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4 **Title:** Ecosystem Metabolism as an Early Warning Indicator of Lake Algal Blooms

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15 All authors conceived of the study. SJT conducted the analyses and wrote the initial
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31 descriptive purposes only and does not imply endorsement by the U.S. Government.

32 **Data Availability Statement**

33 All data used in this analysis are available from publicly available data repositories: the
34 U.S. Geological Survey (USGS) Water Data for the Nation (WDFN; U.S. Geological Survey,
35 2026; <https://doi.org/10.5066/F7P55KJN>) and the National Ecological Observatory Network
36 (NEON; <https://data.neonscience.org/data-products/explore>). Metabolism model inputs,
37 outputs, and associated R scripts are provided in Tassone (2026;
38 <https://doi.org/10.5066/P13AKNWB>).

39 **Abstract**

40 Algal blooms represent ecosystem state shifts that degrade drinking water, restrict
41 recreation, threaten public health, and lower property values. Detecting blooms in advance
42 on management relevant timescales of days to weeks can support proactive intervention.
43 Early warning statistics derived from indicator time series offer a framework for detecting
44 state shifts, but the use of lake metabolic estimates (gross primary production, ecosystem
45 respiration, and net ecosystem production) in this context has been limited. Here, we
46 modeled lake metabolism using water-quality monitoring data from eight U.S. lakes
47 spanning a trophic gradient to test the hypothesis that metabolic estimates serve as
48 effective early warning indicators of algal blooms. Time series of early warning statistics
49 were analyzed using the conventional Kendall's tau approach and a complementary
50 threshold-based approach. The threshold-based approach yielded higher bloom detection
51 rates, longer early warning lead times, and fewer false alarms than the Kendall's tau
52 approach. Across lakes, metabolic metrics detected 86% of blooms, with the strongest
53 early warning signals in oligotrophic, eutrophic, and hypereutrophic systems. However,
54 directly measured water-quality parameters, particularly water temperature and
55 chlorophyll concentration, were the primary early warning indicators of blooms. Overall,
56 these results demonstrate that metabolic estimates can provide early warning signals of
57 bloom development but are secondary to directly measured water-quality parameters,
58 indicating a complementary rather than primary role in early bloom detection.

59 **Keywords**

60 Lake, Metabolism, Production, Respiration, Early Warning, Algal Bloom

61 ***Introduction***

62 Algae are the base of the aquatic food web; however, rapid and often non-linear
63 increases in algae biomass, termed algal blooms, can impair water resources and lead to
64 environmental, social, public health, and economic challenges. The progression and
65 impact of algal growth to nuisance or harmful status has been studied globally, spanning
66 the freshwater-marine continuum (Paerl 1988; Griffith and Gobler 2020; Feng et al. 2024).
67 Management of blooms in inland waters has historically relied on reactive strategies aimed
68 at mitigating impacts after a bloom has occurred (Anantapantula and Wilson 2023).
69 However, advances in sensor technologies and methodologies have increased attention
70 toward detecting early warning signals indicative of impending bloom formation to support
71 proactive bloom management (Almuhtaram et al. 2021; Carey et al. 2022; Xiao et al. 2024).

72 As ecosystems approach a transition, such as shifting from a non-bloom to a bloom
73 condition (Batt et al. 2013a; Ortiz et al. 2020), variability and autocorrelation within
74 indicator time series should theoretically increase and enable the early detection of
75 impending state change (Carpenter 2003; Scheffer et al. 2009; Scheffer et al. 2012). In
76 lakes, experimental studies have provided evidence to support this concept of early
77 warning signals preceding state change (Carpenter et al. 2011; Pace et al. 2017; Wilkinson
78 et al. 2018; Buelo et al. 2022), albeit inconsistently in non-experimental settings (Gsell et
79 al. 2016; Ortiz et al. 2020; O'Brien et al. 2023). Aquatic metabolism, encompassing rates of
80 gross primary production (GPP), ecosystem respiration (ER) and their difference (net
81 ecosystem production [NEP] = GPP - ER), have been proposed as early warning indicator
82 (EWIs) of algal bloom development due to close associations with nutrient concentrations

83 and algal biomass (Batt et al. 2013b; Corman et al. 2023). However, Batt et al. (2013b)
84 provided evidence from a mesotrophic lake with an experimentally manipulated food web,
85 that water-quality parameters related to ecosystem metabolism (e.g., dissolved oxygen
86 [DO], pH, chlorophyll) were more effective EWIs of state change than metabolic
87 parameters. In non-eutrophic lakes (i.e., oligotrophic, mesotrophic), low biotic activity
88 relative to abiotic processes can make it challenging to constrain metabolic estimates
89 (Staeher et al. 2010; Richardson et al. 2017; Jankowski et al. 2021). In contrast, eutrophic
90 and hypereutrophic lakes, characterized by greater nutrient (nitrogen and phosphorous)
91 availability and biotic activity, exhibit stronger metabolic signals and are more prone to
92 algal blooms (Paerl and Paul 2012; Tigli et al. 2025). Consequently, the ability to use
93 metabolic estimates as EWIs of algal blooms may vary systematically among trophic
94 groups (i.e., oligotrophic, mesotrophic, eutrophic, and hypereutrophic).

95 In this study, we revisit lake metabolism metrics (i.e., GPP, ER, NEP) as potential
96 EWIs by evaluating their effectiveness in detecting algal blooms before their onset across
97 multiple lakes spanning the oligotrophic to hypereutrophic gradient. We hypothesized that
98 metabolism-based parameters would be effective EWIs of blooms along the lake trophic
99 gradient, particularly in eutrophic and hypereutrophic lakes where blooms are more
100 frequent, prolonged, and/or severe. We further compared the abilities of metabolism-
101 based indicators and directly measured *in situ* water-quality parameters to identify early
102 warning signals of impending bloom formation. To compare metabolism and water-quality
103 parameters among trophic groups, we evaluated two complementary analytical

104 approaches for detecting early warning signals in lakes: a conventional Kendall's tau-
105 based method and a novel threshold-based approach.

106 **Methods**

107 *Site Description & Data Collection*

108 Lake Anna (ANNA) is an 83 km² reservoir in Spotsylvania, Orange, and Louisa
109 Counties, Virginia, that was constructed in 1972 by damming the North Anna River (Eric
110 Adams and Wells 1984). The reservoir is a popular destination for swimming, boating, and
111 fishing; however, since 2018, the riverine-lake transition zone in the western section of the
112 reservoir has experienced algal blooms exceeding recreational advisory thresholds
113 (Hanlon et al. 2022). The Virginia General Assembly appropriated funds to support
114 investigations into Lake Anna algae blooms and the U.S. Geological Survey (USGS), in
115 partnership with the Virginia Department of Environmental Quality installed water-quality
116 and meteorological monitoring equipment at Red House Point near Ellisville, VA (USGS site
117 no: 01670144; U.S. Geological Survey, 2026). Concurrent monitoring spanned November
118 2023 through December 2024. Water-quality observations were continuously monitored
119 using a YSI Inc. (Yellow Springs, OH) EXO3 Multiparameter Water-Quality Sonde with a
120 sampling frequency of 15-minutes. Algal pigment concentration time series were collected
121 using a bbe-Moldaenke (Schwentinental, Germany) PhycoProbe that differentiated each
122 15-minute chlorophyll observation into algal groups including cyanobacteria, diatoms, and
123 green algae. All water quality and algal pigment time series were collected from a dock 10
124 m from the shoreline at a fixed depth of 1.25 m above the sediment surface. Wind speed
125 and direction were monitored from the Red House dock from a height of 3 m at a sampling

126 frequency of 5 minutes. All monitoring and data quality control followed standard USGS
127 practices (Wagner et al. 2006; Turnipseed and Sauer 2010; Foster et al. 2022).

