

RESEARCH ARTICLE

Effects of river ice break-up on organic-matter dynamics and feeding ecology of aquatic insects

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Abstract

Disturbance shapes the structure and function of aquatic communities and ecosystems, but the dynamics of ice are a less studied dimension of the disturbance-regime of rivers. We investigated effects of a river-ice regime on organic-matter dynamics and feeding ecology of aquatic insects. Samples of biofilm and aquatic insects for gut content analysis were collected monthly from Big Creek, a sixth - order tributary of the Middle Fork Salmon River in central Idaho, USA, during winter 2010–2011. Our results indicate that river ice affects both quantity and quality of organic matter available to, and used by, consumers. Specifically, scour from December and February ice break-up events reduced biofilm biomass by one-half and one-third, respectively, whereas quality (chlorophyll-*a*: ash-free dry mass) increased. Diets of scrapers, *Rhithrogena* (Heptageniidae) and *Biocephala* (Blephariceridae), collector-gatherers, *Baetis* (Baetidae), and collector-filterers, *Simulium* (Simuliidae) appeared to follow patterns of organic matter. Following ice break-up events, diets of these taxa had increased proportions of diatom frustules, which are high-quality food resources due to their relatively high nutrient content. Other taxa, such as collector-gatherers, non-Tanytopodinae (Chironomidae), and the collector-filterer, *Arctopsyche grandis* (Hydropsychidae), consistently consumed high proportions of diatom frustules and insect material, respectively, suggesting they were able to feed more selectively throughout winter. Our study indicates that ice regimes in temperate rivers can affect organic-matter dynamics and feeding ecology of aquatic insects, a possibility that deserves additional investigation, particularly in light of potential changes to the ice regimes of rivers with changing climate.

KEYWORDS

aquatic invertebrates, disturbance, gut-content analysis, organic matter, river ice, winter ecology

1 | INTRODUCTION

Disturbance is a critical factor shaping structure and function of riverine communities and ecosystems (Resh et al., 1988). Flooding, drought, landslides, fire, and human alterations to flow regimes are disturbances affecting river productivity and survival of aquatic organisms. (Poff et al., 1997). These disturbances impact quantity

and quality of organic matter for consumers within aquatic food webs. For instance, droughts are critical periods of organic-matter availability (Lake, 2003), reducing fine particulate organic matter transport, and leading to accumulations of detritus and sediments (Cuffney & Wallace, 1989). Floods transport organic matter to downstream regions and link the mainstem channel to floodplains, where exchange of organic matter and organisms may occur (Poff

et al., 1997). In addition, elevated flows mobilize sediments and riverbed particles, scouring substrate and exposing areas of riverbed for colonization by biofilm communities (Power & Stewart, 1987). New growth of biofilm is considered a high quality food, in part because diatom frustules contain large proportions of lipids and fatty acids (Spaulding & Elwell, 2007). In contrast to floods, the impact of ice regimes has received less attention. In particular, studies are needed that investigate ecological effects of ice dynamics (Scrimgeour, Prowse, Culp, & Chambers, 1994; Prowse, 2001a; Prowse, 2001b; Beltaos, 2007).

Periods of river-ice formation and break-up are critical physical disturbances affecting river ecosystems at high latitudes and altitudes (Scrimgeour et al. 1994, Prowse, 2001b). Ice may form at the water surface, thereby stabilizing water temperatures relative to atmospheric temperatures (Gard, 1963), reducing water velocity (Turcotte, Morse, Bergeron, & Roy, 2011), and lowering concentrations of dissolved oxygen (Prowse, 2001a). Turbulent flows, in contrast, prevent ice formation at the water surface and promote formation of small ice crystals in the water column (frazil ice; Prowse, 2001a, Hirayama et al. 2002). In addition, ice may attach to river substrates forming anchor ice. Anchor ice confines the channel, shields riverbed materials from entrainment, and disturbs river substrates (Prowse, 2001a). Frazil ice affects the viscosity of flowing waters and may scour the riverbed (Reimnitz et al. 1990, Prowse 2001a). Although many types of ice affect physical processes in rivers, ice break-up events may do so disproportionately because ice break-up events result from the rapid degradation of ice cover into large ice flows. This can result in dramatic increases in discharge, water temperature, suspended materials, and intense scouring of the river channel and riparian area (Scrimgeour et al. 1994, Prowse & Culp 2003, Beltaos 2007, Turcotte et al. 2011, Engstrom et al. 2011). Typically, ice break-up events are assumed to occur in spring with warming temperatures; however, they may occur during winter, and the timing and frequency of ice break-up events may be affected by climate change (Scrimgeour et al. 1994, Prowse & Culp, 2003). Previous studies have focused on physical effects of river ice (hydraulic and geomorphic, that is, Prowse, 2001a, Hirayama, Yamazaki, & Tao Shen, 2002), however, less is known regarding the ecological effects of disturbance from river ice (Scrimgeour et al. 1994).

Few studies have addressed how disturbance from river ice affects riverine food webs; river ice may alter the structure of food webs by affecting the distribution of organisms and availability of food. Ice cover and break-up may influence the quantity and quality of organic matter in river ecosystems. For instance, surface ice can decrease light available to primary producers (Steinhart & Wurtsbaugh, 2004), and anchor ice can displace macrophytes (Prowse, 2001b). Additionally, scour from ice break-up may not just temporarily remove primary producers, but stimulate them by providing a clean substrate for growth (Prowse & Culp, 2003). Ice formation and break-up can alter the distribution of fishes and may affect their populations by freezing their eggs (Brown, Power, & Daly, 2011). Furthermore, ice break-up events can displace macroinvertebrates (Brown, Power, & Daly, 2011). However,

cumulative effects on populations of macroinvertebrates and the food webs in which they participate may depend on the dynamics of organic matter resources (i.e., food resources) and trophic ecology of these consumers, which may be altered by scour from ice break-up. Floods can reduce biofilm biomass, increase gross primary production (Power & Stewart, 1987), and increase the quality of food available to aquatic insects (Wellard Kelly et al., 2013). Ice scour may play a similar role in structuring river food webs; however, no study has directly investigated the feeding ecology of aquatic insects in response to a river-ice regime.

