

Effects of spatially heterogeneous lakeside development on nearshore biotic communities in a large, deep, oligotrophic lake

Michael F. Meyer ^{1*,a} Ted Ozersky ² Kara H. Woo ³ Kirill Shchapov ² Aaron W. E. Galloway ⁴
Julie B. Schram ⁴ Emma J. Rosi ⁵ Daniel D. Snow ⁶ Maxim A. Timofeyev ⁷
Dmitry Yu. Karnaukhov ⁷ Matthew R. Brousil ³ Stephanie E. Hampton ^{3,b}

¹School of the Environment, Washington State University, Pullman, Washington

²Large Lakes Observatory, University of Minnesota—Duluth, Duluth, Minnesota

³Center for Environmental Research, Education, and Outreach, Washington State University, Pullman, Washington

⁴Oregon Institute of Marine Biology, University of Oregon, Charleston, Oregon

⁵Cary Institute of Ecosystem Studies, Millbrook, New York

⁶School of Natural Resources, University of Nebraska—Lincoln, Lincoln, Nebraska

⁷Biological Research Institute, Irkutsk State University, Irkutsk, Irkutsk Oblast, Russia

Abstract

Sewage released from lakeside development can reshape ecological communities. Nearshore periphyton can rapidly assimilate sewage-associated nutrients, leading to increases of filamentous algal abundance, thus altering both food abundance and quality for grazers. In Lake Baikal, a large, ultra-oligotrophic, remote lake in Siberia, filamentous algal abundance has increased near lakeside developments, and localized sewage input is the suspected cause. These shifts are of particular interest in Lake Baikal, where endemic littoral biodiversity is high, lakeside settlements are mostly small, tourism is relatively high (~1.2 million visitors annually), and settlements are separated by large tracts of undisturbed shoreline, enabling investigation of heterogeneity and gradients of disturbance. We surveyed sites along 40 km of Baikal's southwestern shore for sewage indicators—pharmaceuticals and personal care products (PPCPs) and microplastics—as well as periphyton and macroinvertebrate abundance and indicators of food web structure (stable isotopes and fatty acids). Summed PPCP concentrations were spatially related to lakeside development. As predicted, lakeside development was associated with more filamentous algae and lower abundance of sewage-sensitive mollusks. Periphyton and macroinvertebrate stable isotopes and essential fatty acids suggested that food web structure otherwise remained similar across sites; yet, the invariance of amphipod fatty acid composition, relative to periphyton, suggested that grazers adjust behavior or metabolism to compensate for different periphyton assemblages. Our results demonstrate that even low levels of human disturbance can result in spatial heterogeneity of nearshore ecological responses, with potential for changing trophic interactions that propagate through the food web.

*Correspondence: michael.f.meyer@wsu.edu

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Additional Supporting Information may be found in the online version of this article.

^aPresent address: U.S. Geological Survey, Observing Systems Division, Madison, Wisconsin

^bPresent address: Carnegie Institution for Science, Biosphere Sciences and Engineering, Pasadena, California

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The release of treated and untreated wastewater into aquatic ecosystems is a common human disturbance that can introduce pollutants and reshape aquatic ecological communities. Nitrogen and phosphorus are among the primary pollutants in wastewater and its associated byproducts, yet these nutrients can also originate from disparate anthropogenic and natural environmental sources, thereby complicating their use as sewage indicators. For example, agriculture (Powers et al. 2016), watershed processes such as melting permafrost (Tornqvist et al. 2014), and changes in terrestrial plant communities (Moran et al. 2012) can all increase allochthonous nutrient inputs similar to sewage. Regardless of the nutrients' source, biological processes can further confound sewage detection. Benthic primary producers, especially those in oligotrophic systems (Hampton et al. 2011; Oleksy et al. 2020), can assimilate nutrients quickly from the water

column (e.g., hours; Hadwen and Bunn 2005), such that elevated nutrient concentrations may not be always observed.

Because nutrients can come from numerous non-sewage sources, indicators consistently associated with sewage loading, such as enhanced $\delta^{15}\text{N}$ stable isotope values (Camilleri and Ozersky 2019), pharmaceuticals and personal care products (PPCPs) (Rosi-Marshall and Royer 2012; Meyer et al. 2019), and microplastics (Barnes et al. 2009), have garnered increasing attention for their usefulness in defining locations of sewage pollution. Stable isotopes, such as $\delta^{15}\text{N}$, have been frequently used to trace sewage pollution (Gartner et al. 2002), yet their potential to indicate sewage can be obfuscated by complex terrestrial (e.g., terrestrial oligotrophication; Craine et al. 2018) and aquatic (e.g., variation within and between trophic levels; Guzzo et al. 2011) processes. In contrast to $\delta^{15}\text{N}$ values, PPCPs explicitly originate from human sources (Rosi-Marshall and Royer 2012; Meyer et al. 2019), where PPCP studies from continental (Kolpin et al. 2002) to colloidal pore (Yang et al. 2016) scales, have shown that concentrations tend to be greatest closer to their source. In addition to identifying areas and periods of sewage-specific pollution, PPCPs have also demonstrated robustness in defining gradients of sewage pollution in river systems, with concentrations being directly proportional to population density and inversely proportional to distance from a densely populated area (Bendz et al. 2005). Similar to PPCPs, microplastics (plastic debris up to 5 mm in size) also have been useful to detect sewage pollution (Li et al. 2018) along gradients of increasing human disturbance (Tanentzap et al. 2021), although they can also originate from non-sewage sources, such as shoreline debris or fishing nets (Moore et al. 2022). In contrast to $\delta^{15}\text{N}$ values and PPCPs, microplastics are typically resistant to degradation (Barnes et al. 2009), providing a signal over a longer time frame than many PPCPs and nutrients in sewage. As a result of each pollutant's association with sewage, co-located $\delta^{15}\text{N}$, PPCP, and microplastic measurements can be used to infer the spatial extent and timing of sewage pollution in an ecosystem. Although microplastics and $\delta^{15}\text{N}$ may originate from non-sewage sources, increases in PPCPs in tandem with either microplastics or $\delta^{15}\text{N}$ values together may robustly indicate sewage inputs. However, instances where PPCPs are not elevated yet microplastics and $\delta^{15}\text{N}$ measurements do increase may be inconclusive, suggest transient sewage inputs, or result from other non-sewage sources, such as atmospheric deposition.

The effects of sewage pollution are frequently first seen in nearshore benthic communities, where nutrients entering from directly adjacent settlements can alter algal species composition, abundance, nutritional quality, as well as food web trophic structure. Increased filamentous algal abundance, for example, has been frequently observed in areas suspected of sewage pollution (Rosenberger et al. 2008; Hampton et al. 2011), likely due to benthic filamentous algae efficiently removing nutrients from the water column (Oleksy et al. 2020). With a changing resource

base, grazing macroinvertebrate communities may likewise shift to include more detritivores or species capable of consuming filamentous algae (Rosenberger et al. 2008). In addition to some grazers' physical difficulty consuming filamentous algae (Mazzella and Russo 1989), there also may be changes in algal nutritional quality, as filamentous algae tend to contain a different mixture of essential fatty acids (EFAs) in comparison to diatoms (Taipale et al. 2013), which dominate periphyton communities in unimpacted ecosystems. In particular, the EFAs 18:3 ω 3 and 18:2 ω 6 are commonly associated with green filamentous algae (Taipale et al. 2013), whereas the EFA 20:5 ω 3 is more associated with diatoms (Taipale et al. 2013). All EFAs are largely synthesized by primary producers, and different algal taxonomic groups produce strongly differentiated multivariate signatures (Taipale et al. 2013; Galloway and Winder 2015). Consumers can acquire fatty acids by grazing (Dalsgaard et al. 2003) or upgrading fatty acids at their own energetic expense (Dalsgaard et al. 2003) and often reflect the fatty acid signatures of their diets. Thus, comparing consumer and producer fatty acid compositions can be used to infer how grazing patterns change in response to increasing sewage pollution.

