

1 **Spatiotemporal decoupling of littoral and lacustrine geosmin dynamics:**

2 **Implications for early warning in drinking water reservoirs**

3 Yuying Gui^{a,b,#} Tengxin Cao^{b,f,#} Jie Yang^c Jihui Qin^d Ming Su^{g,b,f,*} Ziyi Yang^{b,f}
4 Qi Zhang^e Yufan Ai^{b,f} Jiao Fang^b Yingjie Li^{b,f} Yuanhong Xiao^d Zhixiang Hao^c
5 Zhengyan Li^a Min Yang^{b,f}

6 # These authors contributed equally to this work.

7 ^a College of Environmental Science and Engineering, Ocean University of China, Qingdao
8 266100, China.

9 ^b Key Laboratory of Environmental Aquatic Chemistry, State Key Laboratory of Regional
10 Environment and Sustainability, Research Center for Eco-Environmental Sciences, Chinese
11 Academy of Sciences, Beijing 100085, China.

12 ^c Tianjin Hydraulic Research Institute, Tianjin 300061, China.

13 ^d Tianjin Yuqiao Reservoir Authority, Tianjin 301900, China.

14 ^e Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430070, China.

15 ^f University of Chinese Academy of Sciences, Beijing 100049, China.

16 * Corresponding to: [Ming Su \(mingsu@rcees.ac.cn\)](mailto:mingsu@rcees.ac.cn)

17 **Abstract**

18 The relationship between cyanobacterial niche characteristics and the transport dynamics of
19 harmful metabolites to drinking water intakes remains poorly understood. This study integrated
20 a national survey with a five-year high-frequency monitoring program to characterize these dy-
21 namics, focusing on the potent odorant geosmin. The national investigation revealed that 14%
22 of surveyed sites exceeded the odor threshold of 10 ng L^{-1} , indicating a non-negligible risk. In the
23 YQ Reservoir, *Planktothrix agardhii* was identified as a primary producer. Monitoring revealed
24 a distinct spatiotemporal decoupling: shallow littoral zones functioned as production centers
25 where *P. agardhii* biomass peaked 8 days prior to the lacustrine intake. Time-lagged correla-
26 tion analysis indicated that littoral biomass predicts intake geosmin concentrations with a 5-
27 week lead time ($R^2 = 0.41$). Ammonium was identified as the key regulatory factor, exhibiting
28 its strongest correlation with geosmin in littoral zones ($R^2 = 0.37$), though this linkage attenu-
29 ated during transport. This proposed mechanistic transport model and tiered framework shift
30 surveillance from reactive intake sampling to proactive littoral sentinel stations, establishing a
31 critical predictive window for preventive intervention in reservoir-dependent water supplies.

32 **Keywords:** *Geosmin, taste and odor, Early warning, Planktothrix agardhii, Spatiotemporal de-*
33 *coupling*

34 I Introduction

35 The increasing frequency and intensity of harmful cyanobacterial blooms (CyanoHABs) in
36 surface waters, driven by climate change and intensified anthropogenic activities, represent
37 a significant global threat to water security (Feng et al., 2021; Heisler et al., 2008; Huisman
38 et al., 2018; O'neil et al., 2012; Paerl et al., 2001; Paerl and Paul, 2012; Woolway et al., 2020).
39 While CyanoHABs in eutrophic shallow lakes have been extensively characterized (Kosten
40 et al., 2011; Paerl et al., 2011; Reintjes et al., 2022; Rousso et al., 2020; Xu et al., 2009; Zhang
41 et al., 2023), research in reservoir systems remains comparatively limited. In these critical
42 drinking water resources, CyanoHABs directly jeopardize water safety through the production
43 of toxins (Carmichael et al., 2001; Merel et al., 2013; Plaas and Paerl, 2020) and taste-and-odor
44 (T&O) compounds (Burlingame et al., 2017; Lin et al., 2018; Su et al., 2015; Yang et al., 2008).
45 Approximately half of China's source-water reservoirs experience recurrent algal-derived
46 T&O episodes (Sun et al., 2014). Unlike chemical contaminants, cyanobacterial populations
47 exhibit exponential growth under favorable conditions (Asato, 2003; Mehnert et al., 2010),
48 resulting in rapid metabolite release (Ai et al., 2025; Singh et al., 2005) that often exceeds the
49 treatment capacity of conventional water utilities (Cerón-Vivas et al., 2022; Mustapha et al.,
50 2021; Srinivasan and Sorial, 2011).

51 Managing CyanoHABs in reservoirs involves distinct challenges due to spatial and hydraulic com-
52 plexity, which results in less predictable ecological regimes than those in natural lakes (Dordoni
53 et al., 2023; Thornton, 1984). Conventional monitoring strategies, typically concentrated at la-
54 custrine intakes near dams, often fail to capture the heterogeneous distribution of algal biomass
55 and metabolites. Furthermore, the limited hydraulic residence time between the intake and the
56 treatment plant provides an insufficient operational window for intervention. Littoral zones,
57 with their shallow depth, generally warm earlier in spring and maintain higher light availabil-
58 ity throughout the water column compared to deeper offshore areas (Bracchini et al., 2009).
59 These nearshore regions also exhibit stronger sediment-water coupling, evident in diffusive nu-

60 trient fluxes and episodic wind-driven resuspension, which significantly enhance internal nutri-
61 ent supply (Akbarzadeh et al., 2025; Qin et al., 2006). Together, these physicochemical factors
62 (Cefalì et al., 2016; Zohary and Gasith, 2014) create an optimal ecological niche that supports
63 the early proliferation of cyanobacteria. Despite their potential as sentinel sites, these areas
64 are frequently under-monitored, and the mechanistic linkages between littoral zone dynamics
65 and downstream water quality at intakes remain insufficiently quantified.

66 Geosmin and 2-methylisoborneol (MIB) are the primary terpenoid T&O compounds synthesized
67 by cyanobacteria (Jüttner and Watson, 2007; Watson, 2003). Their low molecular weight and
68 chemical stability allow them to penetrate conventional treatment barriers and persist in distri-
69 bution networks (Lin et al., 2018; Zamyadi et al., 2015). While MIB episodes in China have been
70 well studied and managed through hydraulic controls (Lu et al., 2023; Su et al., 2015), geosmin
71 episodes are increasing in frequency across Northern Hemisphere reservoirs (Qiu et al., 2023;
72 Wu et al., 2022). The high phylogenetic diversity of geosmin-producing taxa (AWWA, 2010) com-
73 plicates the identification of biological sources and the development of targeted management
74 strategies, emphasizing the need for research into the ecological niches and growth dynamics
75 of these organisms in littoral zones.

