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Ecology under lake ice

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87 **Statement of Authorship**

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SEH conceived of the project idea. SEH, AWEG, and KHW initiated the project and provided oversight during data collection, integration, and aggregation. SEH, EHS, and TO served on the steering committee. KHW, AWEG, and SGL led QA/QC on the submitted data sets. SMP, TO, RDB, CMO, SS, NRL, EHS, RLN, JDS, RA, and GAW performed exploratory analyses and helped determine scope and structure of manuscript. SMP, SEH, and SGL performed final analyses and designed figures and tables. All other listed authors aggregated data for submission to this project and contributed to interpretation of results and final manuscript text.

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107

108 **Abstract**

109 Winter conditions are rapidly changing in temperate ecosystems, particularly for those that
110 experience periods of snow and ice cover. Relatively little is known of winter ecology in
111 these systems, due to a historical research focus on summer "growing seasons." We
112 executed the first global quantitative synthesis on under-ice lake ecology, including 36
113 abiotic and biotic variables from 42 research groups and 101 lakes, examining seasonal
114 differences and connections as well as how seasonal differences vary with geophysical
115 factors. Plankton were more abundant under ice than expected; mean winter values were
116 42.8% of summer values for chlorophyll *a*, 15.8% of summer phytoplankton biovolume,
117 and 34.4% of summer zooplankton density. Dissolved nitrogen concentrations were
118 typically higher during winter, and these differences were exaggerated in smaller lakes.
119 Lake size also influenced winter-summer patterns for dissolved organic carbon (DOC), with
120 higher winter DOC in smaller lakes. At coarse levels of taxonomic aggregation,
121 phytoplankton and zooplankton community composition showed few systematic
122 differences between seasons, although literature suggests that seasonal differences are
123 frequently lake-specific, species-specific, or occur at the level of functional group. Within
124 the subset of lakes that had longer time-series, winter influenced the subsequent summer
125 for some nutrient variables and zooplankton biomass.

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130 **Introduction**

131

132 Reduced ice cover on lakes and rivers worldwide (Magnuson et al. 2000; Benson et
133 al. 2012) highlights an urgent need for research focused on under-ice ecosystem dynamics
134 and their contributions to whole-ecosystem processes. Recently a global synthesis of
135 summer lake temperature trends in lakes (O'Reilly et al. 2015) revealed that winter ice
136 cover is a major force in determining the characteristics of summer warming trends,
137 demonstrating the cascading effects between seasons. Cross-seasonal cascades can involve
138 both abiotic and biotic variables, such as when winter ice characteristics influence spring
139 and summer algal growth (e.g., Gerten & Adrian 2000; Straile 2002; Adrian et al. 2006;
140 Blenckner et al. 2007). Consequently, in water bodies that freeze, the timing and physical
141 characteristics of ice cover are likely to drive some of the most important biological
142 changes for lakes overall (Salonen et al. 2009; Moore et al. 2009; Benson et al. 2012).

143 Marine research is ahead of freshwater research in studies of under-ice ecology,
144 providing compelling evidence that winter conditions and changes in ice phenology play an
145 important role in sea-ice system dynamics (Arrigo & Thomas 2004; Arrigo et al. 2008;
146 Meier et al. 2014). The presence of ice in marine systems drives primary productivity that
147 is critical for food webs (Lizotte 2001; Grebmeier 2012); for example, ice-associated algae
148 in the Antarctic contribute 25-30% of total annual productivity for the region (Arrigo &
149 Thomas 2004). But for lakes, there is very little information about the physics,
150 geochemistry, and biology under ice, and this knowledge gap severely limits our ability to
151 predict how changes in winter conditions will affect the ecology and productivity of inland
152 waters. A recent study reported that only 2% of peer-reviewed freshwater literature has
153 included under-ice lake processes (Hampton et al. 2015). The paucity of under-ice research
154 in freshwater systems is especially surprising when one considers that half of the world's
155 lakes periodically freeze, i.e. slightly more than 50 million lakes (Verpoorter et al. 2014).
156 Also, the majority of lakes in the world are located between 60° and 66°N where annual ice
157 cover duration currently averages more than 150 days (Weyhenmeyer et al. 2011).

158 The initial and highly influential model of the plankton ecology group (the PEG
159 model; Sommer et al. 1986) hypothesized that winter in ice-covered lakes is a time of
160 limited, if any, activity by primary or secondary producers. The widespread use of the term
161 "growing season" to describe summer months in temperate lakes reflects the prevailing
162 viewpoint of winter as an inactive period. In general, freshwater scientists have assumed

163 that overall biological activity under lake ice is inconsequential or that under-ice primary
164 producers resort to heterotrophy or dormancy, as has been observed in some studies (e.g.,
165 McKnight et al. 2000; Leppäranta 2015), particularly for high-latitude systems with heavy
166 snow coverage. While the PEG model has since been revised (Sommer et al. 2012) with a
167 call for additional winter work, areas of uncertainty range from the identity and activity of
168 plankton to ecosystem-level processes such as whole-lake metabolism and greenhouse gas
169 emissions. The lake studies that have included under-ice work strongly suggest that winter
170 food webs and physical processes are both active and complex, but with few patterns that
171 are readily generalizable (reviewed in Salonen et al. 2009; Bertilsson et al. 2013;
172 Bruesewitz et al. 2015; Hampton et al. 2015).

173 Prior work indicates that winter under-ice conditions can be very similar to, or very
174 different from, the ice-free summer conditions. Depending upon snow characteristics, ice
175 can allow for up to 95% of photosynthetically active radiation (PAR) transmission
176 (Bolsenga & Verderploeg 1992), fueling winter algal blooms that rival those of summer
177 (e.g., Jewson et al. 2009). In Lake Erie, phytoplankton growth and loss rates during winter
178 can be similar to those of summer (Twiss et al. 2014). For certain lakes, the composition of
179 phytoplankton communities is different under ice, dominated by smaller species (e.g.,
180 Wetzel 2001), or conversely dominated by large ice-associated filamentous diatoms (e.g.,
181 Katz et al. 2015; Beall et al. 2016), whereas other lakes do not appear to have distinct
182 seasonal changes in phytoplankton community composition (Dokulil et al. 2014). Although
183 zooplankton biomass generally appears to be lower under ice, changes in community
184 composition can be highly variable across lakes (Dokulil et al. 2014). Even more scarce is
185 information about nutrient and dissolved organic carbon concentrations under the ice that
186 may help to drive many of these plankton dynamics (but see Özkundakci et al. 2016).

187 The pathways through which winter conditions may affect lake ecology throughout
188 the year are similarly diverse. Winter ice conditions have been observed to alter
189 phytoplankton biomass and composition in the subsequent ice-free season (Weyhenmeyer
190 et al. 2008). For zooplankton, early emergence from diapause, synchronized with the
191 timing of warming at the end of winter can be associated with higher summer density for
192 zooplankton grazers (Gerten & Adrian 2000; Adrian et al. 2006). Such carry-over between
193 seasons is not restricted to winter's influence on summer, of course, and there is evidence

194 that under-ice zooplankton dynamics can depend in part on late summer zooplankton
195 biomass (Dokulil et al. 2014). The diversity of responses found by under-ice studies
196 suggests that a synthesis of existing knowledge is greatly needed and would help identify
197 key next steps in winter limnology as well as promote productive collaborations (Hampton
198 et al. 2015).

199 Research that builds a knowledge base about the processes occurring over nearly
200 half the annual cycle for approximately half of the world's lakes is a worthy challenge, with
201 potentially global repercussions. Here we explore differences between winter and summer
202 conditions both across and within lakes, focusing on dynamics of phytoplankton,
203 zooplankton, nutrients, and dissolved organic carbon. We address two overarching
204 questions on under-ice ecology: 1) What is the magnitude and direction of ecological
205 change from winter to summer; and 2) For which variables and to what extent are winter
206 and summer seasons connected, i.e., what is the influence of winter conditions on the
207 following summer season, and the influence of summer conditions on the following winter?
208 We hypothesized that winter biomass and density of phytoplankton and zooplankton are
209 significantly lower than that of summer, due to a low-light environment unfavorable for
210 emergence or growth (e.g., Vincent & Vincent 1982; Cáceres & Schwalbach 2001; Jewson et
211 al. 2009), low temperature (e.g., Özkundakci et al. 2016), or nutrient limitation (e.g.,
212 O'Brien et al. 1992; Özkundakci et al. 2016), and that these differences would be modified
213 by geophysical characteristics of lakes. Further, we hypothesize that lake conditions can
214 carry over across seasons, as suggested in the revised PEG model (Sommer et al. 2012;
215 Domis et al. 2013), such that an understanding of winter conditions will improve
216 understanding of summer conditions, and vice versa. The presence of seasonal carry-over
217 would indicate that winter is not simply a "reset" that leads back to similar spring ice-out
218 conditions year after year, and would suggest revisions to current field and laboratory
219 approaches currently focused on "growing season" dynamics.

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222

223 **Methods**

224 *Data Acquisition*

225 Data were acquired from both an initial literature review to provide baseline
226 expectations for ecological patterns and, much more comprehensively, from a collation of
227 primary data.

228 Literature review. As an initial step toward synthesizing knowledge, we compiled
229 under-ice data for chlorophyll *a* (chl *a*) concentration from a literature survey. We found 14
230 papers for which data would be readily compared to those solicited from primary data
231 contributors (based on criteria in Supplemental Information). From these papers, we
232 compiled data from 17 lakes (Fig. 1), extracting data from text, tables, or from figures. For
233 the literature review effort, we were unable to compare ice-on (winter) and ice-off
234 (summer) data, as only 7 of the lakes in these papers also included biological data during
235 the summer season.

236 Primary data collation. The scientific community was solicited for data on physical,
237 chemical, and biological variables of lakes and reservoirs (hereafter together called “lakes”)
238 during ice cover. We used an open call for participation through electronic mailing lists and
239 professional networks, and then interacted extensively with data contributors. In total, we
240 collated winter under-ice and summer observations between 1940 and 2015 for 101 lakes
241 at 135 unique sampling locations across wide gradients of latitudes, production, and
242 trophic status (Fig. 1). For the Laurentian Great Lakes, most sampling stations were located
243 nearshore or in bays.