To investigate lake littoral community and food web responses to sewage-associated nutrient pollution, we surveyed 40 km of Lake Baikal's shoreline for indicators of sewage pollution and metrics of benthic community composition and structure. Located in Siberia, Lake Baikal is the oldest, most voluminous, and deepest freshwater lake in the world (Hampton et al. 2018), with the majority of Lake Baikal's biodiversity occurring in the littoral zone (Kozhov 1963). Although Lake Baikal's pelagic zone is generally ultra-oligotrophic (O'Donnell et al. 2017), nearshore areas abutting lakeside settlements have shown distinct signs of eutrophication (Kravtsova et al. 2014; Timoshkin et al. 2016). Much of Lake Baikal's shoreline lacks human development, and Baikal's watershed is largely roadless and unpopulated (Moore et al. 2009). Despite low levels of development, uncharacteristic filamentous algal blooms have been occurring throughout the lake since 2010 (Kravtsova et al. 2014; Timoshkin et al. 2016) including cyanobacterial blooms in 2019 (Bondarenko et al. 2021). While increased *Ulothrix* spp. abundance has historically occurred in Lake Baikal in late summer (Kozhov 1963), recent observations of unprecedented filamentous green algae proliferation, especially of *Spirogyra* spp. and *Ulothrix* spp., are thought to be associated with increased nearshore nutrient concentrations (Ozersky et al. 2018). Inadequate wastewater management in lakeside settlements is likely the main driver of these nearshore algal blooms (Timoshkin et al. 2016, 2018), motivating further research to identify the extent to which sewage is altering nearshore communities.

Given the growing evidence that Baikal's nearshore periphyton communities are responding to sewage inputs, our goal was to understand how littoral benthic community composition and interactions may be changing near areas of sewage pollution. This overarching goal was divided into three specific objectives:

1. identify areas of wastewater pollution using several complementary sewage indicators;
2. assess the relationship between sewage indicators and littoral periphyton and macroinvertebrate community composition; and
3. evaluate how trophic relationships among littoral benthic community members are impacted by localized sewage pollution.

We hypothesized that (1) sewage indicators, such as PPCP concentrations, $\delta^{15}\text{N}$, and microplastic densities, would increase with increasing population density and proximity of lakeside development; (2) an increasing sewage signal would correlate with increased dominance of filamentous benthic algae; and (3) increasing filamentous algal abundance would result in changes in the abundance of different macroinvertebrate feeding guilds, reflected in community composition and dietary tracers such as carbon and nitrogen stable isotopes and fatty acids.

Methods

Site description

The vast majority of Lake Baikal's 2100-km shoreline lacks lakeside development (Moore et al. 2009; Timoshkin et al. 2016). Our study focused on a 40-km section of Baikal's southwestern shoreline, which included three settlements of different sizes (Fig. 1). From 19 August 2015 through 23 August 2015, we sampled 14 littoral and 3 pelagic locations along our 40-km transect. Littoral locations were chosen to capture a range of sites with varying degrees of adjacent shoreline development—from “developed” (human settlements along the waterfront) to “undeveloped” (no adjacent human settlements and complete forest cover; Fig. 1; Supporting Information Table S1). Pelagic sites were located 2–5 km offshore from each of the developed sites in water depths of 900–1300 m (Fig. 1; Supporting Information Table S1). As previous investigations of nearshore algal communities near our sampled locations observed increased filamentous algae (Timoshkin et al. 2016, 2018) and cyanobacteria (Bondarenko et al. 2021) in mid-to-late summer, the timing of our sampling was intended to coincide with the annual peaks of tourism and summertime community succession, such that gradients of human disturbance and biological response would likely be most apparent relative to environmental noise. All littoral sites were sampled at approximately the same depth (~1.25 m) at a distance of 8.90–20.75 m from shore (Supporting Information Table S1), which allowed us to collect samples without the need for SCUBA but precluded us from sampling deeper littoral environments. The substrate was consistent among sites and generally was dominated by pebble to boulder-sized rocks.

Three discrete lakeside settlements were located along our 40-km transect. The largest, Listvyanka, is primarily a tourist town of approximately 2000 permanent residents, although tourism can contribute significantly to the town's population with approximately 1.2 million annual visitors (Interfax-

Tourism 2018). The other two settlements are the villages Bolshie Koty and Bolshoe Goloustnoe, which have approximately 80 and 600 permanent residents, respectively. Although Bolshie Koty and Bolshoe Goloustnoe are built along small streams that empty into Baikal, there are no upstream developed sites, meaning that any observed sewage indicators in Baikal most likely originated either from Bolshie Koty or Bolshoe Goloustnoe. None of these settlements have centralized sewage treatment facilities and most residents rely on unlined cesspools (Timoshkin et al. 2018).

Below we briefly describe the data collected along our sampling transect. More detailed methods for sample collection and processing are located in the Supplementary Methods (S1) for this manuscript, the “protocol.pdf” file on the Environmental Data Initiative (Meyer et al. 2020), as well as this analysis's companion data manuscript (Meyer et al. 2022).

Inverse distance-weighted population metric calculation

We recognized that sewage indicator concentrations at each sampling location may be related to a sampling location's spatial position relative to both the size and proximity of neighboring developed sites. Therefore, we calculated an inverse distance-weighted human population metric to compress, into a single metric, information about human population size, density, and location along the shoreline as well as distance between developed sites and sampling locations. Hereafter, the inverse distance-weighted human population metric is referred to as “population metric.” The population metric reflects the idea that sewage pollution should be positively related to increasing human density and inversely related with distance from densely populated areas (sensu Bendz et al. 2005).

Water samples

At both pelagic and littoral sites, water samples were collected for nitrate, ammonium, total phosphorus, chlorophyll, microplastic, and PPCP analysis. Samples were collected by hand from 0.75 m depth for each littoral site and with a bucket from aboard a research vessel for pelagic sites. Supporting Information Table S2 describes summarized concentrations for water column constituents across sampling sites.

Benthic algal collection

At each littoral site, we haphazardly selected three rocks representative of local substrate. A plastic stencil was used to define a surface area of each rock from which we scraped a standardized 14.5 cm² patch of periphyton. Samples were preserved with Lugol's solution and stored in plastic scintillation vials. Additional periphyton was collected in composite from each site for fatty acid and stable isotope analysis. Periphyton identification and enumeration were performed under a compound microscope.

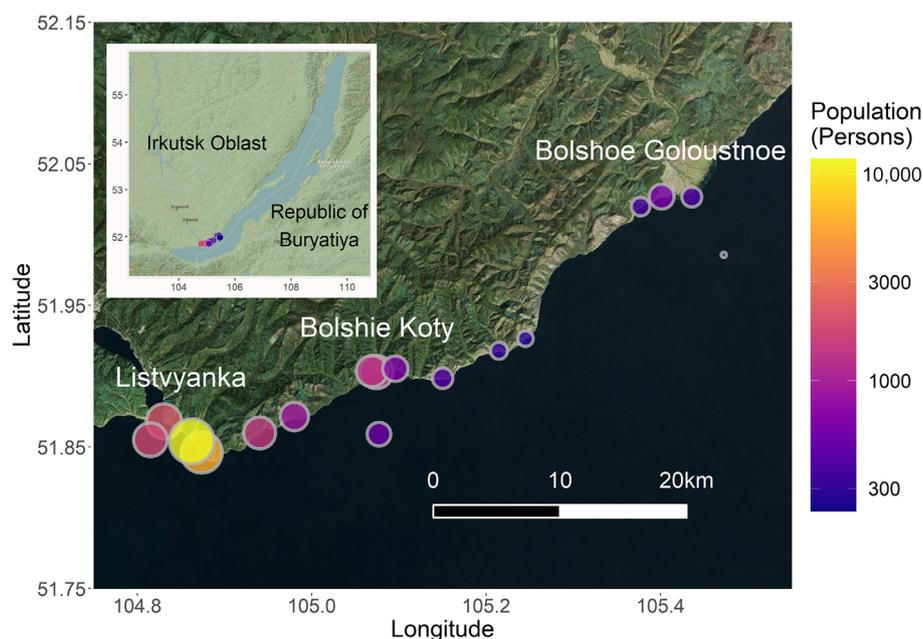


Fig. 1. Map of all sampling locations with sites sized and colored by population metric values for the lakeside developments of Listvyanka, Bolshie Koty, and Bolshoe Goloustnoe. Population metric values are shown on a log-scale to make values across three orders of magnitude more comparable.