The objective of this research was to investigate how disturbance from ice break-up affects dynamics of biofilm organic matter and feeding ecology of aquatic insects. In general, we hypothesized that disturbance by ice alters such food-web dynamics. More specifically, we hypothesized that by scouring the channel of accumulated detritus and exposing fresh substrates to colonization by diatoms, ice break-up would reduce the biofilm quantity (as measured by ash-free dry mass; AFDM), but increase its quality (i.e., ratio of chlorophyll-*a* to ash-free dry mass). Stream biofilm is composed of autotrophic algae, heterotrophic microbes, and detritus; their relative importance can change during biofilm succession and result in changes in chlorophyll-*a* to AFDM ratios over time (Fisher et al. 1982). We predicted that biofilm quality would increase in response to ice break-up. If so, we expected that aquatic insects would respond by consuming a greater proportion of high-quality foods, such as diatoms, following ice break-up, but that insects would respond differentially because of their feeding traits. For example, a shredder may not shift its diet in response to ice break-up events in the same manner as a scraper. A broader aim was to investigate winter ecology in river ecosystems, which is globally understudied. Winter temperatures in the Pacific Northwest of North America are predicted to be strongly affected by climate change (Mote et al., 2003); therefore, river ice regimes are likely to be altered. Results from our research will improve understanding of how climate-induced shifts in ice-regimes may affect aquatic ecosystems.

2 | METHODS

2.1 | Study site

Our research was based at Taylor Wilderness Research Station (TWRS, 45.1019°N and 114.8517°W), within the Frank Church Wilderness in central Idaho, USA. Study locations were in the mainstem of Big Creek, a sixth order river (drainage area: 1444 km²). Big Creek has a natural flow regime and a diverse suite of native macroinvertebrates, encompassing a range of feeding modes that occur in montane rivers within this region and similar regions of the world. Big Creek flows through mountainous terrain with severe changes in elevation from the valleys near TWRS (1,200 m) to high elevation peaks (3,150 m). Annual precipitation ranges from 38 to 50 cm in valleys and from 76 to 100 cm at higher elevations. Most precipitation occurs as snow, resulting in peak flows from May to June. Baseflow conditions occur from late

summer through winter, but mid-winter fluctuations in river discharge associated with river ice were observed during this study. We selected 36 locations (18 paired edge and thalweg sites) along a 3 km segment of Big Creek encompassing pool and riffle habitats that were representative of the geomorphic character of the river.

2.2 | River ice monitoring

We used a combination of techniques to describe patterns in river ice cover and break-up. Monthly sampling trips (December 2010 to March 2011) allowed us to directly observe river-ice cover and conditions before and after break-up events. Additionally, we used cameras (Moultrie, Farmington, NY, USA) to monitor patterns in river ice. Two digital cameras were programmed to record a photo every 30-minutes from December 11, 2010 through February 9, 2011. Lastly, we used a gauge in Big Creek that recorded stage-height to monitor river ice (Northwest Fisheries Science Center, 2007). We identified ice break-up events by loss of surface ice, change in color of water in photographs, and increases in stage height (Figure 1).

2.3 | Biofilm

We sampled biofilm (assemblage of living and dead autotrophs, heterotrophic microbes, and detritus on rocks) monthly from

December 2010 to March 2011. Sampling was stratified by thalweg and edge habitats to represent the range of conditions present and because we expected that these habitats might be differentially impacted by the ice-regime in Big Creek. At each of the 18 locations, three rocks were chosen haphazardly from each habitat type, placed into plastic bags, and transported to the research station for processing. Rocks were kept cool during transport as ambient weather conditions were generally near freezing. The entire surface area of each rock was scrubbed with a wire brush to remove all biofilm (Bergey and Getty, 2006). The composite slurry was subsampled (20–50 mL), filtered onto pre-combusted (400°C for 30 min) and pre-weighed glass-fiber filters (0.7 μm), and frozen immediately. The planar area of sampled rocks was traced onto paper. Rock tracings were converted to planar area with linear regression. Using the planar area method is an accepted technique to scale chlorophyll-*a* measurements to rock size (Bergey and Getty, 2006). This resulted in 36 composite samples (18 thalweg and 18 edge) for each sampling period.

Based on standard methods (APHA, 1998), filters were analyzed for chlorophyll-*a* (chl-*a*) and ash-free dry mass (AFDM). Filters were extracted in methanol for 12 h, analyzed for chl-*a* with a spectrophotometer and corrected for phaeophytin. After extraction, the filters and methanol extract were recombined, dried, weighed, and ashed. Samples were then reweighed to calculate AFDM. Additionally, the chl-*a* values were divided by the corresponding AFDM values to generate the ratio of chl-*a* to AFDM, an indicator of biofilm quality (Naiman, 1983).

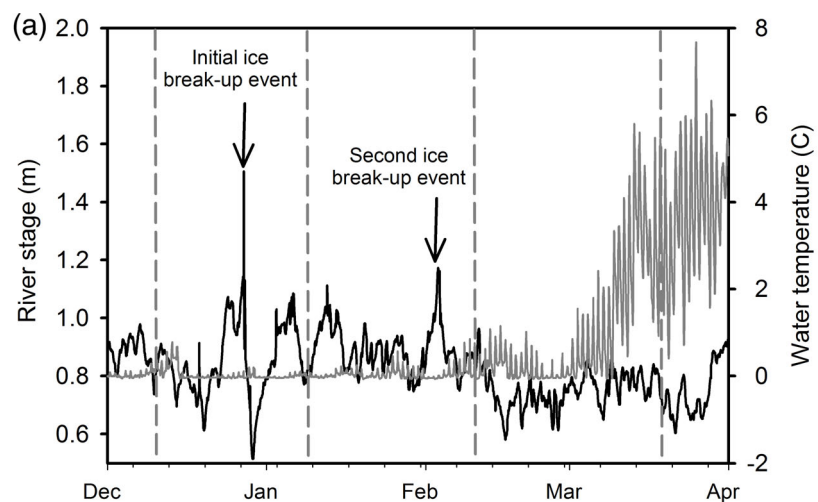


FIGURE 1 Hourly river stage (black lines) and water temperature (grey lines) in Big Creek, Idaho, USA between 1 December, 2010 and 1 April, 2011 (a). Dashed, vertical lines represent dates of sampling events. Representative photos of Big Creek during an ice-out event (b) and the maximum extent of river ice in Big Creek near TWRS (c). Notice river discoloration and transport of large logs in photo (b) and evidence of previous ice break-up events in photo (c)