244 Contributors of primary data used a structured template to report values from
245 winter periods when the lake had complete ice cover (hereafter “winter”), and summer
246 periods when the lake was completely open and, in dimictic systems, stratified (hereafter
247 “summer”). For 10 lakes that were polymictic or lack reliable summer stratification,
248 summer data are from a representative open water period chosen by the primary data
249 contributors, usually midsummer. We asked researchers to provide data aggregated from
250 the photic zone, for each lake and season. Across all lakes, the median sample depth during
251 winter was 2.0 m, and the mean ratio of sample depths (winter:summer) was 1.01. We did
252 not include winter data from those years that did not have ice cover (e.g., Müggelsee
253 sometimes does not freeze). Each seasonal value used in our analysis was computed by the
254 individual data providers (Box S1; Fig. S1). The number of within-season sampling events
255 was reported by researchers for 71% of our compiled seasonal averages; of these, 64% of

256 the winter averages and 79% of the summer averages were based on 3 or more sampling
257 events. When a lake had multiple sampling stations, the stations were generally treated
258 independently. Exceptions were cases where researchers specified multiple stations that
259 were functionally similar and could be pooled in aggregate. After pooling the functionally
260 similar stations, the majority of lakes (84 of 101 lakes) did not retain multiple distinct
261 stations for analyses (see SI).

262 Data availability differed among lakes and variables. For several major variables,
263 paired winter and summer observations were present in at least 30 stations, often over 10
264 years. All stations had at least one variable with both winter and summer data, and the
265 variable-specific sample sizes and periods of record are in Table S1. The median period of
266 record for most variables was 2-3 years. Variables included water temperature (107
267 unique stations with paired winter-summer data), chlorophyll *a* (chl *a* as $\mu\text{g L}^{-1}$; 118
268 stations), total phosphorous (TP as $\mu\text{g L}^{-1}$; 106 stations), total dissolved phosphorus (TDP
269 as $\mu\text{g L}^{-1}$; 72 stations), total nitrogen (TN as $\mu\text{g L}^{-1}$; 75 stations), total dissolved nitrogen
270 (TDN as $\mu\text{g L}^{-1}$; 73 stations), TN:TP (atomic ratio; 74 stations), TDN:TDP (atomic ratio; 66
271 stations), and dissolved organic carbon (DOC as mg L^{-1} ; 81 stations). Our reported values
272 for TDP and TDN are conservative, because not all researchers performed the digestion
273 step. Nonetheless, because common nutrient methods were usually used at a given lake,
274 our approach still captures the relative difference between seasons (winter-summer),
275 except in lakes where the dissolved organic fraction varies substantially between seasons.
276 In addition, 36 stations had data for total zooplankton density (individuals L^{-1}). Group-
277 specific zooplankton counts (proportion of total abundance) for calanoid, cyclopid,
278 *Daphnia*, rotifer, other cladoceran, and unspecified other zooplankton were also available.
279 Methodology for zooplankton data collection differs across programs to a degree that
280 complicates comparisons across lakes for rotifers and unspecified other zooplankton, such
281 that those data were not analyzed here and total zooplankton densities were accordingly
282 adjusted as well. Subsequent references to zooplankton density include *Daphnia*, other
283 cladocerans, cyclopid and calanoid copepods for all 36 stations. For phytoplankton
284 biovolume $\text{mm}^3 \text{L}^{-1}$, there were data for 17 stations. Group-specific phytoplankton counts
285 (proportion of total abundance) for chlorophyte, cryptophyte, cyanophyte, bacillariophyte,
286 dinoflagellate, and other phytoplankter were available at 17 stations. Specific ultraviolet

287 absorbance (SUVA, L mg C⁻¹ m⁻¹), and color (platinum units) were also available at some
288 stations. Although we solicited benthic data, only a few researchers provided data for any
289 type of benthic variable, suggesting a widespread lack of benthic winter sampling. The lake-
290 specific averages for winter and summer conditions, by variable, are shown in Table S2. For
291 chl *a*, TP, TDP, TN, TDN, DOC, and zooplankton density, more than 25% of stations had a
292 period of record ≥ 10 years. The complete dataset is available in the Knowledge Network
293 for Biocomplexity (<https://knb.ecoinformatics.org/>, Hampton et al. 2016).

294 *Data analysis*

295 We approached data analysis in two ways. The first approach was to quantify the
296 average winter-summer differences across all lakes in the data set, identifying major
297 physical features of lakes that affect the magnitude of observed winter-summer differences.
298 The second approach was to examine univariate seasonal dynamics within lakes, including
299 winter-summer differences and winter-summer correlations, using the subset of lakes
300 where longer-term (≥ 10 years) time series were available.

301 Winter-summer differences across lakes. We calculated the mean winter value and
302 the mean summer value for every station and variable, and examined mean winter-summer
303 differences across all lakes in the data set. Magnitude, direction and significance of
304 differences between winter and summer were determined using linear mixed effect (LME)
305 modeling with year as a random intercept (Bates et al. 2015). For the multivariate plankton
306 compositional data, we used permutational analysis of variance (PERMANOVA; Anderson
307 2001) from the *vegan* package in R (“*adonis*” function, Oksanen et al. 2016; R Core Team
308 2016) on sites that had complete cases for both winter and summer communities. To
309 discern major physical variables correlated with the magnitude and sign of winter-summer
310 differences, we used a regression tree approach (*rpart* package in R, Therneau et al. 2015,
311 with applications from Breiman et al. 1984). We used the variable-specific average winter-
312 summer difference as the response variable; the candidate explanatory variables were lake
313 area, lake maximum depth, latitude (absolute), and elevation. Trees were cross-validated
314 and pruned using the complexity parameter value which minimized the cross-validated
315 error. Mean winter-summer difference and standard error of the difference were
316 calculated for each branch of the regression trees. We also used a regression tree approach
317 to analyze average winter-summer difference in plankton community composition as a

318 matrix response (mvpart package in R, Therneau et al. 2014), for both the crustacean
319 zooplankton community and the phytoplankton community data. Candidate explanatory
320 variables included the same four variables as previous trees, as well as winter-summer
321 difference in water temperature and, for zooplankton, the summer chl *a*.

322 Due to differences in the available period of record, the overall winter average can
323 represent 30+ years for some lakes and variables, while for others the overall average
324 represents only one year of data. We expected that variation in sample size might create
325 noise that could obscure differences (Type 2 error), but not suggest differences that do not
326 exist (Type 1 error).

327 Winter-summer differences within lakes. For time series that were available, we
328 examined within-lake differences between winter and summer. For this we used only time
329 series that had ≥ 10 winter values, meaning at least 10 years of data and 20 values overall.
330 To allow a robust examination of winter-summer correlations (below), we used contiguous
331 portions of each time series, allowing no more than 1 data gap. Before examining
332 differences, every time series was detrended using a 7-point moving average filter (3.5
333 years) to account for longer-term trends, and we confirmed that no significant linear trends
334 remained after filtering. With each detrended time series, summer-winter differences were
335 examined using a simple seasonal model

$$336 \quad y_t = b_{ice} * D + b_0 + e \quad (1)$$

337 where b_{ice} is the coefficient describing the winter-summer difference, D is a dummy
338 variable (1 in winter, 0 in summer) that employs the b_{ice} coefficient, b_0 is the intercept
339 (representing the mean summer value), and e is the error term. We then compared the
340 seasonal model (2 parameters) to the simple intercept model (1 parameter, b_0 ,
341 representing the overall mean) using the Akaike Information Criterion corrected for small
342 sample sizes (AIC_c) (Burnham & Anderson 2002). If the seasonal model differed from the
343 simple intercept model by $\Delta AIC_c \geq 2$, we interpreted this result to mean that the time series
344 showed a seasonal difference. Detailed diagnostic plots including raw and detrended time
345 series are provided in Figure S4 for one example lake (Big Muskellunge Lake, chl *a*). For
346 194 of the 238 available time series (82%), residuals from eq. 1 were not autocorrelated at
347 lag 1 according to the Box-Ljung test, and this is demonstrated by the partial
348 autocorrelation plot of the detrended+deseasoned data (Fig. S4). For the other 44 time

349 series, we added a first-order autocorrelated error structure to eq. 1. The percent of time
350 series having winter values greater than summer values, or vice versa, was tabulated by
351 variable.

352 Winter-summer correlations within lakes. Using the same univariate, contiguous,
353 moving-average detrended time series as above (those with >10 winter values), we
354 examined temporal correlations between winter and summer. These included: i)
355 correlations between winter and the previous summer season ($summer_{t-1}$), or summer-
356 into-winter (*SW*) correlations; and ii) correlations between winter and the subsequent
357 summer ($summer_{t+1}$), or winter-into-summer (*WS*) correlations. We determined the sign of
358 seasonal correlations, if present, using a simple model of the detrended data

$$Y_{winter, t} = b_{SW} * Y_{summer, t-1} + b_0 + e \quad (2)$$

359 where t is the index of the time series and b_{SW} is the slope of the relationship between
360 winter and the previous summer. If this *SW* correlation model did not show AIC_c
361 improvement >2 AIC_c units compared to the intercept model (1 parameter, b_0 ,
362 representing the overall mean), the time series was interpreted as not seasonally
363 correlated. We then separately evaluated the corresponding *WS* correlation model, $Y_{summer,$
364 $t+1 = b_{WS} * Y_{winter, t} + b_0 + e$, also using AIC_c . A minority of these *SW* and *WS* correlation
365 models produced autocorrelated residuals, and to these we added a first-order
366 autocorrelated error structure, although this modification did not change the model
367 selection nor the sign of b_{SW} or b_{WS} for any time series. Here a positive *WS* correlation
368 indicates that high summer values follow high winter values, or low summer values follow
369 low winter values. Alternatively, a negative *WS* correlation indicates anti-persistence, such
370 that low summer values follow high winter values, or high summer values follow low
371 winter values. As examples, we illustrate the presence/absence of winter-summer
372 correlations for every chl *a* time series, including *SW* correlations (Fig. S5) and *WS*
373 correlations (Fig. S6). The percent of time series having positive/negative *SW* correlations
374 or positive/negative *WS* correlations was tabulated by variable (Table S5).

