Environ Monit Assess (2025) 197:944
https://doi.org/10.1007/s10661-025-14275-0

RESEARCH

Freshwater bioindicators demonstrate sensitivities to potential changes from climate and mineral development in Alaska

Rebecca Shaftel · Erin Larson · Dan Bogan · Birgit Hagedorn · Dustin Merrigan · Sarah O'Neal · Daniel Rinella · Carol Ann Woody

Received: 12 March 2025 / Accepted: 19 June 2025

Abstract In Bristol Bay, Alaska, headwater streams support the world's largest, most valuable sockeye salmon fishery, but face an uncertain future due to climate change and proposed development. We used a framework based on pre-impact data to identify sensitive taxa and evaluate their potential as freshwater bioindicators for climate change and mineral development in the relatively undisturbed Lime Hills ecoregion of Bristol Bay. We identified sensitive taxa as those associated with distinct stream physical habitat types and those with published sensitivities to expected changes from climate or mineral development (e.g., increasing temperatures, acidity, conductivity, sedimentation, or general pollution). Using a 12-year dataset of stream macroinvertebrates and diatoms, we also investigated patterns over time in community composition and taxa presence. We identified five fish, 23 macroinvertebrate, and 26 diatom bioindicators with high interannual persistence in Bristol Bay wadeable streams that are also sensitive to either habitat change or future stressors. Stream benthic community composition has shifted over the past 12 years for both macroinvertebrates and diatoms, but we found few trends in individual taxa. The final bioindicator list can be used to measure future changes in stream habitats and communities of the Lime Hills ecoregion. Our framework used baseline data that captured both spatial and temporal variability in sensitive taxa and has utility for other pristine subarctic ecosystems prior to potential impacts.

Keywords Biomonitoring · Macroinvertebrate · Diatom · Fish · Bristol Bay · Mining · Climate change

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10661-025-14275-0.

R. Shaftel (✉)
Bureau of Land Management, Anchorage, AK, USA
e-mail: rshaftel@blm.gov

R. Shaftel · E. Larson · D. Bogan · D. Merrigan
Alaska Center for Conservation Science, University of Alaska Anchorage, Anchorage, AK, USA

E. Larson
Alaska Pacific University, Anchorage, AK, USA

B. Hagedorn
Sustainable Earth Research, LLC, Anchorage, AK, USA

S. O'Neal
School of Aquatic and Fisheries Sciences, University of Washington, Seattle, WA, USA

D. Rinella
U.S. Fish and Wildlife Service, Southern Alaska Fish and Wildlife Conservation Office, Anchorage, AK, USA

C. A. Woody
Fisheries Research & Consulting LLC, Fort Collins, CO, USA

Introduction

The Bristol Bay region in Southwest Alaska supports the largest sockeye salmon (*Oncorhynchus nerka*)

Published online: 24 July 2025

runs in the world (Ruggerone & Irvine, 2018). There are nine major river systems that drain into the bay, and the Kvichak and Nushagak rivers have historically produced up to half of the total sockeye salmon in the region. In addition to sockeye salmon, freshwater habitats in these watersheds support the other four species of North American Pacific Salmon (*Oncorhynchus* spp.) and at least 24 other anadromous and resident fish species (Woody, 2018). These populations contribute to valuable commercial, sport, and subsistence fisheries, with economic effects well beyond Alaska. For example, average annual returns of 50 million sockeye salmon have resulted in a direct annual value of $263 million to commercial harvesters and over 8000 jobs (McKinley Research Group, 2021). Salmon are also central to the cultural, spiritual, and economic well-being of Native Alaskans (Carothers et al., 2021), provide important food resources to local subsistence users, and support over 2000 tourism jobs through sportfishing and bear viewing (McKinley Research Group, 2021). Despite their immense local and global value, Bristol Bay salmon fisheries face an uncertain future due to climate change and proposed mineral development.

Climate change is altering freshwater habitats rapidly in western Alaska. These changes include warmer air temperatures (Rantanen et al., 2022) and changes to the form of seasonal precipitation (McAfee et al., 2013), which act in concert to decrease snowpack. Decreased snowpack then influences both the seasonality and magnitude of stream discharge (Wobus et al., 2015) and can lead to losses in thermal diversity across the stream network (Cline et al., 2020; Lisi et al., 2015). Glaciers in the Alaska Range are contributing increasing amounts of runoff to streamflow in some rivers, but annual glacier runoff is expected to peak in the next century, after which runoff will decrease (Huss & Hock, 2018). Glacier retreat may negatively impact salmon populations as streamflows decrease and stream temperatures warm (Pitman et al., 2020). Additional large-scale ecosystem changes may occur in the future from mining that has been proposed in the Bristol Bay region (Seal, 2018) such as direct loss of stream habitats and indirect impacts to water quantity and water quality from development of a large open-pit mine and the associated infrastructure (USEPA, 2014). Measuring ecological impacts of these changes requires development and maintenance of long-term physical, chemical, and biological monitoring networks to distinguish community responses to these stressors from those caused by natural fluctuations in populations.

However, biomonitoring studies typically take place after stressors, such as mining, logging, or urbanization, occur and therefore rely on reference sites and monitoring during recovery to establish baseline conditions (Armitage et al., 2007; Cianciolo et al., 2020; DeNicola & Stapleton, 2014; Hopkins et al., 2013; Kotalik et al., 2021). When feasible, a better approach captures adequate baselines prior to change. A useful baseline should include multiple taxonomic groups and their natural variation to understand heterogeneity in species composition unrelated to stressors (Humphrey et al., 1995). In freshwaters, select taxonomic groups could include benthic invertebrate communities and fish, which differ in mobility and lifespan.

For several reasons, the sampling of multiple biological assemblages (e.g., macroinvertebrates, diatoms, and fish) can improve the detection of impacts to stream habitats (Karr & Chu, 1999). Aquatic organisms have lifespans from days to years and integrate environmental conditions over time (Hodkinson & Jackson, 2005). Depending upon an organism's mobility, they may reflect the aggregate impact of multiple stressors over scales from stream reaches to watersheds. Finally, different taxa within and among communities are sensitive to different types of impacts (Hughes et al., 2000). Biomonitoring using stream communities has been used for a long time to document habitat impacts, especially relative to climate change (Burgmer et al., 2007; Crozier et al., 2021; Durance & Ormerod, 2007; Heino et al., 2009; Lawrence et al., 2010; Piggott et al., 2015), mining (Clements et al., 2000; Hirst et al., 2002; Hodkinson & Jackson, 2005; Hogsden & Harding, 2012; Milner & Piorkowski, 2004; Smucker et al., 2014; Wagener & LaPerriere, 1985), and urbanization (Cuffney et al., 2010; Hodkinson & Jackson, 2005; King et al., 2011; Smucker et al., 2013).

Shifts in freshwater community composition provide an integrated metric of population responses to changing environmental conditions (Kendrick et al., 2019; King & Baker, 2010). Community responses provide important redundancy by capturing multiple sensitive taxa when individual sensitive taxa may be missing from a sample due to chance or variation in population size. Knowledge about the sensitivity of individual taxa to various stressors is important for interpretation of community responses and also provides an alternative response at a finer level of organization (Hodkinson & Jackson, 2005). Identification of indicator taxa within freshwater biological communities (e.g. bioindicators) can provide early signs of degraded habitat conditions and direct links to impairment causes where continuous or regular monitoring of freshwater physical and chemical conditions is not feasible (Carignan & Villard, 2002; Holt & Miller, 2010). Suggested criteria for selecting bioindicators include choosing habitat specialists that can indicate deterioration of specific habitat types, choosing species that respond negatively to human disturbances, or species that respond to a particular stressor (Carignan & Villard, 2002; Hodkinson & Jackson, 2005; Siddig et al., 2016).

Variation in taxa presence or abundance over space and time can yield supplemental information useful for bioindicator selection. Spatial sampling can capture species' habitat preferences or prevalence in a region. Temporal sampling (e.g., within or across years) can capture expected variation in response to natural disturbances, seasonal phenology, or changing habitat conditions (e.g., streamflows, stream temperatures, and chemistry. Developing a monitoring program for freshwater communities in an ecologically important region like Bristol Bay allows for identification of natural communities and bioindicators. These responses can be used to identify habitat alterations from stressors such as climate change or future development.

The objectives of this research in the southern portion of the Lime Hills ecoregion include: (1) identify freshwater taxa in the region that may be sensitive to future impacts from climate change and mineral development, (2) evaluate the list of recorded freshwater taxa as potential bioindicators for the region based on their persistence over time and distribution across wadeable streams, and (3) investigate long-term changes in stream benthic communities. Combined, these objectives provide an important baseline against which any future stream habitat and biological community responses to climate change and potential mineral development in an important ecoregion of Alaska can be assessed. Previous biological monitoring projects in the Nushagak and Kvichak watersheds included a study of stream benthic communities (diatoms and macroinvertebrates) and habitats from 78 hard-bottomed wadeable streams (Bogan et al., 2018) and sampling of freshwater fish communities from 105 headwater streams that resulted in additional regulatory protections for 168 km of streams with anadromous salmon (Woody & O'Neal, 2010). These prior monitoring projects strategically selected sites to meet different objectives and may not represent the range of diversity in communities and habitats in these important watersheds, unlike this study. Based on similar monitoring efforts elsewhere in Alaska, we developed several hypotheses linked to our objectives: (1) Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa that are prevalent in Bristol Bay (Bogan et al., 2018) would be sensitive to a range of stressors and useful for bioindication; (2) identifying bioindicator taxa would be challenging as few taxa are common across the diversity of stream types within an ecoregion and interannual variability can be high (Milner et al., 2006); and (3) we expected that rapid rates of environmental change in Alaska (Rantanen et al., 2022) would be driving changes in freshwater biological communities, even over a single decade.

Methods

To develop an unbiased estimate of freshwater communities and habitats across the full spectrum of habitats in the Lime Hills ecoregion of Bristol Bay (Fig. 1), we used a probabilistic study design in which streams were sampled randomly and had an equal chance of being selected for monitoring. We sampled fish, macroinvertebrates, diatoms, and physical and chemical habitat conditions to address our three objectives focused on identifying sensitive taxa, evaluating potential bioindicators, and assessing long-term changes in benthic communities (Fig. 2). Detailed methods were written previously for project reports that are publicly available online and are summarized here (see Data Availability statement, Hagedorn et al., 2020; Shaftel et al., 2019). We refer readers to these reports and references therein for more detailed descriptions of the field and laboratory methods and analyses (see Data Availability statement).