2.4 | Aquatic insect collection and laboratory processing

At the same locations where biofilm was sampled, we also collected aquatic insects monthly (December 2010 to March 2011) from thalweg and edge habitats with kick-nets (250- μ m mesh). The aim of this sampling was collection of individuals for gut content analysis, not quantitative evaluation of the entire invertebrate community. Individuals were preserved in Kahle's solution (Stehr, 1991). Prior to gut removal, individuals were identified to genus or species, except for Chironomidae, which were identified as non-Tanypodinae (Merritt, Cummins, & Berg, 2008). We examined gut contents of taxa representing four functional groups corresponding to modes of feeding (Cummins & Klug, 1979): scrapers [*Rhithrogena* (Ephemeroptera: Heptageniidae) 4–11 mm and *Bibiocephala* (Diptera: Blephariceridae) 7–13 mm], collector-gatherers [*Baetis* (Ephemeroptera: Baetidae) 3–6 mm and non-Tanypodinae (Diptera: Chironomidae) 8–11 mm], collector-filterers [*Simulium* (Diptera: Simuliidae) 4–7 mm and *Arctopsyche grandis* (Trichoptera: Hydropsychidae) 10–24 mm], and a shredder [*Pteronarcys californica* (Plecoptera: Pteronarcyidae) 8–48 mm]. These taxa were chosen as study organisms because they represent a range of functional feeding groups. In Big Creek, these taxa represented over 50% of benthic abundance and at least 25% of benthic biomass of aquatic invertebrates collected during summer monitoring (Baxter & Minshall, 2016b).

Diets were evaluated with standard techniques for gut-content analysis (Rosi-Marshall, Wellard Kelly, Hall, & Vailas, 2015). Individuals for gut-content analysis were pooled between thalweg and edge habitats (i.e., across all 36 sampling locations). This pooling provided a spatially integrated estimate of the average diets across the overall length of the study reach. The number of individuals per slide (prepared microscope slide of gut-contents from aquatic insects digestive tract, which was pipetted onto slide and sealed with cover slip) varied from one to four, based on the size and gut fullness of insects. Three to seven slides per month were analyzed for each taxon, allowing us to assess whether diets changed over time.

We measured the fractional area of food particles to calculate the proportion of each particle type in diets of aquatic insects. Food particles were identified as amorphous detritus, diatom frustule, diatom stalk, filamentous algae, fungi, leaf material, insect material, and wood with a compound microscope at 200–400 \times (Leica DMRB, Buffalo Grove, IL) mounted with a digital camera (SPOT CCD, Sterling Heights, MI). We identified diatom frustules and diatom stalks separately because stalks were easily distinguished from frustules and because diatom frustules have higher nutritional quality than diatom stalks. We measured the area of 100 particles on each slide along transects (1–5) using ImageJ (National Institutes of Health, Bethesda, MD).

2.5 | Statistical analyses

The overall study design compared biofilm characteristics and diets of aquatic insects in relation to ice break-up. Because our study focused on a single river and did not include a control that lacked ice-break up

events, we used bootstrap analysis to generate confidence intervals on estimates and examined how organic matter resources and diets of aquatic insects varied through time, bracketing ice break-up events. Data were re-sampled with replacement 1,000 times, and the mean and 2.5% and 97.5% quantiles were calculated from the bootstrap distribution. For all metrics, differences were considered significant if 95% confidence intervals (CIs) did not overlap. In addition, we conducted sign analyses (Conover, 1980) to evaluate patterns in the direction of differences following ice break-up events, and Pearson's correlation analyses to investigate relationships among diets of aquatic insects and days since initial ice break-up. For these analyses, p - values <0.05 were considered significant. The timing of our sampling relative to that of two ice break-up events (Figure 1) meant that comparisons before and after these events were separated by 19 and 29 days for the Dec. 27th, 2010 break-up event and 9 and 5 days for the Feb. third, 2011 event, respectively.

Organic matter data from within each monthly sampling period were averaged. We estimated means and 95% CIs for chl- a , AFDM, and chl- a :AFDM of biofilm. We examined differences in biofilm metrics between edge and thalweg habitats by plotting monthly means and 95% CIs for each month. Because biofilm metrics were similar among habitats (i.e., 95% CIs overlapped), values were combined for subsequent analyses. We used sign analyses to investigate direction of differences following ice break-ups.

Aquatic insect diet data from each monthly sampling period were averaged to calculate the proportion of all food-particle types in the diet of each taxon. We examined differences in diets of insects by comparing monthly mean proportions of dominant foods (diatom frustule, amorphous detritus, leaf material, filamentous algae, etc.). We estimated means and 95% CIs for the proportion of each food consumed. For each taxon, the proportions of food resource consumed were re-sampled with replacement 1,000 times, and results were interpreted as previously described.

We used correlation analysis to investigate relationships between diets of aquatic insects and days since initial ice break-up. We compared the proportion of diatom frustules observed in gut-contents with days since initial ice break-up for each taxon. We measured the strength of the linear association with Pearson's correlation coefficient (r). We also used sign analysis to investigate the direction of differences in diets of aquatic insects following ice break-ups. We evaluated the proportion of diatom frustules in gut-contents of insects before and after ice break-ups. Regression, linear, and correlation analyses were performed with SAS (SAS version 9.2, SAS Institute Inc., Cary, NC). Bootstrap and sign analyses were conducted in Microsoft Excel 2008 (Microsoft Corporation, Redmond, WA). Overall, we used a weight-of-evidence approach (sensu Lowell, Culp, & Dubé, 2000, Monteith et al. 2013) whereby results associated with a single variable may not be sufficient to draw a firm conclusion, but when multiple variables are considered, a clear pattern may become evident. This approach would allow us to make comparisons of evidence from different analyses and make inferences based on the preponderance of evidence. Specifically, we used data from long-term weather records, stream channel photos regularly taken by

remote cameras, and stage-height measurements that captured physical disturbance. By comparing these data with responses of biofilm, transported organic matter, and the gut-contents of aquatic insects before and after ice disturbance, this weight-of-evidence approach allowed us to investigate how the foodweb ecology of Big Creek was potentially altered by ice break-up events. This ecosystem approach to physical and ecological monitoring “realizes the complexity of ecological interactions, the intrinsic importance of humans within ecosystems, and the need for a more balanced approach,” (Scrimgeour & Wicklum, 1996).

3 | RESULTS

3.1 | River ice regime

Our study period exhibited snow accumulations that were typical for this region, as indicated by publicly available snow data (SNOTEL) that is systemically collected by the Natural Resources Conservation Service at the Big Creek Summit (Site #337; ~50 km from our study sites; data retrieved from: (<https://wcc.sc.egov.usda.gov/nwcc/site?sitenum=337>)). Overall, our study period (Nov 2010 to Mar 2011) had snow water equivalent values that were ~97% of the normal snow accumulation for the time period encompassing 1981 to 2010. Further, temperature data collected at TWRS indicate that temperatures during our study period (Nov 2010 to Apr 2011) were similar to mean values from 2009 to 2015 (daily mean maximum temperature 6.8 vs. 4.6 C and daily mean minimum temperature -3.9 vs. -3.7 C, respectively; data retrieved from Western Regional Climate Center: <https://wrcc.dri.edu/cgi-bin/rawMAIN.pl?idITAY>). Precipitation accumulations at TWRS during the same timeframe were similar to mean precipitation values from 2009 to 2015 (mean monthly precipitation 2.8 cm vs. 2.5 cm/month, respectively (<https://wrcc.dri.edu/cgi-bin/rawMAIN.pl?idITAY>)). Together, these data sources suggest that our study year represented a relatively typical winter in the Big Creek watershed. (i.e., weight of evidence approach).