376 Results

377 *Seasonal differences across lakes*

378 Indicators of plankton biomass were lower in the winter than during the summer.
379 Across lakes and latitude, average winter chlorophyll *a* (\pm SE) ($5.87 \pm 0.88 \mu\text{g L}^{-1}$, Fig. 2) in

380 the primary data ranged much more widely than in those from our literature survey
381 (Supplemental Fig. S2), although still significantly lower than that of summer (13.6 ± 2.84
382 $\mu\text{g L}^{-1}$, $p < 0.0001$, Table 1). Using the regression tree approach, the shallowest lakes (max
383 depth < 2.93 m, $n = 13$ lakes) showed greatest disparity in chlorophyll, with summers
384 higher than winters by $52.3 \pm 18.2 \mu\text{g L}^{-1}$ (R^2 for chl *a* tree = 0.330). Under-ice
385 phytoplankton biovolume averaged about 1/6th that of the summer average ($n=17$,
386 $p < 0.001$ by LME, Table 1). However, at our coarse level of taxonomic aggregation,
387 phytoplankton community composition did not differ significantly between winter and
388 summer when examined across all lakes (PERMANOVA, $p=0.77$; Fig. 3). Across lakes,
389 average zooplankton density (\pm SE) was significantly lower under ice (27.8 ± 11.2
390 individuals L^{-1}) than during summer (110 ± 30.8 individuals L^{-1} ; $p < 0.001$), and winter
391 crustacean zooplankton community composition differed significantly from that of summer
392 (PERMANOVA; $p=0.05$), with cladocerans generally more abundant in summer (Fig. 3).
393 Regression trees did not provide further insights into plankton community shifts,
394 differentiating only two lakes out of 17, and are not discussed further here. The complete
395 list of summary statistics, for every variable, is shown in Table S3. The PERMANOVA
396 statistical outputs are in Table S4.

397 Dissolved N concentrations tended to be higher during winter, and seasonal
398 differences were more prominent for dissolved N than for dissolved P. Across lakes,
399 average (\pm SE) TDN was approximately 2-fold higher under ice ($707 \pm 129 \mu\text{g L}^{-1}$, Fig. 2)
400 than in summer ($375 \pm 62.2 \mu\text{g L}^{-1}$; $p < 0.001$ by lme). The pattern of higher winter TDN
401 appeared particularly pronounced as maximum depth decreased. Regression trees showed
402 that the 7 shallowest lakes (< 2.10 m) had $2070 \mu\text{g L}^{-1}$ higher TDN on average in winter
403 than summer, 7 lakes of intermediate depths ($5.20 < \text{max depth} < 2.10$ m) had TDN winter
404 values that were $758 \mu\text{g L}^{-1}$ higher than summer on average, while the 59 deeper lakes
405 (> 5.2 m) showed winter TDN values $123 \mu\text{g L}^{-1}$ higher than summer on average (tree $R^2 =$
406 0.722 , Fig. S7). TN was also higher during winter ($p < 0.001$, LME-fitted difference of
407 $+161 \mu\text{g L}^{-1}$), likely as a reflection of higher dissolved N, which typically accounted for the
408 majority of the N pool (winter TDN:TN = 0.807 compared to summer TDN:TN = 0.592).
409 Winter and summer did not differ significantly for TP or TDP according to LME models
410 ($p > 0.2$). DOC concentrations did not differ seasonally ($p = 0.863$ by LME). Interestingly,

411 these DOC patterns clearly varied with lake area and elevation (tree $R^2 = 0.538$, Fig. S7).
412 Regression trees demonstrated that larger ($\geq 0.373 \text{ km}^2$) lakes had 0.145 mg L^{-1} lower
413 DOC in winter compared to summer, while smaller ($< 0.373 \text{ km}^2$), low elevation ($< 366 \text{ m}$)
414 lakes ($n=19$) had 6.69 mg L^{-1} higher DOC in winter, and similarly small lakes at higher
415 elevations also had 0.810 mg L^{-1} higher DOC in winter. Regression tree analyses did not
416 produce significant models for plankton density or phosphorus variables.

417 *Winter-summer differences within lakes*

418 In general, within-lake differences between summer and winter were consistent
419 with differences observed across lakes. For example, chl *a* was lower in winter at 17 of the
420 34 sites (50%) that met our longer-term data criteria (Table 2). The summary statistics for
421 each individual time series are in Table S5. Phytoplankton density was also lower in winter
422 compared to summer in 4 of 4 sites. Similarly, zooplankton densities were significantly
423 lower during winter at 10 of 11 sites (91%); the one exception was a bog lake, Trout Bog
424 (USA), which had a relatively low summer zooplankton density and no detectable winter-
425 summer difference. For nutrients, patterns again differed between N and P. Over 70% of
426 the sites had higher winter TDN (11 of 14) and TN (21 of 30), whereas only 14% of sites
427 had higher winter TDP (2 of 14) and 21% had higher TP (7 of 33). Allequash Lake (Fig. 4)
428 provides an example where TP concentration was lower during winter. DOC was lower
429 during winter at 6 of 26 sites (23%), and higher in winter at 3 sites including Trout Bog,
430 USA, with no differences between winter and summer at the other 17 sites (65%). Three
431 variables lacked differences between summer and winter values at $>50\%$ of sites (TP, TDP,
432 DOC).

433 *Winter-summer correlations within lakes*

434 From a total of 238 time series for different lakes and variables (Table S5), after
435 accounting for trends, our AIC-based approach detected 94 time series (39%) with some
436 form of correlation between winter and the previous summer, or between winter and the
437 following summer. Several individual variables had seasonal correlations in $\geq 33\%$ of the
438 available time series, including chl *a*, phytoplankton density, TDN, TN, and TDP (Table 2).
439 Negative correlations outnumbered the positive correlations, suggesting seasonal anti-
440 persistence. Positive seasonal correlations were absent for chl *a*, zooplankton density, DOC,
441 TP, TDN, and TDP. For chl *a*, negative winter-into-summer (*WS*) correlations (26% of time

442 series) and summer-into-winter (*SW*) correlations (32%) were both relatively common.
443 For TDN, negative *SW* correlations outnumbered negative *WS* correlations (43% vs. 0%),
444 suggesting summer carry over. Overall, the frequency of these winter-summer negative
445 correlations ranged widely among variables.

446 Discussion

447 This global synthesis of under-ice ecology underscores the importance of winter
448 conditions for lake ecology throughout the year. Using multiple approaches, our cross-lake
449 synthesis revealed several clear differences between winter and summer conditions,
450 offering generalizations about winter ecology that have been difficult to infer from prior
451 studies involving one or a few lakes. We also provide new evidence that interseasonal
452 connections are common for several ecological and biogeochemical variables, linking
453 winter to both the previous and subsequent summers. Among our clearest results, primary
454 producers (algae) and consumers (zooplankton) are typically less abundant under ice than
455 in summer, but they maintain substantial populations in winter. Arguably, this may be
456 interpreted as evidence of high winter productivity, and we explore the possibility below.
457 Also clear was the result that winter dissolved nitrogen was consistently higher than
458 summer. While crustacean zooplankton composition showed some general seasonal
459 differences, we found no generalizable differences in phytoplankton community
460 composition between winter and summer at the coarse level of taxonomic aggregation
461 used here. As long-term climate change alters thermal regimes across globally distributed
462 lakes in both summer (O'Reilly et al. 2015) and winter (Magnuson et al. 2000), it is
463 increasingly important to understand how under-ice physical and ecological conditions
464 influence ecology throughout the year. Overall, this work represents an important step
465 towards understanding winter ecology in lakes broadly, as well as the connections to year-
466 round dynamics and whole-lake functionality.

467 Our results indicate seasonal differences in chl *a*, plankton biomass and biovolume,
468 and dissolved nitrogen between winter and summer, both across and within lakes. Despite
469 lower under-ice values, particularly for the shallowest lakes, on average chl *a* was relatively
470 high (42.8% of summer chl *a*) given the shorter photoperiod and variable physical
471 conditions of winter. Indeed, winter levels exceeded those of summer in multiple cases
472 such as Lake Simcoe (Canada), Lake Scharmützelsee (Germany), and Fish Lake (USA)

473 which all had more than 10 years of winter data. Previous under-ice lake studies have
474 reported chlorophyll values as high as 154 $\mu\text{g L}^{-1}$ (Twiss et al. 2012). Conversely some
475 lakes have undetectable chlorophyll levels under ice (e.g., Hawes 1985). While the available
476 winter limnology literature provides evidence that lakes can support an abundance of algae
477 under ice - as demonstrated by genetic (e.g., Bashenkhaeva et al. 2015), pigment (e.g.,
478 Catalan et al. 2002), and cell count (e.g., Phillips & Fawley 2002; Katz et al. 2015) data - it is
479 also important to remember that estimates of algal biomass or primary productivity based
480 on chlorophyll can be skewed seasonally. Intracellular pigment content can change with
481 temperature and light conditions (Kirk 2011), such that smaller seasonal differences in
482 chlorophyll could in part be due to light adaptation leading to increased cellular pigment
483 concentrations.

484 In general, light can be the limiting factor for photosynthesis under ice, with ice
485 conditions and overlying snow producing spatially (e.g., Cloern et al. 1992, Arrigo and
486 Thomas 2004) and temporally (e.g., Tanabe et al. 2008; Bruesewitz et al. 2015)
487 heterogeneous transmission of light and altered spectral distribution (Roulet & Adams
488 1986). The timing and characteristics of winter precipitation, wind, temperature variation,
489 and solar radiation influence variability in under-ice light conditions, including the
490 formation of clear congelation ice which can have higher light transmittance than lake
491 water (Leppäranta 2010). When light is sufficient for photosynthesis, the under-ice
492 environment can be hospitable for algal growth; complex under-ice convection can keep
493 nutrients and algae mixed in the photic zone (Kelley 1997; but see Vehmaa & Solonen
494 2009), and in Lake Baikal the ice itself can provide a vast habitat for attached algae to
495 maintain access to light (Timoshkin 2001; Bondarenko et al. 2012). In relatively dark
496 conditions with low primary production, we might anticipate lower oxygen conditions,
497 greater winter accumulation and subsequent contributions of greenhouse gases to the
498 atmosphere, smaller algal and grazer populations available to initiate population growth at
499 ice-out (Sommer et al. 2012), and less ice-associated algae sloughing off to feed the benthos
500 as summer begins (Bondarenko et al. 2006). Because increased intracellular chlorophyll
501 content may be an adaptation to low light conditions, exhibited by many but not all (Felip &
502 Catalan 2000) phytoplankton, we recommend measuring primary productivity directly, if

503 that is the variable of interest, or measuring both cell density and community composition
504 in order to characterize plankton biomass and identity.