Study area

Our study area included the southern portion of the Lime Hills ecoregion that includes parts of the

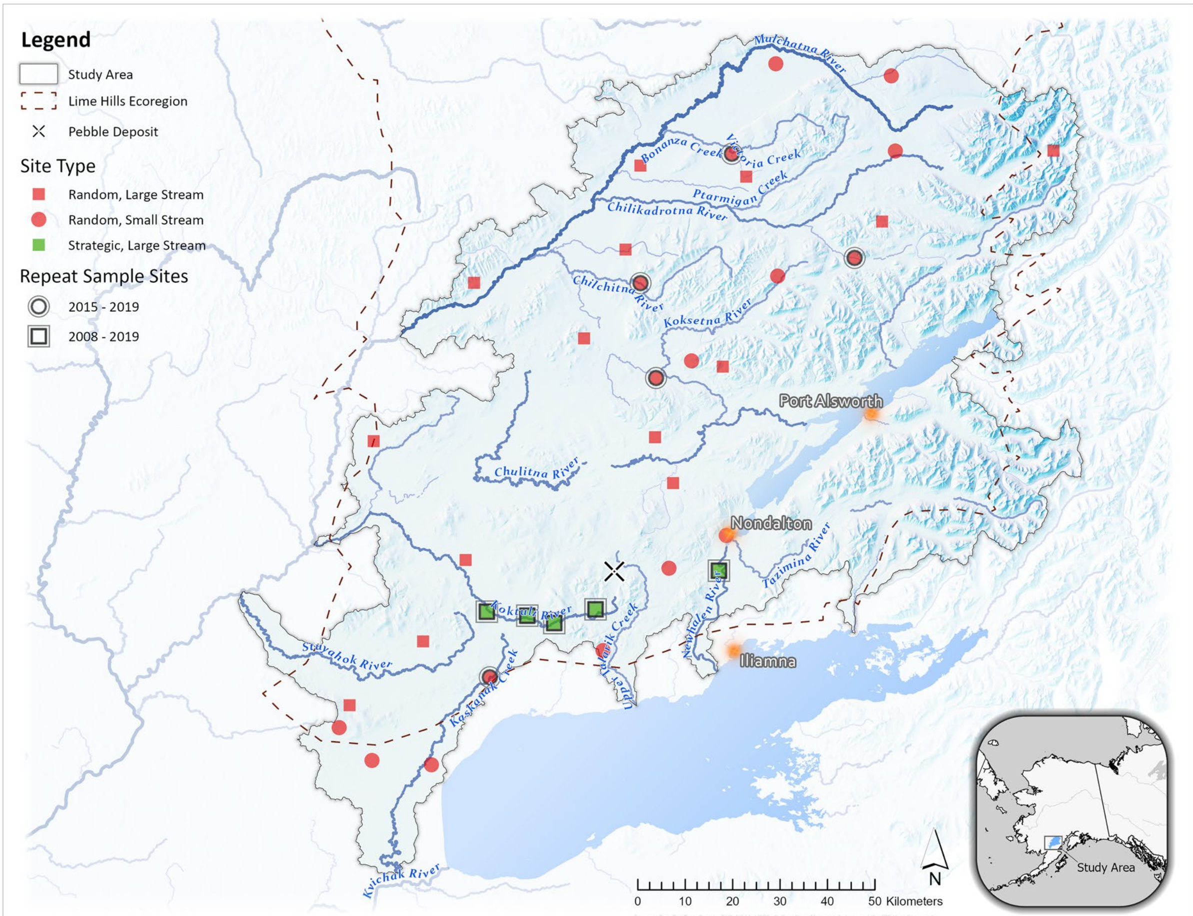

Fig. 1 Map of sampling locations across the study area, which includes the portion of the Lime Hills ecoregion that drains to Bristol Bay. All 35 sites shown on the map were sampled in 2015: 30 randomly selected sites and five strategically selected sites are shown with orange and green colors, respectively. Small (1st and 2nd order) and large (3rd and 4th order) streams were included as strata in the probabilistic study design and are symbolized as circles and squares, respectively. Five sites sampled annually from 2015 to 2019 are indicated by black circles and five long-term sites sampled annually from 2008 to 2019 are indicated by black squares. All repeat sampling sites are located on large streams

Mulchatna River and Kvichak River watersheds (Woody et al., 2014) (Fig. 1). Average monthly air temperatures in Iliamna, the largest community in the study area, are below freezing from November through March. The coldest temperatures occur in January (−7.5 °C), the warmest temperatures occur in July (14.3 °C), and average annual precipitation is 635 mm, approximately one-third of which falls as rain during the summer months (Palecki et al., 2021).

We delineated the study area boundary by selecting all 6th level hydrologic units in the Lime Hills ecoregion that drain to Bristol Bay. These watersheds drain approximately 15,600 km^2 from 15 to 1800 m in elevation and include a potential mining district associated with the Pebble deposit. Several of the large rivers are sourced by glaciers in the Alaska Range, although no glaciers are located within the study area boundary. Shrub and tundra vegetation are common throughout the study area whereas mixed forests are restricted to lower elevations (Nowacki et al., 2002).

Study design

We used a probabilistic study design to sample streams representing Pacific salmon habitat in 2015

Dataset A - Fish, macroinvertebrates, and diatoms from 30 randomly-selected sites sampled in 2015
Dataset B - Macroinvertebrates and diatoms from 5 strategically-selected sites and 5 randomly-selected sites sampled from 2015 to 2019
Dataset C - Macroinvertebrates and diatoms from 5 strategically-selected sites sampled from 2008 to 2019
Dataset D - Physical habitat measurements from 30 randomly-selected sites sampled in 2015
Dataset E - Water chemistry parameters from 30 randomly-selected sites sampled in 2015

Objective 1. Identification of sensitive taxa

1. Used hierarchical cluster analysis and **dataset D** to define physical habitat types.
2. Visually explored differences in physical habitat types using PCA and **datasets D and E** (Figure 3).
3. Used Indicator Species Analysis to associate **dataset A** with physical habitat types.
4. Reviewed published literature to identify taxa with sensitivities to specific stressors associated with climate change and mineral development.
5. Combined lists from steps 3 and 4 into Tables S2-S4.

Objective 2. Evaluation of sensitive taxa as bioindicators

1. Calculated mean abundances and frequencies from **dataset A** using sensitive taxa from Objective 1.
2. Calculated persistence from **dataset B** using sensitive taxa from Objective 1.
3. Evaluated potential bioindicators using overall sensitivity to different stressors, persistence, and frequencies (Figure 4 and Table 1).

Objective 3. Long-term change in benthic communities

1. Harmonized **dataset C** to account for differences in nomenclature and sampling methods over time.
2. Explored changes in community composition using NMS and successional vectors (Figure 5).
3. Analyzed changes in community composition and taxon abundances over time using multivariate generalized linear models.

Fig. 2 Description of datasets and analysis steps for each of three study objectives

(Stevens & Olsen, 2004). Sites were selected from a stream network developed for the Nushagak and Kvichak watersheds (Woll et al., 2012). We restricted site selection to first-through fourth-order streams with gradients of 10% or less. We removed stream reaches inaccessible to salmon (e.g., above waterfalls or above reaches with gradient greater than 20%) and short streams (< 1-km first-order streams). After that filtering, the sample frame consisted of 12,434 km of streams, 72% of which were first- or second-order headwater streams.

We used the spsurvey package in R to select a spatially balanced sample of sites from the final sample frame (Dumelle et al., 2023). One to two streams were sampled every day in June 2015 to total 30 sites (datasets A, D, and E in Fig. 2). The sites included 18 large and 12 small streams (Fig. 1, "Random"). Some sites were rejected during implementation of the study design because they did not represent our target population of wadeable streams (e.g., map error, wetlands, or too steep). After accounting for these rejections, we estimated 6991 km of wadeable streams in the study area (95% CI 5259–8723 km) that are represented by our final set of sample sites. The June sampling period was selected to capture base-flow conditions, and sampling in future years (2016–2019) was also conducted during June. Data were collected within defined stream reaches surrounding the sample point. Stream reaches were defined according to EPA protocol as 40 times the mean wetted width or 150 m, whichever was greater (USEPA, 2013).

We continued our sampling at a subset of sites to capture interannual variability in stream benthic communities and to extend a long-term analysis of benthic community change (datasets B and C in Fig. 2). We sampled ten sites annually from 2016 to 2019 to evaluate taxa persistence (Objective 2), which included five random sites and five long-term monitoring sites (Fig. 1, "Repeat Sampling Sites"). The five long-term monitoring sites were strategically selected in 2008 because of their proximity to the Pebble deposit in the southwest region of the study area, and we used data through 2019 to investigate changes in benthic communities over a 12-year period (Objective 3).

Field and laboratory methods

Water quality measurements included both in situ parameters and samples analyzed after fieldwork which were completed in the Applied Science, Engineering, and Technology (ASET) Laboratory at the University of Alaska Anchorage (UAA). In situ parameters included dissolved oxygen, pH, temperature, and specific conductance. Alkalinity samples were collected and analyzed in the field each day. Laboratory parameters included 26 dissolved and total metals, dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), and total dissolved nitrogen (TDN).

Physical habitat data were collected using the U.S. EPA's National Rivers and Streams Assessment methods (USEPA, 2013). Measurements were collected at 11 transects within each reach and focused on stream substrates, stream channel dimensions (e.g., widths and depths), riparian cover and fish cover in the stream, wood volumes, and reach characteristics (e.g., sinuosity and watershed area). We used the aquamet library (personal communication with Karen Blocksom, U.S. EPA, March 14, 2017) and the R statistical platform (R Core Team, 2023) to calculate physical habitat metrics from the measurements taken at each stream reach.

Fish were sampled by electrofishing using a Smith-Root Model LR-24 backpack electro-fisher (Smith-Root, Vancouver, Washington). We identified all fish to species, except for sculpin (*Cottus* sp.), lamprey (*Lampetra* sp.), and whitefish (*Coregonus* sp.), which were identified to genus. We tallied all fish at each site and released them within 60 min of capture. We standardized fish counts to numbers per 100 m. All fish methods followed an approved IACUC protocol (PI—Ray Hilborn, #3142–01) through the University of Washington.

Macroinvertebrates and diatoms were sampled according to USEPA protocols (2013). Both communities were sub-sampled at 11 transects and composited to form a single sample for the reach. All benthic community samples were processed at UAA.

Macroinvertebrate samples were sub-sampled in the laboratory to obtain a fixed count of 500 +/− 20% organisms. The remaining sample was searched for 5 min to locate additional large and rare taxa. All insects were identified to genus or lowest practical taxonomic level, including Chironomidae. Non-insects were identified to a higher taxonomic level (usually family or order). Taxonomic keys for macroinvertebrates included Pennak (1989), Wiggins (1996), Thorp and Covich (2001) Stewart and Oswood (2006), Merritt et al. (2008), and Andersen et al. (2013).

Diatom samples were processed and slide mounted in the lab. A fixed count of 600 diatom valves was identified to species or lowest practical taxonomic level. The primary taxonomic references used were Patrick and Reimer (1966 and 1975), Krammer and Lange-Bertalot (1986, 1988, and 1991), Krammer (2000, 2002, and 2003), Lange-Bertalot (2001), and Lange-Bertalot et al. (2011). The Diatoms of North America website (diatoms.org) and AlgaeBase (algaebase.org) were used to update the taxonomy as needed.

Data analysis

Identification of sensitive freshwater taxa

We identified sensitive taxa from the fish, macroinvertebrate, and diatom communities using two criteria: (1) taxa that are characteristic of distinct stream types based on physical habitat metrics and (2) taxa that have published sensitivities to climate change or mineral development (Objective 1 in Fig. 2). We focused on identifying taxa from streams representing distinct physical habitat types because we expected they would represent less dynamic conditions than water chemistry samples collected at a single point in time. Additionally, our water chemistry dataset spanned a limited range of conditions that might drive responses in biological communities or represent expected environments from future climate change (e.g., warm stream temperatures) or mineral development (e.g., low pH). We limited our list to taxa that occurred in at least 10% of sites (three or more) in the probabilistic survey. All data analyses were conducted in R (R Core Team, 2023).

We selected 12 physical habitat variables calculated from field measurements to define habitat types: average depth across the reach (cm), bankfull width to depth ratio (unitless), relative bed stability (unitless), mean canopy cover (trees greater than 5 m in height, %), woody debris volume (m^3/100 m), mean channel gradient (%), geometric mean ($\log_{10}$ (mm)) and standard deviation of particle diameters, total residual pool length (m/reach), sinuosity (unitless), elevation (m), and watershed size (km^2). We identified habitat types using hierarchical cluster analysis. Habitat variables were scaled, converted to a distance matrix using Euclidean distances, and grouped using Ward's minimum variance method. We selected the number of physical habitat types by evaluating cluster stability across solutions of two to six groups. We used the R package fpc (Hennig, 2015) to assess cluster stability using 500 bootstrapped samples of the data. Jaccard similarities were used to compare groups in the bootstrap samples with groups in the observed data. The mean Jaccard similarity was calculated over all bootstrap samples. Higher mean similarities indicate stability, and clusters with similarities greater than 0.75 were considered stable, while those less than 0.60 were considered unstable (Hennig, 2007).

