 attributed to rivers and streams could be occurring primarily in lentic systems (Figure
381 2A).

382 Using NiRReLa we estimate that the area-specific rate of N removal by lentic
383 systems globally is approximately $4,805 \text{ kg N km}^{-2} \text{ yr}^{-1}$ (Table 3), approximately half of a
384 previous estimate by Seitzinger et al. (2006; $11,000 \text{ kg N km}^{-2} \text{ yr}^{-1}$), but still well within
385 measured denitrification rates for individual lakes ($181\text{-}38,263 \text{ kg km}^{-2} \text{ yr}^{-1}$ as compiled

386 in Piña-Ochoa and Alvarez 2006). This discrepancy is in part due to our slightly lower
387 global estimate of N removal by lakes and reservoirs of 19.7 Tg yr⁻¹ relative to 31 Tg N
388 yr⁻¹, but mostly due to the lower estimate of the global lake surface used in Seitzinger et
389 al. (2006). Indeed, when we use the NiRReLa estimate of global lake and reservoir
390 surface area, the values for area-specific N removal were comparable between the current
391 analysis and the Seitzinger et al. (2006) estimate (Table 3).

392 Results from NiRReLa suggest that the inclusion of small lakes and reservoirs is
393 crucial for predicting global N removal by lentic systems. NiRReLa model output
394 indicates that small lakes remove more than twice as much N from watersheds as large
395 lakes (9.3 Tg N yr⁻¹ for small lakes versus 3.7 Tg N yr⁻¹ for large lakes), and that small
396 lakes (<50 km²) account for almost half of the N removed by lentic systems (lakes and
397 reservoirs combined) globally (Table 3). This important role of small lakes acting as
398 biogeochemical sinks in the landscape was also observed in a similar analysis assessing
399 the fate of carbon in freshwater aquatic ecosystems (Cole et al. 2007). On a per-unit area
400 basis, small lakes also processed 16% more N than large lakes (Table 3). In interpreting
401 these model results, it is important to remember that the NiRReLa model assumes that all
402 N entering surface waters in each grid cell passes through a small lake, which is most
403 likely not the case. Thus it is likely that NiRReLa somewhat overestimates the role of
404 small lakes in removing N from the landscape. Nonetheless, these results underscore the
405 potential importance of small lakes as sinks for N on the landscape. This analysis does
406 not explicitly include N removal in stream reaches connecting lakes to each other.

407 Humans are actively increasing the number of “lakes” on the landscape via the
408 creation of reservoirs (Takeuchi et al., 2000; Tomaszec and Kozelnick 2003). Therefore

409 understanding the role of reservoirs in the processing of N at the landscape level is of
410 critical importance. Despite the fact that the global abundance of lakes is almost two
411 orders of magnitude greater than that of reservoirs (3.04×10^8 lakes versus 3.77×10^6
412 reservoirs greater than 0.001 km^2 ; Downing et al., 2006), NiRReLa estimated that
413 reservoirs remove roughly 33% of the N removed by lentic systems, accounting for the
414 removal of 6.6 Tg N yr^{-1} , an estimate similar to that made by an independent model of
415 lake N removal (Wollheim et al., In Revision). Despite their comparatively low global
416 surface area and numbers, large reservoirs appear to play as important a role in N
417 removal as large lakes (Table 3). NiRReLa output suggests that approximately equal
418 amounts of N are removed by large reservoirs and large lakes (3.6 Tg N yr^{-1} and 3.7 Tg N
419 yr^{-1} for large reservoirs and large lakes, respectively; Table 3).

420 The parity of large lakes and large reservoirs with respect to N removal most
421 likely results from the fact that reservoirs have large contributing watersheds, and thus
422 relatively large N loading rates (kg N yr^{-1}) compared to large lakes, which generally
423 (though not always) receive their water and N input from a more limited surface area and
424 thereby receive less N input. In the large lake and reservoir dataset utilized for this study
425 the mean drainage ratio (ratio of basin surface area to lake or reservoir surface area) for
426 reservoirs was 83, whereas the ratio was 25 for lakes (Lehner and Döll 2004). The higher
427 drainage ratio of reservoirs resulted in higher N loading to reservoirs than to lakes, on
428 average. The higher V_f values observed for reservoirs in this study play a smaller, though
429 still important, role as well. In reservoirs, flooding of previously terrestrial soils and
430 ecosystems also may lead to an increased availability of highly labile organic matter

431 (Kelly et al., 1997) and bottom water anoxia which should favor denitrification. The
432 greater frequency of reservoirs in areas with high N inputs may also contribute.