128 The National Ecological Observatory Network (NEON) collects high-frequency
129 water-quality and meteorological observations from seven lakes across the Northern
130 Plains, Great Lakes, Southeast, and Tundra ecoclimatic domains of the United States
131 (<https://www.neonscience.org/field-sites>). Of the seven lakes, six were paired, including
132 Prairie Lake (PRLA) and Prairie Pothole (PRPO) in North Dakota (11 km apart), Crampton
133 Lake (CRAM) and Little Rock Lake (LIRO) in Wisconsin (29.5 km), Suggs Lake (SUGG) and
134 Lake Barco (BARC) in Florida (1.6 km), and Toolik Lake, Alaska (TOOK). Watershed area
135 ranges between 0.6-67.6 km² and maximum lake depth ranges between 3.2-27 m. All
136 water-quality observations were collected using a buoy-mounted YSI EXO2 Multiparameter
137 Water-Quality Sonde above the deepest section of the lake at a sampling frequency of 5-
138 minutes. Water temperatures at various depths were recorded from the buoy at a sampling
139 frequency of 1 minute while meteorological observations were measured from fixed
140 heights above the buoy every 2 minutes. NEON lake buoys were removed during winter
141 except at SUGG and BARC. Time series observations were quality assured and controlled
142 by NEON's data quality program, and only approved data were used which encompassed
143 January 2018 through June 2024. All NEON time series were accessed using the
144 *neonUtilities* R package (R Core Team, 2025; Lunch et al. 2024; SI Table 1).

145 *Lake Trophic Status & Algae Bloom Classification*

146 There are many ways to classify the trophic status of inland waters (Meyer et al.
147 2025). In this study, we use the term *trophic group* to refer specifically to four trophic

148 classes—oligotrophic, mesotrophic, eutrophic, and hypereutrophic. The trophic
149 classification of all eight lakes (NEON + ANNA) were based on their median chlorophyll
150 concentration according to the U.S. Environmental Protection Agency National Lake
151 Assessment (U.S. Environmental Protection Agency 2024) as oligotrophic ($\leq 2 \mu\text{g L}^{-1}$),
152 mesotrophic ($2\text{-}7 \mu\text{g L}^{-1}$), eutrophic ($7\text{-}30 \mu\text{g L}^{-1}$), or hypereutrophic ($> 30 \mu\text{g L}^{-1}$). BARC
153 (median = $1.8 \mu\text{g L}^{-1}$) and ANNA ($46.1 \mu\text{g L}^{-1}$) were oligotrophic and hypereutrophic,
154 respectively; TOOK, LIRO, and CRAM were mesotrophic (2.4 , 3.0 , and $3.8 \mu\text{g L}^{-1}$,
155 respectively) while PRPO, SUGG, and PRLA were eutrophic (14.4 , 14.8 , $21.2 \mu\text{g L}^{-1}$,
156 respectively).

157 There is no standard quantitative definition of an algal bloom, though definitions
158 often share commonality in using thresholds of an algal parameter (i.e., pigment
159 concentration, cell counts), above which a system is in a bloom state (Smayda 1997; WHO
160 2003; Stackpoole et al. 2024). Here, blooms were defined using site-specific thresholds
161 calculated as the median of the high-frequency chlorophyll concentration time series plus
162 one standard deviation, such that bloom conditions represent periods of elevated
163 chlorophyll relative to typical conditions within each lake. A lake was classified as being in
164 a bloom state when the daily mean chlorophyll concentration exceeded this threshold. This
165 approach emphasizes within-site anomaly detection rather than cross-site comparability
166 and was selected in part for its ability to delineate bloom and non-bloom periods at the site
167 with the shortest time series (ANNA), where a single, large-magnitude, long-duration bloom
168 event was observed. We acknowledge that this threshold is statistically derived and may
169 not correspond to management-defined bloom conditions; however, this threshold

170 provides a pragmatic framework for identifying blooms within non-experimental lakes with
171 differing baseline conditions. When a bloom was observed, bloom duration was calculated
172 as the difference in days between the bloom end and start date and bloom magnitude as
173 the maximum daily average chlorophyll concentration during the bloom.

174 *Metabolism Model*

175 Daily average metabolic estimates were modeled with a Bayesian model structure
176 using the R package *lakeMetabolizer* (Winslow et al. 2016). Photosynthetically active
177 radiation was estimated for each site using the *calc_light* function from the R package
178 *streamMetabolizer* (Appling et al. 2018a). Likewise, gas transfer velocity was estimated
179 using wind speed and sensor height according to Cole and Caraco (1998) and converted to
180 a gas- and temperature-specific transfer velocity according to Raymond et al. (2012) using
181 *lakeMetabolizer's k.cole.base* and *k600.2.kGAS.base* functions, respectively. Thermocline
182 depth time series were estimated for the NEON lakes using water temperature
183 observations at various depth and the R package *rLakeAnalyzer* (Winslow et al. 2019), with
184 a metalimnion minimum density gradient cutoff of $0.1 \text{ kg m}^{-3} \text{ m}^{-1}$. At ANNA, water
185 temperature observations from multiple depths, collected October 2024 through January
186 2025, indicated no stratification. Lacking a concurrent thermocline depth time series and
187 personal observations of regular wake boat activity in the vicinity of the Red House dock
188 during the growing season, the thermocline depth was set equal to the maximum lake
189 depth from where the observations were collected, 1.8 m. Confidence in each lake's
190 metabolic model was assessed based on the percentage of biologically unrealistic
191 estimates of GPP and ER (i.e., negative GPP and positive ER; Appling et al. 2018b). All GPP

192 estimates < 0 but ≥ -0.5 and ER estimates > 0 but $\leq 0.5 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ were converted to 0
193 (Appling et al. 2018b), and all days with a biologically unrealistic estimate were excluded
194 from analysis (Bernhardt et al. 2022; Tassone 2026).

195 *Early Warning Statistics*

196 Several early warning statistics (EWS) exist (Dakos et al. 2012); however, studies
197 from ecological systems, including lakes, have provided support for the use of standard
198 deviation (SD) and lag-1 autocorrelation (AR1) calculated over rolling windows (Batt et al.
199 2013b; Burthe et al. 2015; Pace et al. 2017; Wilkinson et al. 2018; Ortiz et al. 2020; Buelo et
200 al. 2022). To determine the sensitivity of our results to multiple rolling windows, we
201 calculated SD and AR1 over 7-, 14-, and 21-day windows for each lake using daily averages
202 of metabolism (GPP, ER, NEP) and water-quality parameters (water temperature, pH, DO,
203 turbidity, and log-transformed chlorophyll and specific conductance; hereafter, both
204 metabolism and water-quality parameters are collectively referred to as water-quality
205 parameters) with the R package *tvsews* (Buelo et al. 2022). These rolling window widths
206 were selected based on previous early warning lake algal bloom studies (Wilkinson et al.
207 2018; Ortiz et al. 2020) that have provided evidence for them being long enough to detect
208 signals in EWIs while minimizing false alarms.

209 In EWS time series analysis, a common approach for assessing increases in SD and
210 AR1 is the non-parametric Kendall's tau (τ) coefficient, where a positive and statistically
211 significant τ (p -value < 0.05), calculated as the rank correlation between EWS values and
212 time indicates an increase in variability consistent with an impending bloom (Dakos et al.
213 2012; Gsell et al. 2016; Pace et al. 2017; Buelo et al. 2022). When calculating τ , window

214 widths of 7-, 14-, and 21-days were used to assess the sensitivity of results to the choice of
215 window width. When a bloom was detected early, the early warning lead time for each
216 parameter was calculated as the difference between the date the early warning was
217 detected and the date the bloom started. False alarms were defined as instances when τ
218 was positive and significant but did not overlap the start of a bloom.