Ice formation within our study segment in Big Creek commenced in November 2010 and ice was no longer present by March 2011. We observed surface ice along margins of the river channel from November 2010 to February 2011; however, surface ice was not observed in thalweg habitats for all months. In contrast, we observed frazil and anchor ice from November 2010 to February 2011. The ice regime in Big Creek was dominated by two ice break-up events in December and February (Figure 1(a), see Supplementary Material). We documented the ice break-ups via cameras and stage measurements (Figure 1(b)). The initial ice break-up occurred on December 27, 2010 and a second ice break-up, of lower magnitude than the initial, occurred on February 3, 2011 (Figure 1(a)). Following ice break-up events, we observed a wall of ice (c. 0.3–1.6 m in height) comprised of ice slabs deposited on top of one another along river margins. While the wall of ice on the margins of the river persisted, this feature altered channel morphology, resulting in a narrower, deeper channel than would have otherwise occurred (Figure 1(c)).

3.2 | Biofilm

Biofilm AFDM decreased following two ice break-up events, (Figure 2 (a)). AFDM decreased by 38%, following the ice break-up in December (Figure 2(a)). Subsequently, AFDM decreased by 54% between January and February, following the second ice break-up. Differences in AFDM between January and February were significant (Figure 2(a)). The greatest shift in AFDM occurred between February and March (Figure 2(a)). Overall, AFDM decreased following the two ice break-ups (sign test; $n = 66$, $x = 16$, $p < 0.001$).

Patterns in biofilm chl-*a* were similar to AFDM (Figure 2(b)). Chl-*a* decreased by 23%, following the initial ice break-up in December (Figure 2(b)). In addition, chl-*a* significantly decreased by 41% after the second ice break-up (i.e., between January and February, Figures 1 (a), 2(b)). Chl-*a* increased 103% from February to March, reaching values similar to pre ice break-up conditions (Figure 2(b)). Overall,

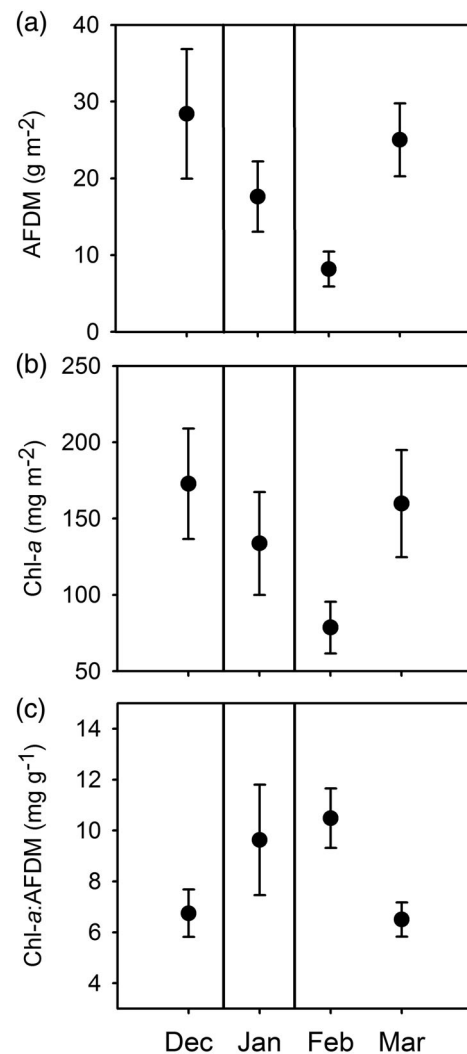


FIGURE 2 Monthly biofilm (Mean \pm 95% CI) ash-free dry mass (a), chlorophyll-*a* (b), and ratio of chl-*a* to AFDM (c) in combined thalweg and edge habitats in Big Creek, Idaho, USA during winter 2010–2011. Vertical, black lines represent dates of ice break-up events