76 This study analyzes recent national survey data to characterize the occurrence of geosmin
77 across China's drinking water sources and presents a five-year, spatially resolved investigation
78 of a representative reservoir. By integrating water chemistry, molecular profiling, and statisti-
79 cal modeling, this research examines the spatiotemporal decoupling between cyanobacterial
80 communities in littoral zones and concentrations at the lacustrine intake. The objectives
81 are to identify the primary cyanobacterial taxa responsible for geosmin production and to
82 demonstrate how population dynamics within littoral hotspots determine downstream odor
83 levels. This work provides an evidence-based framework for shifting from reactive treatment
84 toward proactive, risk-based management of cyanobacterial T&O threats.

85 2 Materials and methods

86 2.1 Study area and sampling design

87 **National-scale geosmin survey.** This study compiles geosmin concentration data from drink-
88 ing water sources across China, representing an extensive national assessment of this odor-
89 ant. The dataset integrates long-term monitoring results with high-quality measurements from
90 established literature, including a survey of 33 reservoirs in Guangdong province (Zhou et al.,
91 2024). To improve data comparability, only quantitative geosmin data from raw water sam-
92 ples analyzed using GC–MS-based methods were included. For risk assessment, a uniform ex-
93 ceedance threshold of 10 ng L⁻¹ was applied across all sites, and values reported below method
94 detection limits (MDLs) were treated as non-exceedance records in the exceedance-rate analy-
95 sis. In total, geosmin data from 214 distinct sampling sites were analyzed to characterize spatial
96 heterogeneity and nationwide occurrence patterns.

97 **Intensive monitoring at a reservoir in northern China.** YQ Reservoir is a large, river-type reser-
98 voir located in northern China, with a total storage capacity of approximately 1.559 billion m³,
99 and serves as an important drinking water source for a major metropolitan area in northern
100 China (Xu et al., 2014; Zhai et al., 2017). In recent years, the reservoir has experienced recurrent
101 seasonal taste-and-odor episodes (Cai et al., 2017; Qiu et al., 2021). Based on bathymetric and
102 hydrodynamic gradients, seven sampling sites (YQ01–YQ07) were established along a littoral-
103 to-lacustrine transect. Site YQ01, located in the deep lacustrine zone (maximum depth of ap-
104 proximately 12 m), was monitored using integrated water column sampling. Sites YQ02–YQ07
105 were situated in shallower littoral and transitional zones (water depth 2–4 m), where surface
106 water samples were collected because the shallow depth and frequent mixing were unlikely to
107 produce persistent vertical stratification (Holgerson et al., 2022). High-frequency sampling (2–
108 3 times per week) was conducted during the annual odor season from 2019 to 2024. Samples
109 for geosmin analysis, water chemistry, and phytoplankton assessment were collected concur-

110 rently, stored at 4 °C in the dark, and processed within 24 hours.

111 2.2 Analytical methods

112 **Geosmin analysis.** Geosmin concentrations were determined via headspace solid-phase mi-
113 croextraction (HS-SPME) coupled with gas chromatography–mass spectrometry (GC-MS; Agi-
114 lent 6890GC-5973MSD) following established protocols (Su et al., 2015). The method detection
115 limit (MDL) for geosmin was 1 ng L⁻¹.

116 **Physicochemical parameters.** Water temperature, pH, dissolved oxygen (DO), and turbidity
117 were recorded *in-situ* using a multiparameter sonde (EXO2, Xylem, USA). Concentrations of am-
118 monium (NH₄⁺-N), total nitrogen (TN), and total phosphorus (TP) were determined spectropho-
119 tometrically following Chinese national standard protocols. Specifically, TN and TP were quan-
120 tified after alkaline potassium persulfate digestion (HJ 636-2012 and GB/T 11893-1989, respec-
121 tively). NH₄⁺-N was measured using the Nessler’s reagent method (HJ 535-2009).

122 **Phytoplankton analysis.** At each sampling station, a 1 L water sample was collected and imme-
123 diately fixed with Lugol’s iodine solution (1% final concentration). After 48 h of static sedimenta-
124 tion, the samples were concentrated to a final volume of 50 mL (Hawkins et al., 2005). For phy-
125 toplankton identification and enumeration, a 0.1 mL aliquot of the concentrate was transferred
126 to a Sedgewick–Rafter counting chamber. Phytoplankton were identified and counted under an
127 upright microscope (Olympus CX23, Tokyo, Japan) at 400× magnification based on morpholog-
128 ical characteristics according to (Hu and Wei, 2006). Multiple microscopic fields were examined
129 for each sample. The phytoplankton cell density (C , cells L⁻¹) was calculated using the follow-
130 ing equation:

$$C = \frac{n \times V_{con}}{V_{count} \times V_{sample}} \quad (1)$$

131 where n is the number of cells counted, V_{con} is the concentrated volume (50 mL), V_{count} is the

132 volume of the counting chamber (0.1 mL), and V_{sample} is the initial sample volume (1 L).

133 **2.3 Molecular characterization and bioinformatics**

134 **Molecular identification of geosmin producers.** Biomass for molecular analysis was collected
135 on 1.2- μ m polycarbonate filters (Millipore) and stored at -80°C . Genomic DNA was extracted us-
136 ing the FastDNA™ Spin Kit for Soil (MP Biomedicals). The *geoA* gene, which encodes geosmin syn-
137 thase in cyanobacteria, was amplified using functional primers 173AF/173AR (Giglio et al., 2008;
138 Su et al., 2013). Taxonomic identification was performed via PCR amplification of the 16S rRNA
139 gene V4 region (primers 515F/806R). Gene fusion was carried out to combine the (*geoA*) and 16S
140 rRNA gene amplicons using the primers (173AF/806R). Amplicons were verified via agarose gel
141 electrophoresis and subjected to high-throughput sequencing. Representative sequences were
142 taxonomically assigned via BLAST searches, and a maximum-likelihood phylogenetic tree was
143 constructed to confirm the identity of the dominant producer.

144 **Bioinformatics pipeline.** The sequencing was performed on the Illumina MiSeq PE300 plat-
145 form (Illumina Inc., San Diego, USA) (Ravi et al., 2018). The raw paired-end sequences were
146 first merged using FLASH (v1.2.11) and processed for quality filtering within the QIIME2 pipeline
147 (v2022.2) (Bolyen et al., 2019). The UPARSE algorithm (v7.0.1090) was used to remove single-
148 tons and chimeras, and the sequences were clustered into Operational Taxonomic Units (OTUs)
149 at a 97% similarity threshold (Edgar, 2013). For the 16S rRNA gene fragments, representative se-
150 quences were taxonomically assigned against the SILVA rRNA reference database (release 138)
151 (Quast et al., 2012).