433

434 **Regional Patterns of Lake and Reservoir N Retention**

435 Considerable regional variability exists in the potential for lakes and reservoirs to
436 act as sinks for N within watersheds (Figure 2). This spatial heterogeneity has heretofore
437 gone largely un-quantified, in part, because there has not been a sufficiently high-
438 resolution model to evaluate it (though see Wollheim et al., In Revision). NiRReLa
439 output indicates that there are a number of regions globally where lakes and reservoirs
440 have the capacity to filter virtually all N loaded to surface waters, whereas in other
441 regions lakes have very little or no capacity to remove N input to the landscape. In
442 general, areas where percent N removal approached or equaled 100% correspond to areas
443 with large lake surface areas, low runoff rates, or both. Regions where lakes and
444 reservoirs have the capacity to remove a large proportion of the N added to the landscape
445 correspond to areas with high lake densities, including boreal regions in Canada,
446 Northern Europe, and Russia, portions of the western US, Eastern Brazil, Sub-Saharan
447 Africa, northern China, Eastern Europe, and Mongolia, and parts of Argentina. The
448 predicted N removal efficiency of lentic systems in many parts of the world seems quite
449 high. However, to the extent we were able to validate these regional patterns they are
450 consistent with observations of watershed N export. For example, using Bouwman et al.
451 (2005) estimates of N inputs to surface waters and measurements of N export at the
452 mouths of rivers from Seitzinger and Harrison (In Press), we calculate that very small
453 fractions of N inputs to surface waters are exported at basin mouths (0.7%, 6.0% and

454 ~8.7% of N inputs to surface waters in the Churchill, Neva and St. Lawrence River
455 Basins, respectively). This contrasts markedly with regions that exhibit relatively low
456 predicted lentic N removal (as a fraction of N input) such as the Mississippi and Amazon
457 Rivers, where much larger fractions are exported.

458 Regions with high estimated per-area rates of lake and reservoir N removal (kg N
459 $\text{km}^{-2} \text{yr}^{-1}$; Figure 2B) are somewhat different than regions where N removal is estimated
460 to approach 100% of the N applied to the landscape (Figure 2A). This pattern occurs
461 because the lake and reservoir locations do not always correspond to regions of highest N
462 input. For example, while a large fraction of N input to lakes and reservoirs is removed
463 in Northern Canada, the rate of N removal is low because of low N inputs in this region.
464 Basins with high rates of lentic N removal (kg N $\text{km}^{-2} \text{yr}^{-1}$) include the St. Lawrence,
465 many of the river basins in southern Scandinavia, the Zambezi River, and several river
466 basins in northeast China.

467

468 **Sensitivity Analysis**

469 A number of insights emerge from the sensitivity analysis described in the
470 methods section, for which a summary of results is presented in Table 4. One of the
471 principal insights resulting from this analysis is that while NiRReLa is relatively sensitive
472 to changes in N loading rates, it is relatively insensitive to alterations in hydrology.
473 Doubling global inputs of water to the landscape (and consequently cutting water
474 residence time in individual systems in half) only decreased predicted lentic N removal
475 (Tg N) by 11% . Decreasing water runoff by 50% resulted in a 15% increase in N
476 removal (Tg N). In contrast to its relatively damped response to changes in hydrology,

477 the NiRReLa model was quite sensitive to changes in N loading. As would be expected
478 based on Eq. 1 above, doubling global inputs of N resulted in a doubling of N removal
479 (Tg N), whereas cutting N inputs in half resulted in a halving of lake and reservoir N
480 removal (Tg N). Using output from the NEWS-DIN model (Dumont et al., 2005) as
481 input to the NiRReLa model resulted in a 23% decrease in estimated global lentic N
482 removal (to 15.2 Tg N yr⁻¹), and this estimate can be considered to be quite conservative.
483 Interactions between runoff and N loading were not explored in this sensitivity analysis,
484 but could be important as one would expect N loading to increase with increasing runoff.
485 Such a relation has been demonstrated for many watersheds globally (Dumont et al.,
486 2005). Runoff dependence of N loading could make N removal either more or less
487 sensitive to changes in hydrology. The net impact depends on the nature of the N loading
488 response to increased runoff.