219 Given the multiple EWS (SD and AR1), EWS window widths, and τ -window widths, a
220 sensitivity analysis was conducted. For each scenario (2 EWS * 3 EWS window widths * 3 τ -
221 window widths = 18 scenarios), three key performance indicators (KPI) were calculated for
222 each trophic group: 1) the fraction of correctly identified blooms (hereafter, detection rate),
223 2) the median number of early warning days, and 3) the fraction of false alarms. To identify
224 the top performing scenario, KPIs were summed across trophic groups within each
225 scenario. However, because a lower false alarm ratio indicates better performance, the
226 inverse of this KPI was calculated prior to summing. To identify the top performing water-
227 quality parameter for each scenario and trophic group, KPIs were normalized and summed
228 as follows:

$$229 \quad \text{Normalized KPI}_i = D_i + L_i + F_i$$

230 where i represents a unique water-quality parameter for each scenario and trophic group.
231 The detection rate (D_i) was min-max normalized such that the highest fraction of correctly
232 identified blooms (x) had a value of one, the lowest had a value of zero and all others were
233 scaled between zero and one.

$$234 \quad D_i = \frac{x - \min(x)}{\max(x) - \min(x)}$$

235 The early warning lead time (L_i) was binarized such that scenarios with an early warning
236 lead time ≥ 7 days were assigned a value of one, and those < 7 days a value of zero. A 7-day
237 threshold was selected to represent a management-relevant response window, though
238 results were robust when using a 3-day threshold. Lastly, the false alarm ratio (F_i) was
239 inverse min-max normalized, such that lower false alarms ratios received higher scores.
240 Normalized KPIs were equally weighted to avoid imposing subjective priorities among
241 detection rates, early warning lead times, and false alarm rates.

242 A complementary, threshold-based approach for analyzing EWI time series was
243 evaluated to assess potential improvements in KPI performance (i.e., a higher detection
244 rate, longer early warnings, and fewer false alarms) relative to the conventional τ -approach.
245 This approach provides an alternative framework for identifying increases in EWI variability
246 that may precede bloom development in non-experimental systems. Rather than assessing
247 temporal trends in EWI with the τ -coefficient, this alternative approach defined a fixed,
248 site- and parameter-specific statistical threshold, above which a system may be entering a
249 period of instability that could be indicative of impending bloom formation (Figure 1). Two
250 definitions of this potential instability threshold (PIT) were explored, the mean and median
251 of the EWI time series. These distribution-based PITs were selected because they
252 characterize the central tendency of the EWI time series, enabling the identification of
253 periods when EWIs were elevated relative to baseline conditions. If an EWI exceeded the
254 PIT for a continuous period but dropped below the threshold for one week or less before
255 exceeding the PIT again, that dip below the PIT was considered part of the same early
256 warning event rather than indicating the end of one event and the start of another event.

257 False alarms were identified as instances when the PIT was exceeded but no bloom
258 occurred during the exceedance or within one week following the return below the PIT.
259 Because multiple EWS metrics, window widths, and PIT definitions were evaluated, a
260 sensitivity analysis analogous to the τ -based approach described above was conducted for
261 the threshold-based approach. All modelling, statistical analyses, and visualizations were
262 conducted in the R environment for statistical computing (R Core Team 2025).

263 **Results**

264 *Algal Blooms*

265 Among the eight lakes, there were 89 algal blooms with a median (25th-75th
266 percentile) duration of 6 (3-17) days and range of 1 and 80 days. The median bloom
267 magnitude was 35.7 (13.1-58.8) $\mu\text{g L}^{-1}$ and ranged between 4.8 and 319 $\mu\text{g L}^{-1}$ (SI Figure 1).
268 ANNA, with the shortest time series, had one bloom while the NEON lakes had between 6
269 and 22 blooms (PRLA and SUGG, respectively; Figure 2).

270 *Metabolism*

271 The range in metabolic estimates generally increased with trophic status, apart from
272 eutrophic and hypereutrophic groups which were similar. GPP ranged between 4.8, 9.3,
273 36.8, and 31.1 $\text{g O}_2 \text{m}^{-2} \text{d}^{-1}$ for oligotrophic, mesotrophic, eutrophic, and hypereutrophic,
274 respectively (Figure 2). Likewise, ER ranged between 5.7, 14.9, 32.7, and 33 $\text{g O}_2 \text{m}^{-2} \text{d}^{-1}$ for
275 oligotrophic, mesotrophic, eutrophic, and hypereutrophic, respectively. Daily occurrences
276 of autotrophy (NEP > 0) were observed across all lakes; however, heterotrophy (NEP < 0)
277 was predominant in five lakes, with ANNA, CRAM, and TOOK being predominantly
278 autotrophic (55%, 57%, and 54% days of autotrophy, respectively; Figure 2).

279 *Early Warning Detection*

280 KPIs from the two sensitivity analyses, one based on Kendall's tau (SI Figure 2) and
281 the other on the EWS threshold (Figure 3), indicated that the threshold approach generally
282 achieved higher detection rates, longer early warning lead times, and fewer false alarms
283 across lake trophic groups regardless of EWS metric, window width, or τ window width. For
284 the Kendall's tau, the detection rates ranged between 0 to 78% with false alarm rates
285 ranging between 90 and 100% (SI Figure 2). When blooms were detected early, median
286 early warning lead times ranged from 1 to 22 days. In contrast, the threshold-based
287 approach yielded detection rates between 46 and 100%, with false alarm rates between 69
288 and 89% and median early warning lead times of 9 to 57 days (Figure 3).

289 Among the threshold-based scenarios, the scenario with the largest normalized KPI
290 score used AR1 calculated over a 7-day rolling window with the PIT set to the mean (Figure
291 3). Under this scenario, and across trophic groups, bloom detection rates ranged from 88 to
292 100%, median early warning lead times ranged from 25 to 54 days, and false alarm rates
293 ranged from 69 to 82%. Within this top performing scenario, median detection rates across
294 water-quality parameters increased from 90% (80-100%) to 100% along the oligotrophic to
295 hypereutrophic gradient, with water temperature and log-transformed chlorophyll both
296 achieving median detection rates of 100% (98-100%; Figure 4). These two parameters also
297 exhibited the longest median early warning lead times, at 40 days (16-77 days) for water
298 temperature and 36 days (13-66 days) for log-transformed chlorophyll. Water temperature
299 produced the lowest false alarm rates for the oligotrophic, mesotrophic, and eutrophic
300 groups at 44, 23, and 32%, respectively. In the hypereutrophic group, the false alarm rates

301 were elevated (> 50%) across all water-quality parameters but were lowest for log-
302 transformed chlorophyll at 67%. Overall, given high detection rates, long early warning lead
303 times, and relatively low false alarm rates, water temperature had the largest normalized
304 KPI among water-quality parameters for bloom early warning in the oligotrophic,
305 mesotrophic, and eutrophic groups, whereas log-transformed chlorophyll had the largest
306 normalized KPI in the hypereutrophic group.

307 Across the 12 threshold-based sensitivity scenarios, the most influential water-
308 quality parameter was identified within each trophic group based on the largest normalized
309 KPI score (Figure 5). Metabolism metrics (GPP, ER, NEP) had the largest normalized KPI in
310 at least one scenario across all trophic groups except for mesotrophic. Across the
311 oligotrophic, eutrophic, and hypereutrophic groups, metabolic metrics had the largest
312 normalized KPI among water-quality parameters in 33 to 58% of scenarios. When
313 aggregated across trophic groups (12 scenarios * 4 trophic groups = 48 trophic-specific
314 scenarios), water temperature was most frequently identified as having the largest
315 normalized KPI (n = 10), followed by GPP (n = 9; SI Figure 3).