152 **2.4 Data processing and statistical analysis**

153 **Temporal aggregation and lagged correlation.** Data were aggregated to weekly means to
154 align time series and reduce noise. To investigate time-lagged relationships, weekly geosmin
155 concentrations were shifted forward by i weeks ($i = 0-7$) and paired with concurrent *Planktothrix*

156 *agardhii* biomass. A log–log linear model was applied:

$$\log_{10}(G) = \alpha + \beta \log_{10}(P) + \varepsilon \quad (2)$$

157 where G is the geosmin concentration (ng L⁻¹) and P is *P.agardhii* cell density (cells L⁻¹). To
158 minimize low-value interference, only paired observations with geosmin > 2 ng L⁻¹ and posi-
159 tive biomass were included. Analysis was restricted to sites with ≥20 valid weekly observations.
160 The coefficient of determination (R^2) was used to identify the optimal lag period (i.e., the early-
161 warning window reported in the main text), and slope significance was evaluated via t-test.

162 **Multivariate and spatial analysis.** Principal component analysis (PCA) was performed on stan-
163 dardized variables to explore multivariate relationships. Zone-specific regressions (littoral, tran-
164 sitional, lacustrine) compared the strength of the ammonium–geosmin linkage. Bathymetric
165 data were spatially interpolated via ordinary kriging to illustrate the reservoir’s depth gradient.
166 All analyses were conducted in R (version 4.4.2) using the *dplyr*, *lubridate*, *stats*, and *ggplot2*
167 packages.

168 3 Results

169 3.1 National survey of geosmin occurrence in drinking water 170 sources

171 We conducted a nationwide survey of 214 sites across 26 provinces to assess geosmin levels in
172 China’s major drinking water sources, including reservoirs and key surface water bodies. Risk
173 potential at each site was evaluated using peak recorded concentrations (Fig. S1). Values var-
174 ied by more than four orders of magnitude, ranging from non-detectable levels to a maximum
175 of 150 ng L⁻¹ in East Coastal China. Across the study area, 14% of sites exceeded the 10 ng L⁻¹
176 odor threshold (Fig. S2). The geospatial distribution showed marked spatial variability; ele-

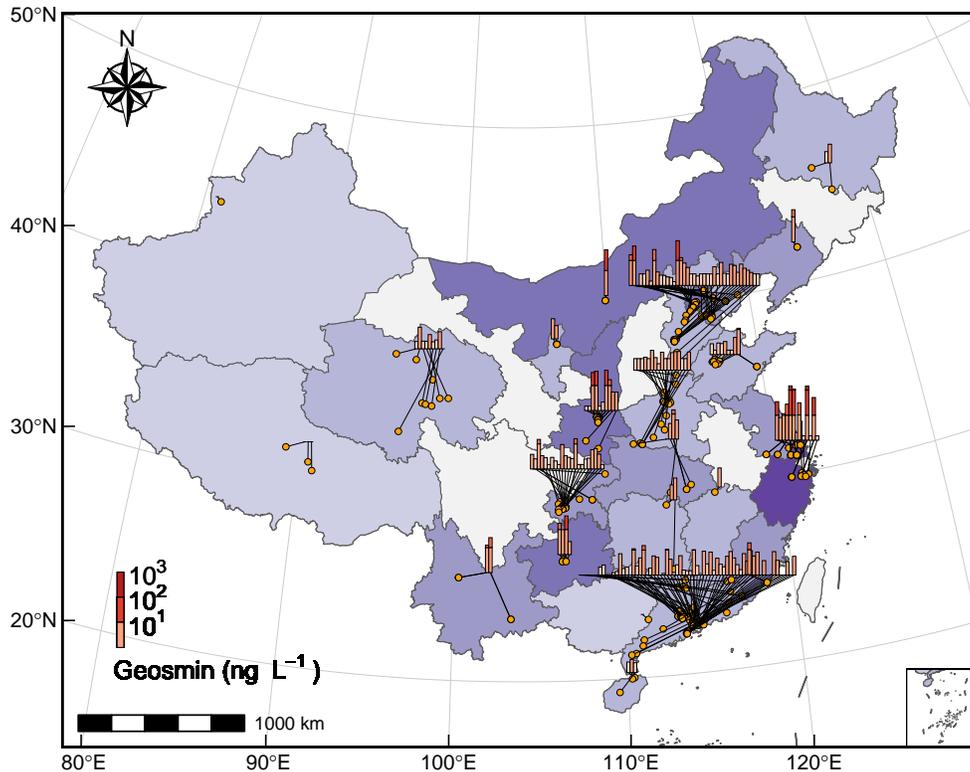


Fig. 1: A multi-scale visualization of geosmin occurrence: linking individual sampling sites to provincial-level aggregates (Provincial/regional aggregate bars (log-scale binned) connected to individual sampling sites. Beijing-Tianjin-Hebei and Jiangsu-Shanghai-Zhejiang are treated as single units to avoid spatial overlap).

177 vated geosmin levels were primarily concentrated in eastern and southern China—specifically
 178 the Yangtze and Pearl River Deltas and parts of North China. In contrast, concentrations re-
 179 mained low or below detection limits throughout the northwest (e.g., Tibet, Xinjiang, and Qing-
 180 hai) and certain central provinces, indicating a clear longitudinal gradient. These results identify
 181 geosmin as a pervasive odorant affecting drinking water quality across diverse climatic and ge-
 182 ographic zones in China.

183 **3.2 Seasonal and interannual dynamics in YQ Reservoir**

184 High-frequency monitoring was conducted at the primary intake (site YQ01) of YQ Reservoir from
 185 2019 to 2024 to characterize temporal geosmin variability (Fig. S3). The longitudinal record
 186 demonstrates a recurrent seasonal pattern (Fig. 2A, Fig. S4A). Concentrations typically remained

187 below 5 ng L⁻¹ during the spring (April–May), followed by an abrupt increase in June. Primary
188 peaks occurred during the July–August period, with secondary elevations persisting through
189 autumn and early winter (October–December) before a gradual decline. The 10 ng L⁻¹ odor
190 threshold was frequently exceeded during the study period. Monthly median values surpassed
191 this threshold in 40% of summer months (July–September) and 100% of autumn/early winter
192 months (October–December), indicating a recurrent odor risk during the warmer half of the
193 year.

194 Interannual analysis (Fig. 2B) revealed a reduction in geosmin levels following the 2019–2020
195 monitoring period, which recorded a median concentration of 2.5 ng L⁻¹. Between 2020 and
196 2024, annual medians stabilized within a range of 5.2 to 10 ng L⁻¹. Statistical differences between
197 years were confirmed by a Kruskal-Wallis test ($\chi^2(4) = 64.3, p < 0.001$). These data suggest a
198 shift in baseline conditions or source inputs after the initial year, although seasonal periodicity
199 remained a consistent feature.