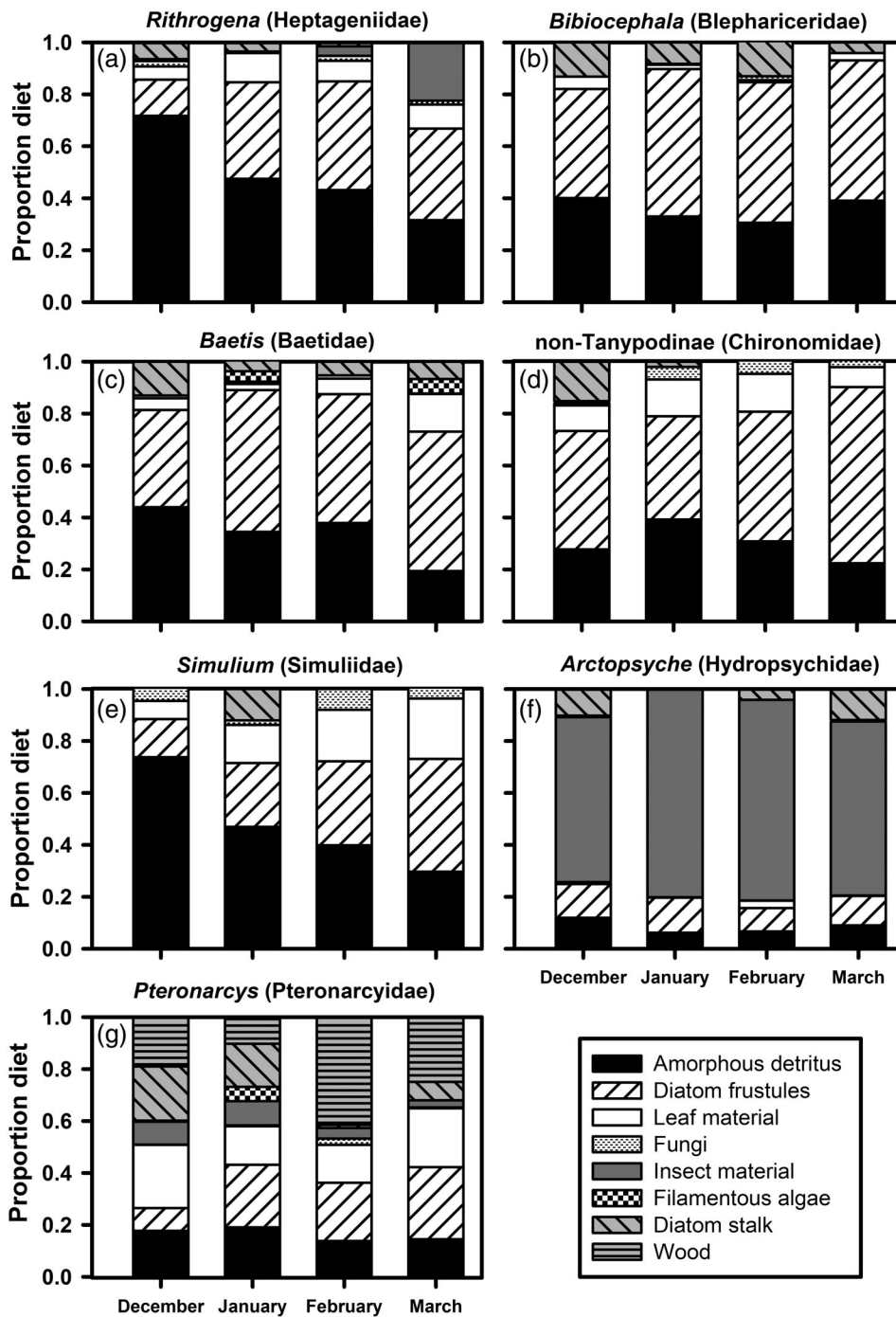


FIGURE 3 Proportion of different food items in the diets of aquatic insects collected from Big Creek in Idaho, USA. Individuals were collected between Dec. 2010 and Mar. 2011. Stacked bars represent the average ($n = 3-7$) proportion of food-particle types in gut-contents of *Rithrogena* (a), *Bibiocephala* (b), *Baetis* (c), non-Tanyptodinae Chironomidae (d), *Simulium* (e), *A. grandis* (f), and *P. californica* (g)

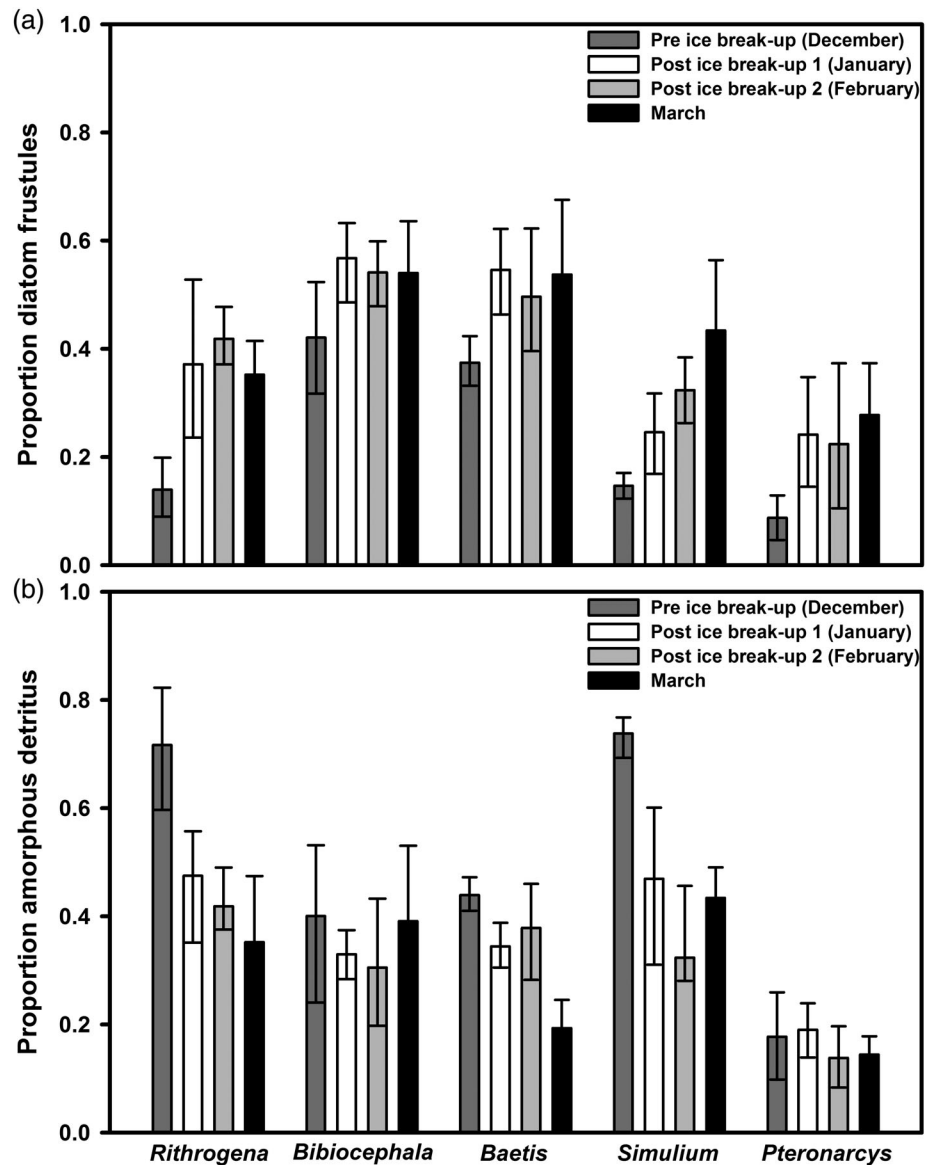
chl-*a* decreased following the two ice break-up events (sign test; $n = 66$, $x = 20$, $p = 0.001$).

The ratio of chl-*a* to AFDM of biofilm, an indicator of quality, exhibited trends opposite to those of AFDM and chl-*a* (Figure 2(c)). When chl-*a* and AFDM were highest (December and March), chl-*a*:AFDM was lowest (Figure 2). Following the initial ice break-up in December, chl-*a*:AFDM decreased 43% (Figure 2(c)). Differences in chl-*a*:AFDM between December and January were significant (Figure 2(c)). From February to March, chl-*a*:AFDM decreased 38%, reaching values similar to pre ice-break-up conditions (Figure 2(c)). Overall, chl-*a*:AFDM increased following the two ice break-up events (sign test; $n = 66$, $x = 18$, $p < 0.001$).