We identified characteristics defining the final habitat types by plotting them on separate physical habitat and water chemistry ordinations and by comparing means. The water chemistry variables included ten dissolved metals (µg/L), DOC (mg/L), DIC (mg/L), TDN (mg/L), pH (unitless), specific conductance (µS/cm), temperature (°C), and dissolved oxygen (mg/L). We used principal components analysis (PCA) to visualize differences in physical habitat and water chemistry conditions across the final habitat types. Variables with absolute skewness greater than one were $\log_{10}$-transformed, and all variables were scaled prior to conducting each PCA on a correlation matrix.

Taxa associated with the physical habitat types were identified using indicator species analysis (ISA, Dufrêne & Legendre, 1997), modified to include taxa with different niche breadths that may be most strongly associated with a combination of habitat types (De Cáceres and Legendre, 2009; De Cáceres et al., 2010). ISA combines relative abundances and frequencies across different groups to generate an indicator value whose significance is evaluated using a randomization procedure. We used a permutation test to identify statistically significant taxa associated with different physical habitats (alpha = 0.05).

As a second method to identify sensitive taxa, we researched published sensitivities to one or more expected changes from mineral development or climate change. Several stressors associated with mineral development were considered, including changes to pH, specific conductance, sedimentation, temperature, and chemical pollution. We also considered increased stream temperature to be a potential impact from climate change. We carried out a comprehensive search of the relevant peer-reviewed scientific literature to identify sensitivities to climate change or mineral development for the seven fish species found at three or more sites in our study. Sensitivity to mineral development was assessed using published sensitivities to metals, pH, sedimentation, and to climate change based on maximum spawning temperatures. For macroinvertebrates and diatoms, we used published databases that provided information on species- or genus-level responses to environmental conditions or stressors. For macroinvertebrates, we used the Freshwater Biological Traits Database (USEPA 2012) and the Aquatic Fine Sediment Biotic Index (Relyea et al., 2012); and for diatoms, we used the Algal Attributes Database (Porter, 2008) and Diatoms of North America website (Spaulding et al., 2021). The supplementary methods (Appendix S1) provides additional information on how we identified fish, macroinvertebrate, and diatom taxa with sensitivities from the published literature.

Evaluation of sensitive freshwater taxa as potential bioindicators

We combined the lists of sensitive taxa using our two criteria and calculated mean abundances associated with the 30 random sites sampled in 2015. For taxa associated with specific habitat types (or combinations of two habitat types), we calculated average abundances for sampling sites belonging to that habitat. Spatial summary statistics were calculated using the sample weights from the study design and the spsurvey library in R (Dumelle et al., 2023). For taxa found at the ten sites repeatedly sampled for 5 years (Dataset B in Fig. 2), we calculated taxon persistence by averaging the number of years a taxon was observed across all sites where it was found (maximum of five). Fish were not sampled after 2015, so persistence values could not be calculated. We used the spatial and temporal summary statistics to identify abundant, common, and/or persistent taxa that might be most useful as bioindicators for future monitoring (Objective 2 in Fig. 2).

We created a list of bioindicator taxa by combining our two criteria used to identify sensitive taxa with information on spatial frequencies and temporal persistence from year to year. Any taxon with fidelity to one of the stream habitat types and high interannual persistence (3 or more years, 60%) were considered useful bioindicators of habitat change. Any taxon with one or more published sensitivities, high interannual persistence (3 or more years, 60%), and high frequency in wadeable streams (10 or more sites, 33%) were considered useful bioindicators of future stressors from climate change or development.

Long-term change in stream benthic communities

To investigate trends in macroinvertebrate and diatom communities over the past decade, we used samples collected from 2008 to 2019 at five long-term monitoring sites (Fig. 1, Objective 3 in Fig. 2). We harmonized taxonomic nomenclature and sampling methods over the 12-year study period prior to analysis (see supplemental methods in Appendix S1). To investigate long-term changes in benthic community composition, we compared beta diversity at the long-term monitoring sites using non-metric multidimensional scaling ordination (NMS, Clarke, 1993). Prior to running NMS, we removed rare taxa that were found in less than 5% of samples and $\log_{10}$-transformed abundances to lessen the influence of abundant taxa. The NMS ordination was based on a matrix of Bray–Curtis distances. We selected an interpretable number of dimensions that also had acceptable stress (<20, McCune et al., 2002). We plotted the changes in beta diversity over time for each site using successional vectors. The NMS ordination and multivariate analysis of variance were run using the vegan package in R (Oksanen et al., 2022).

We used a model-based approach to analyze changes in benthic communities and taxon abundances over time using multivariate generalized linear models (GLM, Wang et al., 2012). We fit the models using a negative binomial distribution for each of the two benthic communities and tested for significant differences in abundances over time (i.e., year covariate) that could vary by site (e.g., site by year interaction term). Significance was tested by calculating p values from resampling the data 999 times using the mvabund package in R (Wang et al., 2012).

Results

The population of 30 random sites had mean watershed area of 19 km^2 (95% CI 12–27) and mean elevation of 329 m (95% CI 282–375). Mean specific conductance was 60 $\mu S\ cm^{-1}$ (95% CI 51–68) and mean pH was 7.3 (95% CI 7.2–7.4), both of which are within common ranges for freshwater streams. Mean dissolved oxygen was 11.7 $mg\ L^{-1}$ (95% CI 11.3–12.1), mean water temperature was 8.1 °C (95% CI 6.9–9.4), and mean alkalinity was 22 $mg\ L^{-1}$ $CaCO_3$ (95% CI 19–26).

Eleven fish taxa were sampled from 27 of the random sites in 2015. Two small, high-gradient streams were fishless, and one site was not sampled due to equipment problems. Although fish diversity was low, sculpin, Dolly Varden (*Salvelinus malma*), and coho salmon (*Oncorhynchus kisutch*) were found at many sites throughout the study area. Sculpin were the most common fish encountered and occurred at 85% of all sites, followed by Dolly Varden (67%) and coho salmon (41%). Other fish encountered at four or fewer sites ($\leq$15%) included Alaska blackfish (*Dallia pectoralis*), lamprey (*Lampetra* sp.), ninespine stickleback (*Pungitius pungitius*), rainbow trout (*O. mykiss*), sockeye salmon (*O. nerka*), burbot (*Lota lota*), Arctic grayling (*Thymallus arcticus*), and longnose sucker (*Catostomus catostomus*).

Insects dominated the macroinvertebrate genera identified from the random sites, comprising 86% (101 out of 117 genera). Of the remaining 16 genera, seven were arachnids, five were snails or clams, two were amphipods, and two were leeches. Non-insect macroinvertebrates identified to the family or higher level included annelid worms (Clitellata), nematodes (Nematoda), flatworms (Platyhelminthes), mites (Trombidiformes and Sarcoptiformes), pond snails (Lymnaeidae), ramshorn snails (Planorbidae), and amphipods (Amphipoda). Insect diversity was distributed throughout six different orders with Diptera (true flies) exhibiting the highest diversity (65 genera and eight families), followed by Trichoptera (caddisflies, 16 genera and eight families), Plecoptera (stoneflies, ten genera and five families), Ephemeroptera (mayflies, eight genera and four families), and Coleoptera (beetles, two genera and one family). The order Diptera comprised the largest component of site richness, averaging 18 taxa across all sites, followed by Trichoptera and Ephemeroptera with four taxa each and Plecoptera with two. Site richness was driven by diversity in the family Chironomidae (non-biting midges), averaging 16 genera, followed by two each for Limnephilidae (northern case-constructing caddisflies), Simuliidae (black flies), and Heptageniidae (flat-headed mayflies).

Benthic diatoms from the random sites were represented by 284 taxa from 68 genera. The most diverse genera were *Eunotia* and *Gomphonema*, each with 25 different taxa, followed by *Pinnularia* (20), *Navicula* and *Nitzschia* (15), *Encyonema* (13), and *Psammothidium* (10). *Achnanthidium minutissimum* was the only diatom encountered in all 30 sites. Other commonly encountered diatoms were *Fragilaria vaucheria* (28 sites), *Aulacoseira alpigena* and *Staurosirella pinnata* (27 sites), *Odontidium mesodon* and *Tabellaria flocculosa* (strain IV) sensu Koppen (26 sites), and *Encyonema silesiacum* and *Eucocconeis laevis* (25 sites). Rare taxa dominated the diatom community, with over 45% (129 out of 284) of taxa encountered in only one of the 30 sites sampled in 2015, and with 49 additional taxa encountered at the repeat sites 2016–2019.

Identification of sensitive freshwater taxa

We identified three stream habitat types using 12 physical habitat variables across the random sites (Dataset D in Fig. 2). The three-group solution had the highest mean stability (0.77 versus 0.68–0.71 for other solutions), and individual cluster stabilities across all bootstrap samples were 0.84, 0.74, and 0.77 for habitat types 1 through 3, respectively. Physical habitat conditions varied among the three habitat types (Fig. 3 and Figure S1). Habitat type 1 (“Higher Gradient Coarse Substrate”) included 17 high gradient (95% CI 3.2–6.4%), small streams with the shallowest average depths and coarse substrates (mean diameters equal to coarse gravel) leading to high bed stability (Fig. 3 and Figure S1). Habitat type 2 (“Sandy”) included eight small streams with low canopy cover, depths in between the other two habitat types, and the highest variability in substrate composition, which resulted in smaller average substrate sizes (mean diameters equal to sand) and lower bed stability (Fig. 3 and Figure S1). Habitat type 3 (“Larger Woody”) included five large and deep wadeable streams with the highest canopy cover, wood densities, and sinuosity; and intermediate substrate sizes (mean diameters equal to fine gravel, Fig. 3 and Figure S1). Water chemistry was similar among stream habitats 1 and 3 (Figure S2). Stream habitat type 2 had more variable and higher concentrations of aluminum, barium, iron, manganese, sodium, vanadium, and DOC (Figure S2).

Stream taxa associated with physical habitat types included two fish, 18 macroinvertebrates, and ten diatom taxa. Twenty-two taxa were associated with individual habitat types, and eight macroinvertebrates were associated with combinations of types 1 and 3 or 2 and 3. A single diatom taxon was associated with stream habitat 1: higher-gradient coarse substrate streams. Lower gradient, sandy streams of stream habitat 2 had several characteristic taxa that included two fish (Alaska blackfish and ninespine stickleback), five macroinvertebrates (three genera of non-biting midges, one caddisfly, and one snail), and three diatoms. Larger woody streams associated with stream habitat 3 had five macroinvertebrate (two genera of non-biting midges, two mayflies, and one caddisfly) and six characteristic diatom taxa. Two macroinvertebrates (one non-biting midge and one caddisfly) were associated with stream habitats 2 and 3, which may indicate a preference for lower gradient habitats or smaller substrates. Six macroinvertebrates (three non-biting midges, one caddisfly, one stonefly, and one mayfly) were associated with stream habitats 1 and 3, which may indicate a preference for larger or more stable substrates.