316 ***Discussion***

317 Algal blooms were observed across all trophic groups, and early warning signals
318 derived from metabolic estimates were capable of detecting blooms across trophic
319 groups, although detection rates varied among groups. When bloom detection was
320 successful, metabolic indicators preceded blooms at management-relevant timescales,
321 typically days to weeks but up to five months in advance. However, metabolic parameters
322 were not the most influential indicators, based on normalized KPI scores, in the threshold-

323 based scenario with the strongest early-warning results and did not emerge as the most
324 influential indicator in any of the mesotrophic scenarios. Their reduced early-warning
325 capacity in mesotrophic lakes may indicate weaker coupling between algal biomass and
326 ecosystem metabolism, where abiotic drivers such as mixing and light availability can
327 obscure biologically driven signals (Staeher et al. 2010; Richardson et al. 2017; Jankowski et
328 al. 2021; Farruggia et al. 2026). Additionally, the mesotrophic lakes in this study were
329 located at northern latitudes (e.g., Wisconsin and Alaska), where seasonal ice cover
330 required removal of buoy-deployed monitoring equipment. Consequently, bloom events
331 occurring during ice-impacted periods may have been missed (Salmi and Salonen 2016;
332 Reinl et al. 2023). Overall, these results indicate that while metabolic estimates can
333 provide actionable early warning signals, particularly in oligotrophic, eutrophic, and
334 hypereutrophic systems, their normalized KPI scores were generally secondary to directly
335 measured water-quality parameters, indicating a complementary rather than primary role
336 in early bloom detection.

337 Broadly, our results align with prior studies demonstrating that water-quality
338 parameters can provide early warning of impending ecosystem state change in lakes,
339 including algal blooms (Wilkinson et al. 2018; Ortiz et al. 2020; Buelo et al. 2022). The
340 secondary role of derived metabolic estimates relative to the directly measured water-
341 quality parameters in mesotrophic lakes is consistent with Batt et al. (2013b) who observed
342 similar patterns in a single, experimentally manipulated mesotrophic lake. Further, results
343 from the Kendall's tau sensitivity analysis were consistent with prior studies that have
344 highlighted challenges in the application of early warning signals in non-experimental lakes

345 (Gsell et al. 2016; O'Brien et al. 2023). These challenges may indicate limitations in the
346 trend-based approach, which can be insensitive to abrupt or non-monotonic changes in
347 early warning signals. In contrast, our results suggest that a threshold-based approach,
348 applied to the same underlying EWI time series used in the trend-based approach, may
349 increase algal bloom detection and reduce false alarm rates in non-experimental lakes.
350 Lastly, our results support growing recognition of aquatic metabolism as an informative
351 suite of metrics for environmental management (Jankowski et al. 2021).

352 False alarm rates were elevated for both analytical approaches but were lower (<
353 50%) for certain combinations of trophic groups (i.e., oligotrophic, mesotrophic, and
354 eutrophic) and water-quality parameters (i.e., water temperature) using the threshold-
355 based approach. False alarms may arise from asynchronous bloom dynamics within the
356 algal community (George et al. 2023). For instance, in Lake Anna, a spring green-algae
357 bloom triggered an early warning signal despite its low magnitude relative to the total
358 chlorophyll concentration. Additionally, while this study utilized relatively simple and
359 transferable distribution-based approaches to defining algal blooms and potential
360 instability thresholds across multiple lakes, studies have used other thresholds
361 (Stackpoole et al. 2024). Lowering thresholds may improve detection rates but also
362 increase false alarms, highlighting a tradeoff between early warning sensitivity and
363 specificity. This tradeoff demonstrates a broader challenge in proactive water-quality
364 management—acting on an early warning signal that turns out to be a false alarm or failing
365 to act during the early stages of a real event. Although responding to false alarms can strain
366 limited resources, it can also reinforce management preparedness, analogous to fire drills,

367 by maintaining readiness to intervene during early bloom development before ecological
368 and socioeconomic impacts escalate. Future efforts could adjust thresholds to align with
369 management needs to improve the reliability and efficacy of EWS frameworks as a lake
370 management bloom-detection tool (Biggs et al. 2009; Scheffer et al. 2012; George et al.
371 2023). Management-specific thresholds integrated with spatial water-quality monitoring
372 programs or spatially explicit predictive water-quality models could be utilized to evaluate
373 the effectiveness of ecosystem metabolism as a spatial, intra-lake EWI (Buelo et al. 2022;
374 Caballero et al. 2025). Likewise, 73% of bloom events were detected by multiple water-
375 quality parameters, indicating redundancy among EWIs and utility in ensemble early
376 warning systems that integrate multiple indicators of change rather than relying on a single
377 indicator (Gsell et al. 2016; Almuhtaram et al. 2021; Laitinen and Lahti 2022).

378 This study demonstrates that across diverse trophic conditions and a broad
379 geographic range, estimates of aquatic ecosystem metabolism detected a substantial
380 proportion of blooms (86%), though their normalized KPI scores were generally lower than
381 those of directly measured water-quality parameters, particularly in mesotrophic systems.
382 Given the rapid, non-linear growth of algae during the onset of blooms, early detection
383 provides opportunities for water-quality management intervention before blooms escalate
384 to nuisance or harmful levels (Biggs et al. 2009; Crépin et al. 2012; Pace et al. 2017).
385 However, these windows of intervention were typically open for days to weeks, so resource
386 monitoring programs with a low sampling frequency may fail to capture them. This study
387 highlights the importance of high-frequency water-quality monitoring and the utility of
388 coordinated monitoring networks in supporting early warning systems.