Benthic invertebrate collection

At each littoral site, three kick-net samples were collected for assessment of benthic community composition and abundance. Separate collections were conducted for invertebrate fatty acid and stable isotope analyses. Invertebrates were collected using a D-net and by hand. Six ethanol-preserved samples of the 42 collected were not well-preserved and were excluded from further analyses, in order to reduce errors in identification. Supporting Information Table S3 contains a full list of macroinvertebrate taxa included in this analysis.

Food web characterization

To characterize littoral food webs, we analyzed periphyton and macroinvertebrate carbon and nitrogen stable isotopes and fatty acid profiles. Supporting Information Table S4 contains a full list of fatty acids quantified. Because some samples thawed during transit to the United States, we focus only on samples that were completely frozen. Carbon and nitrogen stable isotope as well as fatty acid analyses were performed using standard methods described in Meyer et al. (2022).

Inferring food web structure

In order to assess food web structure, we compared stable isotopes and fatty acids in periphyton resources with those in amphipods. Stable isotope values of bulk periphyton and different amphipod species were measured for a given sampling location. Because periphyton stable isotope samples were measured for the aggregate community, periphyton could only be used as a single potential resource for amphipods, meaning it was not possible to use our stable isotope data alone to infer

diet shifts for amphipod grazers. In contrast, algal fatty acid signatures tend to be consistent for closely related taxa (Galloway and Winder 2015), allowing us to use published Baikal algal fatty acid profiles with consumer fatty acid profiles from our sampling campaign to evaluate more taxon-specific, algae-amphipod trophic interactions. We used a Bayesian mixing model to infer the relative abundance of potential resources in amphipod diets using the MixSIAR framework (Stock et al. 2018a,b). This modeling procedure involved three data inputs:

1. *Consumer fatty acids*: These data were collected from our sampling at Lake Baikal.
2. *Source fatty acids*: Because our collected fatty acid data considered periphyton species in composite, we used published Baikal taxon-specific fatty acid profiles to define characteristic diatom (Shishlyannikov et al. 2018) and *Ulothrix* spp. (Osipova et al. 2009) signatures. The relatively large benthic alga *Draparnaldia* spp. creates mats that can be discretely sampled, in addition to the composite periphyton samples, such that we included *Draparnaldia* spp. fatty acid profiles as distinct sources.
3. *Trophic discrimination factors (TDFs)*: TDFs reflect shifts in fatty acid concentrations between trophic levels. To the best of our knowledge, there are no published TDFs for Baikal amphipods' fatty acids. Therefore, we calculated TDFs from fatty acid concentrations quantified for Antarctic marine amphipods (Schram et al. 2019), which likely experience similar physiological and metabolic demands as those in Lake Baikal. To ensure TDF estimates were

conservative across consumers and resources, we averaged each fatty acid's TDF, such that a given fatty acid's TDF was identical for each potential resource.

The model building procedure used uninformative prior distributions for each resource, a chain length of 100,000 with 50,000 burn-in, thin of 50, and 3 Monte Carlo Markov Chains. Chain convergence was assessed with a Gelman-Rubin diagnostic, which was below 1.005 for all model runs. Model fit was assessed by calculating root-mean-square error (RMSE) twice: first, between a sample's predicted consumer fatty acid proportions and a sample's actual consumer fatty acid proportions, and second, between mean predicted fatty acids and mean actual consumer fatty acid proportions. Because TDFs for this analysis were based on marine taxa, we assessed posterior sensitivity to TDF variation by increasing TDF standard deviations by 5%, 10%, 25%, 50%, and 100%, and then re-running the model. This routine allowed us to assess both the potential for TDF variation to alter quantitative results as well as qualitative interpretations of the mixing model. Although MixSIAR has demonstrated robustness to deviations in TDFs and complexity of mixed resource inputs (Guerrero and Rogers 2020), this sensitivity analysis was designed to exceed errors that can arise from differences in mixing model methodologies and prescribed error structures. Each iteration of the sensitivity analysis produced a similar posterior result as the original TDFs. The accompanying R script "07_foodweb_analysis.R" details the exact data aggregation, model construction, and model validation procedures and can be accessed from the project's Open Science Framework portal (Meyer et al. 2015).

Statistical analyses

To identify areas of wastewater pollution with sewage indicators (Objective 1), total phosphorus, nitrate, ammonium, microplastic density, summed caffeine and paraxanthine/1,7-dimethylxanthine, acetaminophen/paracetamol, cotinine, and summed PPCP concentrations were log-transformed and regressed against log-transformed population metric using a linear model. Summed PPCP concentrations are defined as the sum of all PPCP residue concentrations above minimal detection limits and have been used in prior studies to reflect accumulated sewage loadings (Kolpin et al. 2002; Richmond et al. 2018). Residuals were assessed for normality and homogeneity of variance.

To increase confidence that our observed sewage indicator patterns were not a product of a limited sample size, we also performed a permutational analysis to compare how our actual results compared to a randomly permuted dataset. This process involved randomly permuting sewage indicator variables, regressing the respective sewage indicator against human population, and then extracting the p -values and R^2 values for the model. This routine was repeated 5000 times for each sewage

indicator to generate a distribution of p -values and R^2 value that could have been possible, given our observed data. We then compared models' p -values and R^2 values generated from non-permuted data to those from permuted datasets. If indeed models generated from observed data were describing a non-random process, p -values and R^2 values should be located at the tail end of the permuted values' distribution. To summarize our original p -values and R^2 values in the context of those from models with permuted datasets, we report the percent of p -values less than and R^2 values greater than those from models generated from non-permuted datasets. This permutation routine is documented in more detail in the accompanying R script "02_sewage_indicator_analysis.R."

To assess if benthic community composition was associated with increasing sewage indicators (Objective 2), periphyton and macroinvertebrate abundance data were each analyzed with a consistent multivariate workflow. First, replicates were averaged to characterize algal and macroinvertebrate compositions, and taxonomic groups representing less than 1% of the inter-site community were removed from analysis, in order to reduce the influence of rare species on results. Second, community compositions for both periphyton and macroinvertebrates were visualized using non-metric multidimensional scaling (NMDS) with a Bray-Curtis similarity metric. The NMDS plot suggested that sites generally separated by increasing PPCP concentrations and our population metric (see Supporting Information Table S2). To test whether sites' benthic communities significantly differed between co-located PPCP concentrations and human population, we first used k-medoids (Supporting Information Figs. S2, S3), also known as non-hierarchical partitioning around the medoids, as well as weighted pair-group centroid clustering (WPGMC; Fig. S4) as a hierarchical clustering approach to identify an optimal number of groupings. We then performed three permutational multivariate analyses of variance (PERMANOVA) with 999 permutations: the first where community compositions were responses to the groups identified through clustering, the second where community compositions were responses to the continuous population metric, and the third where community compositions were responses to summed PPCP concentrations. When significant differences were identified, post hoc similarity percentages (SIMPER) analysis was performed following the PERMANOVA to identify which taxa contributed to 85% of the cumulative variance that most influenced group separation, which allowed us to identify a subset of most influential taxa.