200 **3.3 Phytoplankton community dynamics and key cyanobacterial** 201 **genera**

202 Phytoplankton composition data from YQ Reservoir (site YQ01, 2019–2024) were analyzed to
203 assess the relationship between community dynamics and geosmin occurrence (Fig. 2B). To-
204 tal phytoplankton biomass (log₁₀-transformed cell density) demonstrated seasonal variability,
205 with minimum values in winter (January–March, ~10⁷ cells L⁻¹) followed by an increase starting
206 in April. Biomass peaked during summer (July–September, >10⁸ cells L⁻¹) and remained ele-
207 vated through autumn (October–December) before declining in late winter, a trajectory consis-
208 tent with observed geosmin fluctuations.

209 Cyanobacteria dominated the assemblage throughout most of the monitoring period, with
210 peak biomass recorded from June to October. Within this group, filamentous genera associated
211 with geosmin production followed distinct successional patterns. *Planktothrix agardhii* and

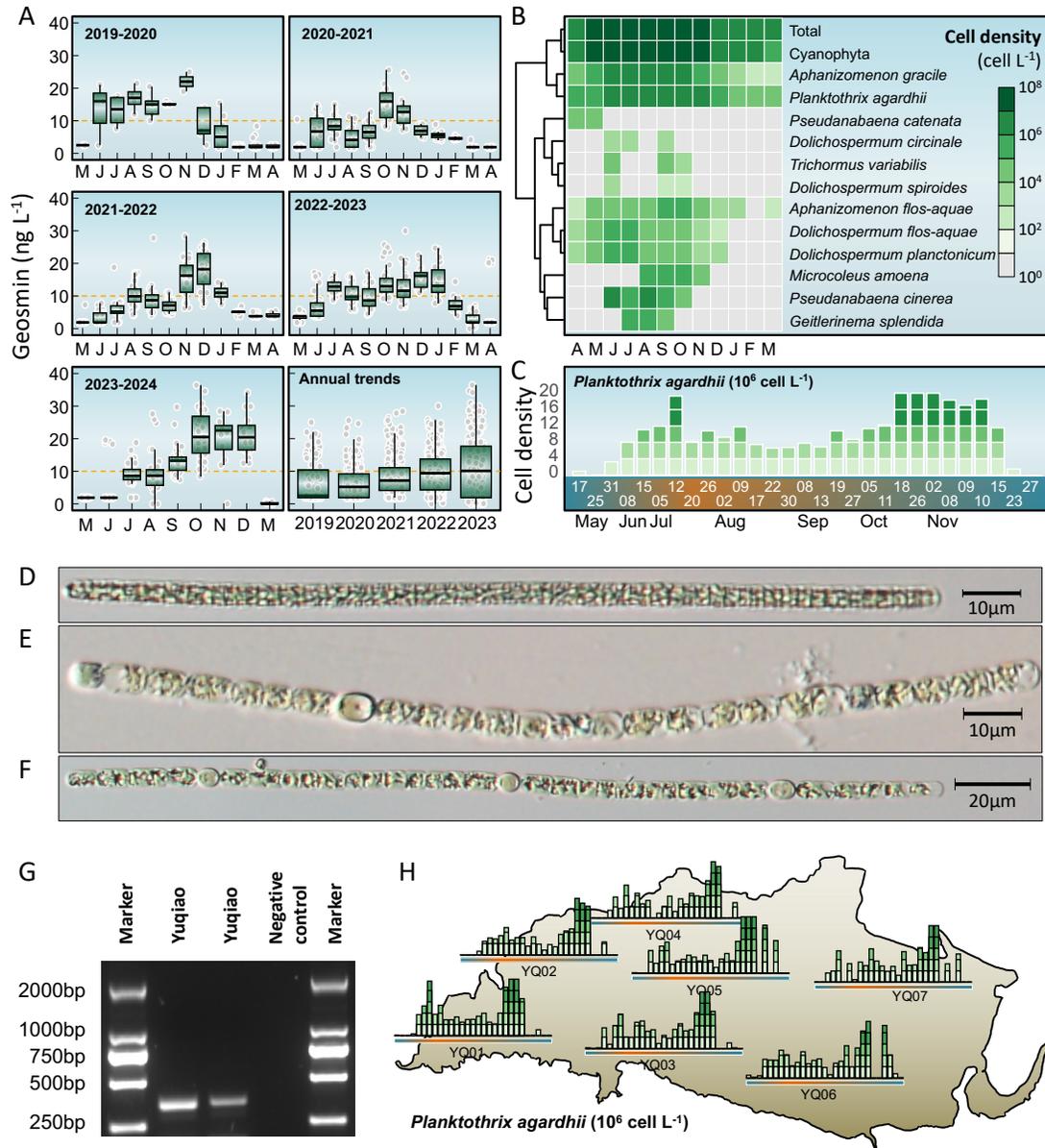


Fig. 2: Long-term dynamics of geosmin and phytoplankton community in YQ Reservoir (2019–2024). (A) Seasonal and interannual variations in geosmin concentrations at the main water intake (site YQ01). (B) Heatmap showing monthly \log_{10} -transformed biomass ($\log_{10}(X + 1)$) of total phytoplankton, total cyanobacteria, and key geosmin-producing cyanobacterial genera. (C) Temporal patterns of *Planktothrix agardhii* biomass across sampling sites. (D–F) Microscopic images of primary geosmin producers (*P. agardhii*, *Dolichospermum* and *Aphanizomenon*). (G) Agarose gel electrophoresis image for the molecular identification of geosmin producers. (H) Spatial mapping of seasonal *P. agardhii* biomass variations at representative sampling sites overlaid on the reservoir map.

212 *Aphanizomenon gracile* were present year-round but reached maxima in summer and autumn.

213 In contrast, *Pseudanabaena catenata* was primarily restricted to spring (April–May). Several

214 *Dolichospermum* species (e.g., *D. circinale*, *D. flos-aquae*, *D. planctonicum*) and *Aphanizomenon*
215 *flos-aquae* emerged in late spring, proliferated during summer, and declined by late autumn.
216 Other taxa, including *Trichormus variabilis*, *Microcoleus amoenus*, and *Pseudanabaena lim-*
217 *netica*, occurred sporadically, with peaks confined to specific intervals between June and
218 August.

219 The synchronization of elevated geosmin concentrations with high cyanobacterial biomass—
220 particularly during blooms of *Planktothrix*, *Dolichospermum* and *Aphanizomenon*—points to a bi-
221 ological origin for the odor episodes. The temporal succession of these specific taxa likely drives
222 the characteristic bimodal geosmin peaks observed during the summer and autumn months.

223 **3.4 Identification and spatiotemporal distribution of the primary** 224 **geosmin producer**

225 Screening of 16S rRNA and *geoA* gene sequences identified the genera *Planktothrix*, *Dolichosper-*
226 *um*, and *Aphanizomenon* as the primary geosmin producers in YQ Reservoir (Fig. 2D-2G). Due
227 to the high diversity and dynamic succession of filamentous cyanobacteria observed over the
228 five-year monitoring period, taxonomic identification at the species level remains inconclusive
229 based on current evidence. For subsequent analysis, *P. agardhii* was selected as the representa-
230 tive taxon for subsequent analysis because it showed a more persistent temporal pattern than
231 other candidate producers across the monitoring period (Fig. 2B–C) and exhibited the strongest
232 correlation with geosmin concentrations (Fig. S4B).