505 Phytoplankton biovolume was lower under ice than in the summer on average,
506 consistent with chl *a* values, when all lakes were considered together. However, we did not
507 detect systematic seasonal differences in phytoplankton community composition that
508 could be generalized among all lakes. The lack of detectable difference does not imply that
509 algal communities in each lake did not change from season to season; rather, this result
510 suggests that generalizations about “winter” or “summer” taxa are difficult to make at the
511 coarse level of taxonomic grouping we used. Moreover, it is rare for monitoring programs
512 to quantify picoplankton, which constitute substantial portions of algal communities in
513 summer and winter (Callieri & Stockner 2002; Bondarenko et al. 2012), such that their
514 contributions to our results are unknown. Previous studies indicate that many if not all
515 lakes do harbor relatively distinct winter and summer algae, frequently with differences
516 occurring at species level (Kozhova & Izmet’eva 1998; Dokulil et al. 2014; Özkundakci et
517 al. 2016), division level (Carey et al. 2016), or by functional traits (Özkundakci et al. 2016)
518 with winter assemblages characterized by taxa that are more tolerant to cold and low-light
519 conditions. Despite constraints by cold temperature, light limitation or altered mixing
520 under the ice, winter species diversity has been found to be rather high (Salonen et al.
521 2009). Moreover, for Müggelsee, a lake located in a geographical transition phase of
522 becoming ice-free more frequently with current and projected climate warming
523 (Livingstone and Adrian 2009) it has been shown that different phytoplankton
524 communities were favored across a gradient of mild to strong winter severity, associated
525 with the key functional traits of motility, nutritional mode (autotrophy, heterotrophy,
526 mixotrophy) and the ability to form resting stages (Özkundakci et al. 2016).

527 As algal communities adjust to ice cover, seasonal shifts in higher trophic levels such
528 as zooplankton would also be anticipated. In this study, average winter zooplankton
529 density declined to roughly one third that of summer - lower but still substantial enough to
530 suggest that many of these relatively short-lived grazers actively feed and reproduce under
531 ice. In the absence of live primary producers or residual producer biomass, presence of
532 zooplankton under the ice can be explained by the consumption of other carbon sources
533 such as chemolithotrophs (e.g., methane-oxidizing bacteria), or detritus. For example,

534 planktonic heterotrophs and phototrophs, and benthic algae under the ice can provide
535 alternative diet sources throughout winter for zooplankton in some lakes (Karlsson &
536 Sävström 2009; Rautio et al. 2011; Hampton et al. 2015), while cyclopoids may prey on
537 other zooplankton (Ventura & Catalan 2008). Further, as in marine systems (Lee et al.
538 2006), some freshwater grazers may be able to use lipid stores accumulated in prior
539 seasons; lipid percentage in zooplankton samples collected from a lake in northern Finland
540 varied from over 60% in early winter to approximately 20% in late winter (Syväranta &
541 Rautio 2010).

542 The composition of crustacean zooplankton differed across seasons, with summer
543 characterized by more cladocerans such as *Daphnia*. These taxa are generally associated
544 with greater presence in summer months, with temperature and photoperiod offering cues
545 for hatching, and growth fueled by higher temperature and food availability (Adrian et al.
546 2006). Even so, as we observed for phytoplankton, it seems likely that many differences
547 between summer and winter zooplankton community composition may be lake-specific,
548 species-specific or better captured by functional trait grouping. Many zooplankton are
549 strict diapausing species that disappear from the water column into sediments during
550 winter (Nilssen & Elgmork 1977; Ventura & Catalan 2005; Larsson & Wathne 2006), but
551 several copepod species in high-latitude lakes of Europe and Canada have been shown to
552 reach peak density in mid-winter (Rigler et al. 1974; Rautio et al. 2000; Scharfenberger et
553 al. 2013) undergoing diapause during summer. Further, a variety of rotifers are well known
554 to proliferate under ice (e.g., Pennak 1968; Dokulil & Herzig 2009; Virro et al. 2009; Melnik
555 et al. 2008). Other studies also report persisting populations of *Daphnia* under the ice
556 (Snow 1972; Larsson & Wathne 2006; Slusarczyk 2009) but data are still somewhat scarce.
557 Our study suggests that when aggregating species to coarse taxonomic groups we may see
558 some expected differences, but will miss out on the complexity of plankton composition,
559 dynamics and functionality illustrated in the few detailed single-lake winter studies. It is
560 not necessarily the overall abundance or biomass of major taxonomic groups which differ
561 between seasons or change with global warming – but the species per se and the relative
562 species composition (reviewed in Adrian et al. 2009). While this is well known for summer,
563 information on species and functional trait composition during winter is indeed scarce.
564 Given that the ice itself provides a vast potential substrate for attached algae and an

565 associated community of metazoans (Bonderenko et al. 2012), and that common sampling
566 methods do not target this microhabitat, a major advance in winter limnology would be the
567 broader assessment of primary producers at this ice-water interface where some lakes
568 have shown extraordinarily high algal biomass and activity (e.g. Timoshkin 2001;
569 Bondarenko et al. 2012; Twiss et al. 2012). Further, shifts from autotrophy to mixotrophy
570 and heterotrophy clearly occur in some communities under ice (e.g. Rhode 1955,
571 Özkundakci et al. 2016), and examining how this trait varies from winter to summer likely
572 will yield important insights for ecosystem-level carbon cycles.

573 TDN and TN were higher under ice based on both our cross-lakes approach (Table
574 1) and a within-lakes time series approach (Table 2), while winter DOC was variable but
575 more similar to that of summer. The higher concentrations of dissolved N likely reflect
576 winter nutrient mineralization (Cornett & Rigler 1979; Nürnberg et al. 1986, Catalan 1992)
577 providing continued N inputs, while dissolved N uptake may be lower under winter
578 conditions due to low temperature and light, and possibly less denitrification. More
579 specifically, these results indicate that within the first few meters of the water column,
580 dissolved N accumulates disproportionately under ice relative to P, especially in shallower
581 lakes according to the regression tree analysis. A possible explanation is that benthic N
582 mineralization and nitrification dominate winter N cycles in shallow lakes, whereas the
583 higher water volume:surface area ratios in deeper lakes may limit N mineralization per
584 unit volume and perhaps increase the role of pelagic uptake by phytoplankton. While the
585 cross-lakes approach (Table 1) suggested that winter DOC was similar to summer on
586 average, the regression tree analysis indicated DOC was unique among our variables, with
587 opposing patterns in two distinct lake groups. More specifically, larger lakes (>0.373 km²)
588 had lower DOC in winter, while smaller lakes (<0.373 km²) had higher DOC in winter,
589 especially those occurring at lower elevation (<366 m). These smaller, lower elevation
590 lakes also tended to have higher DOC overall, possibly resulting in especially dark
591 conditions under ice. The dynamics of DOC can be influenced by multiple interacting
592 factors such as lower terrestrial carbon input during cold winters (Lepistö et al. 2014),
593 sustained benthic metabolism, uptake of DOC by bacteria (Tulonen et al. 1994), and
594 photodegradation (Wetzel 2001), but few studies have partitioned DOC sources and

595 processing during winter. DOC dynamics under ice clearly represent a key area for future
596 research.

597 In revising the PEG model, Sommer et al. (2012) speculate that winter activity
598 should have effects on phytoplankton and zooplankton in the subsequent season; indeed,
599 we found evidence for strong winter-summer linkage for some lakes and variables. In lakes
600 that had longer time series, such as the Laurentian Great Lakes, northern Wisconsin lakes,
601 northern Europe lakes, and Canadian lakes, the influence of winter conditions on the
602 following summer's value differed among variables. Winter and summer were often
603 negatively related, such that high winter values were associated with low values from the
604 adjacent summer, or low winter values were associated with high values from the adjacent
605 summer (Fig. S5, Fig. S6, Table S5). Among variables in our analysis, these negative cross-
606 seasonal relationships were particularly frequent for zooplankton density and chl *a*,
607 although several other variables also had negative winter-summer correlations in >20% of
608 the available time series. In the case of chl *a*, one explanation for antagonistic winter-
609 summer dynamics is that high winter production may reduce the pelagic nutrient pool,
610 strengthening P limitation or Si limitation in the following summer, in turn reducing
611 summer production. For zooplankton, one possible explanation for negative winter-
612 summer correlations could be that high prior zooplankton abundance or composition
613 reduces the availability of readily-ingestible phytoplankton at the beginning of the next
614 season. Many studies have suggested that overwintering populations can boost summer
615 populations and vice versa (e.g. Sommer et al. 2012). A clear next step would be to examine
616 temporal trends at the population level for zooplankton. Overall, evidence is increasing
617 among independent studies for the prevalence of carryover between seasons. Coherent
618 responses in algal and zooplankton phenology associated with conditions related to the
619 winter North Atlantic Oscillation, which determines winter weather conditions across large
620 parts of Europe, provide well studied examples (Weyhenmeyer et al. 1999; Gerten & Adrian
621 2000; Straile et al. 2003; Blenckner et al. 2007; Straile et al. 2012). Similarly, the severity of
622 winter influenced spring nutrient concentrations in Lake Peipsi (Blank et al. 2009).
623 Altogether such seasonal connections strongly favor previous calls to "close the loop"
624 (Salonen et al. 2009) and study the full annual cycle in order to understand lake dynamics,
625 particularly as lake temperature rises worldwide (O'Reilly et al. 2015). Though winter

626 conditions often present logistical challenges to field sampling, we should not dismiss
627 opportunities that are within reach and could greatly increase our basic understanding of
628 winter ecology.