Seven fish occurred at three or more random sites. We used published papers to assign sensitivities to acidic conditions, metals pollution, high water temperatures, and fine sedimentation (detailed citations in Appendix S1 and Table S1). Four of the six taxa with pH information available preferred neutral or alkaline conditions. Three of the six taxa with information available on metals pollution were intolerant of it. All taxa had temperature preference and fine sedimentation tolerance information available. Four taxa of the seven with temperature tolerance information prefer cool temperatures, and two taxa are intolerant of fine sedimentation. Excepting

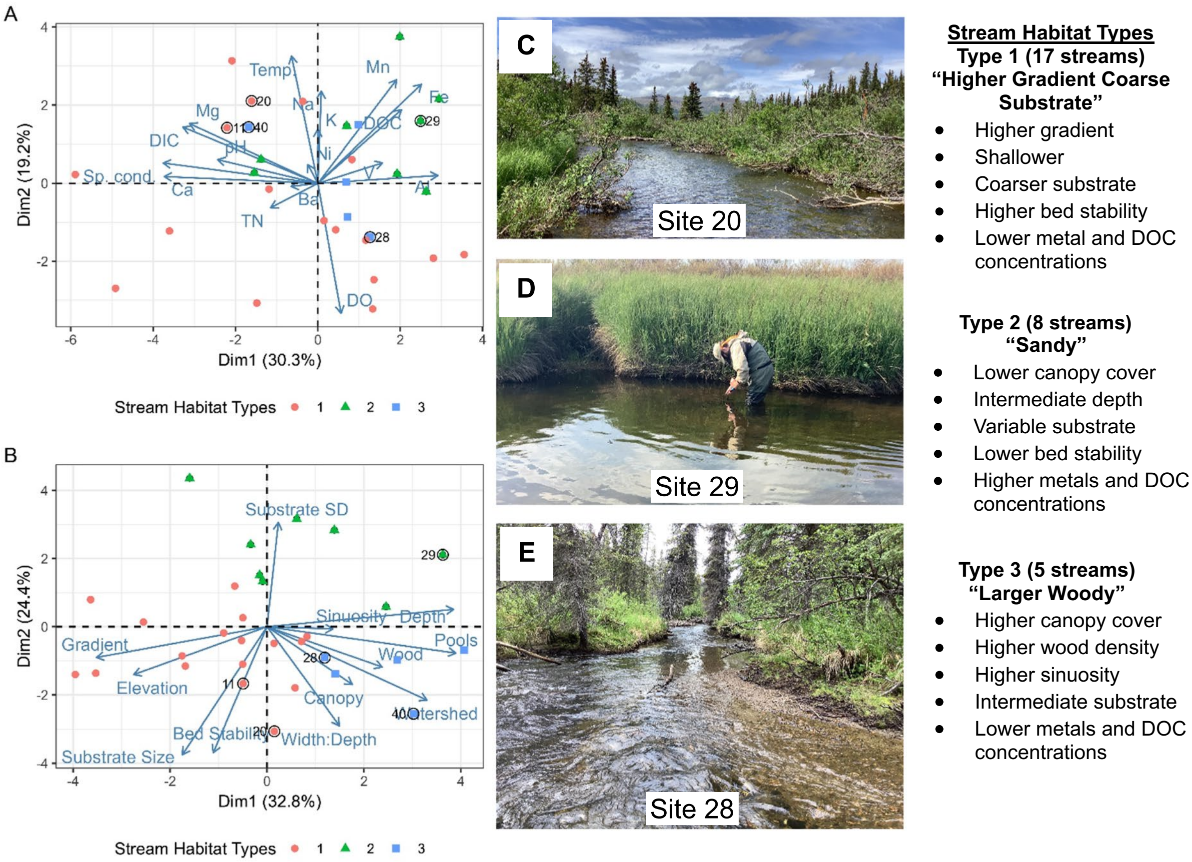

Fig. 3 The first two factors (Dim1 and Dim2) of principal components analysis of dissolved load (**A**) and physical habitat (**B**) for 30 streams sampled in 2015 indicating covariation among variables and differences among stream habitat types. Five probabilistic sites sampled annually from 2015 to 2019 are outlined with black circles. Example photos from a site representing each habitat type are shown (**C**–**E**) with descriptions of the habitat type

ninespine stickleback (*Pungitius pungitius*), which were tolerant of metals, sedimentation, and high temperatures, the remaining six fish taxa were sensitive to at least one environmental condition related to mining (Table S2).

Seventy-one macroinvertebrate genera that were found at three or more random sites were merged with the Freshwater Biological Traits Database (USEPA, 2012) and the Aquatic Fine Sediment Biotic Index (Relyea et al., 2012). Pollution tolerance information was available for 63 (89%) of the genera and 22 had mean tolerance values less than three indicating taxa sensitive to pollution. Of the 41 genera (58%) with information on pH preferences, six preferred neutral to alkaline conditions, indicating sensitivities to acidity. Thermal preferences were available for 47 genera (66%) and, with additional investigation of Alaskan species preferences, we determined that 11 preferred cold or cold-cool water temperatures. Finally, we identified 15 genera and one species (*Baetis bicaudatus*) with sensitivities to fine sediment that ranged from extremely sensitive (only one genus, *Ecclisomyia*) to slightly sensitive. The combined list of macroinvertebrates with at least one identified sensitivity included 30 genera and one species (Table S3).

Of 125 diatom taxa that occurred at three or more random sites, 110 (88%) had entries in the Algal Attributes Database (Porter, 2008). Pollution tolerance information was available for 67 (54%) of the diatom taxa, and 48 were identified as being sensitive to pollution. Information on pH preferences was available for 85 (68%) of the diatom taxa, and 64 preferred neutral to alkaline conditions. All but one of the 19 (15%) diatom taxa with information on conductivity preferred habitats with low specific conductance. Motility information from the Diatoms of North America website (Spaulding et al., 2021) was available for 94 (75%) diatom taxa, and we used best professional judgment to fill in motility information for an additional 27 (22%) taxa. Eighty-four diatom taxa were either non-motile, weakly motile, or slightly motile, suggesting sensitivity to sediment pollution. The combined list of diatoms with at least one identified sensitivity included 111 taxa (Table S4).

Evaluation of sensitive freshwater taxa as potential bioindicators

The two criteria used to identify sensitive freshwater taxa produced lists with low overlap. Six fish taxa had published sensitivities to one or more stressors, two had fidelity to stream habitat type 2, and only one taxon met both criteria (Table S2). For the macroinvertebrates and diatoms, only eight (20% of all macroinvertebrate and 7% of all diatom sensitive taxa) had fidelity to a stream habitat type and at least one published sensitivity (Tables S3 and S4). Almost all of the sensitive taxa in the macroinvertebrate and diatom communities (40 out of 41 macroinvertebrate genera and 113 out of 115 diatom taxa) were found in the ten repeat sampling sites and could be evaluated for their persistence from year to year.

Of the seven sensitive fish taxa, five were considered useful bioindicators (Table 1). Alaska blackfish and ninespine stickleback were associated with stream habitat type 2, sandy streams with low canopy cover, and variable substrate types (Table 1). Coho salmon, Dolly Varden, and sculpin occurred frequently in wadeable streams and had at least one published sensitivity (Table 1 and Fig. 4).

Forty-one sensitive macroinvertebrate taxa occurred at three to 26 sites (Table S3). Relative densities were highly variable across sites ranging from less than one to over 800 organisms per square meter. One taxon was not found at any of the repeat sampling sites, and the remainder occurred at one to ten sites with 15 genera found at all ten sites. Temporal persistence ranged from 1 to 4.8 years, and eight taxa had mean persistence greater than 4 years meaning that they were observed 80% of the times sampled. Seven macroinvertebrate genera were sensitive to three stressors, and the most sensitive taxa occurred at a range of frequencies across the study area (Fig. 4). Genera found at more sites sampled in 2015 also had higher average persistence values (Fig. 4). Twenty-three macroinvertebrate genera were identified as potential bioindicators (Table 1). Of 13 macroinvertebrate bioindicators with high persistence and fidelity to stream habitat types, five also had published sensitivities to at least two stressors. Another ten macroinvertebrate bioindicators were common in wadeable streams (range = 11–26 sites, mean = 19) and had published sensitivities to one or more stressors.

One hundred and fifteen sensitive diatom taxa occurred at two to 20 sites (Table S4). Relative abundances ranged from less than 1 to 100%, but only 12 taxa had average relative abundance greater than 10%. Diatom taxa occurrence at the repeat sampling sites ranged from one to ten, and 14 taxa were found at all ten sites. Persistence ranged from 1 to 4.8 years, and 13 taxa had mean persistence greater than 4 years. Twenty-three diatom taxa were sensitive to three or more stressors and occurred across a range of frequencies (Fig. 4). Similar to macroinvertebrates, diatoms that occurred more frequently in streams across the study area had higher temporal persistence (Fig. 4). Twenty-six diatom taxa were identified as potential bioindicators (Table 1). Five had fidelity to stream habitat 3, which were characterized by high riparian cover and large wood. The remaining 21 diatom bioindicators were sensitive to one or more stressors and were commonly found in wadeable streams (range = 11–30 sites, mean = 19).

Long-term changes in benthic communities

The ordinations of long-term macroinvertebrate and diatom beta diversity ($n = 12$ years) resulted in three dimensions (stress = 14 for macroinvertebrates and 10 for diatoms, Fig. 5). Diatom communities were more distinct among sites than macroinvertebrates and neither ordination showed strong directional change over time (Fig. 5). The multivariate GLM indicated a significant change in the macroinvertebrate community over time (Deviance = 162.7, p value = 0.001) and the interaction between year and site was not significant (Deviance = 294.5, p value = 0.494) indicating that the trends were the same across sites. There were changes in two macroinvertebrate genera from

Table 1 Fish, macroinvertebrate, and diatom bioindicators of climate change and mineral development in the Lime Hills ecoregion of Bristol Bay. This list includes two types of taxa with high year to year persistence (60% of years): those with fidelity to a specific habitat type or those with adequate spatial frequency (33% of sites) and at least one published sensitivity. Note that temperature information was not available for diatoms, and conductivity information was not available for fish or macroinvertebrates. A full list of bioindicators can be found in the online Supplementary Information. *NA*, no sensitivity information for a stressor was found in the literature. 0 = published literature indicates no sensitivity to a stressor. 1 = published literature indicates taxon is sensitive to a stressor (see definitions of sensitivity for each stressor in the Methods). Taxa are ordered from lowest to highest frequencies (fish) or persistence (macroinvertebrates and diatoms)

Community	Taxon name	pH	Poll	Cond	Temp	Sed	Sum	Habitat[a]	Freq	Pers
Fish	*Dallia pectoralis*	1	NA	NA	0	0	1	2	4	NA
Fish	*Pungitius pungitius*	NA	0	NA	0	0	0	2	3	NA
Fish	*Oncorhynchus kisutch*	1	1	NA	1	1	4	All	11	NA
Fish	*Salvelinus malma*	0	0	NA	1	0	1	All	18	NA
Fish	*Cottus* sp.	0	1	NA	1	0	2	All	23	NA
MI	*Isoperla*	0	1	NA	0	NA	1	All	15	3.1
MI	*Polypedilum*	NA	NA	NA	NA	NA	NA	2	12	3.3
MI	*Parakiefferiella*	NA	NA	NA	NA	NA	NA	2	8	3.3
MI	*Suwallia*	1	1	NA	0	1	3	All	16	3.4
MI	*Zapada*	1	1	NA	0	NA	2	1 and 3	25	3.5
MI	*Conchapelopia*	NA	NA	NA	NA	NA	NA	2	11	3.5
MI	*Baetis bicaudatus*	NA	NA	NA	NA	1	1	All	23	3.5
MI	*Zapada* (excluding *cinctipes*)	NA	NA	NA	NA	1	1	All	23	3.5
MI	*Rhyacophila*	0	1	NA	0	0	1	1 and 3	17	3.6
MI	*Fossaria*	sss	NA	NA	NA	NA	NA	2	4	3.7
MI	*Drunella*	NA	1	NA	1	1	3	3	12	3.8
MI	*Ephemerella*	0	1	NA	0	0	1	All	11	3.8
MI	*Glossosoma*	0	1	NA	0	1	2	3	12	3.9
MI	*Dicranota*	NA	1	NA	NA	0	1	All	22	3.9
MI	*Onocosmoecus*	0	0	NA	1	NA	1	All	21	3.9
MI	*Cinygmula*	NA	1	NA	1	1	3	1 and 3	23	4.2
MI	*Tvetenia*	NA	NA	NA	NA	NA	NA	1 and 3	24	4.3
MI	*Stempellina*	0	1	NA	1	NA	2	All	12	4.4
MI	*Eukiefferiella*	NA	NA	NA	NA	NA	NA	1 and 3	26	4.5
MI	*Cricotopus*	NA	NA	NA	NA	NA	NA	2 and 3	21	4.5
MI	*Brachycentrus*	1	1	NA	0	1	3	2 and 3	17	4.6
MI	*Pagastia*	0	1	NA	NA	NA	1	All	26	4.7
MI	*Lebertia*	NA	NA	NA	1	NA	1	All	26	4.8
Diatoms	*Achnanthidium pyrenaicum* (Hustedt) Kobayasi	1	1	NA	NA	1	3	3	4	3.0

Table 1 (continued)