489 The observed difference in model response to changes in hydrologic and N-
490 loading is a function of the relations between model inputs and model response variables.
491 The relation between percent N removal and water residence time is log-linear (Eq. 2)
492 whereas the relation between N load and N removal is linear. This suggests that the
493 location of N inputs relative to the location of lakes and reservoirs is an important
494 determinant of the effectiveness of lakes and reservoirs in removing N from surface
495 waters (i.e. N inputs upstream from lakes and reservoirs will be subject to retention
496 within lentic systems whereas N inputs downstream from those systems will not). This is
497 also an uncertainty in the model worthy of future investigation. Taken together, these
498 insights suggest that, in general, N removal within lentic systems will be more sensitive
499 to land-use change than climate change at the global scale, though this is certain to vary

500 substantially by region. Climate could also significantly alter N transfers to surface
501 waters by altering the balance of runoff and evapotranspiration, but it is difficult to
502 predict the magnitude, or even the direction, of this effect as increased runoff is likely to
503 cause greater N inputs but lower water residence times.

504 In addition, in order to assess the NiRReLa model's sensitivity to uncertainty in V_f
505 we ran the model using arithmetic mean V_f (6.8 and 13.6 m yr⁻¹ for lakes and reservoirs,
506 respectively), low V_f (25th percentile), and high V_f (75th percentile) values. Using mean
507 V_f values for the NiRReLa model in place of median values increased global lentic TN
508 retention by 3.4 Tg N yr⁻¹. This range of variation in V_f resulted in a variation in model
509 output that ranged between 11.8 and 25 Tg N retained globally. Hence a 3.4-fold
510 increase in V_f for lakes and a 6.2-fold increase in V_f for reservoirs resulted in an
511 approximate doubling of global N removal in lakes and reservoirs. Hence, the NiRReLa
512 model is less sensitive to variation in V_f than to changes in N loading.

513 We also examined how changes in the parameterization of the Pareto distribution
514 of lakes and reservoirs affected N removal by varying the parameter “ c ” in equations 4, 5
515 and 10 in Downing et al. (2006) plus or minus one standard error. The change in model
516 predictions resulting from this perturbation was minimal (Table 4). Finally, we examined
517 the influence of the smallest lakes and reservoirs by excluding them from our analysis.
518 Removing reservoirs smaller than 0.01 km² from the analysis decreased the N removal in
519 lentic systems by 0.8%; removing lakes smaller than 0.01 km² decreased our estimate of
520 small-lake N removal by 8.1%. Limiting our analysis to only lakes and reservoirs
521 available in the most comprehensive global lake and reservoir database decreased our
522 estimate of global lentic N removal by 9.8%, highlighting the importance of including the

523 smallest lakes (0.001-0.1 km²). If the surface area of small lakes is greater than we have
524 estimated, then NiRReLa most likely underestimates TN retention by such systems.

525

526 **Uncertainties and Future Directions**

527 Here we have presented a higher resolution, spatially explicit, global analysis of
528 lake and reservoir N removal than has previously been published. The NiRReLa model is
529 a promising new tool that provides insight into global rates and spatial organization of N
530 removal within lentic systems. The model provides initial estimates of the relative
531 importance of natural versus man-made lakes (reservoirs) and indicates factors to which
532 N removal within lakes and reservoirs is likely to be sensitive.

533 Clearly a number of questions remain unanswered. For example the NiRReLa
534 model does not distinguish between N removal via denitrification and N removal via
535 other pathways such as sediment N burial or consumptive water use. Denitrification is
536 clearly an important component of total lake N removal, and in many studies this process
537 accounts for the majority of N removed from lake and reservoir waters (Jensen et al.,
538 1990; Jensen et al., 1992; Saunders and Kalff 2001). However, it is likely that there are
539 systems where sediment N burial, transient storage in macrophyte stands, and
540 consumptive water use are important N sinks (e.g. Kelly 2001). A rough estimate using
541 Cole et al. (2007) estimates of C burial along with an estimate of sediment C:N ratios (9-
542 28; Brahney et al., 2006) suggests that sediment N burial could account for anywhere
543 between 25-250% of the total NiRReLa-based estimate of N removal. A somewhat
544 different approach using reported annual area-specific rates of denitrification in 21 lakes
545 (1,760-45,080 kg N km⁻² yr⁻¹ mol N Piña-Ochoa and Álvarez-Cobelas 2006) and our