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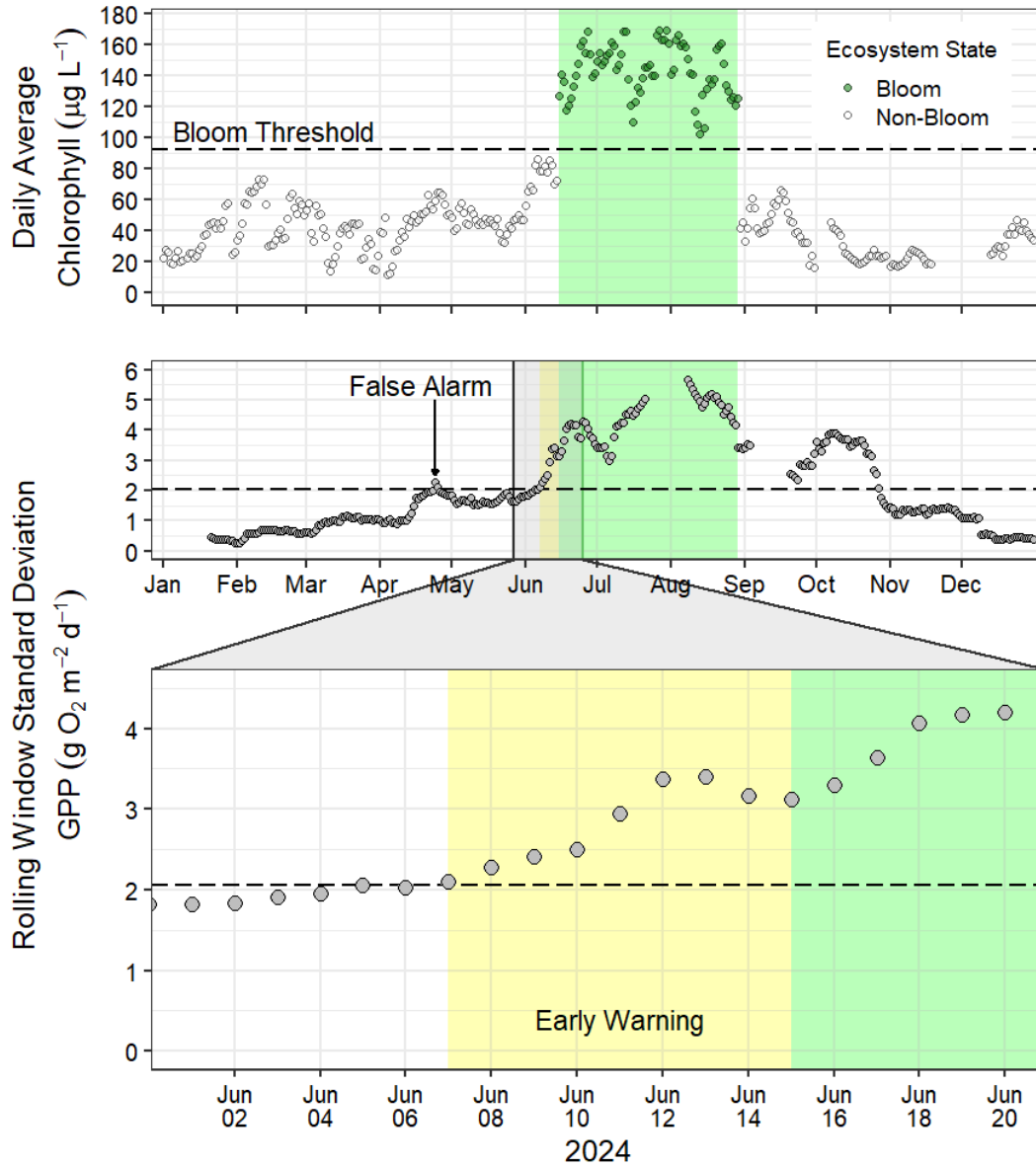
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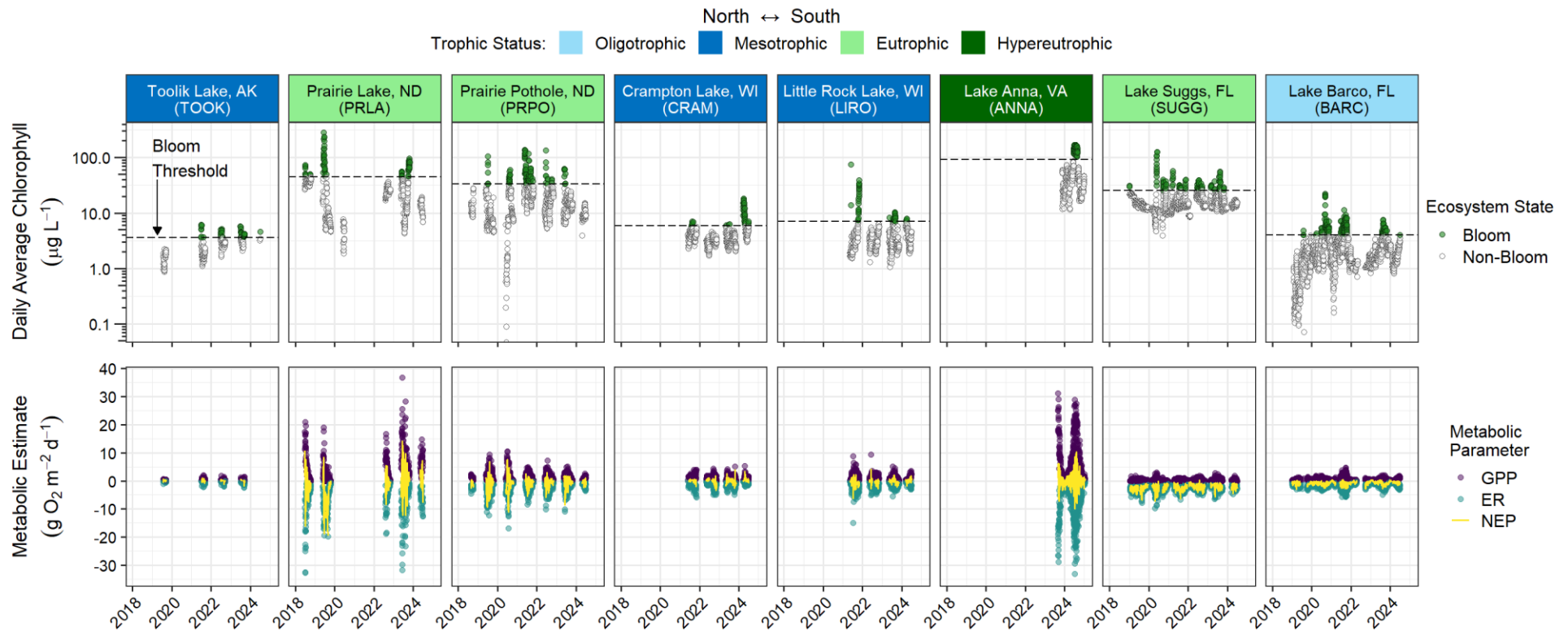
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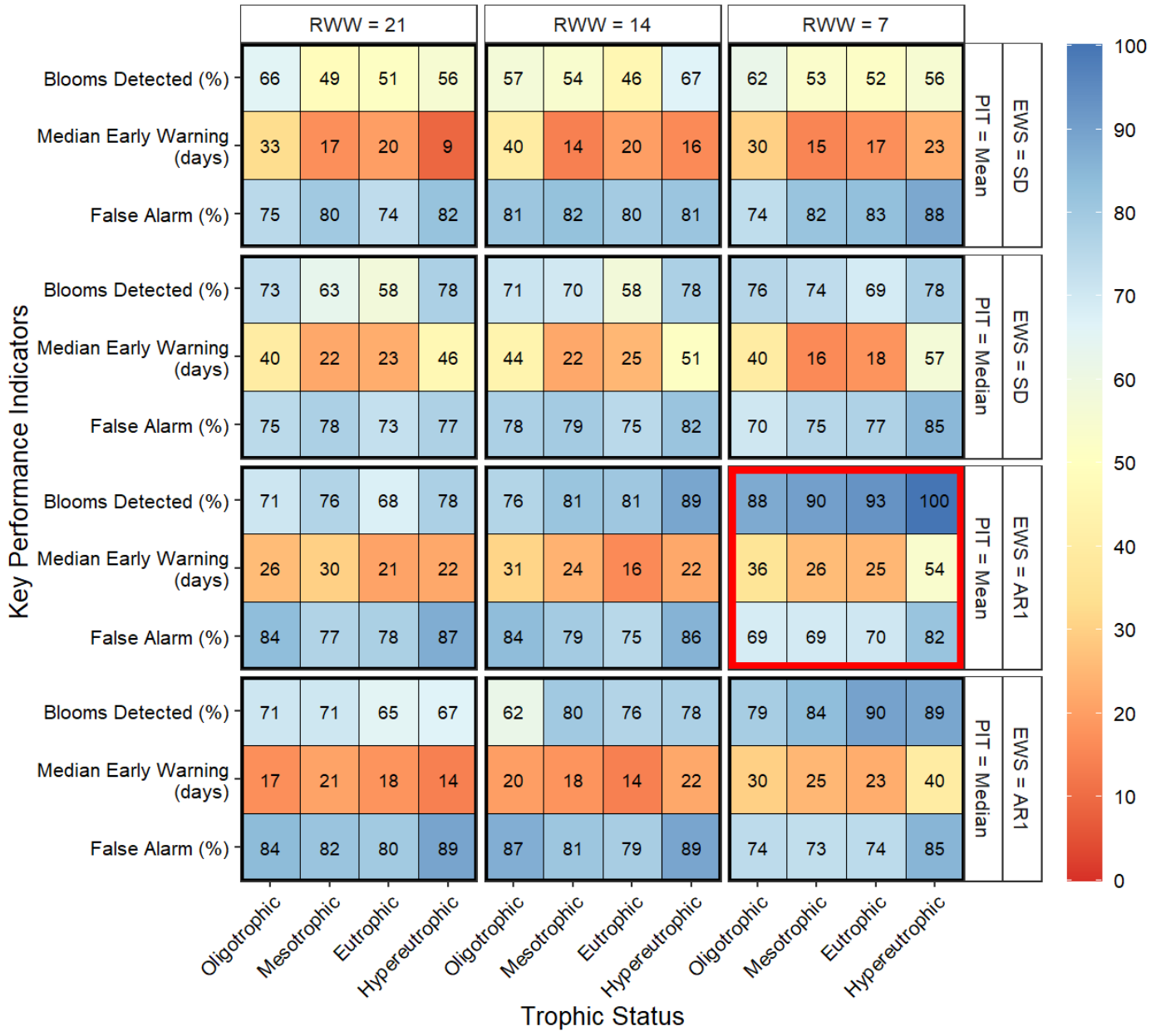
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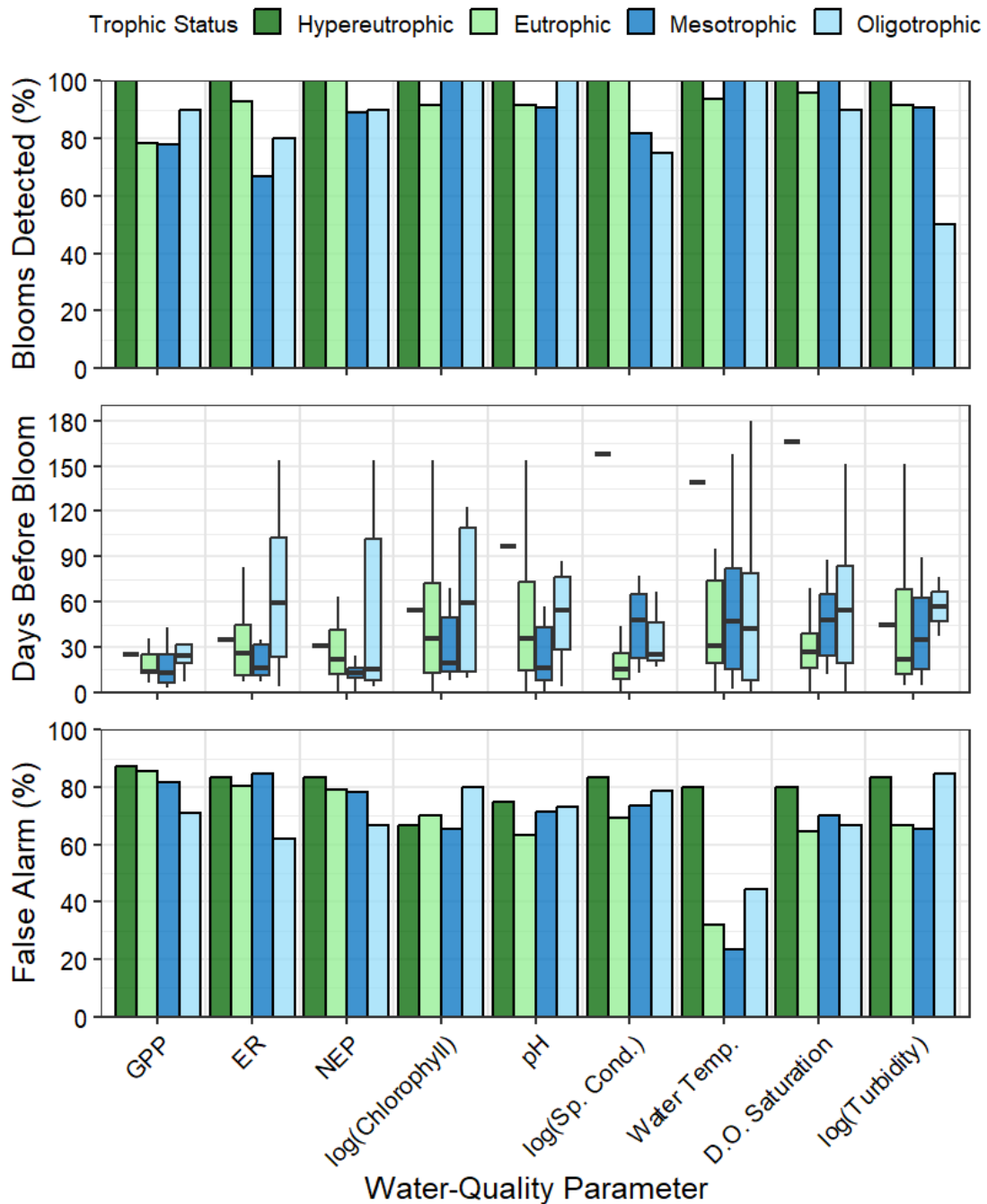
586 Figure 1. Example from Lake Anna, VA of using a rolling window standard deviation of gross
 587 primary production (GPP) to detect an algae bloom before it occurs. Daily average
 588 chlorophyll time series with the dashed line representing the fixed site-specific algae
 589 bloom threshold (top). Chlorophyll concentrations above the threshold indicate bloom
 590 conditions, while concentrations below indicate non-bloom conditions. The shaded green
 591 region indicates the duration of the bloom. The middle and bottom time series are the
 592 rolling window standard deviation for GPP, with the dashed line representing the site- and
 593 parameter-specific fixed potential instability threshold (PIT). The shaded yellow region
 594 represents the early warning lead time when the rolling window standard deviation exceeds
 595 the PIT prior to a bloom. False alarms occur when the rolling window standard deviation
 596 exceeds the PIT without bloom development within one week of return below the PIT.