629
630 *Implications*

631 We are losing ice without a deep understanding of what ecological processes are at
632 stake. Our synthesis demonstrates that under-ice environments in lakes are biologically
633 dynamic, and that in some cases understanding winter can help to predict summer
634 conditions, highlighting the importance of expanding our knowledge of under-ice
635 dynamics. Climate change is already altering lake conditions by increasing summer water
636 temperatures (O'Reilly et al. 2015) and decreasing winter ice duration (Magnuson et al.
637 2000; Benson et al. 2012; Shuter et al. 2013). While our study identifies some of these basic
638 patterns across and within lakes, how climate change will influence seasonal differences
639 and connections, as well as the nature of any feedbacks associated with these potential
640 changes, remains unclear. Long-term changes in lake ice already have been associated with
641 shifts in the timing of under-ice phytoplankton blooms (Adrian et al. 1999; Blenckner et al.
642 2007). Here, paleolimnology may offer useful insights into how lakes responded during
643 periods of warming, through the analysis of microfossils in sedimentary records. For
644 example, Smol et al. (2005) show that global warming over the past 150 years has resulted
645 in wide-scale reorganization of circumpolar lake ecosystems through shortening of the
646 winter season, with highest changes in beta-diversity occurring at the most northern
647 latitudes. Over longer timescales, declining winter ice conditions, inferred from
648 chrysophyte cysts, suggest that European Pyrenees lakes gradually warmed from the early
649 Holocene to c. 4000 years ago (Pla & Catalan 2005). While in ancient lakes such as Baikal,
650 we can look to previous warm periods such as the Last Interglacial (125,000 years ago)
651 which reveal a decline in ice-associated diatoms, but greater abundance in species that
652 require either strong mixing conditions or extended summer stratification (Rioul &
653 Mackay 2005).

654 Effects of shortening ice duration may present the most straight-forward scenarios
655 to consider. Predicting the influence of climate change on other ice characteristics, such as
656 clarity, may be a more difficult task. Observed and anticipated shifts in precipitation, wind,

657 and solar radiation patterns associated with climate change are heterogeneous across and
658 within regions, and can greatly alter the under-ice environment by changing the amount of
659 incident light that penetrates the ice. Surface snow accumulation of as little as 10 cm can
660 reduce light penetration to levels insufficient for photosynthesis and convective mixing
661 that influences algal suspension as well as nutrient concentrations in the photic zone
662 (Granin et al. 2000; Mackay et al. 2006; Jewson et al. 2009; Salmi & Salonen 2016). As with
663 many aspects of climate change, the extremes and the timing of shifts, in addition to
664 average changes, are important (reviewed in Adrian et al. 2012).

665 **Conclusion**

666 Our results suggest two principles that should motivate future work: 1) knowledge
667 of under-ice conditions within lake ecosystems may help to refine expectations of how lake
668 conditions, dynamics and functionality will unfold over the next season; 2) under-ice
669 observations, and measures of seasonal connectivity or dis-connectivity between seasons,
670 may enhance our ability to detect and understand ecological responses to lake warming,
671 especially when monitoring is sustained over the long-term. Both of these ideas are
672 testable, but only in the presence of long-term paired winter-summer lake data. Thus, while
673 most lakes can be expected to experience shorter winter ice duration and longer summers,
674 our capability to predict the ecosystem-wide impacts is constrained by our limited
675 knowledge of under-ice ecology and also accurate down-scaled climate predictions that
676 allow us to anticipate under-ice physical conditions. However, as our study demonstrates,
677 lake conditions are not the simple result of weather conditions during the current season
678 but can also depend upon external and internal forces operating on the ecosystem in
679 previous seasons. Our capacity to predict effects of warming waters and shortening ice
680 duration on lake ecosystems, and the resources they provide to society, will depend in part
681 on our ability to rapidly accumulate more knowledge of winter ecology and its influence on
682 ecological processes throughout the year. In the future, we predict that there will be no
683 more “off-seasons” for freshwater ecologists.

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705 **References**

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1073 Table 1. Winter-summer differences expressed across lakes. Linear mixed models were used, with a random intercept for year.

1074

Variable	# winter obvs	# paired obvs	Fitted difference (+=higher in winter)	s.e. of difference	Intercept (typical summer value)	s.e. of intercept	p-value of difference	p-value of intercept
chl <i>a</i> (µg/L)	119	118	-5.06	0.661	9.13	0.612	<<0.001	<<0.001
phyto biovolume (mm ³ /L)	17	17	-12.8	1.85	14.7	1.31	<<0.001	<<0.001
crustacean zoop density(no./L)	36	36	-41.8	5.82	54.8	4.15	<<0.001	<<0.001
DOC (mg/L)	82	81	-0.0559	0.324	5.53	0.418	0.863	<<0.001
TDN (µg/L)	78	73	262	44.0	300	38.8	<<0.001	<<0.001
TDN:TDP (as atoms)	71	66	27.5	40.6	161	29.6	0.498	<<0.001
TDP (µg/L)	73	72	3.97	3.18	11.8	2.83	0.213	<<0.001
TN (µg/L)	76	75	161	23.1	552	23.7	<<0.001	<<0.001
TN:TP (as atoms)	75	74	24.0	6.44	88.3	4.89	<<0.001	<<0.001
TP (µg/L)	107	106	-1.35	1.95	27.1	1.98	0.488	<<0.001
water temp (°C)	113	107	-15.1	0.19	16.2	0.202	<<0.001	<0.001

1075 Table 2. Summary of winter-summer differences and winter-summer correlations from
 1076 univariate time series of individual lakes. Correlations for summer-into-winter (*SW*) and
 1077 winter-into-summer (*WS*) are both shown. Zooplankton groups are referenced here as
 1078 counts L⁻¹ (calculated from reported proportion of total zooplankton density). Note that for
 1079 chl *a* and phytoplankton density only 3 lakes reported both variables with sufficient data to
 1080 include in our time series analysis, such that patterns are not readily compared between
 1081 these variables.

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Variable	# of time series	Seasonal difference present (% of time series)		Sign of summer-winter slope* (% of time series)				
		winter> summer	winter< summer	SW pos	SW neg	WS pos	WS neg	Any pos or neg
chl <i>a</i>	34	9	50	0	32	0	26	47
phyto density	4	0	100	25	0	25	0	50
crustacean zooplankton density	11	0	91	0	18	0	9	18
DOC	26	12	23	0	15	0	4	19
TDN	14	79	7	0	43	0	0	43
TDP	14	14	0	0	21	0	14	36
TN	30	70	3	0	33	3	10	47
TP	33	21	21	0	18	0	12	30
water temp	20	0	100	5	0	5	5	15

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1084 * Sign of the summer-winter slope determined using detrended data and AIC selection.