Community	Taxon name	pH	Poll	Cond	Temp	Sed	Sum	Habitat[a]	Freq	Pers
Community	**Taxon Name**	**pH**	**Poll**	**Cond**	**Temp**	**Sed**	**Sum**	**Habitat[a]**	**Freq**	**Pers**
Diatoms	*Encyonema latens* (Krasske) Mann	NA	NA	NA	NA	1	1	3	11	3.0
Diatoms	*Staurosira construens* var. *venter* (Ehrenberg) Hamilton	1	1	NA	NA	1	3	All	11	3.3
Diatoms	*Nitzschia perminuta* (Grunow) Peragallo	1	1	NA	NA	0	2	All	17	3.4
Diatoms	*Gomphonema ventricosum* Gregory	NA	NA	NA	NA	NA	NA	3	4	3.5
Diatoms	*Planothidium lanceolatum* (Brébisson) Lange-Bertalot	1	0	NA	NA	1	2	All	17	3.5
Diatoms	*Ulnaria ulna* (Nitzsch) Compére	1	0	NA	NA	1	2	All	13	3.7
Diatoms	*Gomphonema micropus* Kützing	1	NA	NA	NA	NA	1	All	23	3.7
Diatoms	*Fragilaria capucina* Desmazieres	1	0	1	NA	1	3	All	17	3.7
Diatoms	*Diatoma tenuis* Agardh	1	0	NA	NA	1	2	All	16	3.8
Diatoms	*Pseudostaurosira brevistriata* (Grunow) Williams and Round	1	1	NA	NA	1	3	All	17	3.8
Diatoms	*Meridion circulare* (Greville) Agardh	1	1	NA	NA	1	3	All	16	3.9
Diatoms	*Gomphonema parvulum* (Kützing) Kützing	1	0	NA	NA	NA	1	All	19	4.0
Diatoms	*Eucocconeis laevis* (Østrup) Lange-Bertalot	1	1	NA	NA	1	3	All	25	4.1
Diatoms	*Fragilaria gracilis* Østrup	1	NA	NA	NA	1	2	All	23	4.2
Diatoms	*Reimeria sinuata* (Gregory) Kociolek et Stoermer	1	1	NA	NA	NA	2	All	22	4.2
Diatoms	*Odontidium mesodon* (Ehrenberg) Kützing	1	1	1	NA	1	4	All	26	4.4
Diatoms	*Staurosirella pinnata* (Ehrenberg) Williams and Round	1	1	NA	NA	1	3	All	27	4.4
Diatoms	*Tabellaria flocculosa* (strain IV) sensu Koppen	0	NA	1	NA	1	2	All	26	4.4
Diatoms	*Aulacoseira alpigena* (Grunow) Krammer	0	1	NA	NA	1	2	All	27	4.4
Diatoms	*Achnanthidium minutissimum* (Kützing) Czarnecki	0	1	NA	NA	1	2	All	30	4.6
Diatoms	*Encyonema silesiacum* (Bleisch) Mann	1	1	NA	NA	1	3	All	25	4.6
Diatoms	*Fragilaria vaucheriae* (Kützing) Petersen	1	0	NA	NA	1	2	All	28	4.8
Diatoms	*Hannaea arcus* (Ehrenberg) Patrick	1	NA	NA	NA	1	2	All	20	4.8
Diatoms	*Frustulia vulgaris* (Thwaites) De Toni	NA	NA	NA	NA	NA	NA	3	2	NA
Diatoms	*Gomphonema olivaceoides* var. *denestriata* Foged	NA	NA	NA	NA	NA	NA	3	2	NA

MI, macroinvertebrates; *Poll*, pollution; *Cond.*, conductivity; *Sed*, sediment; *Temp*, temperature; *Freq.*, frequency; *Pers.*, persistence; *NA*, not available

[a]Habitat type 1 = small, higher gradient streams; 2 = sandy, low cover streams; 3 = gravel bed streams with large wood; All = all habitat types

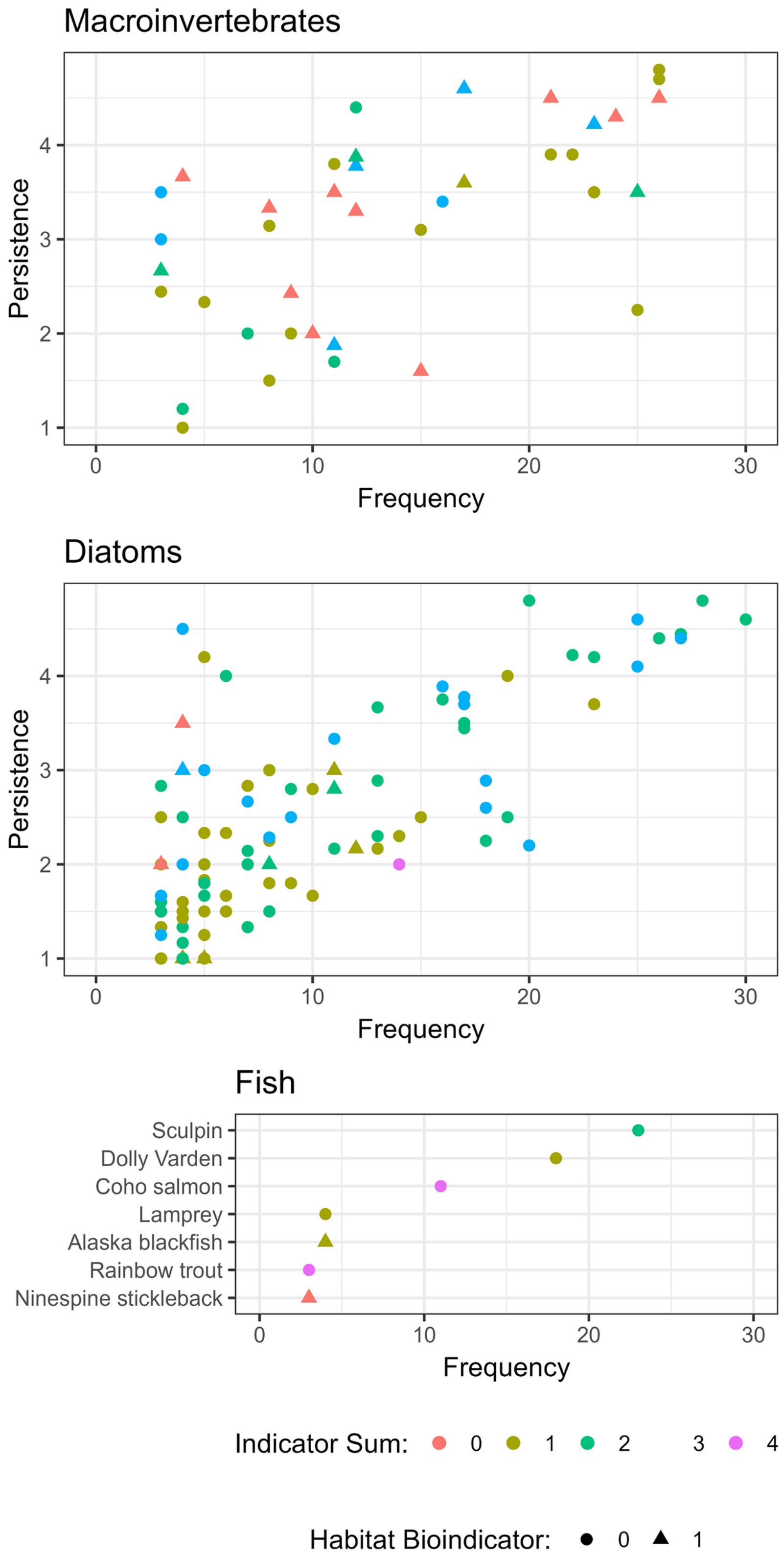

Fig. 4 Spatial frequency versus temporal persistence for macroinvertebrate and diatom sensitive taxa along with spatial frequencies for seven sensitive fish taxa. Frequencies are from random sites (maximum of 30), and persistence is the average number of years a taxon was observed across ten repeat sampling sites (maximum of 5). The indicator sum is a metric of taxon sensitivity and reflects the number of stressors to which a taxon responds negatively. Habitat bioindicators are taxa with high fidelity to a single stream habitat type or a combination of stream habitat types

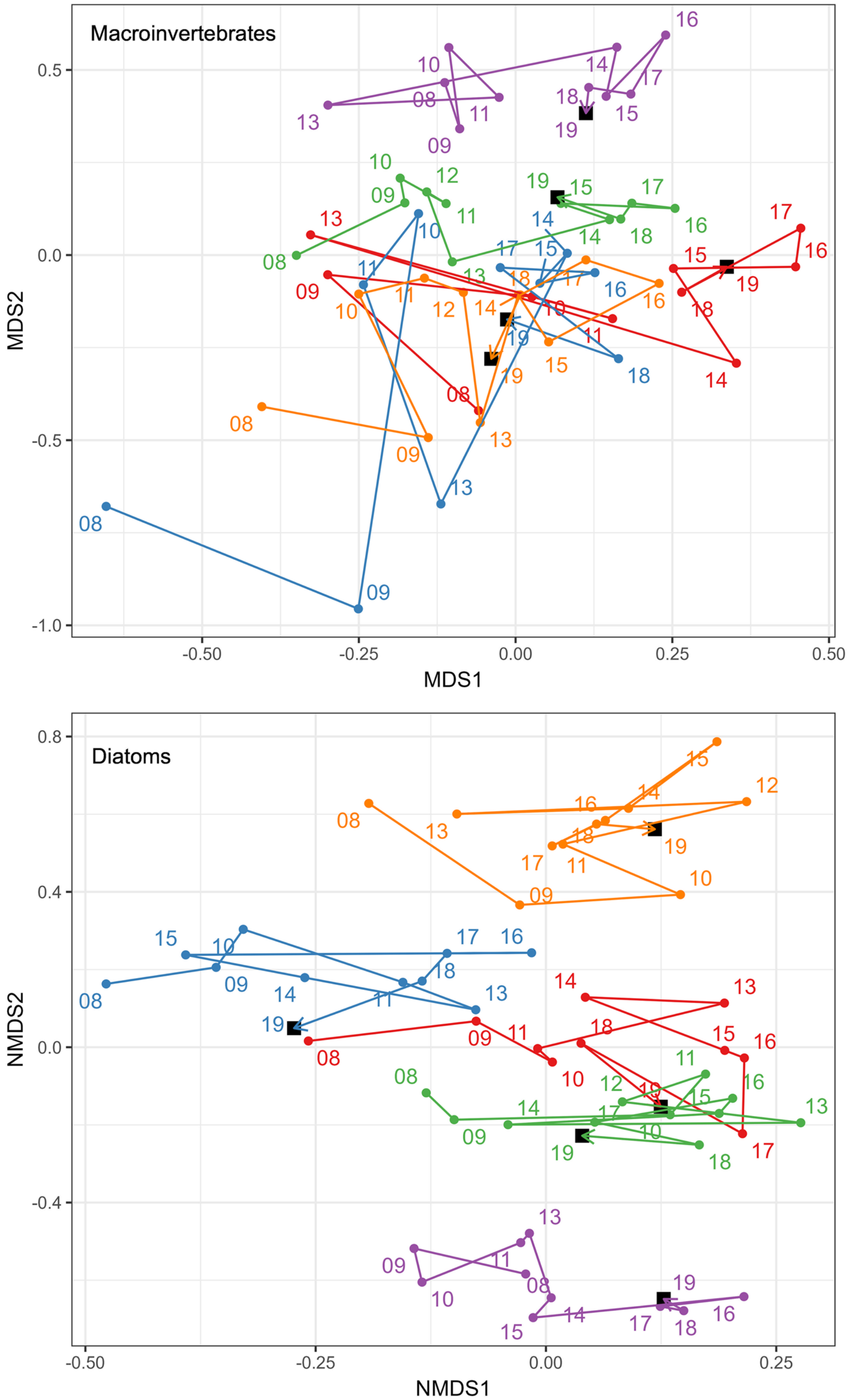

Fig. 5 First two axes of non-metric multi-dimensional scaling ordination of macroinvertebrate and diatom communities sampled at five sites from 2008 to 2019. Points in the ordination represent one sample from a stream and year. The first axis was rotated to align with the year variable; black boxes indicate communities sampled in 2019, the final year of sampling; and colors indicate different streams

the family Chironomidae (non-biting midges): *Heleniella* increased in abundance (Deviance = 19.943, p value = 0.002), while *Brillia* decreased in abundance (Deviance = 10.987, p value = 0.07). The multivariate GLM indicated significant changes in the diatom community over time (Deviance = 3364, p value = 0.029) with a significant interaction term between year and site (Deviance = 868, p value = 0.001), indicating different trends among sites. There were no significant changes in relative abundances for individual diatom taxa (p values > 0.1). We also explored changes in nine coldwater macroinvertebrate taxa that occurred at the long-term sampling sites since we lacked information on stream temperatures over the 12-year period. The coldwater taxa exhibited high interannual variability, but no clear patterns in abundance over time (Figure S3).