3.3 | Aquatic insect gut-content analysis

Overall, diets of five taxa (*Rithrogena*, *Bibiocephala*, *Baetis*, *Simulium*, and *P. californica*) appeared to follow the temporal patterns of organic matter that were observed pre- and post- ice break-up. These taxa consumed greater proportions of diatom frustules following ice break-up (sign test; $n = 58$, $x = 19$, $p = 0.006$). Changes in the proportion of diatom frustules in gut-contents of these taxa were greatest following the initial ice break-up (sign test; $n = 29$, $x = 19$, $p < 0.001$). In contrast, two taxa (non-Tanyptodinae Chironomidae and *A. grandis*) did not follow patterns observed in organic matter. Rather, these insects

FIGURE 4 Monthly (Mean \pm 95% CI) proportion of diatom frustules (a) and amorphous detritus (b) in gut-contents of aquatic insects collected from Big Creek in Idaho, USA. Proportions of diatom frustules increased and amorphous detritus decreased in diets of aquatic insects following ice break-up. Dark gray bars represent diets in December 2010 prior to ice break-up, white bars represent diets in January 2011 following initial ice break-up event, light gray bars represent diets in February 2011 following second ice break-up event, and black bars represent diets in March 2011



consistently consumed high proportions of diatom frustules and insect material.

Diets of the scraper mayfly, *Rhithrogena*, consisted of amorphous detritus (49%), diatom frustules (32%), leaf material (8%), insect material (7%), and diatom stalks (2%; Figure 3(a)). The proportion of diatom frustules in their gut-contents was significantly lower in December, prior to ice break-up, than all other months (Figure 4(a)). Following the initial ice break-up, the proportion of diatom frustules increased significantly by 166% from December and January (Figure 4(a)). We observed a significant, positive relationship between days since initial ice break-up and the proportion of diatom frustules in *Rhithrogena* gut-contents (Pearson; $n = 24$, $r = 0.48$, $p = 0.017$). In contrast to diatom frustules, the proportion of diatom stalks, a lower-quality food resource, was greatest in December, prior to ice break-up, and decreased through March (Figure 3(a)). Similar to the pattern of diatom stalks, the proportion of amorphous detritus was significantly greater in December than

all other months (Figure 4(b)). Overall, gut-contents of *Rhithrogena* were composed of a greater proportion of diatom frustules following ice break-up, which also corresponded with a reduction in proportions of diatom stalks and amorphous detritus.

Diets of the scraper midge, *Bibiocephala*, consisted of diatom frustules (52%), amorphous detritus (36%), diatom stalks (10%), and leaf material (2%; Figure 3(b)). Similar to *Rhithrogena*, the proportion of diatom frustules in gut-contents was lowest in December, prior to ice break-up (Figure 4(a)). Additionally, the proportion of amorphous detritus was greatest in December, and decreased following ice break-ups in December and February (Figure 4(b)). There was not, however, a significant correlation between days since initial ice break-up and the proportion of diatom frustules (Pearson; $n = 28$, $r = 0.26$, $p = 0.177$). In general, diets of *Bibiocephala* were composed of a greater proportion of diatom frustules following ice break-ups, and this corresponded with a reduction in the proportion of amorphous detritus.

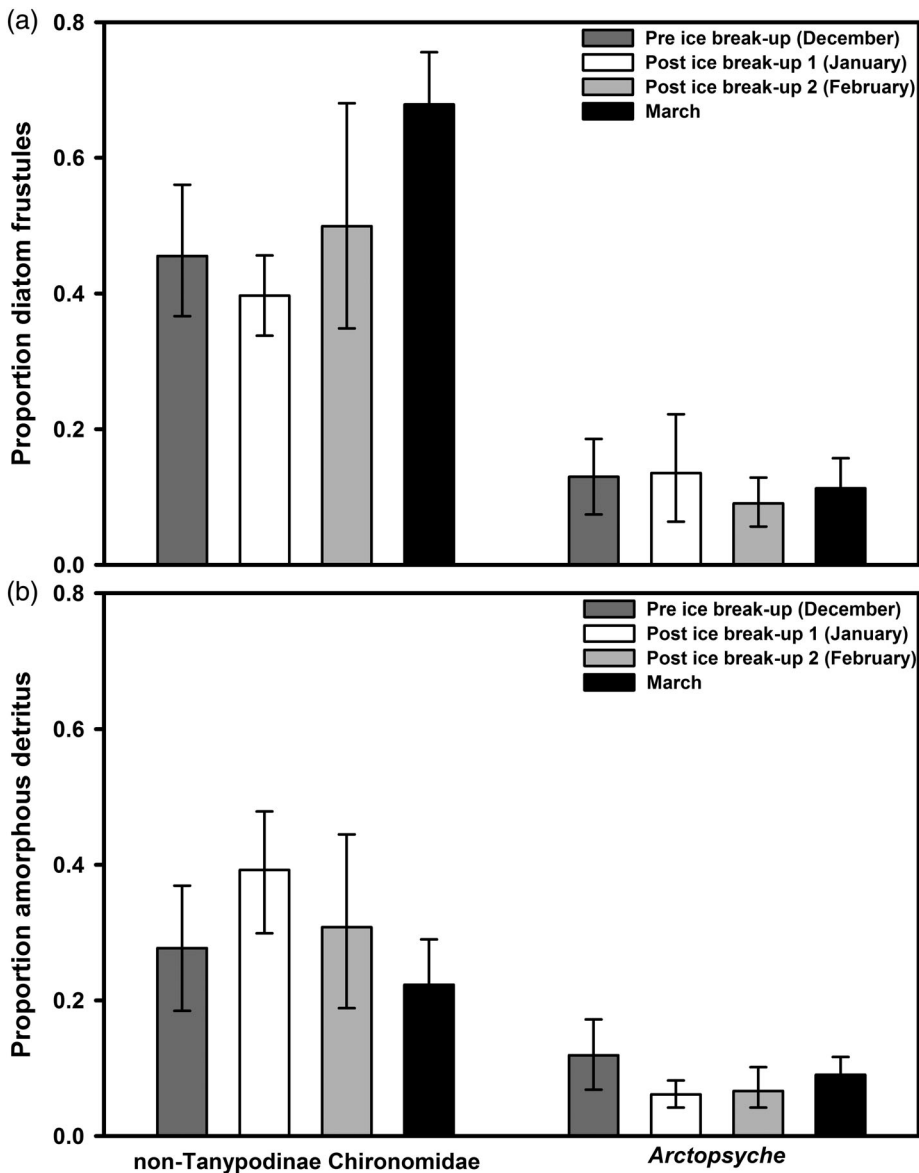


FIGURE 5 Monthly (Mean \pm 95% CI) proportion of diatom frustules (a) and amorphous detritus (b) in gut-contents of aquatic insects collected from Big Creek in Idaho, USA. Proportions of diatom frustules and amorphous detritus were not affected by ice break-up events. Dark gray bars represent diets in December 2010 prior to ice break-up, white bars represent diets in January 2011 following initial ice break-up event, light gray bars represent diets in February 2011 following second ice break-up event, and black bars represent diets in March 2011