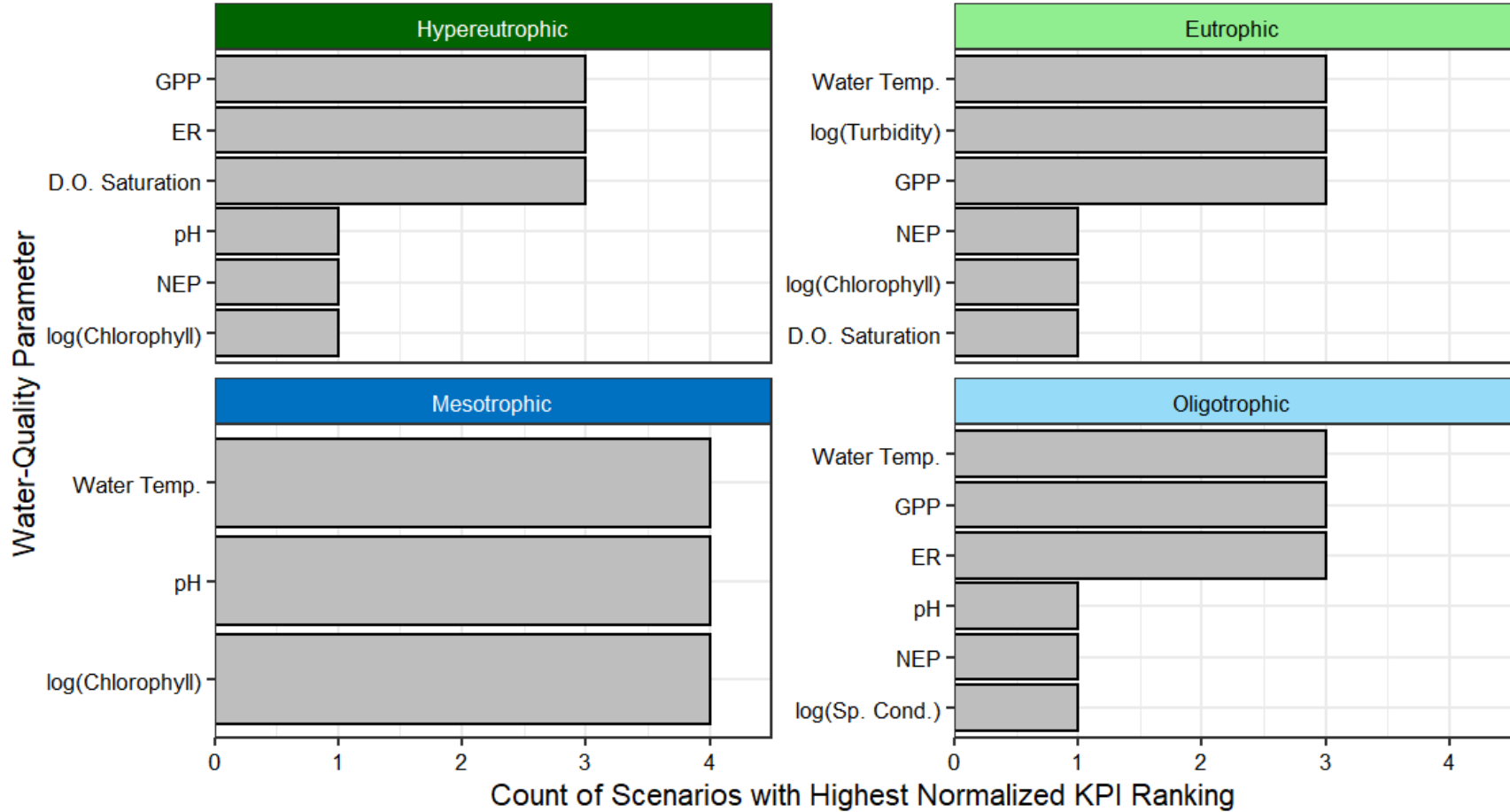
597 Figure 2. Time series of daily average chlorophyll concentrations (top row) and ecosystem metabolism (bottom row) for eight
 598 lakes, arranged geographically from north to south. Lake names are color-coded according to trophic status. Horizontal
 599 dashed lines mark the site-specific algal bloom thresholds, defined as the median chlorophyll concentration plus one
 600 standard deviation. Concentrations above the threshold are shown in green (indicating bloom conditions), while those below
 601 the threshold are white (non-bloom conditions). Metabolism metrics include gross primary production (GPP, purple points),
 602 ecosystem respiration (ER, teal points), and net ecosystem production (NEP, yellow lines).