233 Spatial monitoring in 2023 demonstrated a clear biomass gradient; littoral sites (YQ03, YQ04,
234 YQ06, and YQ07, Fig. S3) maintained significantly higher cell densities than the lacustrine site
235 (YQ01). Maximum biomass reached 5.6×10^7 cells L⁻¹ at littoral locations, nearly double the peak
236 of 3.9×10^7 cells L⁻¹ recorded at the lacustrine abstraction point. Biomass exceeded the 2×10^7
237 cells L⁻¹ threshold in 8.7% of littoral samples, compared to 8.6% at YQ01. Unlike the ephemeral
238 peaks of other cyanobacteria, *P. agardhii* persisted throughout the warm season (Fig. 2C).

239 The progression of bloom events ($\geq 2 \times 10^7$ cells L⁻¹) followed a spatial sequence from the lit-
240 toral zone toward the dam (Fig. 2H). For example, YQ05 reached this threshold 8 days before
241 YQ01. This temporal lag suggests that littoral zones function as primary proliferation centers,
242 with subsequent advection driving the geosmin peaks observed at the lacustrine intake.

243 **3.5 Distinct spatiotemporal patterns of two geosmin episodes**

244 Two distinct odor episodes were identified in YQ Reservoir during 2023 (April–August and
245 August–December). Spatial mapping of monthly average geosmin concentrations at seven
246 representative sites revealed contrasting trajectories between littoral and lacustrine regions
247 (Fig. 3).

248 During the first episode (April–August), littoral sites (YQ02, YQ03, YQ04, YQ06, and YQ07)
249 recorded elevated concentrations in spring (April–June), ranging from 0 to 21.2 ng L⁻¹. These
250 values declined by August to between 0.6 and 5.8 ng L⁻¹. In contrast, the lacustrine site
251 (YQ01) and the transitional site (YQ05) exhibited a delayed response; concentrations increased
252 progressively from April minima to reach a peak in August at 8.5 ng L⁻¹.

253 The second episode (August–December) showed a reversed spatiotemporal gradient. Littoral
254 sites reached peak concentrations in October, ranging from 0 to 36.4 ng L⁻¹, before decreasing
255 by December. Conversely, the lacustrine site (YQ01) exhibited a monotonic increase throughout
256 the period, reaching 24.2 ng L⁻¹ in December. Site YQ05 demonstrated an intermediate transi-
257 tion, with concentrations declining in November.

258 These divergent trajectories (Fig. 3) indicate a systematic spatiotemporal decoupling: littoral
259 zones demonstrate earlier onset and decline during both episodes, while the lacustrine region
260 shows delayed and prolonged elevations. This pattern reflects the integrated effects of initial
261 production in littoral hotspots and subsequent advective transport toward the central reservoir.

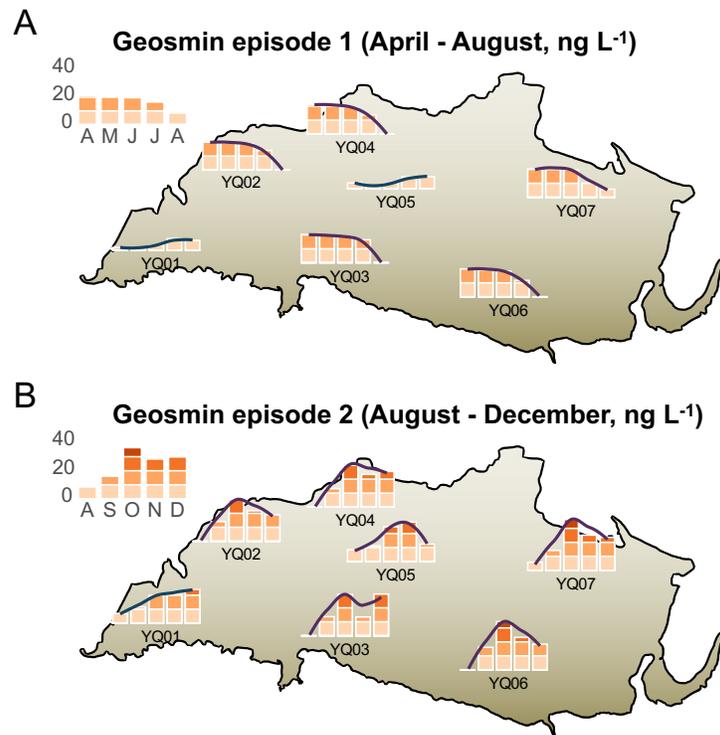


Fig. 3: Spatial mapping of monthly mean geosmin concentrations during Episode 1 (April–August, A) and Episode 2 (August–December, B) in YQ Reservoir.

3.6 Predictive relationship between *Planktothrix agardhii* dynamics and geosmin episodes

Time-lagged correlation analyses were performed between *Planktothrix agardhii* biomass and geosmin concentrations at the near-littoral site YQ05 and the lacustrine site YQ01 (Fig. 4A, Fig. S8). The analysis demonstrated divergent temporal coupling between the two locations. At YQ05, the strongest correlation ($R^2 = 0.5, p < 0.001$) occurred at zero lag, indicating that geosmin levels fluctuated synchronously with local *P. agardhii* density. In contrast, the correlation at the lacustrine site YQ01 was weakest at zero lag but increased with time, peaking at a 5-week lag ($R^2 = 0.41, p < 0.001$). This offset indicates that *P. agardhii* biomass functions as a concurrent indicator in the littoral production zone but acts as a leading indicator for geosmin risk at the distal lacustrine intake.

273 Regression models were established using the optimal lag periods for each site (Fig. 4B). For
274 YQ05 (zero lag), the relationship followed the equation: $\log_{10}(\text{geosmin}) = 0.244 + 0.288 \times \log_{10}(P.$
275 *agardhii* biomass). For YQ01 (5-week lag), the model was: $\log_{10}(\text{geosmin}) = 0.558 + 0.196 \times$
276 $\log_{10}(P. \textit{agardhii}$ biomass). The higher slope observed at YQ01 suggests a potential amplifica-
277 tion of geosmin concentrations during transport from littoral zones to the reservoir center.

278 Bi-weekly time series further illustrate this temporal phasing (Fig. 4C). At YQ05, *P. agardhii* and
279 geosmin peaks were closely aligned, whereas at YQ01, biomass peaks preceded major odor
280 episodes by approximately 6.7 weeks. This consistent lag serves as a predictive window; when *P.*
281 *agardhii* biomass at YQ05 exceeded 5.0×10^7 cells L⁻¹, geosmin at the lacustrine intake surpassed
282 the 10 ng L⁻¹ threshold within 4–6 weeks in 61.9% of observations. These results support the use
283 of near-littoral monitoring for forecasting odor risks at central abstraction points.