Diets of the collector-gatherer mayfly, *Baetis*, consisted of diatom frustules (49%), amorphous detritus (34%), diatom stalks (7%), leaf material (7%), and filamentous algae (2%; Figure 3(c)). The proportion of diatom frustules was lowest (Figure 4(a)), and the proportion of diatom stalks was highest (Figure 4(b)), in December. Following the initial ice break-up, the proportion of diatom frustules increased by 46% between December and January (Figure 4(a)). The proportion of amorphous detritus was greatest in December (Figure 4(b)) and decreased by 22% between December and January (Figure 4(b)). Overall, diets of *Baetis* were composed of greater proportions of diatom frustules following ice break-ups, which also corresponded with a reduction in proportions of diatom stalks and amorphous detritus.

Diets of the collector-gatherer Chironomidae (non-Tanytopodinae) consisted of diatom frustules (51%), amorphous detritus (30%), leaf material (12%), diatom stalks (4%), and fungi (3%; Figure 3(d)). The proportion of diatom frustules in their guts was greatest in March, when the proportion of amorphous detritus was lowest (Figure 5).

Between December and February, the proportion of diatom frustules ranged from 40–50% and did not differ following ice break-up events (Figure 5(a)). Diatom stalks accounted for 15% and 2% of gut-contents in December and January, respectively, but were not observed in guts from February or March, following two ice break-ups (Figure 3(d)). Overall, non-Tanytopodinae Chironomidae consumed high proportions of diatom frustules, and their diets did not shift significantly following ice break-up.

Diets of the collector-filterer black fly, *Simulium*, consisted of amorphous detritus (49%), diatom frustules (29%), leaf material (16%), fungi (5%), and diatom stalks (3%; Figure 3(e)). The proportion of diatom frustules was lowest in December and increased through March (Figure 4(a)). We observed a significant positive relationship between days since initial ice break-up and the proportion of diatom frustules (Pearson; $n = 21$, $r = 0.70$, $p < 0.001$). Correspondingly, the proportion of amorphous detritus was significantly greater in December than all other months and decreased through February (Figure 4(b)). Following

the initial ice break-up, the proportion of amorphous detritus decreased by 36% (Figure 4(b)). Overall, *Simulium* consumed a greater proportion of diatom frustules following ice break-ups, which also corresponded with a reduction in the proportion of amorphous detritus consumed.

Diets of the collector-filterer caddisfly, *A. grandis*, were dominated by insect material, (72%), with smaller proportions of diatom frustules (12%), amorphous detritus (8%), and diatom stalks (7%; Figure 3(f)). On average, the proportion of insect material ranged from 64–80% and did not differ significantly following ice break-up (Figure 3(f)). Diatom frustules composed <14% of gut-contents for all months and did not differ following ice break-up (Figure 5(a)). However, as exhibited by other taxa, the proportion of amorphous detritus was greatest in *A. grandis* gut contents in December, prior to ice break-up (Figure 5(b)).

Finally, diets of the shredder stonefly, *P. californica*, included the greatest variety of all taxa examined. The diets of *P. californica* consisted of wood (24%), diatom frustules (21%), leaf material (19%), amorphous detritus (16%), diatom stalks (11%), and insect material (6%; Figure 3(g)). Consistent with several other insects, the proportion of diatom frustules was lowest in December, and increased by 176% following the initial ice break-up (Figure 4(a)). We observed a significant, positive relationship between days since initial ice break-up and the proportion of diatom frustules in their gut-contents (Pearson; $n = 28$, $r = 0.42$, $p = 0.025$). In contrast to diatom frustules, the proportion of diatom stalks decreased from December through February (Figure 3(g)). The proportion of wood in gut-contents was lowest in January and increased by 302% from January to February, following the second ice break-up (Figure 3(g)). Leaf material composed 15–24% of gut-contents for all months and did not differ following ice break-up (Figure 3(g)). Overall, diets of *P. californica* were composed of greater proportions of diatom frustules following ice break-ups, which corresponded with a reduction in the proportion of diatom stalks.

4 | DISCUSSION

Our study demonstrates ice break-up can affect river ecosystems in temperate zones, specifically via changes in organic matter dynamics and feeding ecology of aquatic insects. Disturbance by river ice affected both quantity and quality of organic matter available to aquatic insects. Biofilm biomass (AFDM and chl-*a*) was greatest prior to ice break-up. Scour from ice break-up reduced AFDM and chl-*a*, while its quality (chl-*a*:AFDM) increased. Diets of most aquatic insects we studied (*Rhithrogena*, *Bibiocephala*, *Baetis*, *Simulium*, *P. californica*) appeared to follow patterns of organic matter in response to disturbance by river ice. These taxa consumed greater proportions of diatom frustules, a high-quality food resource, following two ice break-up events. In contrast, two taxa (non-Tanypodinae Chironomidae and *A. grandis*) consistently consumed large proportions of diatom frustules and insect material, both high-quality foods. In contrast to our results, a recent study found that flooding disturbance decreased

biofilm dry weight, exhibited no significant effect on biofilm C:N, and shifted the stable isotope signatures of invertebrates towards relatively more allochthony vs. autochthony (i.e., Larson, Poff, Atkinson, & Flecker, 2018). Although that study did not present resource quality metrics based on chl-*a*:AFDM, disturbance by ice break-up may be distinctive, in part because such events may occur during times of the year not characterized by flooding. Nonetheless, the combination of such results indicate that invertebrate diets can shift with disturbance, and ours is one of the first studies to directly evaluate organic matter resources and insect trophic ecology following disturbance by river ice. Our observations were limited to a single montane, free-flowing river; therefore, we suggest additional ecological studies of river ice regimes be conducted in other regions to investigate the extent to which these patterns can be generalized.