546 estimate of global lake and reservoir surface area ($4.05 \times 10^6 \text{ km}^2$; Table 3) suggests that
547 between 47 and 182 Tg N yr⁻¹ (206-498% of the NiRReLa-based estimate of total N
548 removal) could be denitrified in lakes and reservoirs. Though far from establishing the
549 relative importance of different N removal pathways in lentic systems, and though even
550 measurement-based estimates of N removal are quite uncertain, together, these rough
551 calculations suggest that NiRReLa-based estimates of lentic N removal are quite
552 conservative. Due to the high degree of uncertainty, these calculations also suggest that
553 understanding lentic N removal is an important goal for future investigations.

554 In addition, the sensitivity of the NiRReLa model to N inputs raises the question
555 whether there is a N-saturation threshold for lakes. This potential is not evident in our
556 calibration dataset, but if such a threshold exists, it would have important implications for
557 the capacity of lake and reservoir systems to act as buffers for N enrichment of surface
558 waters on the landscape.

559 Given the general trend toward higher rates of biological and physical processing
560 with increased temperatures in many systems, we were somewhat surprised not to find a
561 significant relation between latitude and apparent settling velocity for N. However, this
562 is consistent with a general lack of empirical evidence for a relation between latitude and
563 denitrification rates (Piña-Ochoa Álvarez-Cobelas 2006). It may also be that differences
564 in lake and reservoir mixing regimes at different latitudes (Lewis 1983) obscure a simple
565 relation between temperature and lake and reservoir N apparent settling velocities.

566 The apparent relative importance of small ($<0.1 \text{ km}^2$) reservoirs in controlling N
567 removal along flow paths within watersheds suggests that an important area for future
568 research is an improved understanding of the spatial distribution and biogeochemical role

569 of such systems. Similarly, NiRReLa assumes a simple hydrologic linkage of small lakes
570 with large lakes on the landscape. This simplistic view could certainly be improved in
571 future models as appropriate data becomes available to support such enhancements.
572 Other issues that merit further investigation and may result in substantial model
573 improvements include lake and reservoir hydrology and mixing regimes, an improved
574 representation of inflow seasonality, and an improved representation of N cycling,
575 including the balance between nitrification, denitrification, sediment organic matter
576 burial, and N mineralization in lentic systems.

577 Finally, this analysis should not be interpreted as an argument for the construction
578 of dams as a mitigation strategy for coastal N delivery. Though reservoirs appear to be
579 an important site for N removal within watersheds at regional and global scales, it is far
580 from certain that the net impact of reservoir construction is a reduction in N transport to
581 coastal systems. In part, the impact of reservoir construction on downstream N transport
582 is a function of reservoir morphology, with narrow, deep reservoirs actually decreasing N
583 removal compared to the original river reach. In addition, and probably more
584 importantly, irrigation water made available by dams may increase the amount of land
585 available for intensive agriculture and hence facilitate elevated rates of N application to
586 the landscape. An improved understanding of the relation between reservoir operation
587 and downstream N transport may lead to more effective N management strategies.

588

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597

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720

721

722 **Table and Figure Captions:**

723 **Table 1 :** List of references, geographical location, and ranges of morphological and
724 hydrological variables of the lakes and reservoirs used in the determination of
725 different parameter estimates of the NiRReLa model.

726

727 **Table 2.** Comparison of average apparent settling velocities for N (V_f) among different
728 system classifications. Values used in the NiRReLa model are italicized in bold. *
729 denotes a significant difference among systems using a LSD-Tukey test in a 1-way
730 ANOVA. All other comparisons were statistically not significantly different
731 ($P>0.05$).

732 **Table 3.** Results of NiRReLa N removal estimates at the global scale for different aquatic
733 system classes. Surface area represents the global surface as estimated by NiRReLa
734 for small lakes and reservoirs ($0.001-50 \text{ km}^2$) and large lakes and reservoirs (> 50
735 km^2). NiRReLa-based estimates of total surface area, total N removal, and per-area N
736 removal are compared with estimates from Seitzinger et al. 2006.