284 **3.7 Environmental drivers of geosmin and proposed transport** 285 **pathway**

286 Clear spatial gradient in nutrient loading and algal response was observed in YQ Reservoir (Fig.
287 S9). The littoral sites exhibit the highest vulnerability to organic enrichment, particularly during
288 the summer. In this period, the littoral zone reaches a peak mean Chl-a of 0.072 mg L⁻¹, which
289 is significantly higher than the 0.061 mg L⁻¹ observed in the lacustrine zone. This spatial dis-
290 parity is mirrored in the Chemical Oxygen Demand (COD) and turbidity levels, with littoral sites
291 showing higher COD (5.87 mg L⁻¹) and lower Secchi Disk transparency (50.6 cm) than the deeper
292 water sites. In contrast, the lacustrine zone displays higher stability regarding immediate or-
293 ganic surges but acts as a major sink for nitrogen. During winter, the Total Nitrogen (TN) in the
294 lacustrine zone reaches a maximum of 3.56 mg L⁻¹, a level higher than those found in the lit-
295 toral or transitional areas during the same season. The transitional sites serve as a buffer, with
296 water chemistry parameters like pH and TP typically falling between the littoral peaks and the
297 lacustrine lows.

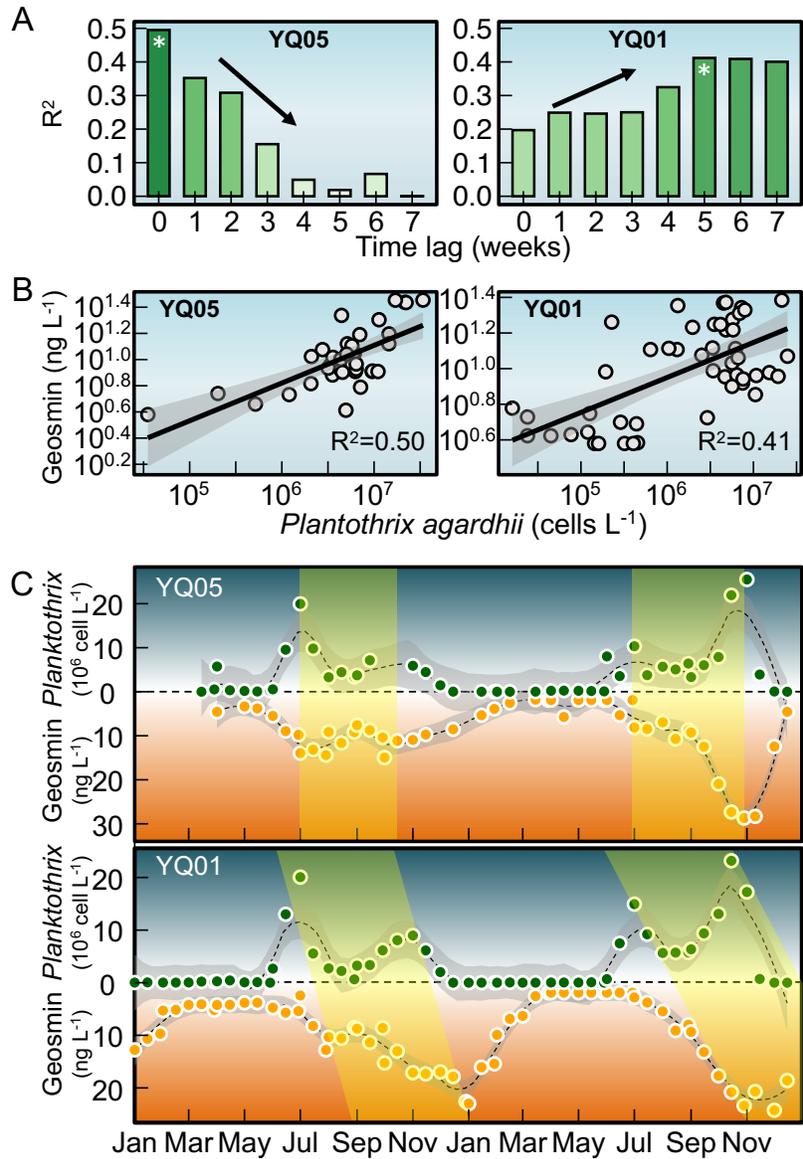


Fig. 4: Time-lagged relationships between *Planktothrix agardhii* biomass and geosmin concentrations at near-littoral and dam sites. (A) Correlation coefficients (R^2) between *P. agardhii* biomass and geosmin at different lag periods (0–5 weeks) for site YQ05 (near-littoral) and YQ01 (dam intake). (B) Linear regression models at optimal lag periods: zero lag for YQ05 and 5-week lag for YQ01. (C) Scatter plots with fitted regression lines showing the quantitative relationships between *P. agardhii* biomass and geosmin at each site.

298 Principal component analysis (PCA) identified ammonium (NH_4^+-N) as the variable most
 299 strongly associated with geosmin variability in the PC1–PC2 plane (Fig. 5A). The first two
 300 principal components accounted for 60.6% of total variance. PC1 (43.5%) represented a
 301 thermal-nutrient productivity axis, characterized by high loadings for temperature (0.342),

302 total phosphorus (TP, 0.39), and chlorophyll-a (Chl-a, 0.428). PC2 (17.1%) represented a
303 nitrogen availability axis, dominated by ammonium (-0.449) and total nitrogen (TN, 0.432).
304 Geosmin exhibited moderate positive loadings on both PC1 (0.122) and PC2 (0.229), suggesting
305 that variability is driven by a combination of thermal-nutrient status and nitrogen availability.

306 Log-log regressions between ammonium and geosmin were performed across three reservoir
307 zones: littoral (YQ02–YQ04, YQ06–YQ07), transitional (YQ05), and lacustrine (YQ01) (Fig. 5B). A
308 clear spatial gradient in correlation strength was observed, with the highest R^2 at littoral sites
309 (0.365), followed by YQ05 (0.203), and the lacustrine site YQ01 (0.035). This attenuation sug-
310 gests that the ammonium-geosmin linkage is most direct in production zones and undergoes
311 progressive decoupling during transport toward the lacustrine intake.

312 Based on these results and the observed spatiotemporal dynamics of *Planktothrix agardhii*, a
313 transport pathway for odor episodes is proposed (Fig. 5C). Shallow littoral areas (depths < 4–5 m)
314 serve as primary sites for ammonium accumulation, *P. agardhii* proliferation, and geosmin pro-
315 duction. Advective transport then moves cells and dissolved geosmin from these littoral zones
316 through the transitional region (YQ05) to the lacustrine intake (YQ01). This framework integrates
317 the spatial gradient in nutrient-geosmin coupling, the observed temporal lags between zones,
318 and the bathymetric influence on water residence times. These elements provide a mechanis-
319 tic basis for the origin and delayed manifestation of geosmin episodes at the reservoir's primary
320 abstraction point.