603 Figure 3. Results of the threshold-based sensitivity analyses for each lake trophic group as
 604 they relate to the three key performance indicators (KPI). Twelve scenarios were tested
 605 corresponding to each combination of early warning statistic (EWS = SD or AR1), EWS-
 606 rolling window width (RWW = 7, 14, 21-days), and potential instability threshold (PIT =
 607 mean or median of the site- and parameter-specific EWS). The bolded red scenario
 608 involving the AR1 EWS, 7-day RWW, and mean PIT was the scenario with the highest
 609 summed KPI values (with false-alarm rate inversely scaled because lower values indicate
 610 better performance) across lake trophic groups.



611 Figure 4. Key performance indicators (bloom detection rate [top], early warning lead time
 612 [middle], and false alarm rate [bottom]) for each trophic group across all metabolism and
 613 water-quality parameters. Results represent the threshold-based sensitivity analysis
 614 corresponding to the scenario with the highest summed KPI values. The hypereutrophic
 615 boxplots appear as a line because there was only one bloom for this trophic group. The
 616 upper and lower hinges of the boxplot represent the 75th and 25th percentiles, the horizontal
 617 line represents the median, and the whiskers represent 1.5 times the range between the
 618 75th and 25th percentiles.



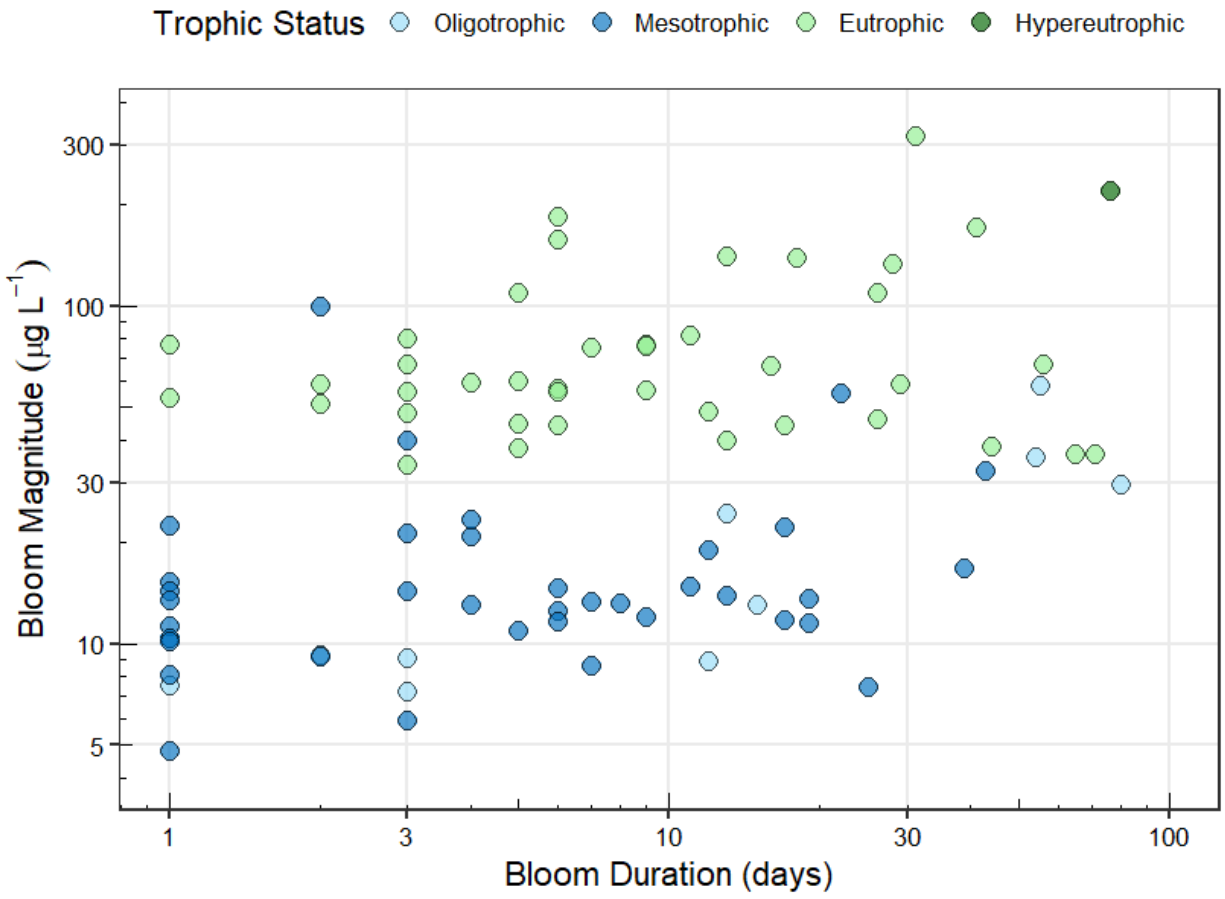
619 Figure 5. Counts of top-performing metabolism and water-quality parameters, based on the highest normalized KPI score, for
 620 each of the 12 threshold-based sensitivity-analysis scenarios by trophic groups.