737

738 **Table 4.** Results from a model sensitivity analysis. * signifies sensitivity analysis was
739 only run on small lakes and reservoirs.

740

741 **Figure 1.** Comparison between measured percent N removal and NiRReLa-modeled
742 percent N removal in lakes (closed diamonds) and reservoirs (open triangles) for
743 which N removal data exist. The 1:1 line is also shown.

744

745 **Figure 2.** NiRReLa-modeled global distribution of percent N removal by lakes and
746 reservoirs in panel A. Panel B shows N removal by lakes and reservoirs kg N km^{-2}
747 yr^{-1} .

748 **Table 1** : List of references, geographical location, and ranges of morphological and hydrological variables of the lakes and reservoirs
 749 used in the determination of different parameter estimates of the NiRReLa model.
 750

Latitude	Lake or reservoir	n	Location	Surface Area (km ²)	mean Z [†] (m)	Residence Time (yr)	% N Removal	V _f	H ₁ [†] (m yr ⁻¹)	Reference
Boreal	lake	2	Switzerland	2.7 - 6.1	2.5 - 5.4	0.85 - 1.81	17.9 - 39.7	0.7 - 1.26	1.38 - 6.38	Ahlgren et al. 1994
Boreal	lake	6	Denmark	0.11 - 1.04	1.9 - 12	0.03 - 0.36	22.7 - 55.3	11.3 - 20.4	14 - 74.2	Andersen 1974
Boreal	lake	4	Denmark	0.16 - 23	1 - 2.6	0.05 - 1.75	41.4 - 54.4	0.61 - 16.9	1.08 - 21.9	Jeppesen et al. 1998
Boreal	lake	1	Estonia	270	2.8	0.88	53	2.41	3.18	Nõges et al. 1998
Boreal	lake	2*	Estonia	0.13	3.6	1.11 - 1.49	58 - 80	2.81 - 3.88	2.41 - 3.24	Nõges 2005
Boreal	lake	16	Denmark	N/A	0.9 - 5.6	0.02 - 0.69	11.0 - 57	2.7 - 12.8	4.2 - 100	Windolf et al. 1996
Boreal/ Temperate	lake	9	ON, Canada	0.12 - 0.71**	2.4 - 12.4	0.06 - 25	7.0 - 99	1.18 - 8.59	0.42 - 118	Kelly et al. 1987
Temperate	lake	1	US/ Canada	58016	84	100	66	0.91	0.84	Ayers 1970
Temperate	lake	1	Italy	1.81	45	4.7	40	4.89	9.57	Calderoni et al. 1978
Temperate	lake	4	ON, Canada	N/A	3.3 - 12.2	0.3 - 3.7	24 - 61	2.11 - 4.64	2.2 - 13.6	Dillon & Molot 1990
Temperate	lake	2	IA, US	1.09 - 14.68	1.5 - 2.9	0.4 - 1.6	50.2 - 82.2	2.62 - 3.13	1.81 - 3.75	J. Downing unpubl.
Temperate	lake	1	Germany	7.18	4.85	0.13	16.6	6.69	36.88	Dudel & Kohl 1992
Temperate	lake	2	Switzerland	5.2 - 38	33 - 84	4.1 - 14.1	78.8 - 87.4	12.3 - 1249	5.96 - 8.05	Mengis et al. 1997
Temperate	lake	7	ON, Canada	0.32 - 270	5 - 14.2	1.6 - 5.35	36 - 73	1.98 - 2.95	1.59 - 5.77	Molot & Dillon 1993
Temperate	lake	5	SK, Canada	7.7 - 20.20	6 - 14.4	0.4 - 1.3	41 - 80	4.52 - 19.3	8.57 - 20.5	Patoine et al. 2006 & Leavitt et al. 2007
Temperate	lake	8	QC, Canada	0.71 - 22.6	3 - 25.9	0.15 - 8.96	6.07 - 57.9	0.6 - 9.89	2.9 - 30.7	Y. Prairie unpubl.
Tropical	lake	9	Latin America/ Caribbean	1.11 - 1078.5	1.0 - 16	0.04 - 98.5	13.9 - 99.7	0.92 - 26.4	0.16 - 114	Salas & Martino 1991
Temperate	reservoir	2	IA, US	0.35 - 1.99	2.3 - 2.5	0.18 - 0.3	37.2 - 69.6	5.95 - 9.91	8.3 - 12.8	J. Downing unpubl.
Temperate	reservoir	6	France	21 - 48 **	3.5 - 8.9	0.03 - 0.62	12 - 54.5	7.2 - 19.2	12.26 - 150	Garnier et al. 1999
Temperate	reservoir	4	US	390 - 832	10 - 55	0.8 - 3.7	0 - 80	0 - 20.12	6.3 - 14.9	Kelly 2001
Temperate	reservoir	1	CA, US	104.4	17.26	0.01	0	0	1400	Teodoru & Wehrli 2005
Temperate	reservoir	4	SK, Canada	0.50 - 430	1.4 - 21.9	0.05 - 12.6	23 - 99	2.9 - 32.2	0.63 - 28	Patoine et al. 2006 & Leavitt et al. 2007
Tropical	reservoir	18	Latin America/ Caribbean	3.8 - 250	2.2 - 26.4	0.002 - 1.92	0.04 - 68.5	0.01 - 81	10.3 - 1250	Salas & Martino 1991