321 **4 Discussion**

322 **4.1 Geosmin prevalence in Chinese drinking water sources**

323 National survey data indicate that geosmin contamination is widespread across China's primary
324 drinking water sources, with 14% of sites exceeding the 10 ng L⁻¹ odor threshold ((AWWA, 2010)).
325 These results identify geosmin as a pervasive water quality challenge, consistent with obser-

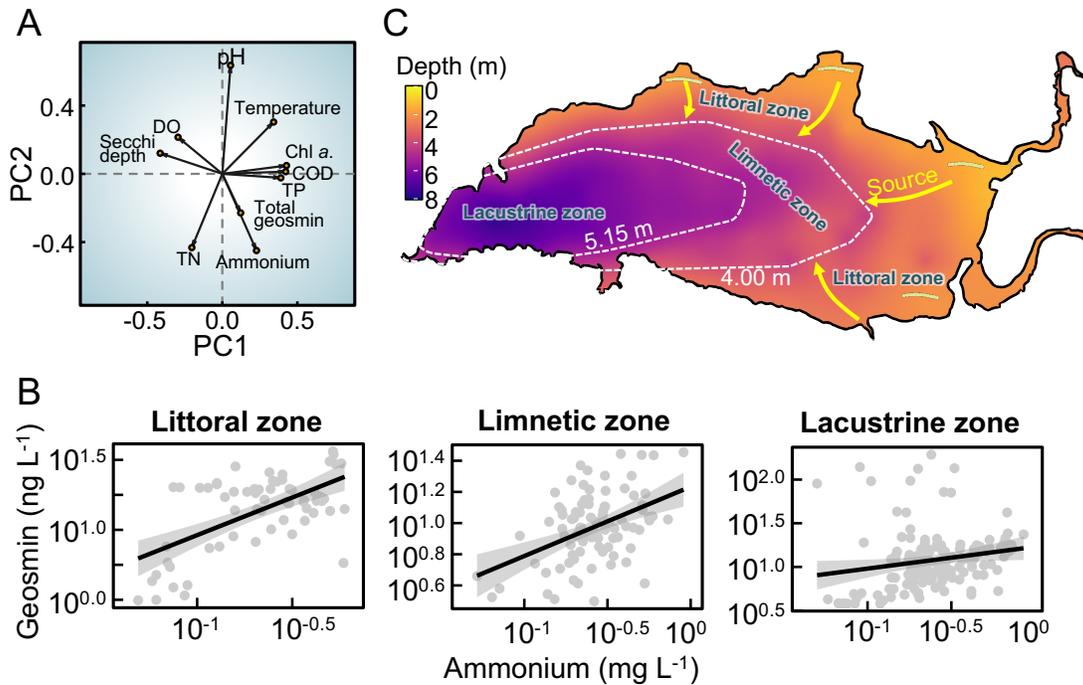


Fig. 5: Environmental drivers and conceptual transport pathway of geosmin in YQ Reservoir. (A) Principal component analysis (PCA) biplot showing relationships between geosmin and key environmental variables. (B) Log-log regressions between ammonium concentration and geosmin across littoral, transitional (YQ05), and dam (YQ01) zones. (C) Bathymetric map of YQ Reservoir depicting the proposed transport pathway from littoral production zones to the central water intake.

326 vations in other climatological regions (Devi et al., 2021; Lin et al., 2018). The observed spa-
 327 tial heterogeneity—specifically the higher concentrations within the Yangtze and Pearl River
 328 Deltas—suggests that regional climatic conditions, watershed land use, and nutrient loading
 329 are primary determinants of geosmin risk. Given its low odor threshold and resistance to con-
 330 ventional treatment processes (Cook et al., 2001; Mustapha et al., 2021; Zamyadi et al., 2015),
 331 geosmin poses significant operational challenges for water utilities (Srinivasan and Sorial, 2011)
 332 and impacts compliance with water safety objectives such as Sustainable Development Goal 6
 333 (Arora and Mishra, 2022). Consequently, these risks drive substantial investment in advanced
 334 treatment technologies and proactive source management (Yuan and Hofmann, 2022).

4.2 Littoral zones as production centers and spatiotemporal decoupling

While actinomycetes are established sources of geosmin in freshwater sediments (Gerber, 1979; Gerber and Lechevalier, 1965; Guo et al., 2024; Jensen et al., 1994), the synchronous peaks of *Planktothrix agardhii* biomass and geosmin at littoral sites ($R^2 = 0.5$), combined with the molecular identification of the *geoA* gene (Fig. 2D, F), confirm a cyanobacterial origin in YQ Reservoir. This supports the consensus that cyanobacteria are the primary biotic source of odorants in well-oxygenated reservoir water columns (Chislock et al., 2021; Hooper et al., 2023; Izaguirre, 1992; Pham et al., 2020; Su et al., 2013; Suurnäkki et al., 2015). Detection of *geoA*-harboring cyanobacteria (Giglio et al., 2011; Giglio et al., 2008; Kutovaya and Watson, 2014) in this oxygenated environment indicates that geosmin is primarily derived from cyanobacterial activity, aligning with studies linking specific blooms to odor episodes globally (Churro et al., 2020; Hayashi et al., 2019; John et al., 2018).

Monitoring data identify littoral zones as critical ecological niches for *P. agardhii* proliferation. The filamentous morphology and low-light adaptation of *P. agardhii* facilitate its dominance in shallow, intermittently mixed littoral environments (Cao et al., 2025; Jia et al., 2019; Komárek and Johansen, 2015; Su et al., 2019). These traits allow for optimal light harvesting under the variable regimes typical of nearshore areas (Scott and Marcarelli, 2012; Zohary and Gasith, 2014). The high correlation between ammonium and geosmin specifically in littoral zones ($R^2 = 0.37$) points to nitrogen availability from shoreline inputs as a key regulator. The positive correlation observed in situ in the reservoir is consistent with physiological evidence from laboratory studies on geosmin-producing cyanobacteria, which have shown that elevated ammonium concentrations can stimulate cyanobacterial growth and thereby increase overall geosmin production capacity (Canizales et al., 2021; Flores and Herrero, 2005; Saadoun et al., 2001; Yang et al., 2023). Thus, these findings collectively suggest that ammonium availability may serve as an indicator of geosmin production potential. Together, these results support the view that littoral zones act

361 as the primary production centers for geosmin in YQ Reservoir.