Discussion

Measuring impacts from current and future stressors in freshwater ecosystems require well designed studies of baseline conditions. In the Bristol Bay region of Alaska, both changing climatic conditions and proposed mineral development may alter the pristine freshwater habitats that support productive salmon fisheries. The freshwater bioindicator framework developed here provides a unique opportunity for measuring future change because monitoring occurred prior to significant impacts, sampling relied on a probabilistic study design, and both spatial and temporal dynamics of bioindicators were measured and used for evaluating bioindicator effectiveness.

By using a probabilistic study design, we uncovered more unique taxa than previous strategic sampling of 78 hard-bottom wadeable streams. Historic sampling of stream benthic communities identified 137 unique macroinvertebrate taxa representing 116 genera (Bogan et al., 2018). Random sampling in this study from less than half the number of sites resulted in 164 unique macroinvertebrate taxa representing 117 genera. The same pattern emerged for diatoms with approximately 44% more diatoms identified in this study as compared to previous sampling (289 versus 201 taxa) when comparing the 600 valve counts. These findings reinforce the importance of random site selection, which reduces bias (conscious or not) and increases the likelihood of sampling across the range of available habitats and the freshwater taxa they support.

This framework for selecting freshwater bioindicators has some limitations. Climate change is one of two key stressors targeted by this framework, but rising air temperatures and changing precipitation patterns over the past century in Alaska (Druckenmiller et al., 2022; Stewart et al., 2022) may have already elicited shifts in community composition (Milner et al., 2023). Despite this fact, we believe our selection of bioindicator taxa provides meaningful results for two reasons: (1) we found limited changes in taxon abundances over the past 12 years of monitoring and (2) current stream temperatures in this region are below thresholds that would limit distributions of coldwater benthic taxa (Lisi et al., 2015). These results suggest that major shifts in taxon response to climate change have not yet occurred.

A second limitation to our bioindicator framework was our reliance on published information for taxon sensitivities to expected changes. For fish and diatoms, most of the literature applied to species documented in our study, so we expect taxa responses to be similar over their Alaska range. One exception could be physiological tolerances that exhibit plasticity over a species' range resulting in different tolerances to stressors targeted in our framework (e.g., Eliason et al., 2011). For macroinvertebrates, most of the published information applied to *genera,* and different species and tolerance levels across regions could make our list of macroinvertebrate bioindicators less accurate. Potential solutions to improve our understanding of macroinvertebrate responses to stressors could include using genomics to improve taxonomic resolution and additional sampling of taxa along stressor gradients in Alaska.

This study provides a potential strategy for monitoring before an anticipated impact or for leveraging pre-existing long-term monitoring after an impact occurs. This strategy operates by selecting potential bioindicators based on literature-derived tolerance values and then characterizing their spatial distribution and persistence over time. We confirmed our hypothesis that it would be challenging to identify useful bioindicators for wadeable streams as two fish, 18 macroinvertebrates, and 89 diatoms had published sensitivities, but did not meet our criteria for persistence or frequency. EPT taxa, which have well known sensitivities to water quality, were important bioindicators for our region, comprising approximately 50% of the final macroinvertebrate bioindicator taxa. Having a long-term dataset in advance can allow researchers to complement published sensitivities to pollution or other impacts with locally relevant information about habitat preferences and landscape heterogeneity, based on temporal and spatial responses of baseline communities. For example, the literature review found that coho salmon and rainbow trout were sensitive to all four published stressors, but these two species were only found at a small number of sites, making them useful as indicators at a subset of sites in the region. Sockeye salmon, which are of particular economic and social importance in the region, were rare in our sampled habitats due to a lack of overlap with their spawning habitats and the lakes where they typically rear. They should be considered in future monitoring efforts given that the headwater streams sampled in this study support downstream lakes and larger river systems where they migrate and spawn (Colvin et al., 2018).

Depending upon future scenarios, changes in bioindicators can be used to plan restoration actions, guide adaptive management, and conserve important freshwater habitats. Changes to bioindicators under a future development scenario may signal impacts to physical or chemical conditions in streams and could be used to trigger strategic sampling to identify sources of impairment and adapt mitigation strategies associated with development activities (e.g., road-building or mining). Under a future climate scenario, changes to bioindicators may indicate losses of freshwater habitat diversity or biodiversity that are important for sustaining and stabilizing salmon fisheries (Schindler et al., 2015). These future changes may be measured using strategic partnerships, such as this study, or as part of national monitoring frameworks, such as the Bureau of Land Management's Assessment, Inventory, and Monitoring framework and USEPA's National Aquatic Resource Surveys. The high cost of accessing remote sites in Bristol Bay precludes regular sampling, but a multi-pronged strategy that focuses on continuous monitoring of habitat changes (e.g., stream temperature and streamflow at strategic sites) alongside less frequent (e.g., 10–20 years) probabilistic sampling of sites should be used to inform potential biological responses to environmental change, mineral exploration, or development in this critical area.

High natural interannual variability in stream biological communities can pose challenges for interpreting responses to external impacts and limit the effectiveness of biological monitoring programs (Milner et al., 2006). Some macroinvertebrate taxa were found at repeat sampling sites at least 80% of the years studied, while others were only detected once. A long-term biomonitoring study on amphibians in Grand Teton and Yellowstone National Parks found similar fluctuations (Ray et al., 2022). In some cases, taxa documented as sensitive in the literature might also be spatially rare or not very persistent. Those characteristics could make them less locally or regionally useful as indicator taxa, because their disappearance or absence may be due to allee effects, for example rather than mining-caused pollution. Our study found that most taxa occupying a wide range of sites were also temporally persistent. Prevalent taxa with known sensitivities to impacts may be useful bioindicators, but could also represent metapopulation source and sink dynamics. In that case, their presence at impacted sites is due to a constant influx of migrants from neighboring communities, rather than a lack of habitat impacts (Pajunen et al., 2020). The most useful bioindicators in wadeable streams are sensitive, persistent over time (in the absence of a stressor), and have known stream habitat associations–based on their frequency in a distinct stream habitat type or commonness in wadeable streams. We identified 23 macroinvertebrate genera and 26 diatom taxa that met this standard and may have the highest value in detecting future change. Thus, having a pre-existing long-term baseline of stream communities in the Bristol Bay region can help disentangle nuanced responses to future environmental impacts, such as climate change and mining.

Our investigation into changes in stream benthic communities over a recent 12-year period in the Lime Hills ecoregion of Bristol Bay indicated significant change in benthic community composition over time, but limited changes in individual taxon relative abundances. Similar work investigating macroinvertebrate community responses in Interior Alaska reported significant changes in the overall community in addition to changing abundance patterns for five stoneflies and one mayfly over a 22-year sampling period (Milner et al., 2023). In this study, the only taxa with changing abundances over our sampling period were in the family Chironomidae, which have high diversity in Arctic ecosystems (Lento et al., 2022; Oswood, 1989), but are often not identified beyond the family level. Other studies support the idea that climate change is shifting freshwater communities, as temperatures warm and precipitation patterns change. Freshwater species distribution models across sites in the contiguous 48 US States indicated strong responses of diatoms, macroinvertebrates, and fish to climate variables and dramatic reductions in coldwater taxa under future projections (Pound et al., 2021). The potential loss of coldwater fish and macroinvertebrates identified in our literature review include taxa indirectly (e.g., macroinvertebrates as food for stream fishes) and directly important to subsistence users (e.g. coho salmon and Dolly Varden) whose loss could have implications for food security in the region. Additionally, several of the coldwater taxa we identified have high value for bioindication (e.g., sculpin and coho salmon and the mayflies *Drunella* and *Cinygmula*).

Measuring taxon-specific responses to climate change is challenging without multi-decadal datasets due to variable abundances from year to year (Figure S3, Milner et al., 2006) caused by variation across timescales. For example, sampling at the same time each year (e.g., an index period) is designed to capture organisms at similar phenological stages, but differences in spring breakup and early summer temperatures lead to differences in the presence of taxa with spring emergence (Finn et al., 2022). Additionally, multi-decadal climate phenomena such as El Niño can affect temperature and precipitation patterns that drive community composition and abundance and mask patterns of long-term change (Lawrence et al., 2010). Despite these challenges, long-term datasets provide a valuable contribution to our understanding of shifting freshwater biodiversity that may alter ecosystem functions (Lento et al., 2023; Shipley et al., 2022). Long-term datasets can also be coupled with climate data to model future species' distributions under climate change.

Climate change has already altered freshwater habitats in Alaska, and the demand for critical minerals will increase mineral exploration activity and potential development, making baseline monitoring particularly timely. Several avenues for future research could improve our bioindicator selection framework and ability to measure freshwater community change in response to these stressors. Responses of Alaskan fish, macroinvertebrates, and diatoms to selected stressors (e.g., sediment, temperature, pH, conductivity, and pollution) could be investigated by sampling along stressor gradients in regions with impacted streams (e.g., urban areas or mines). This approach would confirm taxon responses to changing conditions and allow for better predictions of altered stream food webs, biodiversity, and stream function.

Regional trait information for freshwater taxa could also increase predictive power linking changes in taxonomic composition to changes in ecosystem function. Many trait databases are based on studies from distinct geographic areas, and traits may exhibit more plasticity than suggested by those trait assignments. For example, trophic traits have been found to be very flexible in aquatic insects, with taxa shifting their resource use depending on food availability and quality (Collins et al., 2015; Larson et al., 2018). Emerging genetics tools may also improve our understanding of taxon presence and biodiversity. Recent investigations into macroinvertebrate diversity using DNA metabarcoding in Interior Alaska revealed 20 new chironomid taxa (Webb et al., 2022). These new taxa could have high value for bioindication once their autoecological information (e.g., life cycle, voltinism) and stressor tolerances are described. Efforts to establish a DNA barcode library for Alaskan arthropods are underway (Sikes et al. 2017), and as more taxa are added, DNA barcoding will become an increasingly viable method for bioassessment. As climate change effects continue to intensify, baseline studies can be used to detect signals of climate change in population dynamics. For example, all five of the fish bioindicators identified in this study are anticipated to experience negative impacts to their distributions due to climate change (Krabbenhoft et al., 2020). Finally, we recommend continued support of long-term datasets to document freshwater biodiversity under baseline conditions prior to further taxonomic shifts due to climate change or development.

Conclusions

A probabilistic survey of biological communities in wadeable streams in the Lime Hills ecoregion of Bristol Bay revealed bioindicators that are persistent over time and could be used to measure changes to stream habitats or water quality. The final bioindicator list includes taxa from multiple communities (fish, macroinvertebrates, and diatoms) with different lifespans and mobility. A 12-year dataset of benthic communities from streams in the same ecoregion indicated changing composition over time. This survey was conducted in a relatively undisturbed ecoregion of western Alaska impacted by climate change and proposed for mineral development, and these findings could be applied to similar subarctic ecosystems. Our findings show the value of collecting information on freshwater biodiversity prior to major development and provide a unique baseline for measuring impacts to streams from a rapidly changing climate.