To assess whether benthic food webs restructured with increasing sewage indicator concentrations (Objective 3), fatty acid data were analyzed in a manner similar to periphyton and macroinvertebrate abundance data. First, species' fatty acid profiles were visualized by performing NMDS with Bray-Curtis similarity for all organisms' relative fatty acid abundance (Supporting Information Figs. S5, S6). These NMDS plots suggested that periphyton fatty acids differentiated based on sewage indicator concentrations. Among all taxa and sites, the fatty acids 18:3 ω 3, 18:1 ω 9, and 20:5 ω 3 had among the

highest coefficients of variation (Supporting Information Table S5), enabling comparisons between sites. To increase the robustness of our analysis, we expanded our approach to include major fatty acids within each taxonomic group, including 18:2 ω 6 (abundant in green algae); 16:1 ω 7 and 14:0 (abundant in diatoms); and 16:0 (abundant in both green algae and diatoms) (Taipale et al. 2013). To evaluate how relative fatty acid abundance may relate to sewage pollution, we assessed patterns among these seven fatty acids with both multivariate and univariate approaches. Within a multivariate framework, we created two NMDS plots with Bray–Curtis similarity, one just with primary producer (Supporting Information Fig. S7) and the other with macroinvertebrate (Supporting Information Fig. S8) fatty acid profiles. Because multivariate patterns suggested fatty acid profiles may relate to sewage pollution, we regressed a filamentous: diatom fatty acid ratio (Eq. 1)

$$\frac{18:3\omega3\% + 18:1\omega9\% + 18:2\omega6\% + 16:0\%}{20:5\omega3\% + 16:1\omega7\% + 16:0\% + 14:0\%} \quad (1)$$

against log-transformed summed PPCP concentrations as well as our population metric using a linear model. In addition, we evaluated how three EFAs (18:3 ω 3, 18:2 ω 6, and 20:5 ω 3), lipids thought to accumulate in animal tissues because they are largely synthesized by primary producers (Kelly and Scheibling 2012; Taipale et al. 2013), may differ in abundance across the sewage gradient. Therefore, we similarly regressed the ratio of $\frac{18:3\omega3\% + 18:2\omega6\%}{20:5\omega3\%}$ against log-transformed summed PPCP concentrations as well as our population metric using a linear model. Together, these regressions allowed us to assess how food web interactions may have changed along our disturbance gradient. As with sewage indicators, we recognized that these regression analyses and the associated interpretations may be compromised by a limited sample size. To ensure the robustness of these trends, we performed a permutational analysis similar to sewage indicators.

All packages and software used to aggregate, analyze, and visualize data are provided in the accompanying Supplemental Methods. All data, including .kml files used to calculate the population metric, are publicly available from the Environmental Data Initiative repository (Meyer et al. 2020), and all R scripts are available from the GitHub repository of this project's Open Science Framework account (Meyer et al. 2015).

Results

Water samples

Nearshore water nitrate ($R^2 = 0.01$, $p = 0.68$; Fig. 2A), ammonium ($R^2 = 0.17$, $p = 0.11$; Fig. 2B), total phosphorus ($R^2 = 0.14$, $p = 0.14$; Fig. 2C), chlorophyll *a* (Chl *a*) ($R^2 = 0.11$, $p = 0.20$; Fig. 2D), summed caffeine and paraxanthine ($R^2 = 0.11$, $p = 0.11$; Supporting Information Fig. S9), and acetaminophen/paracetamol ($R^2 = 0.06$, $p = 0.33$; Supporting

Information Fig. S9) concentrations were not significantly correlated with our population metric. Summed PPCP ($R^2 = 0.26$, $p = 0.04$; Fig. 2E) and cotinine ($R^2 = 0.38$, $p = 0.01$; Supporting Information Fig. S9) concentrations as well as $\delta^{15}\text{N}$ values in macroinvertebrate tissue ($R^2 = 0.33$, $p = 0.02$; Fig. 2F) were significantly related with our population metric. In the littoral zone, detected PPCPs included caffeine, 1,7-dimethylxanthine/paraxanthine (main human metabolite of caffeine), cotinine (main human metabolite of nicotine), and acetaminophen/paracetamol (Supporting Information Table S2). Other measured PPCPs, including carbamazepine, diphenhydramine, thiabendazole, amphetamine, methamphetamine, 3,4-methylenedioxyamphetamine (MDA), 3,4-methylenedioxymethamphetamine (MDMA), morphine, phenazone, sulfachloropyridazine, sulfamethazine, sulfadimethoxine, sulfamethazole, trimethoprim, and cimetidine, were not detected.

Microplastics were detected in samples from both littoral and pelagic sites (Supporting Information Table S2). Bead microplastics were only detected near Listvyanka. Fibers (mean = 0.85 microplastics L^{-1} , SD = 1.21 microplastics L^{-1}) and fragments (mean = 0.83 microplastics L^{-1} , SD = 1.35 microplastics L^{-1}) were the most abundant types of microplastics across all sites, whereas beads were relatively rare (mean = 0.08 microplastics L^{-1} , SD = 0.31 microplastics L^{-1}). Microplastic densities were not significantly correlated with our population metric ($R^2 = 0.01$, $p = 0.65$; Fig. 2G), although more types of microplastics were generally observed near areas with higher population metric values, such as Listvyanka.

Permutational analyses corroborated these findings. Models using total phosphorus, nitrate, ammonium, Chl *a*, and microplastics tended to have R^2 values and p -values similar to randomized datasets (Supporting Information Fig. S10). Model estimates for summed PPCP concentrations and $\delta^{15}\text{N}$ values were both within the tail 5% of values generated from permuted data (Supporting Information Fig. S11).

Periphyton

Major taxonomic groupings of periphyton consisted of diatoms, Tetrasporales, *Spirogyra* spp., and *Ulothrix* spp. K-medoids (Supporting Information Figs. S2A, S3A) and WPGMC (Supporting Information Fig. S4A) cluster analyses of periphyton abundance demonstrated two groupings capture most variance, and visual inspection of relative periphyton community abundance. NMDS suggested groupings were related to population metric values (Fig. 3A). PERMANOVA results demonstrated that periphyton communities were significantly different based on population metric groupings ($R^2 = 0.52$, $p = 0.001$) and continuous population metric values ($R^2 = 0.43$, $p = 0.001$), but not with increasing PPCP concentrations ($R^2 = 0.56$, $p = 0.26$). Post hoc SIMPER results with population metric groupings suggested that these differences were primarily associated