362 The subsequent weakening of ammonium–geosmin correlation at the lacustrine intake ($R^2 =$
363 0.03) reflects the decoupling of biological production from observed concentrations during
364 transport. This spatial decoupling is quantified by the 8-day lag in bloom development between
365 littoral sites and the dam, representing a period of physical advection and continued metabolic
366 accumulation. During this process, the observed delay at the lacustrine intake may partly
367 reflect intracellular geosmin release associated with cell lysis during downstream transport. As
368 *P. agardhii* cells are transported toward the dam, where conditions become less favorable for
369 growth, some cells may undergo lysis and release intracellular geosmin into the water column
370 (Dubourg et al., 2015; Jia et al., 2019). In addition, geosmin concentrations at the lacustrine
371 intake may be further affected by multiple physical and biogeochemical attenuation processes,
372 including dilution through mixing with geosmin-poor water, microbial degradation (Clerc et
373 al., 2021; Hammond et al., 2021; Hoefel et al., 2009), volatilization across the air–water interface
374 (Soyluoglu et al., 2022), and photochemical transformation (e.g., UV degradation) (Kim et al.,
375 2016; Mustapha et al., 2021).

376 **4.3 Implications for monitoring and management**

377 The conceptual mechanism depicted in Fig. 6 illustrates that maximum geosmin production is
378 localized in littoral zones before advective transport through the limnetic zone. This sequence
379 demonstrates a limitation in intake-centric monitoring: by the time geosmin reaches the lacus-
380 trine zone, the window for preventive intervention is minimal (Mohanty et al., 2024; Zamyadi et
381 al., 2015). The identified 4–6 week lag between littoral proliferation and lacustrine contamina-
382 tion establishes a quantifiable window for risk mitigation. This estimate is supported by both
383 the 5-week optimal lag identified from weekly lagged-correlation analysis and the 6.7-week de-
384 lay inferred from the observed time-series pattern, which together indicate a comparable multi-
385 week early-warning interval despite differences in method. By deploying littoral sentinel sites,

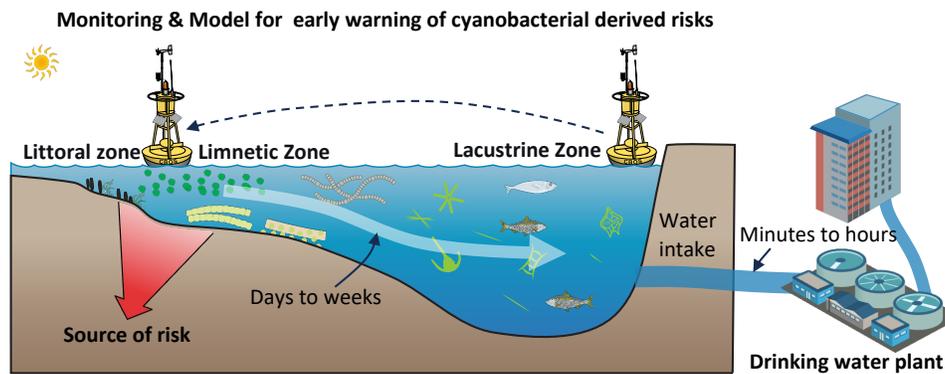


Fig. 6: Conceptual model of littoral-initiated geosmin transport and its implications for monitoring strategy. A sketch illustrating the spatiotemporal progression of geosmin episodes: (1) high metabolic activity of cyanobacteria (e.g., *Planktothrix agardhii*) in the littoral zone, driven by nutrient inputs and favorable light conditions; (2) advection of produced geosmin and biomass into the limnetic zone, resulting in a transport lag; (3) accumulation of geosmin in the lacustrine zone (dam intake), posing an immediate treatment challenge; and (4) the proposed monitoring shift from conventional reactive intake-focused sampling to proactive early detection in littoral zones, providing critical warning time for preventive measures.

386 utilities can move beyond reactive crisis management—such as emergency high-dose activated
 387 carbon application—toward preventive catchment-based strategies. This lead time is further
 388 supported by the lagged correlation at YQ01 ($R^2 = 0.41$ at 5 weeks). This interval allows for opti-
 389 mized treatment costs and proactive resource allocation to intercept risks during the incipient
 390 growth phase, aligning with modern water safety frameworks (Recknagel et al., 2017).

391 This monitoring framework is most applicable to reservoirs where odor production is dominated
 392 by littoral hotspots (Izydorczyk et al., 2008). Because the warning lag may vary among systems,
 393 it should be calibrated according to reservoir-specific characteristics, including hydrodynamic
 394 conditions, shoreline-to-intake distance, water residence time, and the spatial distribution of
 395 odor-producing cyanobacteria (Chong et al., 2018; Shin et al., 2022; Song et al., 2023). Systems
 396 dominated by deep-water or benthic producers may require modified sentinel-station strate-
 397 gies (Gaget et al., 2020; Izaguirre and Taylor, 2007; Su et al., 2017). In addition, the biomass
 398 threshold of 5.0×10^7 cells L^{-1} at YQ05 should be regarded as a preliminary indicator rather than
 399 a fixed decision threshold (Almuhtaram et al., 2021; Recknagel et al., 2017). Accordingly, it is bet-
 400 ter used as a practical reference for sentinel monitoring and early intervention. Exceedance at lit-
 401 toral stations may serve as an early-warning signal to intensify surveillance and, where feasible,

402 support operational measures such as selective withdrawal or hydrodynamic control to limit
403 the transport of geosmin-rich water toward critical intake depths (Lehman et al., 2009; Song et
404 al., 2023, 2023).

405 While the current dataset captures robust seasonal and interannual trends, longer-term obser-
406 vations are required to evaluate these dynamics under shifting climate scenarios. Furthermore,
407 while *P. agardhii* is the dominant producer in this system, other reservoirs may be driven by dif-
408 ferent taxa, such as *Dolichospermum* or *Aphanizomenon* (Choo et al., 2025; Izaguirre and Taylor,
409 2004; Su et al., 2013).

410 Future research should focus on: (1) integrating molecular tools to characterize the diversity
411 and expression of geosmin synthesis genes, (2) coupling ecological monitoring with high-
412 resolution hydrodynamic modeling to refine transport time estimates, and (3) conducting
413 cost-benefit analyses to evaluate the economic feasibility of expanded littoral monitoring. By
414 establishing quantifiable early-warning indicators based on the littoral-to-lacustrine transport
415 mechanism, this work provides a technical foundation for improving drinking water security.

416 **5 Conclusions**

417 This study demonstrates that geosmin risk in drinking water reservoirs is governed by a system-
418 atic spatiotemporal decoupling, whereby shallow littoral zones function as primary production
419 hotspots, with odor manifestation at the lacustrine intake lagging by several weeks. This quan-
420 tifiable lag transforms the monitoring paradigm, establishing that proactive surveillance of lit-
421 toral cyanobacteria provides a critical early-warning window, thereby enabling a shift from re-
422 active treatment toward predictive, source-water management for ensuring drinking water se-
423 curity.

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