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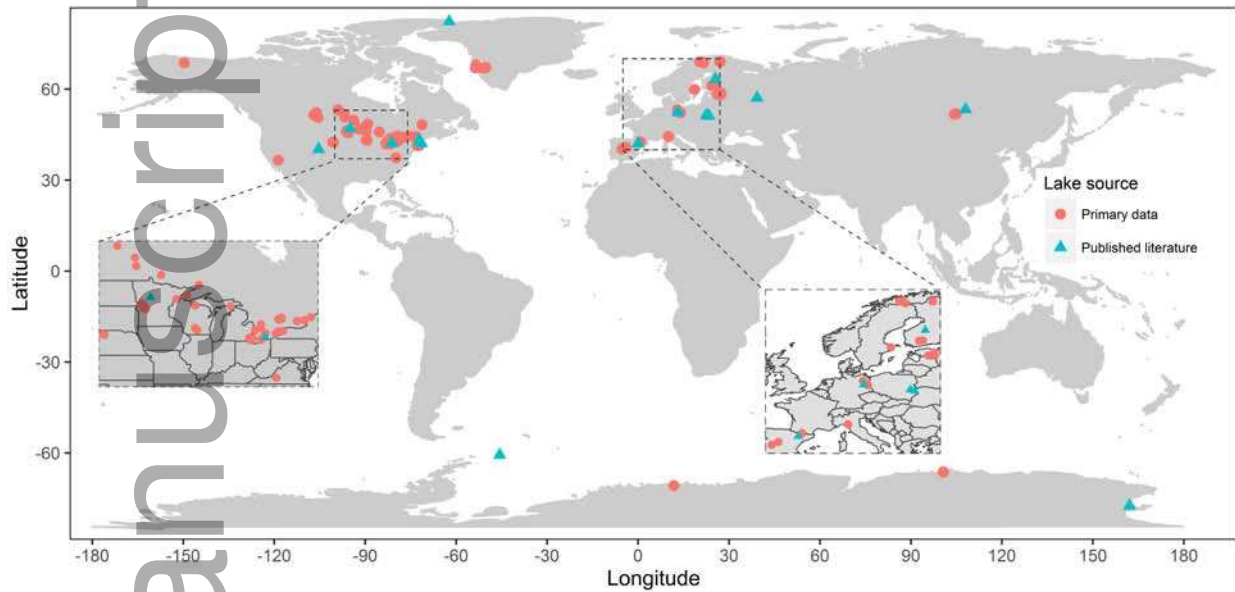
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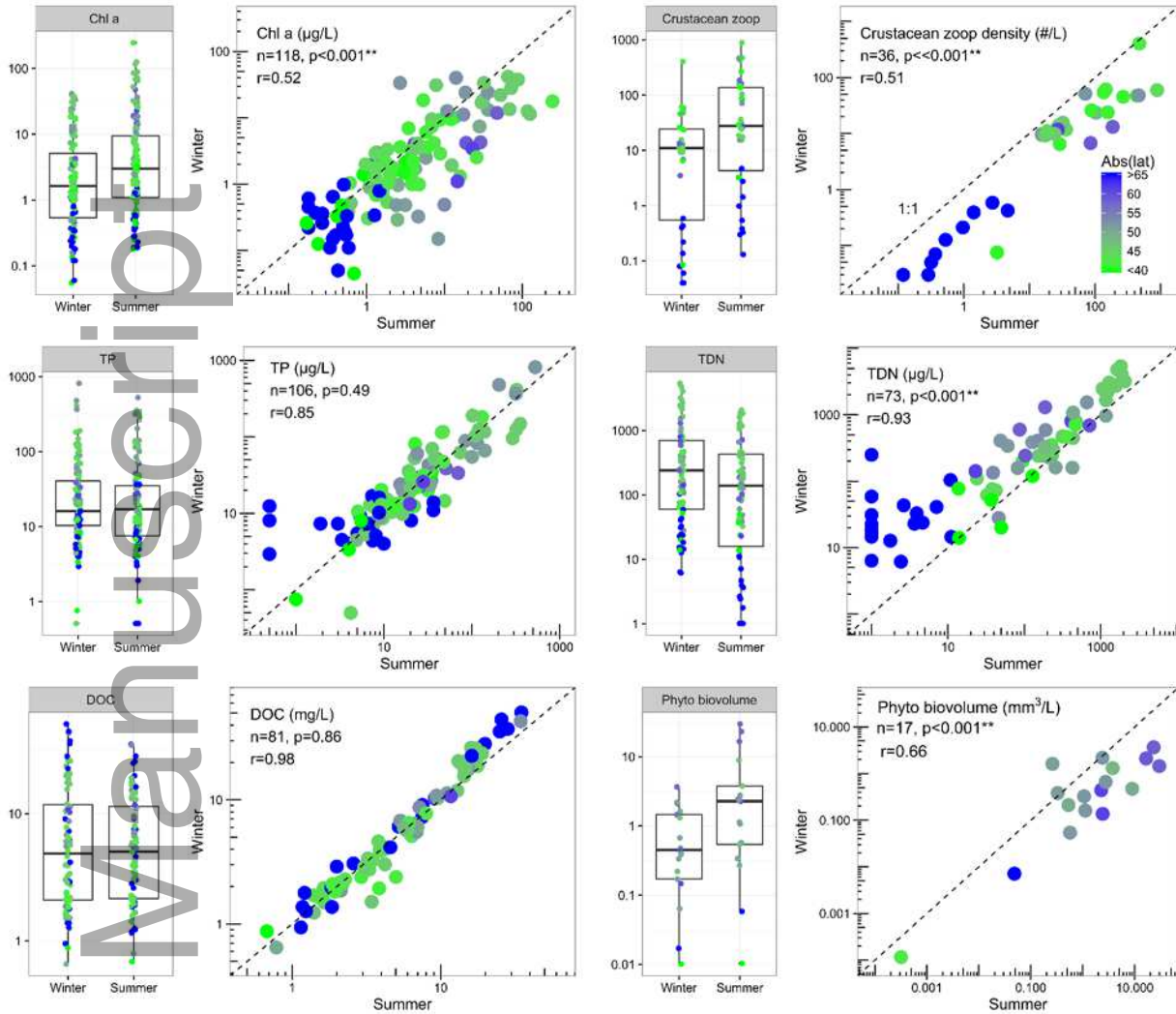
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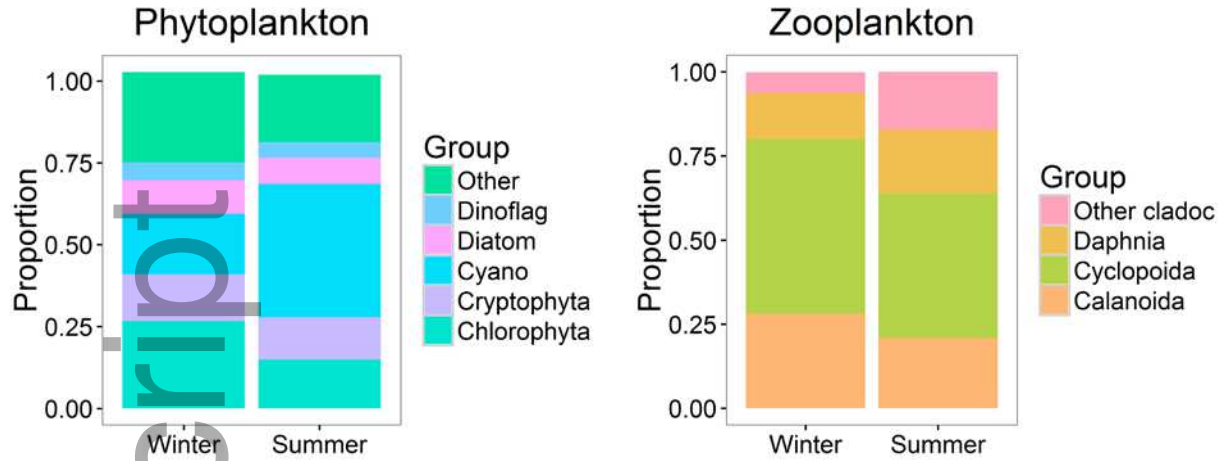
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Figure 1. Map of lakes/sampling stations included in the full synthesis under-ice dataset (i.e., “primary data”) and the published literature review. See Figure S2 for comparison of aggregated chl *a* between primary data and published literature samples.



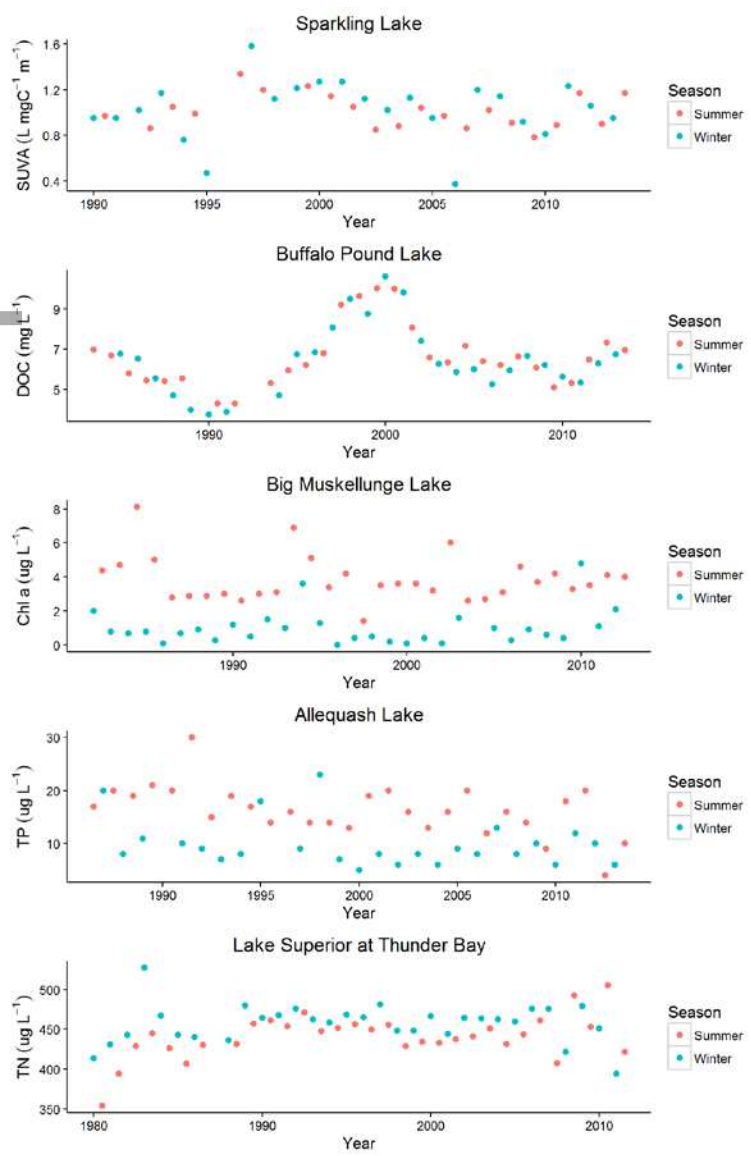
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Figure 2. Average ice-on (winter) versus ice-off (summer) conditions across lakes for major limnological variables. Boxplots show all reported available ice-on and ice-off data. Each point represents the cross-year average from one sampling location; color indicates latitude (absolute). Scatterplots show the paired ice-on-ice-off values at a given each location. P-values are from lme models. Scales are logarithmic.