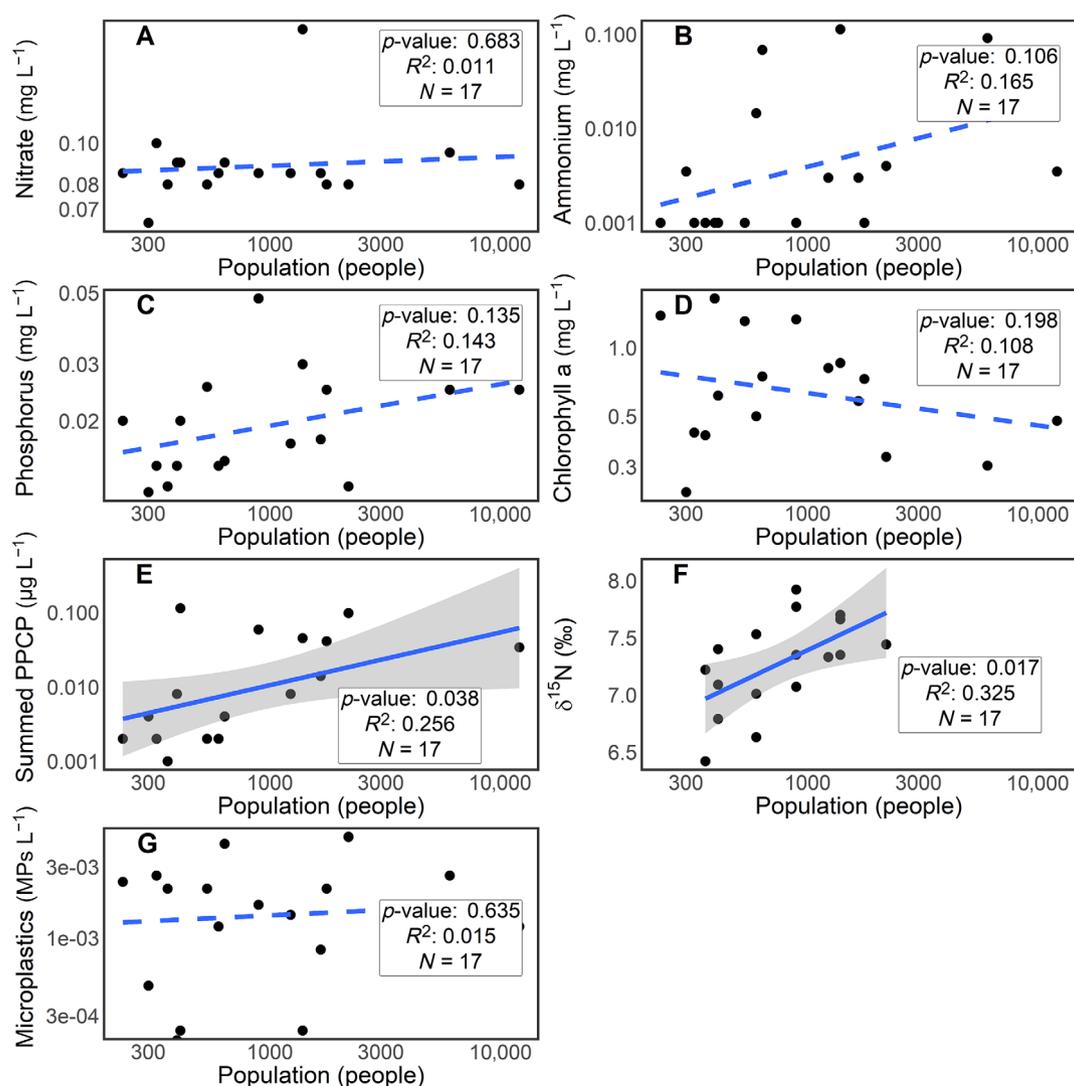


Fig. 2. Nitrate (A), ammonium (B), total phosphorus (C), Chl *a* (D), summed PPCP (E), macroinvertebrate $\delta^{15}\text{N}$ (F), as well as microplastic density (G) values regressed against log-transformed human population metric values. Statistical results are from linear regressions. Solid lines with error envelopes indicate significant relationships, whereas non-significant models have dotted regression lines without error envelopes.

with sites that had higher *Ulothrix* spp. and *Spirogyra* spp. relative abundance.

Macroinvertebrates

Taxonomic groupings included five amphipod genera: *Eulimnogammarus*, *Poekilogammarus*, *Cryptoropus*, *Brandtia*, and *Pallasea*; six mollusk families: Planorbidae, Valvatidae, Baicaliidae, Benedictidae, Acroloxidae, and Maackia; flatworms; caddisflies; isopods; and leeches (summarized in Supporting Information Table S3). K-medoid cluster analysis of macroinvertebrate community composition suggested two or three major groupings would capture most variance (Supporting Information Figs. S2B, S3B), whereas WPGMC analyses suggested two groupings would enable all sites except for one to be assigned a cluster (Supporting

Information Fig. S4B). Because both forms of hierarchical and non-hierarchical clustering suggested two groupings as optimal, we proceeded using two groupings. NMDS suggested clusters were related to population metric values (Fig. 3B). PERMANOVA results supported the hypothesis that macroinvertebrate communities significantly differed both among population metric groupings ($R^2 = 0.19$, $p = 0.02$) and along the continuous gradient of increasing population metric values ($R^2 = 0.19$, $p = 0.02$) and summed PPCP concentrations ($R^2 = 0.19$, $p = 0.02$). Post hoc SIMPER analyses with population metric groupings suggested that *Poekilogammarus*, *Eulimnogammarus*, Valvatidae, Caddisflies, *Brandtia*, Baicaliidae, Planorbidae, *Cryptoropus*, and flatworms contributed the greatest differences between population metric groupings.

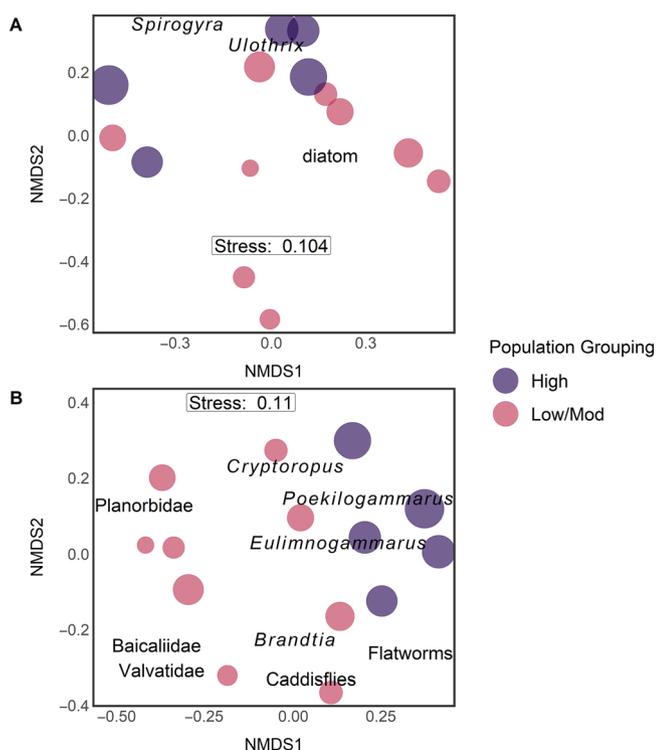


Fig. 3. Periphyton (A) and macroinvertebrate (B) NMDS with Bray-Curtis dissimilarity. Points are sized by log-transformed population metric values and colored by population metric groupings. Taxonomic labels represent species scores, which are weighted averages of species contributions from site scores.

Food web characterization: Stable isotopes and fatty acids

For grazers, $\delta^{15}\text{N}$ values significantly increased with population metric values ($p = 0.01$; Figs. 2B, 4A). Periphyton $\delta^{15}\text{N}$ values did not significantly increase with population metric

values ($p = 0.27$). In contrast, $\delta^{13}\text{C}$ values were not related with our population metric for either periphyton or macroinvertebrates.

With respect to fatty acids, macroinvertebrates tended to be characterized by monounsaturated fatty acids (MUFAs) and long-chain (i.e., ≥ 20 -carbons) polyunsaturated fatty acids (LCPUFAs), whereas periphyton tended to be characterized by short-chain (i.e., 16- and 18-Carbons) polyunsaturated fatty acids (SCPUFAs) (Table 1; Supporting Information Table S4; Figs. S5, S6). When comparing proportions within taxa across an increasing sewage gradient, periphyton SCPUFA proportions tended to increase and periphyton SAFA proportions generally decreased (Supporting Information Fig. S12). In contrast, benthic macroinvertebrate fatty acid proportions tended to remain consistent across the entire gradient (Supporting Information Fig. S12).

With respect to food web structure, stable isotope isospaces suggested that amphipods along our transect likely consumed periphyton (Fig. 4A). Results from our Bayesian mixing model (Supporting Information Fig. S13; RMSE = 0.105) further implied that diatom-associated fatty acids constituted approximately 84.6% (SD = 2.38%) of amphipods' diets, whereas *Draparnaldia* spp. and *Ulothrix* spp. fatty acid signatures constituted 8.7% (SD = 2.39%) and 6.7% (SD = 2.03%), respectively (Fig. 4B).

When assessing how grazing patterns may change over disturbance gradients, our analyses focused mainly on the fatty acids consistently associated with filamentous green algae (i.e., 18:3 ω 3, 18:1 ω 9, 18:2 ω 6, and 16:0) as well as diatoms (i.e., 20:5 ω 3, 16:1 ω 7, 14:0, and 16:0). For periphyton, the ratio of green filamentous: diatom-associated fatty acids significantly increased with an increasing PPCP concentration ($R^2 = 0.62$; $p = 0.04$, Fig. 5; Supporting Information Figs. S14,

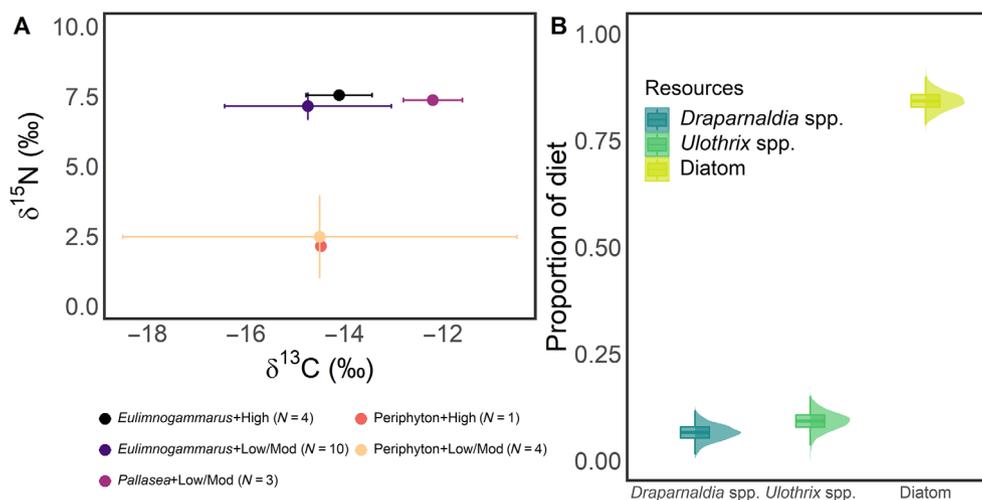


Fig. 4. Food web structure analyses as assessed by $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ stable isotopes (A) and fatty acids (B) using a Bayesian mixing model to estimate the proportion of three algal resources in the diets of *Eulimnogammarus vittatus* and *Eulimnogammarus verrucosus*. Mean and standard deviation $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values for littoral amphipods and periphyton are grouped by population metric values (Supporting Information Table S3).