Acknowledgements In memory of Kristy Jeffries and Daniel Chythlook, close friends, coworkers, and accomplished environmental scientists. We are grateful to Tim Troll for supporting our research and Stan Hermens for safely transporting our crews. We would also like to thank the staff from the Alaska Department of Fish and Game who collected samples in 2012 and provided lab support.

Author contribution Conceptualization: RS, DB, BH, EL, DR, CAW. Developing methods: RS, DB, BH, DM, SON, CAW. Conducting the research: RS, DB, BH, EL, DM, SON, CAW. Data analysis: RS, DB, BH, EL, DM, SON, CAW. Data interpretation: RS, DB, BH, EL, DM, DR, SON, CAW. Preparation of figures and tables: RS, DM, EL. Writing: RS, DB, BH, EL, DM, DR, SON, CAW.

Funding This project was funded by the U.S. Fish and Wildlife Service, the Bristol Bay Heritage Land Trust, the Alaska Department of Environmental Conservation, the National Fish and Wildlife Foundation, the World Wildlife Fund, and the Center for Science in Public Participation.

Data availability Monitoring datasets used for this research are publicly provided on Zenodo: https://doi.org/10.5281/zenodo.15889793. No novel code was used for this research, and R libraries used for reproducing analyses are provided in the methods.

Declarations

Ethics approval All authors have read, understood, and have complied as applicable with the statement on "Ethical responsibilities of Authors" as found in the Instructions for Authors. All fish methods followed an approved Institutional Animal Care and Use Committee protocol (PI—Ray Hilborn, #3142–01) through the University of Washington.

Competing interests The authors declare no competing interests.

References

Andersen, T., P. S. Cranston, and J. H. Epler, editors. (2013). *The larvae of Chironomidae (Diptera) of the Holarctic region – Keys and diagnoses*. Insect Systematics & Evolution.

Armitage, P. D., Bowes, M. J., & Vincent, H. M. (2007). Long-term changes in macroinvertebrate communities of a heavy metal polluted stream: The river Nent (Cumbria, UK) after 28 years. *River Research and Applications, 23*, 997–1015.

Bogan, D., D. Rinella, R. Shaftel, and D. Merrigan. (2018). Macroinvertebrate and diatom communities in headwater streams of the Kvichak and Nushagak River watersheds, Bristol Bay, Alaska. In C. A. Woody, editor. *Bristol Bay Alaska: Natural Resources of the Aquatic and Terrestrial Ecosystems*. J. Ross Publishing, Plantation, FL.

Burgmer, T., Hillebrand, H., & Pfenninger, M. (2007). Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates. *Oecologia, 151*, 93–103.

Carignan, V., & Villard, M.-A. (2002). Selecting indicator species to monitor ecological integrity: A review. *Environmental Monitoring and Assessment, 78*, 45–61.

Carothers, C., Black, J., Langdon, S., Donkersloot, R., Ringer, D., Coleman, J., Gavenus, E., Justin, W., Williams, M., Christiansen, F., Samuelson, J., Stevens, C., Woods, B., Clark, S. J., Clay, P., Mack, L., Raymond-Yakoubian, J., Sanders, A., Stevens, B., & Whiting, A. (2021). Indigenous peoples and salmon stewardship: A critical relationship. *Ecology and Society*. https://doi.org/10.5751/ES-11972-260116

Cianciolo, T. R., McLaughlin, D. L., Zipper, C. E., Timpano, A. J., Soucek, D. J., & Schoenholtz, S. H. (2020). Impacts to water quality and biota persist in mining-influenced Appalachian streams. *Science of the Total Environment, 717*, 137216.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology, 18*, 117–143.

Clements, W. H., Carlisle, D. M., Lazorchak, J. M., & Johnson, P. C. (2000). Heavy metals structure benthic communities in Colorado mountain streams. *Ecological Applications, 10*, 626–638.

Cline, T. J., Schindler, D. E., Walsworth, T. E., French, D. W., & Lisi, P. J. (2020). Low snowpack reduces thermal response diversity among streams across a landscape. *Limnology and Oceanography Letters, 5*, 254–263.

Collins, S. M., Kohler, T. J., Thomas, S. A., Fetzer, W. W., & Flecker, A. S. (2015). The importance of terrestrial subsidies in stream food webs varies along a stream size gradient. *Oikos, 125*, 674–685.

Colvin, S. A. R., Sullivan, S. M. P., Shirey, P. D., Colvin, R. W., Winemiller, K. O., Hughes, R. M., Fausch, K. D., Infante, D. M., Olden, J. D., Bestgen, K. R., Danehy, R. J., & Eby, L. (2019). Headwater streams and wetlands are critical for sustaining fish, fisheries, and ecosystem services. *Fisheries, 44*, 73–91.

Crozier, L. G., Burke, B. J., Chasco, B. E., Widener, D. L., & Zabel, R. W. (2021). Climate change threatens Chinook salmon throughout their life cycle. *Communications Biology, 4*, 1–14.

Cuffney, T. F., Brightbill, R. A., May, J. T., & Waite, I. R. (2010). Responses of benthic macroinvertebrates to environmental changes associated with urbanization in nine metropolitan areas. *Ecological Applications, 20*, 1384–1401.

De Caceres, M., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology, 90*, 3566–3574.

De Cáceres, M., Legendre, P., & Moretti, M. (2010). Improving indicator species analysis by combining groups of sites. *Oikos, 119*, 1674–1684.

DeNicola, D. M., & Stapleton, M. G. (2014). Benthic diatoms as indicators of long-term changes in a watershed receiving passive treatment for acid mine drainage. *Hydrobiologia, 732*, 29–48.

Druckenmiller, M. L., R. L. Thoman, and T. A. Moon. (2022). Arctic Report Card 2022.

Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs, 67*, 345–366.

Dumelle, M., Kincaid, T., Olsen, A. R., & Weber, M. (2023). Spsurvey: Spatial sampling design and analysis in R. *Journal of Statistical Software, 105*(3), 1–29.

Durance, I., & Ormerod, S. J. (2007). Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biology, 13*, 942–957.

Eliason, E. J., Clark, T. D., Hague, M. J., Hanson, L. M., Gallagher, Z. S., Jeffries, K. M., Gale, M. K., Patterson, D. A., Hinch, S. G., & Farrell, A. P. (2011). Differences in thermal tolerance among sockeye salmon populations. *Science, 332*, 109–112.

Finn, D. S., Johnson, S. L., Gerth, W. J., Arismendi, I., & Li, J. L. (2022). Spatiotemporal patterns of emergence phenology reveal complex species-specific responses to temperature in aquatic insects. *Diversity and Distributions, 28*, 1524–1541.

Hagedorn, B.H., R. Shaftel, D. Bogan, L. Jones, and C. Woody. 2020. Water quality evaluation of streams in the Lime Hills ecoregion of Bristol Bay. A report prepared for the Alaska Department of Environmental Conservation. Sustainable Earth Research, LLC and Alaska Center for Conservation Science, University of Alaska Anchorage. Anchorage, AK.

Heino, J., Virkkala, R., & Toivonen, H. (2009). Climate change and freshwater biodiversity: Detected patterns, future trends and adaptations in northern regions. *Biological Reviews of the Cambridge Philosophical Society, 84*, 39–54.

Hennig, C. (2007). Cluster-wise assessment of cluster stability. *Computational Statistics & Data Analysis, 52*, 258–271.

Hennig, C. (2015). *fpc: Flexible procedures for clustering*. R package version 2.2-13. https://CRAN.R-project.org/package=fpc

Hirst, H., Jüttner, I., & Ormerod, S. J. (2002). Comparing the responses of diatoms and macroinvertebrates to metals in upland streams of Wales and Cornwall: Diatoms, macroinvertebrates and metals. *Freshwater Biology, 47*, 1752–1765.

Hodkinson, I. D., & Jackson, J. K. (2005). Terrestrial and aquatic invertebrates as bioindicators for environmental monitoring, with particular reference to mountain ecosystems. *Environmental Management, 35*, 649–666.

Hogsden, K. L., & Harding, J. S. (2012). Anthropogenic and natural sources of acidity and metals and their influence on the structure of stream food webs. *Environmental Pollution, 162*, 466–474.

Holt, E. A., & Miller, S. W. (2010). Bioindicators: Using organisms to measure environmental impacts. *Nature Education Knowledge, 3*, 8.

Hopkins, R. L., Altier, B. M., Haselman, D., Merry, A. D., & White, J. J. (2013). Exploring the legacy effects of surface coal mining on stream chemistry. *Hydrobiologia, 713*, 87–95.

Hughes, R., Paulsen, S., & Stoddard, J. (2000). EMAP-surface waters: A multi-assemblage, probability survey of ecological integrity in the U.S.A. *Hydrobiologia, 422*, 429–443.

Humphrey, C. L., Faith, D. P., & Dostine, P. L. (1995). Baseline requirements for assessment of mining impact using biological monitoring. *Austral Ecology, 20*, 150–166.

Huss, M., & Hock, R. (2018). Global-scale hydrological response to future glacier mass loss. *Nature Climate Change, 8*, 135–140.

Karr, J. R., & Chu, E. W. (1999). *Restoring life in running waters: Better biological monitoring*. Island Press.

Kendrick, M. R., Hershey, A. E., & Huryn, A. D. (2019). Disturbance, nutrients, and antecedent flow conditions affect macroinvertebrate community structure and productivity in an arctic river. *Limnology and Oceanography, 64*, S93–S104.

King, R. S., & Baker, M. E. (2010). Considerations for analyzing ecological community thresholds in response to anthropogenic environmental gradients. *Journal of the North American Benthological Society, 29*, 998–1008.

King, R. S., Baker, M. E., Kazyak, P. F., & Weller, D. E. (2011). How novel is too novel? Stream community thresholds at exceptionally low levels of catchment urbanization. *Ecological Applications, 21*, 1659–1678.

Kotalik, C. J., Cadmus, P., & Clements, W. H. (2021). Before-after control-impact field surveys and novel experimental approaches provide valuable insights for characterizing stream recovery from acid mine drainage. *Science of the Total Environment, 771*, 145419.

Krabbenhoft, T. J., Myers, B. J. E., Wong, J. P., Chu, C., Tingley, R. W., Falke, J. A., Kwak, T. J., Paukert, C. P., & Lynch, A. J. (2020). FiCli, the fish and climate change database, informs climate adaptation and management for freshwater fishes. *Scientific Data, 7*, 124.

Krammer, K., and H. Lange-Bertalot. (1986). Bacillariophyceae. 1. Teil: Naviculaceae In: Ettl, H., J. Gerloff, H. Heynig and D. Mollenhauer (eds.). Spektrum Akad. Verl, Heidelberg Berlin.

Krammer, K., and H. Lange-Bertalot. (1988). Bacillariophyceae. 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae In: Ettl, H., J. Gerloff, H. Heynig and D. Mollenhauer (eds.). Spektrum Akad. Verl, Heidelberg Berlin.

Krammer, K., and H. Lange-Bertalot. (1991). Bacillariophyceae. 3. Teil: Centrales, Fragilariaceae, Eunotiaceae In:

Ettl, H., J. Gerloff, H. Heynig and D. Mollenhauer (eds.). Spektrum Akad. Verl, Heidelberg Berlin.

Krammer, K. (2000). The genus Pinnularia. Gantner, Ruggell/Liechtenstein.

Krammer, K. (2002). The genus Cymbella. Gantner, Ruggell/Liechtenstein.

Krammer, K. (2003). Cymbopleura, Delicata, Navicymbula, Gomphocymbellopsis, Afrocymbella. Gantner, Ruggell/Liechtenstein.

Lange-Bertalot, H., M. Bąk, A. Witkowski, and N. Tagliaventi. (2011). Eunotia and some related genera. Gantner, Ruggell/Liechtenstein.

Lange-Bertalot, H. (2001). Navicula sensu stricto, 10 genera separated from Navicula sensu lato, Frustulia. Gantner, Ruggell/Liechtenstein.