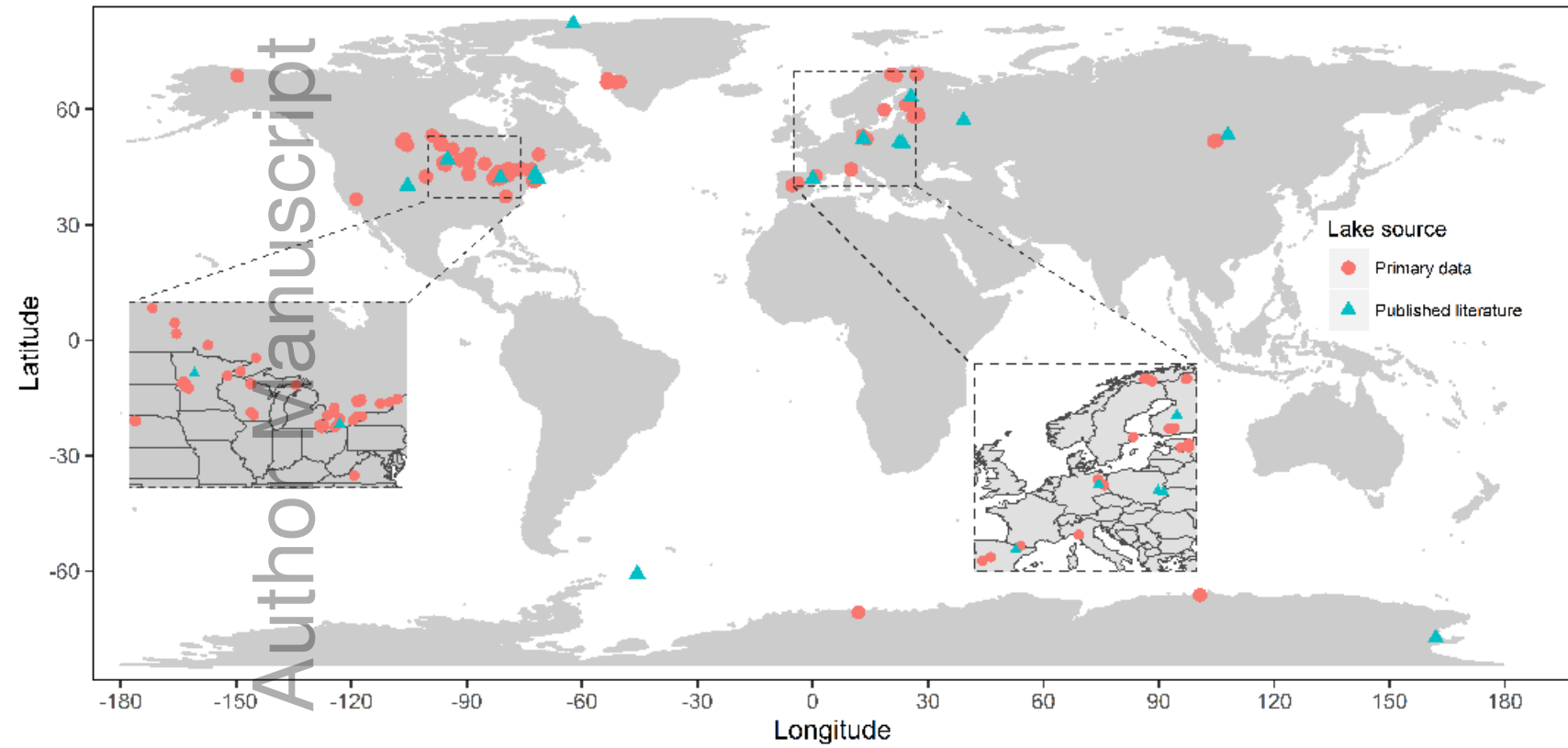


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Figure 3. Average community composition for major phytoplankton and crustacean zooplankton groups during the winter and summer seasons, expressed as a proportion of total density.

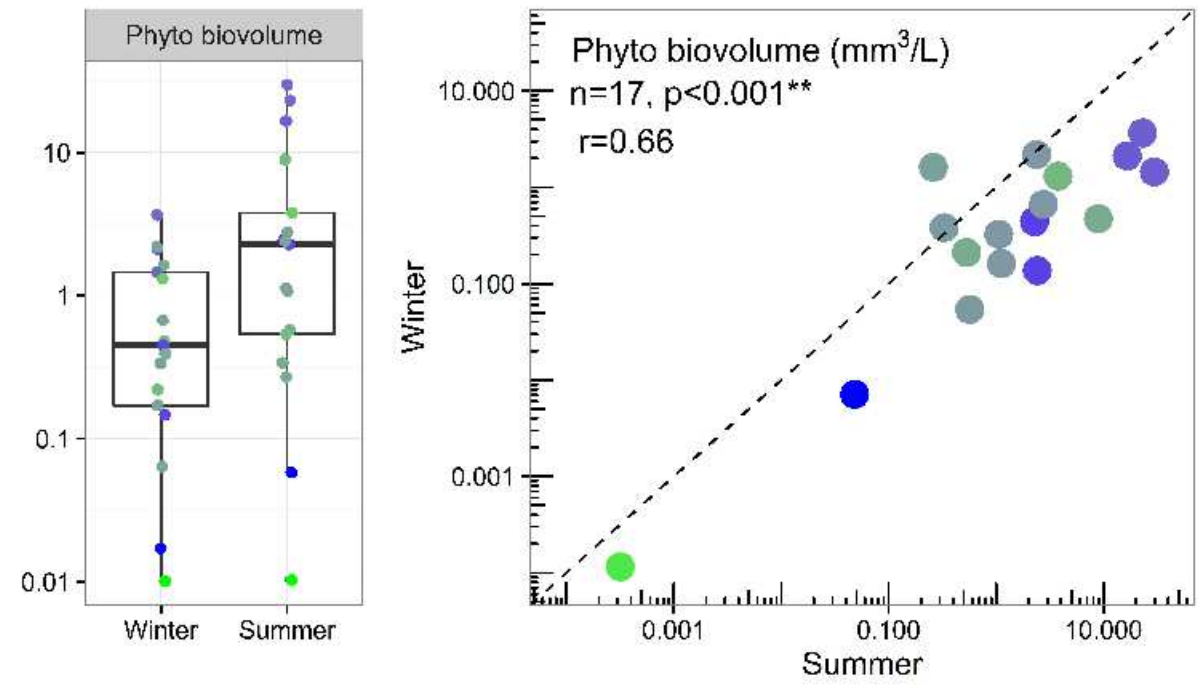
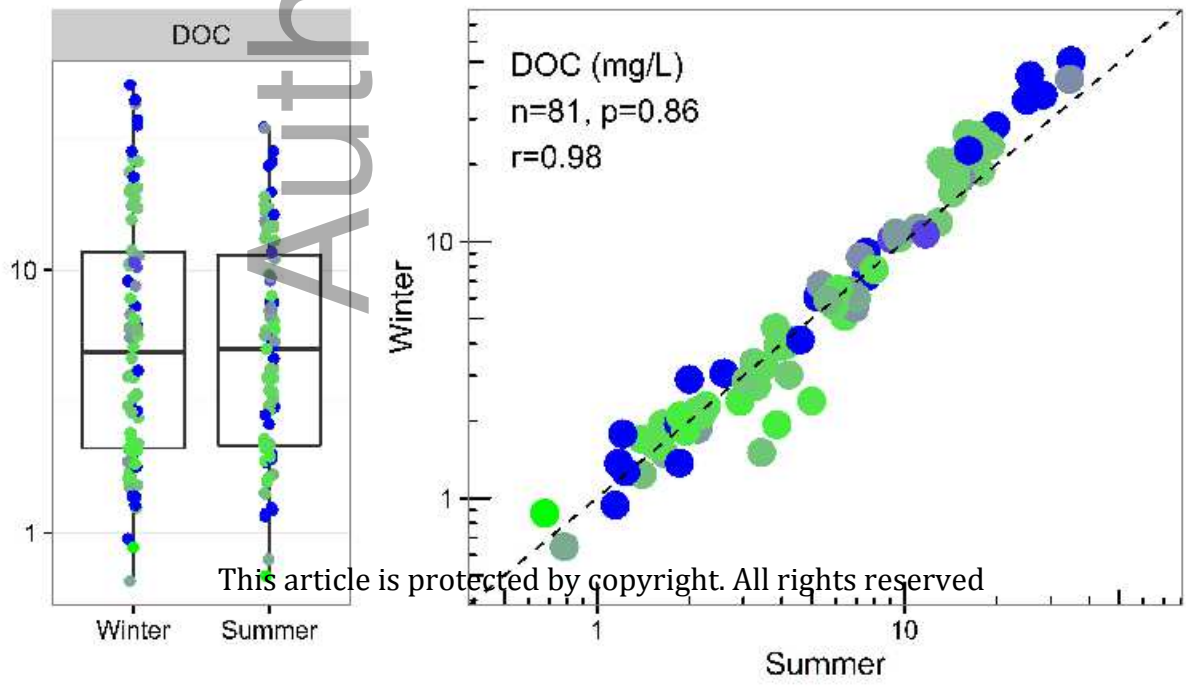
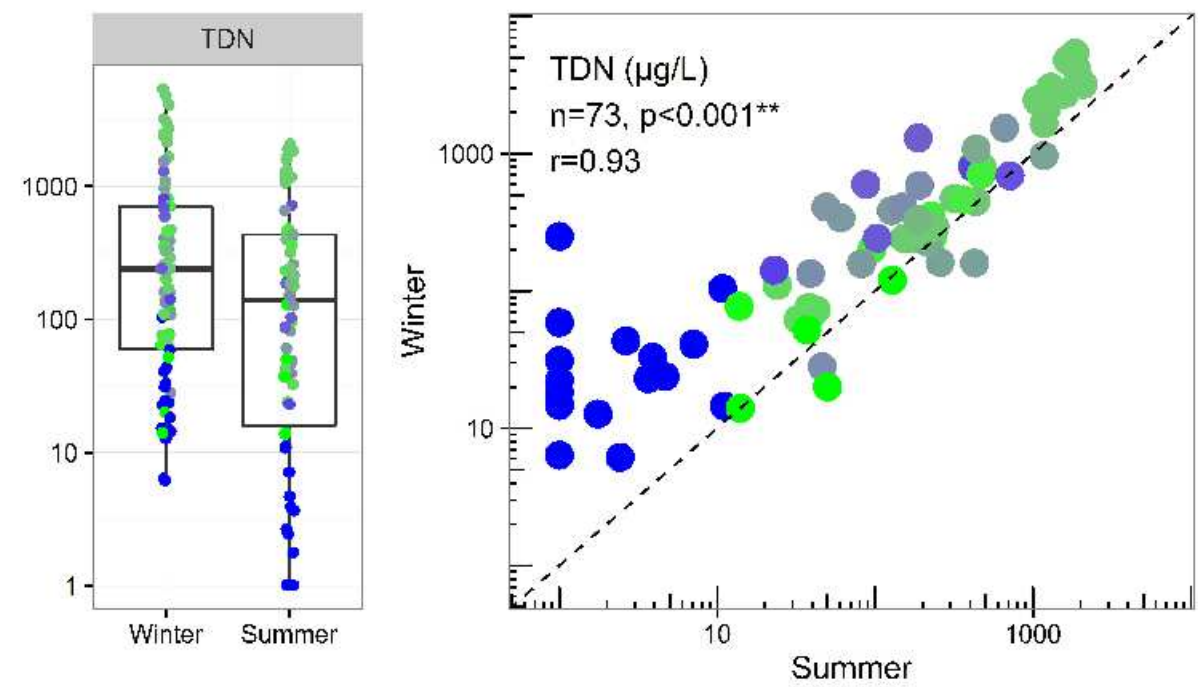
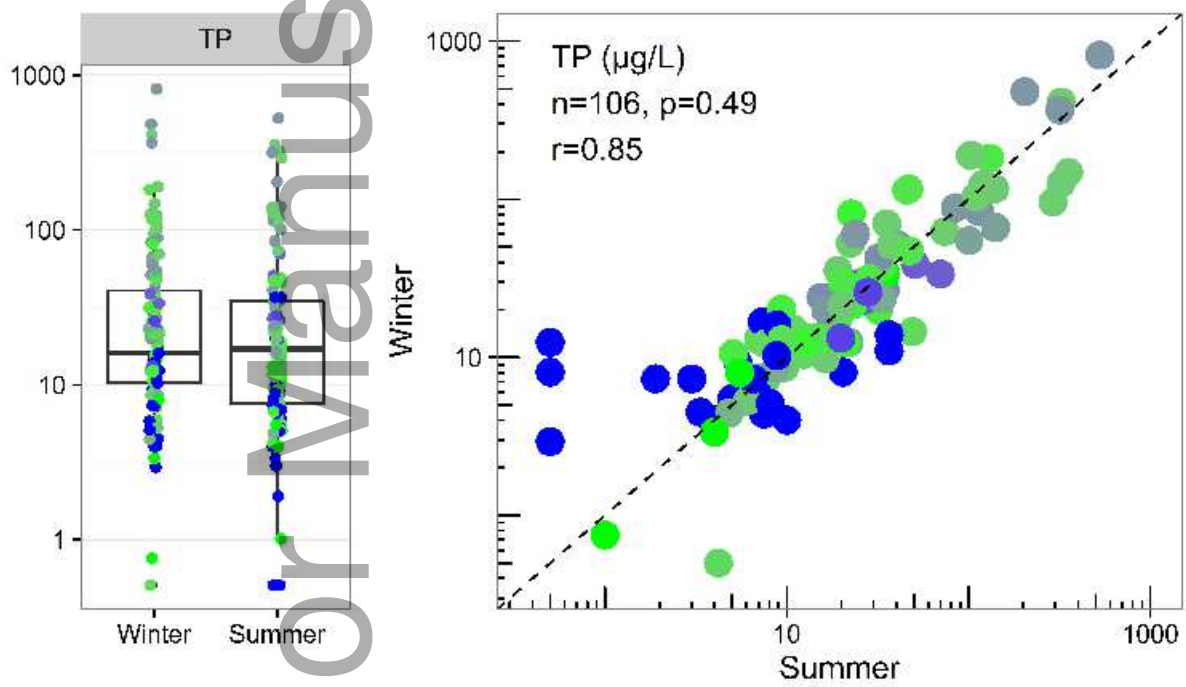
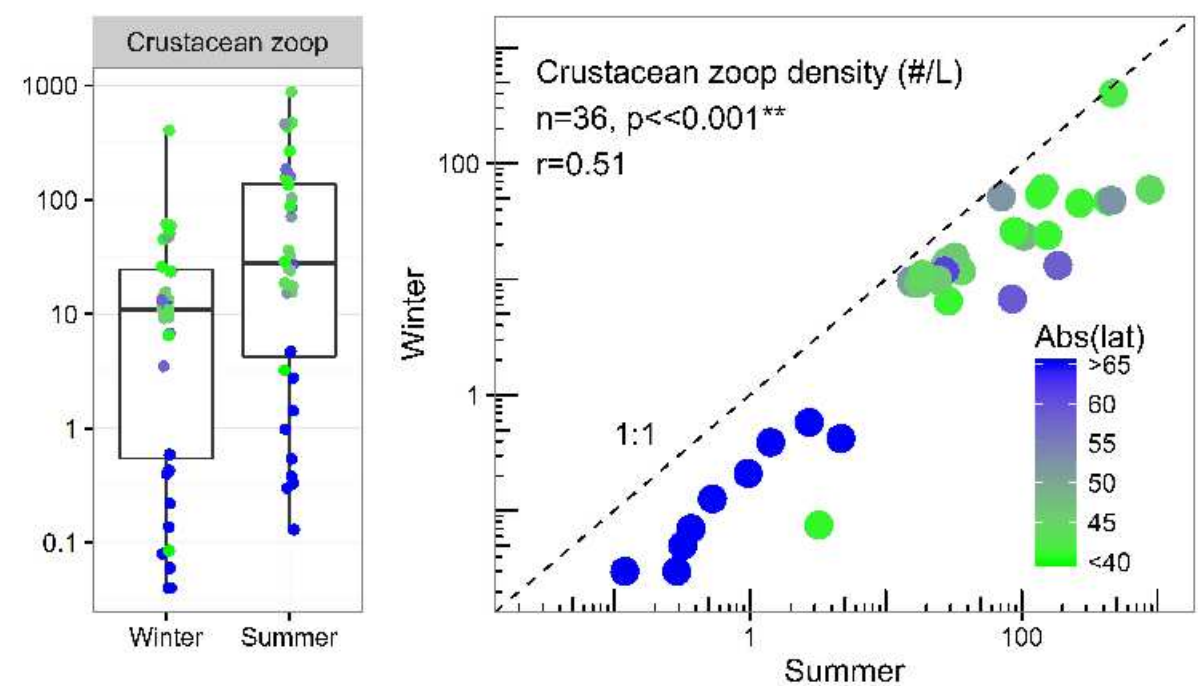
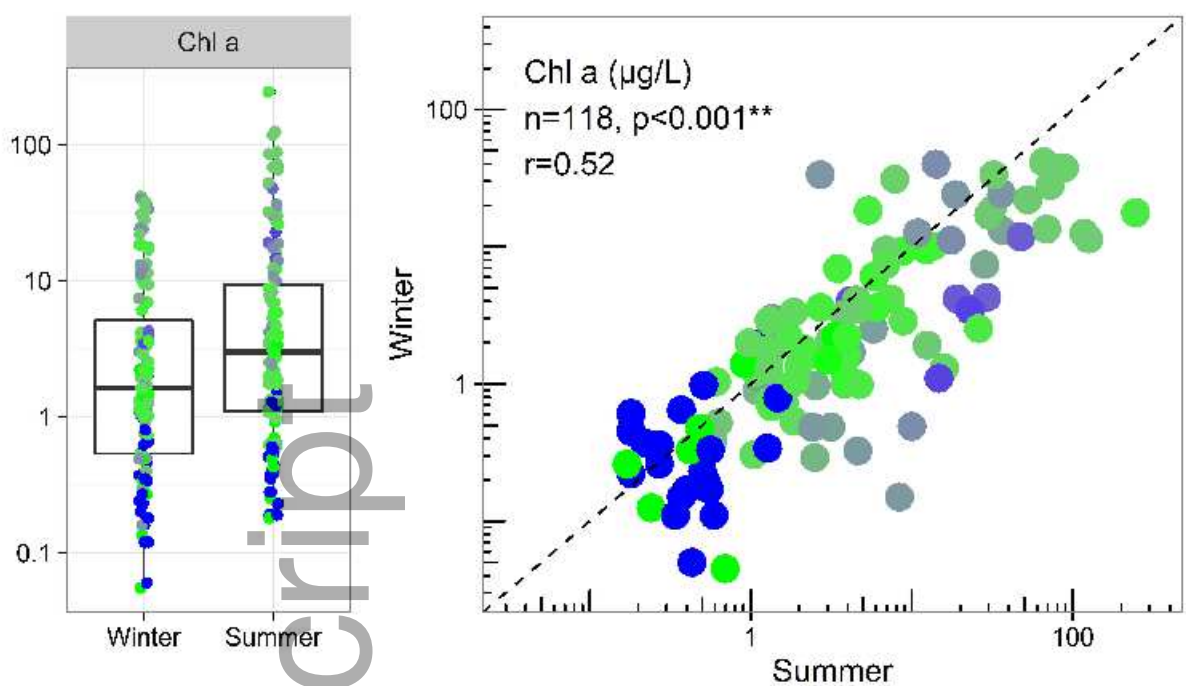