Table 1. Mean inter-site fatty acid proportion of each fatty acid grouping for each taxon. Standard deviations are reported in parentheses. These groups include SAFA, MUFA, and SCUFA as well as LCPUFA.

Taxon	Number of sites	Branched	SAFA	MUFA	SCUFA	LCPUFA
<i>Draparnaldia</i> spp.	4	0.000 (0.000)	0.189 (0.014)	0.088 (0.030)	0.710 (0.045)	0.012 (0.004)
<i>Eulimnogammarus cyaneus</i>	2	0.002 (0.000)	0.248 (0.015)	0.309 (0.009)	0.182 (0.033)	0.259 (0.038)
<i>Eulimnogammarus verrucosus</i>	6	0.000 (0.000)	0.240 (0.061)	0.385 (0.017)	0.187 (0.036)	0.188 (0.051)
<i>Eulimnogammarus vittatus</i>	6	0.001 (0.000)	0.241 (0.025)	0.371 (0.039)	0.216 (0.021)	0.171 (0.032)
<i>Pallasea cancellus</i>	3	0.001 (0.000)	0.187 (0.062)	0.359 (0.027)	0.171 (0.051)	0.282 (0.021)
Periphyton	7	0.000 (0.000)	0.284 (0.048)	0.092 (0.054)	0.550 (0.102)	0.073 (0.006)
Snail	3	0.002 (0.000)	0.194 (0.018)	0.123 (0.005)	0.211 (0.021)	0.470 (0.034)

S15) but not necessarily with an increasing population metric ($p = 0.08$; Supporting Information Figs. S16, S18). *Eulimnogammarus verrucosus* fatty acid ratios were not significantly related with either increasing population metric (Supporting Information Fig. S16) or increasing PPCP concentrations (Fig. 5), but *Eulimnogammarus vittatus* filamentous : diatom ratios decreased with an increasing population metric ($p = 0.01$; Supporting Information Fig. S16) but not PPCP concentrations (Fig. 5). When focusing solely on the EFAs 18:3 ω 3, 18:2 ω 6, and 20:5 ω 3, the same patterns were observed in both periphyton and amphipods (Fig. 5; Supporting Information Fig. S16). Permutational analyses for both regression analyses supported these trends. The

p -values and R^2 values estimated for periphyton models were within the 5% margins in comparison to models produced with a randomized dataset (Supporting Information Figs. S14, S15, S17, S18). Model estimates for both *E. verrucosus* and *E. vittatus* were more reflective of those observed from randomized datasets (Supporting Information Figs. S14, S15, S17, S18).

Discussion

Our combined results corroborate previous findings (Timoshkin et al. 2016, 2018) that sewage pollution is entering Lake Baikal's nearshore area and likely is responsible for

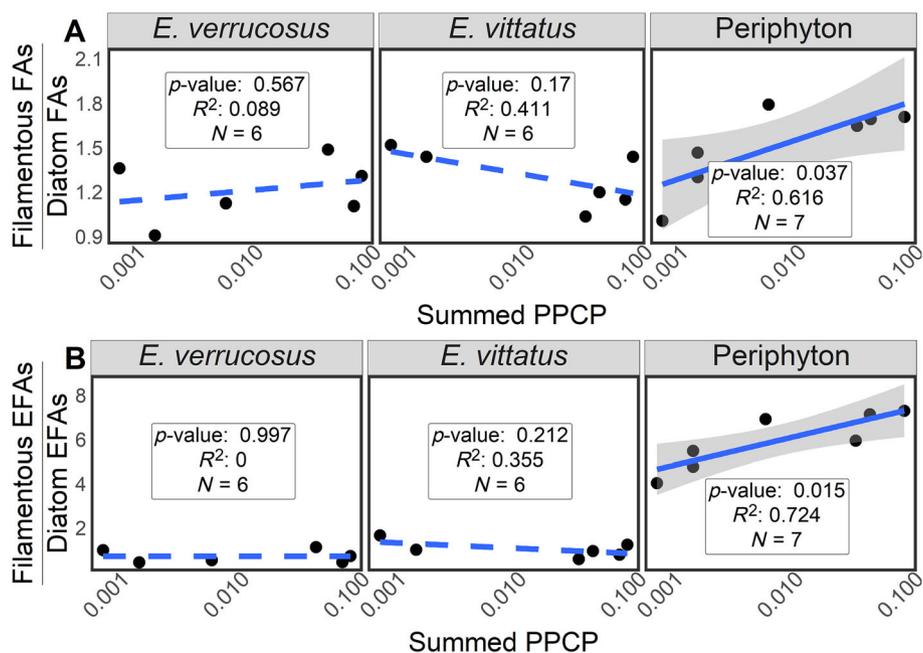


Fig. 5. Ratio of filamentous: diatom-associated fatty acids (A) and essential fatty acids (B) across our PPCP gradient. Our first analysis (A) focused solely on green filamentous algal fatty acids (i.e., 18:3 ω 3, 18:1 ω 9, 18:2 ω 6, and 16:0 relative to diatom fatty acids (i.e., 20:5 ω 3, 16:1 ω 7, 16:0, 14:0) in relation to increasing summed PPCP concentrations. Our second analysis (B) focused solely on the essential fatty acids (i.e., 18:3 ω 3, 18:2 ω 6, and 20:5 ω 3), which further highlights the trends observed in periphyton and macroinvertebrate grazers. Statistical results are from linear regressions. Solid lines with error envelopes indicate significant relationships, whereas non-significant models have dotted regression lines without error envelopes. Sample sizes are uneven among taxonomic groups due to some samples thawing upon transport to the United States from Siberia. See Meyer et al. (2021) for more details.

changes in nearshore benthic communities. Unlike previous studies, we were able to incorporate several highly specific indicators of sewage pollution and food web structure to describe direct, quantitative relationships between human development and ecological responses.

Relating human settlements to sewage indicator concentrations

In agreement with our expectations, some sewage pollution indicators in the nearshore of Lake Baikal were associated with size of and distance from human settlements. Summed PPCP concentrations, macroinvertebrate $\delta^{15}\text{N}$ values, and, to some degree, total phosphorus as well as ammonium concentrations increased with population metric values. Summed detected PPCP concentrations defined a sewage gradient that increased with the population metric. With the exception of cotinine, which significantly increased with an increasing population metric (Supporting Information Fig. S9), other individual PPCP concentrations showed weaker relationships, likely due to individual PPCP concentrations being highly heterogeneous in natural systems (Richmond et al. 2018). Sewage gradients created by highly localized settlements are noteworthy considering that Baikal's shoreline, including our study area, is largely free of lakeside development (Moore et al. 2009). Furthermore, the use of sewage-associated indicators, such as PPCPs and $\delta^{15}\text{N}$, proved necessary for defining sewage gradients. The use of nutrients as indicators alone would not reveal sewage pollution gradients, since nutrients were not strongly correlated with population metric values and could come from diverse sources. For example, melting permafrost in Lake Baikal's watershed (Anisimov and Reneva 2006) and the Selenga River basin (Tornqvist et al. 2014) as well as climate-driven changes in mixing processes (Swann et al. 2020) have the potential to contribute substantial nutrient loadings to the nearshore. While nutrients also could be contributed by agriculture (Powers et al. 2016) and changing terrestrial plant communities (Moran et al. 2012), these are not currently known to be major sources of elevated nutrients in the Baikal watershed, relative to sewage (Timoshkin et al. 2016, 2018), changing mixing patterns (Swann et al. 2020), forest fires (Kulikova et al. 2020), and permafrost melt (Anisimov and Reneva 2006).