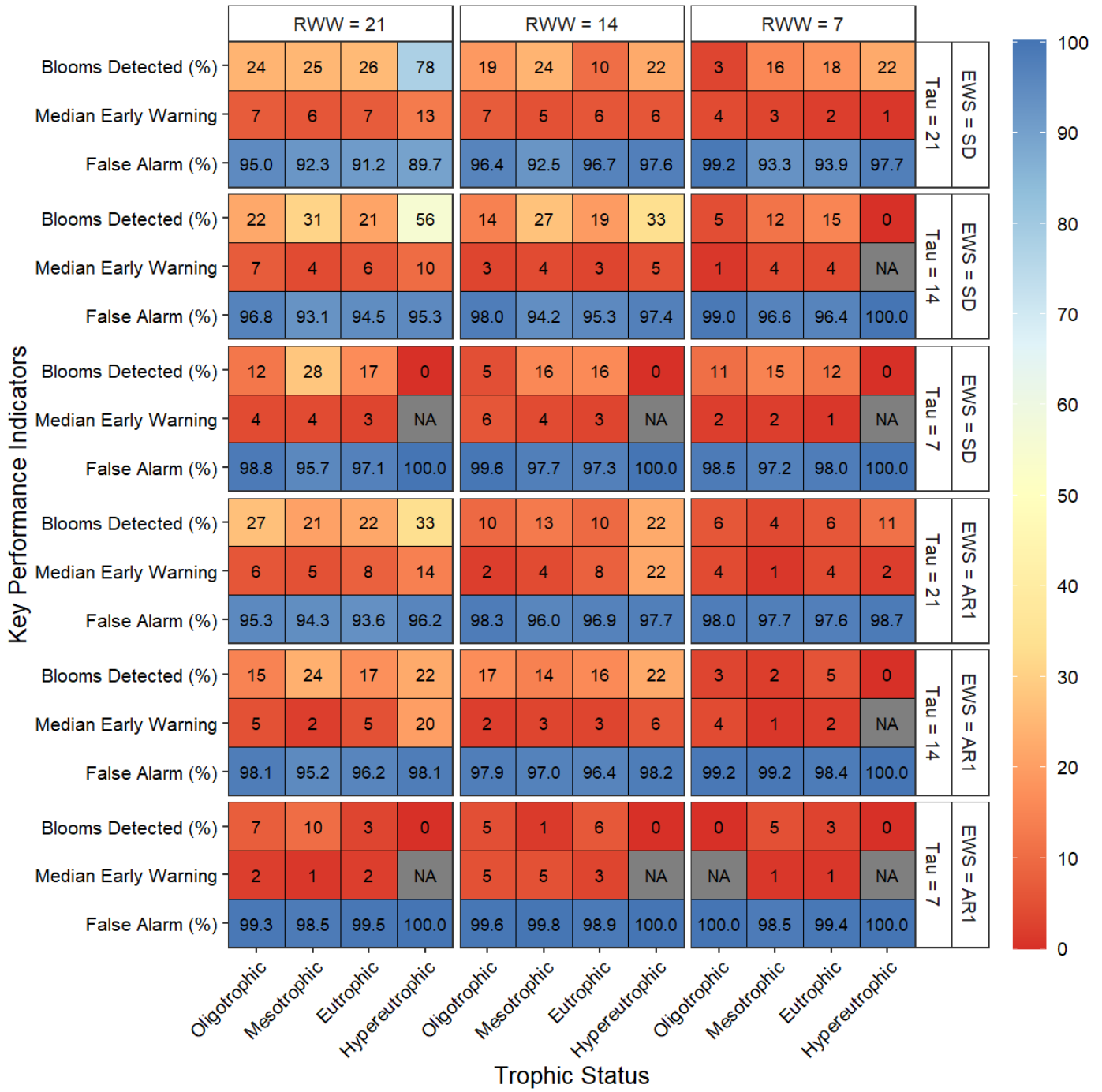
621 **Supplemental Information**

622 SI Table 1. National Ecological Observatory Network (NEON) datasets used in this study.

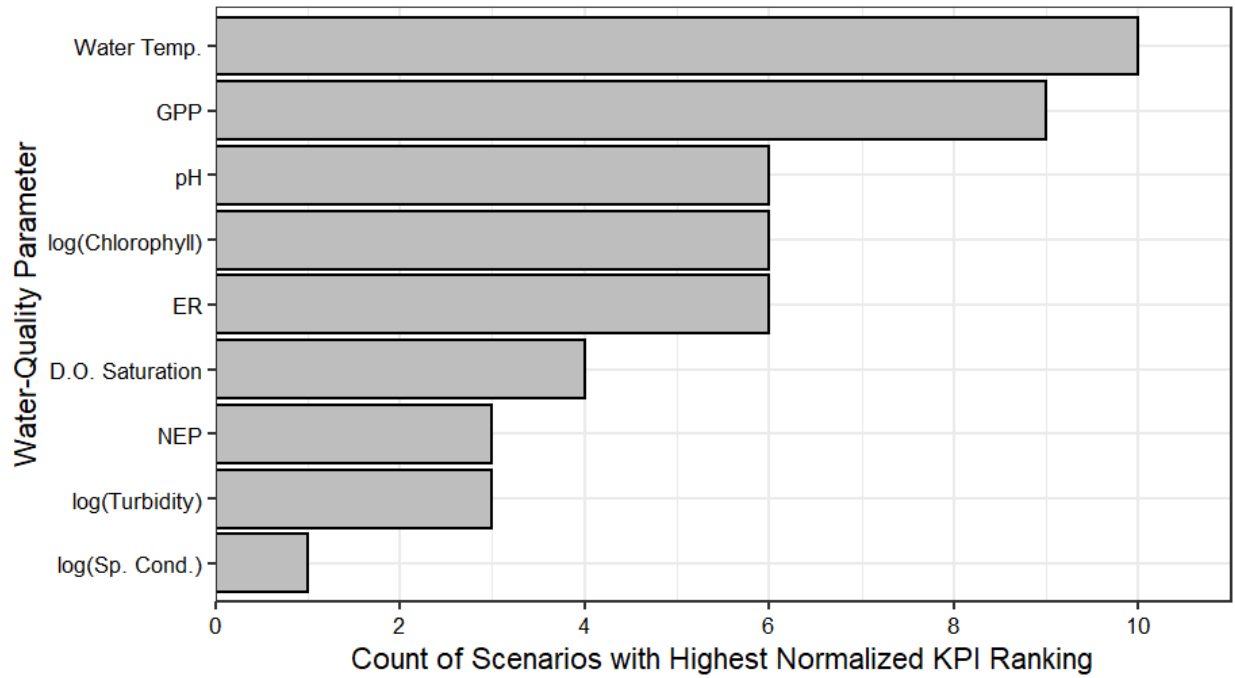
Parameter	Unique Identifier	Citation
Water quality	DP1.20288.001	NEON (National Ecological Observatory Network). Water quality (DP1.20288.001), RELEASE-2025. https://doi.org/10.48443/03mj-t174 . Dataset accessed from https://data.neonscience.org/data-products/DP1.20288.001/RELEASE-2025 on June 13, 2025.
Temperature at specific depth in surface water	DP1.20264.001	NEON (National Ecological Observatory Network). Temperature at specific depth in surface water (DP1.20264.001), RELEASE-2025. https://doi.org/10.48443/06xg-mz55 . Dataset accessed from https://data.neonscience.org/data-products/DP1.20264.001/RELEASE-2025 on June 18, 2025.
Windspeed and direction above water on-buoy	DP1.20059.001	NEON (National Ecological Observatory Network). Windspeed and direction above water on-buoy (DP1.20059.001), RELEASE-2025. https://doi.org/10.48443/w72m-nx46 . Dataset accessed from https://data.neonscience.org/data-products/DP1.20059.001/RELEASE-2025 on June 17, 2025.
Photosynthetically active radiation at water surface	DP1.20042.001	NEON (National Ecological Observatory Network). Photosynthetically active radiation at water surface (DP1.20042.001), RELEASE-2025. https://doi.org/10.48443/rerd-cr90 . Dataset accessed from https://data.neonscience.org/data-products/DP1.20042.001/RELEASE-2025 on June 17, 2025.
Barometric pressure above water on-buoy	DP1.20004.001	NEON (National Ecological Observatory Network). Barometric pressure above water on-buoy (DP1.20004.001), RELEASE-2025. https://doi.org/10.48443/aym4-6h05 . Dataset accessed from https://data.neonscience.org/data-products/DP1.20004.001/RELEASE-2025 on June 17, 2025.

623





626 SI Figure 2. Results of the Kendall's tau-based sensitivity analysis for each lake trophic
 627 group as they relate to the three key performance indicators (KPI).



628 SI Figure 3. Counts of the top-performing metabolism and water-quality parameters based
 629 on the highest normalized KPI score, for each of the 12 threshold-based sensitivity-analysis
 630 scenarios summed across trophic groups.