4.1 | Organic matter dynamics affected by ice regime

We documented that disturbance by ice can affect river organic matter dynamics. Congruent with our initial prediction that ice break-up would reduce biofilm biomass, both AFDM and chl-*a* decreased following ice break-up. In contrast, biofilm quality (chl-*a*:AFDM) increased following ice break-up. Such wintertime dynamics may be more important than generally acknowledged. For instance in Big Creek, AFDM and chl-*a* biomass were greater in winter than observed as part of summer monitoring (Davis et al. 2013; Baxter & Minshall, 2016a) (200% and > 1,200%, respectively), and quality was >200% higher in winter than summer. Moreover, biofilm C:N followed patterns of chl-*a*:AFDM, providing additional evidence that biofilm quality increased following ice break-up events, though elemental analyses of biofilm was limited ($n = 10$) (Blackadar, 2013). Additionally, we visually documented a reduction of thick, brown mats of diatoms covering the riverbed following ice break-up. Two, large diatoms dominated the mats collected from rocks prior to ice break-up, *Cymbella janischii* and *Didymosphenia geminata*; both species grow attached to substrates by vertical, mucopolysaccharide stalks (Bahls, 2007; Blanco & Ector, 2009). These species, which are native to the United States, can occur as “nuisance blooms” when they grow large amounts of stalks that cover riverbeds (Bahls, 2007; Blanco & Ector, 2009). Scour from ice break-up may export accumulated organic matter of lower quality (detritus, diatom stalks, etc.) and expose areas of riverbed for colonization by organisms (diatom frustules, algae, etc.) that provide high-quality (increased chl-*a*:AFDM) organic matter to consumers. This is consistent with prior research showing that floods can reduce organic matter quantity and increase quality (Power & Stewart, 1987).

4.2 | Response of aquatic insect feeding to ice disturbance

Diets of the scrapers, *Rhithrogena* and *Bibiocephala*, a collector-gatherer, *Baetis*, and a shredder, *P. californica*, followed patterns of biofilm

(chl-*a*:AFDM). In December, prior to ice break-up, diets of *Rhithrogena*, *Bibiocephala*, and *Baetis* were composed of high proportions of amorphous detritus and low proportions of diatom frustules. Following ice break-up events that increased organic matter quality (chl-*a*:AFDM), the proportion of amorphous detritus and diatom stalks decreased and the proportion of diatom frustules increased in diets of these taxa. The shredder *P. californica* exhibited similar patterns, though its diet was more diverse. Following ice break-up, their consumption of diatom stalks decreased and frustules increased. All of these taxa are known to reside in fast-flowing waters and in cobble habitats, and our results are generally consistent with previous observations describing what food resources these insects typically consume (Merritt, Cummins, & Berg, 2008), but also suggest their foraging ecology may shift in response to river ice disturbance. Following ice break-up events, diets of *Rhithrogena*, *Bibiocephala*, *Baetis*, and *P. californica* shifted rapidly to include a higher proportion of diatoms. Scouring floods can decrease primary producer biomass, while providing fresh substrate for diatoms that are more palatable to aquatic insects to colonize (Grimm & Fisher, 1989). In addition, floods may promote diversity of aquatic producers, allowing the species most palatable to aquatic insects to persist (Elger et al. 2004). Ice break-up may perform a similar role by increasing availability of high-quality foods to aquatic insects.

Similar to other taxa whose diets followed patterns of biofilm, diets of collector-filtering blackflies (*Simulium*) were composed of a high proportion of amorphous detritus and a low proportion of diatom frustules prior to ice break-up, whereas the proportion of amorphous detritus decreased and diatom frustules increased following ice break-up. Increased proportions of diatoms in transport may have increased the proportion of diatoms frustules in gut-contents of *Simulium* following ice break-ups. *Simulium*'s filter-feeding may track the availability of organic matter resources in seston (Wellard Kelly et al., 2013). Fine particulate organic matter (FPOM) is an important food source to filter feeders such as *Simulium*. Based on sampling we conducted as part of this study we observed that, similarly to biofilm, chl-*a* of transported FPOM decreased following ice break-ups (Blackadar, 2013). This suggests *Simulium* may respond to changes in organic matter resources driven by winter ice dynamics.

In contrast to other insect taxa, diets of the collector-gatherer (non-Tanypodinae Chironomidae), and the collector-filterer, (*A. grandis*) did not appear to follow patterns in organic matter as closely. Chironomids consistently consumed large proportions of diatom frustules. Similarly, *A. grandis* consistently consumed primarily insect material. Previous research has documented the ability of chironomids to select for high quality algal resources (Henriques-Oliveira, Nessiman, & Dorvillé, 2003); we hypothesize their mobility and feeding mode allowed them to select for diatom frustules, even within thick biofilm mats. Likewise, our observations of *A. grandis* reflect the reports of others (e.g., Benke & Wallace, 1980) by suggesting that *A. grandis* can selectively harvest resources from their nets (i.e., insect material, diatoms). To evaluate this more thoroughly, studies that link invertebrate trophic

ecology and secondary production measures (e.g., Benke & Wallace 1980) in the context of river ice dynamics will be needed. Taken together, our findings suggest feeding mode traits may mediate the sensitivity of insect diets to organic matter dynamics associated with river ice.

Although disturbance has been shown to affect resource availability, seasonal dynamics may also contribute to shifts in quantity and quality of organic matter and food ingested by aquatic insects (Biggs & Close, 1989). Food resource switching by aquatic insects may occur when resource availability changes seasonally (Mihuc & Minshall, 1995). Although organic matter and resource consumption may vary seasonally, the magnitude and direction of change following disturbance events within a short time frame over which temperature and day length varied little indicate that disturbance by ice may affect both quantity and quality of organic matter available to, and used by, riverine insects.

Several characteristics of our study limit potential inferences and point to the need for future investigations. Since we did not evaluate changes in community composition of organisms contributing to organic matter resources, we could not directly investigate patterns in resource use by aquatic insects compared with their availability. Bacteria and fungi can be abundant in amorphous detritus and are important food resources to aquatic insects (Findlay, Meyer, & Smith, 1986, Hall & Meyer, 1998, Halvorson et al., 2016). We did not assess the role of bacteria or fungi in our study. Additionally, we did not analyze differences in resource consumption compared with their relative assimilation. Moreover, carbon and nitrogen assimilation for aquatic insects can be higher from low quality food resources (Compson et al. 2015, Compson et al. 2018, Siders et al. 2018). This study also did not assess how invertebrate recruitment and populations may be affected by changes in the relative availability of higher quality biofilm relative to lower quality detrital resources. Future studies that evaluate changes in organic matter composition in response to ice formation and break-up, assess the role of bacteria and fungi in insect diets, and incorporate relative assimilation to calculate insect productivity are needed to further understand the role ice regimes play in aquatic foodwebs.

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DATA AVAILABILITY STATEMENT

Data are available from the corresponding author, [RJB] upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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