Larson, E. I., Poff, N. L., Atkinson, C. L., & Flecker, A. S. (2018). Extreme flooding decreases stream consumer autochthony by increasing detrital resource availability. *Freshwater Biology, 63*, 1483–1497.

Lawrence, J. E., Lunde, K. B., Mazor, R. D., Bêche, L. A., McElravy, E. P., & Resh, V. H. (2010). Long-term macroinvertebrate responses to climate change: Implications for biological assessment in mediterranean-climate streams. *Journal of the North American Benthological Society, 29*, 1424–1440.

Lento, J., Culp, J. M., Levenstein, B., Aroviita, J., Baturina, M. A., Bogan, D., Brittain, J. E., Chin, K., Christoffersen, K. S., Docherty, C., Friberg, N., Ingimarsson, F., Jacobsen, D., Lau, D. C. P., Loskutova, O. A., Milner, A., Mykrä, H., Novichkova, A. A., Ólafsson, J. S., … Goedkoop, W. (2022). Temperature and spatial connectivity drive patterns in freshwater macroinvertebrate diversity across the Arctic. *Freshwater Biology, 67*, 159–175.

Lento, J., Lau, D. C. P., Brittain, J. E., Culp, J. M., & Goedkoop, W. (2023). Macroinvertebrate traits in Arctic streams reveal latitudinal patterns in physiology and habits that are strongly linked to climate. *Frontiers in Ecology and Evolution, 11*, Article 1209612.

Lisi, P. J., Schindler, D. E., Cline, T. J., Scheuerell, M. D., & Walsh, P. B. (2015). Watershed geomorphology and snowmelt control stream thermal sensitivity to air temperature. *Geophysical Research Letters, 42*, 3380–3388.

McKinley Research Group, L. L. C. (2021). *The economic benefits of Bristol Bay salmon*. Anchorage.

McAfee, S. A., Guentchev, G., & Eischeid, J. K. (2013). Reconciling precipitation trends in Alaska: 1. Station-based analyses. *Journal of Geophysical Research: Atmospheres, 118*, 7523–7541.

McCune, B., J. B. Grace, and D. L. Urban. (2002). *Analysis of ecological communities*. 2nd printing. MjM Software Design, Gleneden Beach, Or.

Milner, A. M., & Piorkowski, R. J. (2004). Macroinvertebrate assemblages in streams of interior Alaska following alluvial gold mining. *River Research and Applications, 20*, 719–731.

Milner, A. M., Conn, S. C., & Brown, L. E. (2006). Persistence and stability of macroinvertebrate communities in streams of Denali National Park, Alaska: Implications for biological monitoring. *Freshwater Biology, 51*, 373–387.

Milner, A. M., Loza Vega, E. M., Matthews, T. J., Conn, S. C., & Windsor, F. M. (2023). Long-term changes in macroinvertebrate communities across high-latitude streams. *Global Change Biology, 29*, 2466–2477.

Nowacki, G. J., Spencer, P., Fleming, M., Brock, T., & Jorgenson, T. (2002). *Unified ecoregions of Alaska: 2001*. USGS Open-File Report 2002-297. https://doi.org/10.3133/ofr2002297

Oksanen, J., G. L. Simpson, and F. G. Blanchet. (2022). Vegan: Community ecology package.

Oswood, M. W. (1989). Community structure of benthic invertebrates in interior Alaskan (USA) streams and rivers. *Hydrobiologia, 172*, 97–110.

Pajunen, V., Kahlert, M., & Soininen, J. (2020). Stream diatom assemblages as environmental indicators – A cross-regional assessment. *Ecological Indicators, 113*, Article 106183.

Palecki, M., Durre, I., Applequist, S., Arquez, A., & Lawrimore, J. (2021). *U.S. climate normals 2020: U.S. monthly climate normals (1991-2020)*. NOAA National Centers for Environmental Information. Iliamna AP

Patrick, R., and C. W. Reimer. (1966). The diatoms of the United States, exclusive of Alaska and Hawaii V1. The Academy of Natural Sciences of Philadelphia, Philadelphia, PA.

Patrick, R., and C. W. Reimer. (1975). The diatoms of the United States, exclusive of Alaska and Hawaii V2. The Academy of Natural Sciences of Philadelphia, Philadelphia, PA.

Pennak, R. W. (1989). *Fresh-water invertebrates of the United States: Protozoa to mollusca* (3rd ed.). Wiley.

Piggott, J. J., Salis, R. K., Lear, G., Townsend, C. R., & Matthaei, C. D. (2015). Climate warming and agricultural stressors interact to determine stream periphyton community composition. *Global Change Biology, 21*, 206–222.

Pitman, K. J., Moore, J. W., Sloat, M. R., Beaudreau, A. H., Bidlack, A. L., Brenner, R. E., Hood, E. W., Pess, G. R., Mantua, N. J., Milner, A. M., Radić, V., Reeves, G. H., Schindler, D. E., & Whited, D. C. (2020). Glacier retreat and Pacific Salmon. *BioScience, 70*, 220–236.

Porter, S. D. (2008). *Algal attributes: An autecological classification of algal taxa collected by the National Water-Quality Assessment Program*. U.S. Geological Survey Data Series.

Pound, K. L., Larson, C. A., & Passy, S. I. (2021). Current distributions and future climate-driven changes in diatoms, insects and fish in U.S. streams. *Global Ecology and Biogeography, 30*, 63–78.

R Core Team. (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment, 3*, 1–10.

Ray, A. M., Hossack, B. R., Gould, W. R., Patla, D. A., Spear, S. F., Klaver, R. W., Bartelt, P. E., Thoma, D. P., Legg, K. L., Daley, R., Corn, P. S., & Peterson, C. R. (2022). Multi-species amphibian monitoring across a protected landscape: Critical reflections on 15 years of wetland monitoring in Grand Teton and Yellowstone National Parks. *Ecological Indicators, 135*, 108519.

Relyea, C. D., Minshall, G. W., & Danehy, R. J. (2012). Development and validation of an aquatic fine sediment biotic index. *Environmental Management, 49*, 242–252.

Ruggerone, G. T., & Irvine, J. R. (2018). Numbers and biomass of natural- and hatchery-origin pink salmon, chum salmon, and sockeye salmon in the North Pacific Ocean, 1925–2015. *Marine and Coastal Fisheries, 10*, 152–168.

Merritt, R. W., K. W. Cummins, and M. B. Berg, editors. (2008). *An introduction to the aquatic insects of North America*. Fourth Edition. Kendall/Hunt, Dubuque, IA.

Schindler, D. E., Armstrong, J. B., & Reed, T. E. (2015). The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment, 13*, 257–263.

Seal, R. (2018). Mineral resources of the Bristol Bay watershed and their environmental characteristics. In C.A. Woody (Ed.), *Bristol Bay Alaska: Natural Resources of the Aquatic and Terrestrial Ecosystems*. J. Ross Publishing, Plantation, FL.

Shaftel, R., Bogan, D., Hagedorn, B., Jeffries, K., Jones, L., Merrigan, D., O'Neal, S., Rinella, D., & Woody, C. A. (2019). *Monitoring stream habitats and biological communities in the Lime Hills ecoregion of Bristol Bay*. Alaska Center for Conservation Science, University of Alaska Anchorage. Anchorage, AK.

Shipley, J. R., Twining, C. W., Mathieu-Resuge, M., Parmar, T. P., Kainz, M., Martin-Creuzburg, D., Weber, C., Winkler, D. W., Graham, C. H., & Matthews, B. (2022). Climate change shifts the timing of nutritional flux from aquatic insects. *Current Biology, 32*, 1342-1349.e3.

Siddig, A. A. H., Ellison, A. M., Ochs, A., Villar-Leeman, C., & Lau, M. K. (2016). How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in Ecological Indicators. *Ecological Indicators, 60*, 223–230.

Sikes, D. S., Bowser, M., Morton, J. M., Bickford, C., Meierotto, S., & Hildebrandt, K. (2016). Building a DNA barcode library of Alaska's non-marine arthropods. *Genome, 60*, 248–259.

Smucker, N. J., Detenbeck, N. E., & Morrison, A. C. (2013). Diatom responses to watershed development and potential moderating effects of near-stream forest and wetland cover. *Freshwater Science, 32*, 230–249.

Smucker, N. J., Drerup, S. A., & Vis, M. L. (2014). Roles of benthic algae in the structure, function, and assessment of stream ecosystems affected by acid mine drainage. *Journal of Phycology, 50*, 425–436.

Spaulding, S. A., Potapova, M. G., Bishop, I. W., Lee, S. S., Gasperak, T. S., Jovanoska, E., Furey, P. C., & Edlund, M. B. (2021). Diatoms.org: Supporting taxonomists, connecting communities. *Diatom Research, 36*, 291–304.

Stevens, D. L., & Olsen, A. R. (2004). Spatially balanced sampling of natural resources. *Journal of the American Statistical Association, 99*, 262–278.

Stewart, B. C., Kunkel, K. E., Champion, S. M., Frankson, R., Stevens, L. E., Wendler, G., Simonson, J., & Stuefer, M. (2022). *Alaska state climate summary 2022*. NOAA Technical Report NESDIS, NOAA/NESDIS, Silver Spring.

Stewart, K. W., & Oswood, M. W. (2006). *The stoneflies (plecoptera) of Alaska and western Canada*. Caddis Press.

Thorp, J. H., & Covich, A. P. (Eds.). (2001). *Ecology and classification of North American freshwater invertebrates* (2nd ed.). Academic Press.

U.S. Environmental Protection Agency. (2012). Freshwater biological traits database (Final Report). U.S. Environmental Protection Agency, Washington, DC, EPA/600/R-11/038F.

U.S. Environmental Protection Agency. (2013). National Rivers and Streams Assessment 2013-2014: Field operations manual – wadeable. U.S. Environmental Protection Agency, Office of Water, Washington, DC.

U.S. Environmental Protection Agency. (2014). An assessment of potential mining impacts on salmon ecosystems of Bristol Bay, Alaska. Region 10, Seattle, WA. EPA 910-R-14–001.

Wagener, S. M., & LaPerriere, J. D. (1985). Effects of placer mining on the invertebrate communities of interior Alaska streams. *Freshwater Invertebrate Biology, 4*, 208–214.

Wang, Y., Naumann, U., Wright, S. T., & Warton, D. I. (2012). Mvabund— An R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution, 3*, 471–474.

Webb, J. M., Cole, M. B., & Simmons, T. (2022). DNA barcoding takes bioassessment further: New distribution records for aquatic macroinvertebrates from Alaskan National Parks. *Proceedings of the Entomological Society of Washington, 124*, 131–149.

Wiggins, G. B. (1996). *Larvae of the North American Caddisfly Genera (Trichoptera)*. University of Toronto Press.

Wobus, C., Prucha, R., Albert, D., Woll, C., Loinaz, M., & Jones, R. (2015). Hydrologic alterations from climate change inform assessment of ecological risk to Pacific salmon in Bristol Bay, Alaska. *PLoS ONE, 10*, e0143905.

Woll, C., Albert, D., & Whited, D. (2012). *A preliminary classification and mapping of salmon ecological systems in the Nushagak and Kvichak watersheds*. The Nature Conservancy. https://www.conservationgateway.org/ConservationByGeography/NorthAmerica/UnitedStates/alaska/sw/cpa/Documents/TNC_A_Salmon_Ecological_Systems_Model_Nushagak_Kvichak.pdf

Woody, C. A., & O'Neal, S. L. (2010). *Fish surveys in headwater streams of the Nushagak and Kvichak river drainages*. Fisheries Research and Consulting.

Woody, C. A., Shaftel, R., Rinella, D., & Bogan, D. (2014). *Long-term monitoring plan for wadeable streams, Lime Hills Ecoregion, Kvichak and Nushagak watersheds*. Center for Science in Public Participation and University of Alaska Anchorage.

Woody, C. A. (2018). Freshwater Non-Salmon Fishes of Bristol Bay. In C.A. Woody (Ed.), *Bristol Bay Alaska: Natural Resources of the Aquatic and Terrestrial Ecosystems*. J. Ross Publishing, Plantation, FL.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.