This is the first study we know of to detect PPCPs in Lake Baikal, a large lake in a sparsely populated watershed. We detected PPCPs nearshore but not at our three offshore sites, suggesting that sewage inputs in Baikal become diluted as pollutants move out of the nearshore area. Beyond Lake Baikal, these data are important for furthering our understanding of PPCP prevalence in lakes, as lakes have remained far less represented in the PPCP literature (7% of publications) in comparison to lotic and subsurface systems (66% of the PPCP literature; Meyer et al. 2019). This literature imbalance creates opportunities to assess how PPCPs, and sewage pollution more broadly, may lead to differing ecological responses in lotic and

lentic systems. As lakes tend to have longer hydraulic residence times relative to rivers and streams, pollutants entering lakes may be more prone to accumulate in certain areas and create hot spots within the larger system (Meyer et al. 2019). In the case of our data, comparing contemporaneous littoral and pelagic PPCP concentrations revealed littoral-pelagic sewage gradients, as PPCPs were potentially degraded, metabolized or accumulated by biota, preserved within sediments, or diluted to undetectable concentrations. Furthermore, while we focus on PPCPs as indicators of sewage, they may also be directly harmful to biota, as previous studies have shown that PPCPs, even at concentrations we observed in Lake Baikal, can elicit biological responses from physiological (Feijão et al. 2020) and behavioral effects (Brodin et al. 2013) to food web bioaccumulation (Richmond et al. 2018) and ecosystem processes (Robson et al. 2020). Although our study was not designed to evaluate the ecotoxicological effects of PPCPs themselves, future studies could address effects of PPCPs on nearshore Baikal biota by using in situ sewage gradients as a guide to understanding typical ranges and variation of PPCP concentrations.

In contrast to PPCP concentrations and $\delta^{15}\text{N}$ values, microplastics were not associated with our population metric and may be poor proxies for sewage pollution in Lake Baikal. In addition, microplastics may originate from non-sewage sources, such as fishing nets (Moore et al. 2022), may be influenced by seasonal runoff patterns and watershed-scale properties (Lebreton et al. 2017), and may be subject to complex transport dynamics such as atmospheric deposition (Evangelidou et al. 2020), although atmospheric deposition in Siberia may be low relative to rates experienced globally (Brahney et al. 2021). Because of their long degradation time, microplastics may indicate accumulated pollution, which likely enables wider distribution (Hendrickson et al. 2018). Microplastic concentrations in Baikal, as quantified by our methods, may be poor proxies for capturing pollution from seasonally varying human populations or identifying sewage pollution more broadly. It is worth noting that since the time of our field sampling, evidence has accumulated that the methods we followed likely dramatically underestimated (Brandon et al. 2020) microplastic abundance. Recent studies also suggest that microfibers can easily be mischaracterized as microplastics when they are actually natural in origin (Lusher et al. 2020; Suaria et al. 2020) although our estimates should be highly conservative as we enumerated only artificially colored microplastics (e.g., neon red, no visible biological structures) and not clear or transparent microplastics.

Although we focus here on microplastics as an indicator of sewage pollution, microplastics themselves are increasingly shown to cause deleterious ecological consequences, such as disrupting food web dynamics by altering grazing patterns (Green 2016) and providing carbon substrate for microbial growth (Romera-Castillo et al. 2018). Recent investigations of microplastics in Lake Baikal near Bolshie Koty (BK) used

analogous methods and measured similarly low concentrations of larger microplastics (e.g., <330 μm ; Karnaukhov et al. 2020); yet methods that quantify smaller microplastics have enumerated 2–3 orders of magnitude more microplastics per volume than we recorded (Moore et al. 2022). Moore et al. (2022), however, attributed the majority of microplastics in Lake Baikal as originating from shoreline debris and not sewage pollution. Nevertheless, when considering Lake Baikal's large volume, Karnaukhov et al. (2020) noted that the number of plastic pieces may well exceed those observed in other lakes, such as Lake Hovsgol (Free et al. 2014) and many lakes worldwide (Tanentzap et al. 2021; Supporting Information Fig. S19). Together these growing uncertainties around the abundance and transport of microplastics in Lake Baikal suggest that microplastic pollution in Lake Baikal and freshwater systems elsewhere deserves increased attention.

Relating sewage indicators with benthic algal communities

Congruent with our hypotheses, increasing sewage indicators tended to be associated with higher relative abundance of filamentous taxa in periphyton. Previous studies investigating Baikal's periphyton composition noted that areas adjacent to human development often had an increased relative abundance of filamentous algae such as *Ulothrix* spp. and *Spirogyra* spp. (Timoshkin et al. 2016, 2018). Lake Baikal's southwestern shore historically experiences short *Ulothrix* spp. blooms in late August (Kozhov 1963), potentially confounding sewage signals with an annually occurring phenomenon. Although the potential does exist for both diatoms and filamentous taxa to increase in numerical abundance with increasing sewage pollution, our data are consistent with the results of Timoshkin et al. (2016) and show that relative abundance of filamentous algae is greatest near areas of higher lakeside development.

Even as community composition shifted with increasing sewage indicator concentrations, periphyton $\delta^{15}\text{N}$ values did not differ along our transect. Previous studies in marine (Gartner et al. 2002) and freshwater (Camilleri and Ozersky 2019) systems have shown sewage-associated increases in $\delta^{15}\text{N}$ values in algal samples and through the food web. Like PPCPs in our study, $\delta^{15}\text{N}$ values are often most enriched near the source of sewage pollution and can decrease over several kilometers with concentrations varying based on species-specific uptake rates and mixing processes (Gartner et al. 2002). While previous studies using $\delta^{15}\text{N}$ values in macroalgae and vascular macrophytes have successfully tracked sewage gradients (Gartner et al. 2002), periphyton $\delta^{15}\text{N}$ as a sewage indicator potentially can be confounded by terrestrial $\delta^{15}\text{N}$ contributions such as agricultural runoff (Chang et al. 2012). In our study, periphyton $\delta^{15}\text{N}$ values may be explained by periphyton's typically high cell turnover rates (e.g., days; Swamikannu and Hoagland 1989) that dampened isotopic patterns, $\delta^{15}\text{N}$ -accumulating algal taxa being grazed more readily by macroinvertebrates (Rosenberger et al. 2008), or co-limitation dynamics between ammonium and nitrate (Piñón-Gimate et al. 2009).

Fatty acid analyses suggested that changes in periphyton community composition altered the nutritional quality of periphyton across the pollution gradient. Periphyton fatty acid profiles from sites with higher sewage pollution had higher cumulative proportions of 18:3 ω 3, 18:1 ω 9, 18:2 ω 6, and 16:0 relative to cumulative 20:5 ω 3, 16:1 ω 7, 16:0, and 14:0 fatty acid proportions. This pattern likely reflects the higher abundance of green algae relative to diatoms (Osipova et al. 2009; Galloway and Winder 2015; Shishlyannikov et al. 2018), which we observed from our periphyton community composition analysis (Fig. 3A). Together, our periphyton composition and fatty acid results suggest that Baikal's near-shore periphyton communities near human lakeside developments are more dominated by filamentous green algae and have lower nutritional content.