* same system 2 different years

** some data not available (N/A)

† Z is mean depth for a given lake or reservoir and H₁ is hydraulic load.

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752

753 **Table 2.** Comparison of average N apparent settling velocities (V_f) among different
 754 system classifications. Values used in the NiRReLa model are italicized in bold. *
 755 denotes a significant difference among systems using a Tukey test in a 1-way ANOVA
 756 on the log transformed data. All other comparisons were statistically not significantly
 757 different ($P>0.05$).
 758

Axis of Comparison	Systems Compared	n	V_f	SD
Overall mean		115	8.91	10.27
System type	Lakes	80	<i>6.83*</i>	5.8
	Reservoirs	35	<i>13.66*</i>	15.5
N-form	Total N	89	9.92	11.15
	NO ₃	24	5.66	5.34
Surface Area	>50 km ²	13	8.01	10.83
	<50 km ²	76	9.76	11.66
Latitude (Lakes only)	Boreal	36	7.74	5.77
	Temperate	35	5.13	4.63
	Tropical	9	9.81	8.38
Latitude (Reservoirs only)	Temperate	17	9.35	8.36
	Tropical	18	17.72	19.53

759 **Table 3.** Results of NiRReLa N removal estimates at the global scale for different aquatic
 760 system classes. Surface area represents the global surface as estimated by NiRReLa for
 761 small lakes and reservoirs (0.001-50 km²) and large lakes and reservoirs (> 50 km²).
 762 NiRReLa-based estimates of total surface area, total N removal, and per-area N removal
 763 are compared with estimates from Seitzinger et al. 2006.
 764

Waterbody Type	Surface area (km²)	N retained globally (Tg N yr⁻¹)	N retained per unit area (kg N km⁻² yr⁻¹)
Small Lakes	2.6×10 ⁶	9.3	3,577
Large Lakes	1.2×10 ⁶	3.7	3,083
All Lakes	3.8×10⁶	13.0	3,421
Small Reservoirs	9.8×10 ⁴	3.0	30,612
Large Reservoirs	1.5×10 ⁵	3.6	24,000
All Reservoirs	2.5×10⁵	6.6	26,400
<i>Reservoirs and Lakes Combined</i>	4.1×10⁶	19.7**	4,805
Other Lake Model			
Seitzinger et al. 2006	2.8×10 ⁶	31 (19-43)	11,000
	4.1×10 ⁶	31.0	7,660*