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 1129 Figure 4. Example time series that demonstrate the temporal patterns encountered for
 1130 different lakes and variables. Panel 1: first order autoregressive structure, SUVA in
 1131 Sparkling Lake, Wisconsin, USA; 2: first order autoregressive structure with moving
 1132 average, DOC in Buffalo Pound Lake, Saskatchewan, Canada; 3: seasonal difference, chl *a* in
 1133 Big Muskellunge Lake, Wisconsin, USA; 4: seasonal difference with moving average, TP in
 1134 Allequash Lake, Wisconsin, USA; 5: seasonal difference with first order autocorrelation
 1135 structure and moving average, TN in Lake Superior at Thunder Bay, Ontario, Canada.

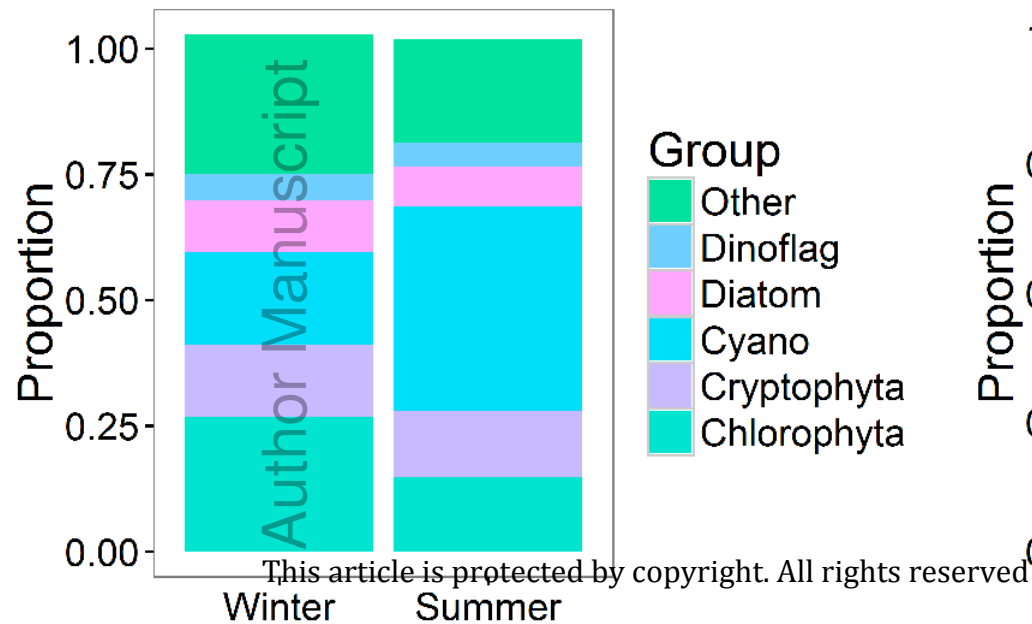


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