Among the array of fatty acids synthesized in algal communities, EFAs are most likely to be taxonomically associated with, and influenced by, changing community composition. EFAs are a subgroup of PUFAs that are prone to accumulating in organisms and are usually synthesized by primary producers (Taipale et al. 2013; Galloway and Winder 2015). Among the eight common EFAs (Taipale et al. 2013), 18:3 ω 3, 18:2 ω 6, and 20:5 ω 3 had the highest coefficients of variation between sites (Supporting Information Table S5). Because these three EFAs demonstrated the greatest variation between sites, our analyses focused on how their relative abundances related to PPCP concentrations and population metric values. The fatty acids 18:3 ω 3 and 18:2 ω 6 have been previously associated with filamentous algae, such as Baikalian *Ulothrix* spp. (Osipova et al. 2009) and *Draparnaldia* spp., whereas 20:5 ω 3 has been associated with Baikalian diatoms (Shishlyannikov et al. 2018). These differences in EFAs can be consequential for higher trophic levels, as 20:5 ω 3 is associated with increased growth and reproductive rates in zooplankton (Brett and Müller-Navarra 1997). In contrast, 18:3 ω 3 is a precursor to 20:5 ω 3, but the energy cost for aquatic grazers to upgrade 18:3 ω 3 to 20:5 ω 3 may be too metabolically expensive relative to simply consuming 20:5 ω 3 directly from diatom primary producers (reviewed in Brett and Müller-Navarra 1997). Comparing the ratio of filamentous green algae to diatoms could therefore function as proxy for each algal taxon's relative abundance and potentially offer insights into feeding patterns for the grazers.

Relating sewage indicators with macroinvertebrate feeding guilds

In assessing benthic consumer communities' responses to changing periphyton, our data suggest macroinvertebrate guilds reshape with increasing sewage pollution. Our results support the general conclusion of Timoshkin et al. (2016) that Baikalian mollusk abundance tends to decrease with increasing sewage pollution. Decreased mollusk abundance may have several causes, including low tolerance for increased concentrations of PPCPs or other components of sewage (Timoshkin

et al. 2016), inability to consume filamentous algae (Mazzella and Russo 1989), or filamentous algae not offering the proper nutrition (Lowe and Hunter 1988). In contrast to mollusks, amphipods were generally prevalent at all littoral sites, regardless of sewage indicator concentrations. *Brandtia* spp. was the only amphipod genus less abundant with sewage indicator signals. This genus tends to be associated with endemic sponges (Taakhteev & Didorenko, 2015), which may also be decreasing in abundance near areas of lakeside development (Timoshkin et al. 2016). *Eulimnogammarus* spp., one of the most speciose Baikal genera (Takhteev and Didorenko 2015), was prevalent at all sites, and $\delta^{15}\text{N}$ values in its tissue increased significantly with increasing population metric values but not enough to suggest that amphipods became detritivorous or carnivorous (e.g., less than 2‰ $\delta^{15}\text{N}$). Unlike periphyton, amphipods' increasing $\delta^{15}\text{N}$ values with indicators of sewage pollution may relate to amphipods having longer cellular turnover rates (e.g., weeks) relative to periphyton. Consequently, amphipods' enhanced $\delta^{15}\text{N}$ values suggest that amphipods may be integrating sewage-derived nutrients into the food web. While we did not test amphipod tissues for other sewage indicators such as PPCPs and microplastics, the potential for some PPCPs to accumulate in food webs has been recently demonstrated, with ecological ramifications remaining uncertain (Richmond et al. 2018). These combined results suggest that mollusk abundance and amphipod $\delta^{15}\text{N}$ values may be longer-term indicators of sewage pollution in Baikal, where mollusk abundance may be indicative of community compositional shifts and amphipod $\delta^{15}\text{N}$ values are indicative of how wastewater-derived nutrients may be entering the food web.

In contrast to variation in $\delta^{15}\text{N}$ values, amphipod fatty acid profiles did not differ markedly between sites (Fig. 5; Supporting Information Figs. S14–S18). Amphipods from all collected sites expressed consistent 20:5 ω 3 signatures relative to 18:3 ω 3 and 18:2 ω 6. Consumers usually accumulate fatty acids from their food source. Yoshii's (1999) study as well as our own stable isotope data suggest that Baikal's benthic, littoral amphipods are likely a combination of grazers and omnivores. Because fatty acid profiles in amphipods largely reflected fatty acid signatures in periphyton, our data suggest that amphipods likely continue grazing on periphyton, despite the food resource changing in community composition and nutritional content. In particular, results from our mixing model suggest that diatoms constitute a large majority of amphipods' diets (Fig. 4B), even though diatoms tended to be less abundant in periphyton communities relative to filamentous taxa along the gradient of increasing sewage pollution (Fig. 3A). As a consequence, amphipods may be compensating for the shifting nutritional quality of periphyton through at least three potential mechanisms. First, amphipods may selectively consume diatoms as opposed to filamentous algae. When living diatoms become less abundant, amphipods may become detritivorous, as detrital fatty acids tend to reflect the composite fatty acids of the

community (Vonk et al. 2016). Because amphipods' fatty acid signatures still reflected a diatom-associated diet (Figs. 4B, 5; Supporting Information Fig. S16), our results imply that even detritivorous amphipods may rely on decomposing diatoms for maintaining consistent nutrition along the disturbance gradient. Second, amphipods themselves (Pilecky et al. 2021) or symbionts (Yoshioka et al. 2019) may upgrade fatty acids by investing energy to convert C18 fatty acids to C20 fatty acids. Third, amphipods may migrate to deep littoral zones (e.g., 10–100 m), where diatoms may be more abundant, but then return to shallow littoral areas where breeding occurs (e.g., < 10 m; Takhteev and Didorenko 2015). Regardless of the exact mechanism, our data suggest that food web interactions and the intensity of those interactions would change with increasing sewage pollution and may impose an energetic cost through amphipods' differential grazing patterns.

Conclusions

Over the past decade, Lake Baikal has shown signs of near-shore eutrophication, despite the pelagic zone remaining ultra-oligotrophic. While Baikal receives nutrients from multiple sources, sewage-specific indicators used in this study implicate wastewater pollution as one of the sources of nutrients. Our results demonstrate how patchy hot spots of lakeside development at Baikal can create gradients in sewage concentrations and ecological responses. Unlike previous work, our approach pairs community abundance data (i.e., periphyton and macroinvertebrate counts) and nuanced dietary tracers (i.e., fatty acids) to assess benthic community and food web consequences of sewage pollution. While sewage pollution may lead to changing resources for macroinvertebrate grazers, Baikal's amphipods appear to be compensating either (1) by increasingly grazing on diatoms, (2) by switching from herbivory to detritivory, or (3) by consuming less desirable food and upgrading fatty acids. In all of these cases, our results suggest shifting community interactions and may imply an energetic cost for amphipods, as they expend energy either by foraging selectively for diatoms or by catabolizing certain essential fatty acids.

Future trajectories: A call for increased nearshore monitoring

Our results underscore the importance of nearshore monitoring in detecting sewage pollution in large lakes. While pelagic samples are representative of the lake's overall status, nearshore sampling aids managers in identifying pollution loading before the entire system is affected (Hampton et al. 2011). Beyond Baikal, several large, deep, oligotrophic lakes have also experienced localized sewage pollution with nearshore biological responses (Jacoby et al. 1991), despite pelagic measurements suggesting oligotrophic status (Jacoby et al. 1991; Rosenberger et al. 2008; Hampton et al. 2011). Once eutrophication of the open water has occurred, mitigation can involve complex socio-economic factors (Carpenter

et al. 1999), require system-specific information (Jeppesen et al. 2005), and necessitate long-term strategies (Tong et al. 2020). Because nutrients may enter systems from numerous sources, incorporating sewage-specific indicators, such as PPCPs, may be helpful to identify sewage-associated nutrient pollution and assess heterogeneities in sewage loading along a shoreline. When PPCP data are available and paired with co-located benthic community composition and food web data, managers can take system-specific actions to mitigate ecological consequences before sewage concentrations are detected throughout the lake. Across larger spatial and temporal scales, these paired PPCP-biological samples have potential to offer a synoptic view of the impacts of sewage pollution, enabling regional and local monitoring to coordinate mitigation strategies.

Data availability statement

The data from this study are publicly available at the replicate level from the Environmental Data Initiative (Meyer et al. 2020) as well as the Open Science Framework repository (Meyer et al. 2015).

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Conflict of Interest

None declared.

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