765 * per-area estimate determined using NiRReLa lentic surface area estimate

766

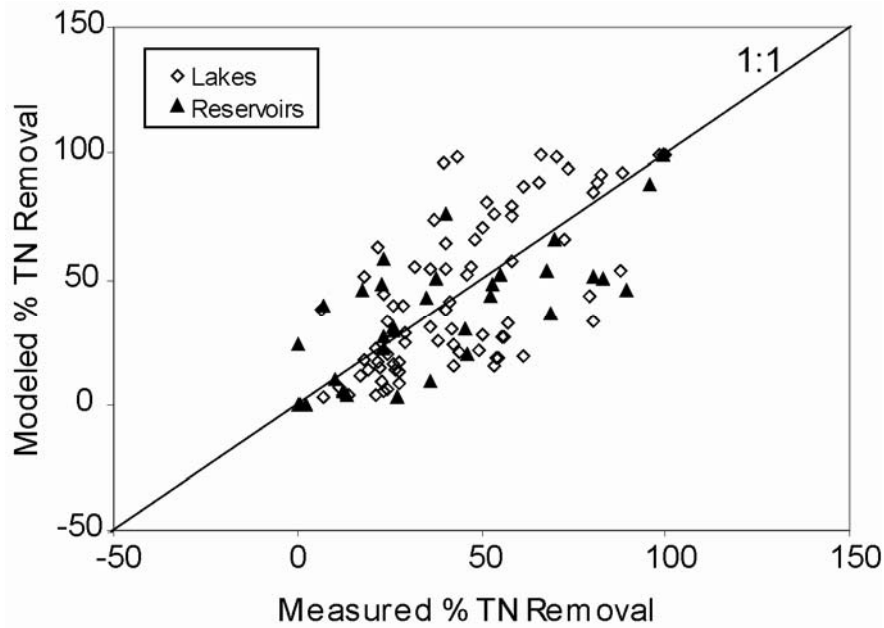
767 **does not sum because of rounding

768 **Table 4.** Results from a model sensitivity analysis. * signifies sensitivity analysis was only run on small lakes and reservoirs.

Parameter	Δ Input	Δ Prediction(%)	Range of Predicted Lake & Reservoir N Retention (Tg yr ⁻¹)
Runoff	Half-Double	-11% to +15%	17.5-22.7
N Inputs	Half-Double	-50% to +100%	9.85-39.4
V_f	25 th percentile-75 th percentile (2.2-7.56 m yr ⁻¹ and 3.15-19.41 m yr ⁻¹ for lakes and reservoirs, respectively)	-30% to +17%	13.7-25.1
c for lakes	± 1 S.E.	-0.1% to +0.1%	*12.3-12.4
c for reservoirs	± 1 S.E.	-1.6% to -1.6%	*12.1-12.4
Minimum Lake Area	Raised to 0.01 km ²	-8.1%	*11.3
Minimum Reservoir Area	Raised to 0.01 km ²	-0.8%	*12.2
Minimum Lake and Reservoir Area	Raised to 0.01 km ²	-9.8%	*11.1
Small Lake and Reservoir Cutoff	Used only documented lakes and reservoirs (>0.1 km ²)	-24.9%	14.8
N Inputs	Run with NEWS-DIN output	-22.8%	15.2

769

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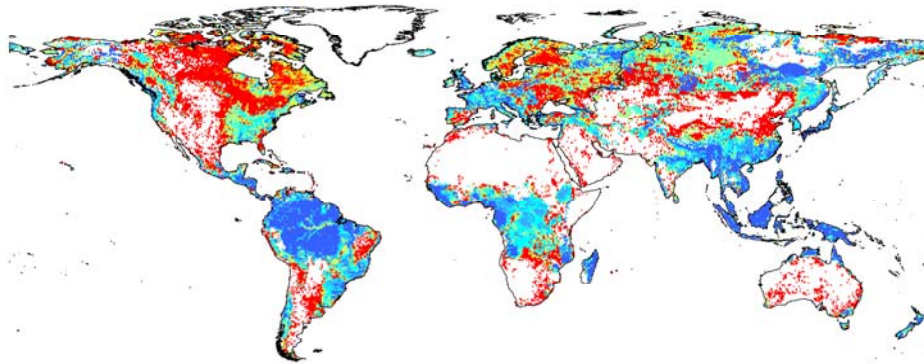
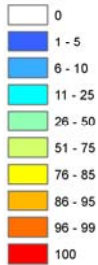


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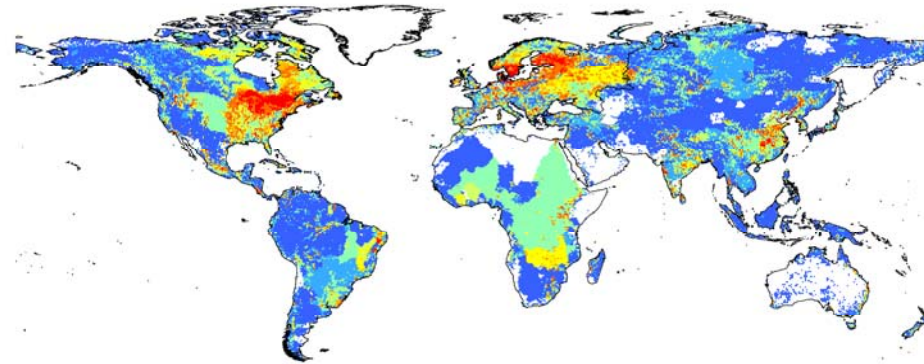
772 **Figure 1.** Comparison between measured percent N removal and NiRReLa-modeled
773 percent N removal in lakes (open diamonds) and reservoirs (closed triangles) for which N
774 removal data exist. The 1:1 line is also shown.

A

% TN Retained
In Lakes and
Reservoirs

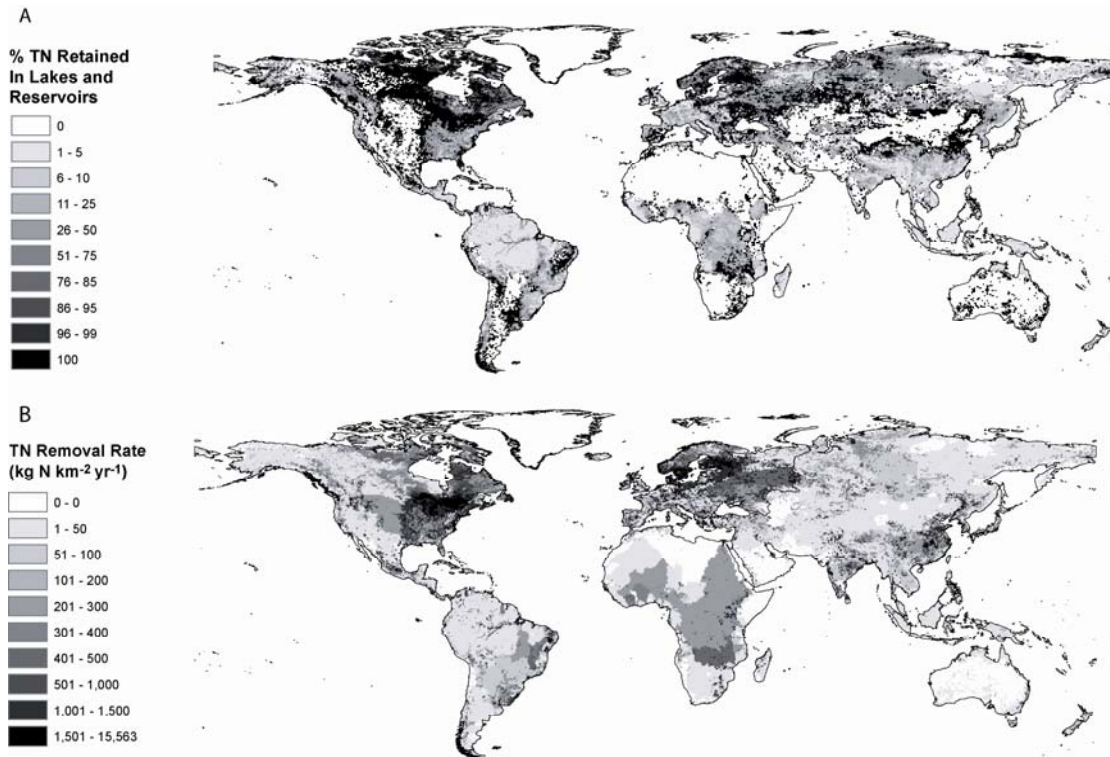


B
TN Removal Rate
(kg N km⁻² yr⁻¹)



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Figure 2. NiRReLa-modeled global distribution of percent N removal by lakes and reservoirs in panel A. Panel B shows N removal by lakes and reservoirs kg N km⁻² yr⁻¹.



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Figure 2. NiRReLa-modeled global distribution of percent N removal by lakes and reservoirs in panel A. Panel B shows N removal by lakes and reservoirs kg N km⁻² yr⁻¹