Abundance of Stream Invertebrates in Winter: Seasonal Changes and Effects of River Ice

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The association between anchor ice and stream invertebrate density in the drift and on the substrate were studied in the Grand River, Ontario, over two winters. Under certain climatic and geomorphological conditions, anchor ice can form a thick blanket on the bottom of rivers and streams. There were almost thirty times more aquatic insects in the drift on mornings after anchor ice developed than when anchor ice did not occur. Both Diptera (mostly chironomids) and Trichoptera were more abundant in the drift when frazil slush was present. During both winters the total density of insects in the drift decreased as the seasons progressed, regardless of the presence or absence of anchor ice on the day of sampling. Within drift samples taken after anchor ice events this relationship was seen in the orders of Diptera and Trichoptera. There was also a decline in the total number of insects in the surface layer of substrate as the winter progressed, particularly in the families of Chironomidae and Simuliidae. Anchor ice and frazil slush appear to be significant factors in invertebrate dispersal and their role in the winter ecology of aquatic invertebrates deserves much more study.

Key Words: Frazil slush, anchor ice, aquatic invertebrate, fish, dispersal, drift, Ontario.

During fall and winter, stream invertebrates are exposed to much different conditions than during warmer seasons. Colder temperatures result in a lower metabolism, and ice formations can cause drastic changes to habitats. During cold weather, subsurface ice commonly forms in areas with moderate to high turbulence. In turbulent areas not covered with surface ice, water temperatures can drop below 0.0°C; this is known as supercooling (Tsang 1982). While the water is supercooled, small ice crystals (called frazil ice) form in the water column. When these ice crystals adhere to the substrate they form anchor ice. Anchor ice can form thick blankets on the bottoms of rivers and streams (Tsang 1982). When stream temperatures increase, or anchor ice becomes thick enough to become buoyant, it lifts off of the stream bottom, carrying with it pieces of substrate, macrophytes, and aquatic invertebrates. This ice, called frazil slush, then becomes incorporated into the flow of the river and transports invertebrates downstream.

Due to the lack of equipment specialized for winter sampling, and to harsh working conditions, few papers have been published on winter invertebrate drift and the effect of anchor ice on invertebrate transport. Some authors suggest that anchor ice has no permanent effect on the removal of invertebrates from the substrate (Brown et al. 1953; Benson 1955). During observations at the Pigeon River, Michigan, Benson (1955) concluded that the daily release of anchor ice from the stream bottom served as a mechanism for the downstream dispersal of bottom organisms, although, the overall depletion of benthic fauna as a result of this was negligible. Brown et al. (1953) viewed aquatic organisms floating alongside dense masses of slush in the West Gallatin River, Montana, thus supporting the hypothesis that anchor ice may temporarily increase the number of bottom organisms in the drift. Similar to Benson (1955) however, their results also showed no decrease in the overall abundance of bottom invertebrates during the winter months.

Other authors suggest that anchor ice, and the scouring that occurs as a result, not only frees aquatic invertebrates from the substrate into the water column but continuously changes the benthic composition of the stream bed over the winter months (Maciolek and Needham 1952; O'Donnell and Churchill 1954; Reimers 1957). Reimers (1957) stated that areas where anchor ice commonly occurred experienced a gradual depletion in benthic fauna due to repeated scouring of the streambed. During Reimers' study at Convict Creek, California, there was a considerably lower food intake by trout midway through the winter in these habitats, which suggests lower availability of food after repeated anchor ice events.

These contradictory results make it unclear whether the severity and frequency of anchor ice events throughout the winter can change the forage available to fish or progressively reduce the benthic population through repeated disturbance. When we observed that masses of frazil slush were transporting sediment and debris downstream, we began collecting samples of the frazil slush for examination and followed up with a benthic survey. Our objective was to determine whether anchor ice events are associated with changes in the density of stream invertebrates in the drift and on the substrate. To achieve this goal, both drift and substrate samples were collected during periods when anchor ice occurred and when it was absent.

Study Area and Methods

The study was conducted along a 10 km reach of the Grand River (43°38'-43°4'N, 80°26'-80°2'W), Ontario in the Elora Gorge Conservation Area. The river channel in the study area has a relatively low gradient (mean 1.4 m km^{-1}) and flows in an open valley.

Invertebrates in the drift were collected during periods when anchor ice was present and when it was not present over two winters (21 January–20 March 1998 and 16 December 1998–23 February, 1999; Table 1). For drift samples with frazil slush, the amount of drift sampled (m^3) was determined by multiplying the amount of frazil slush collected (20–23 litres) by the estimated fraction of frazil in the drift and converting the units to cubic metres. The fraction of frazil slush in the drift was estimated by taking samples of the water column with a graduated cylinder and recording the ratio of frazil slush to water. Repeated samples were taken and the mean was used to estimate the fraction of frazil slush in the drift. The drift net (opening of 0.05 m^2, 2 mm mesh size) was deployed for a maximum of 3–5 minutes for each sample, depending on the amount of frazil slush in the drift. For drift samples without frazil slush, the amount of water sampled (m^3) was measured by multiplying the area of the net opening (0.09 m^2) by the water velocity ($m \cdot s^{-1}$) and the amount of time (s) that the net was in the flow. Dual drift nets, each with a net opening of 0.09 m^2 and mesh size of 180 micrometers collected drift for 30–60 minutes per sample. Drift samples were collected between 09:00 and 13:00. All samples were filtered through 180-micrometer mesh, then preserved in 85% ethanol. Samples with frazil slush were melted before being filtered. Organisms were counted and identified to family, when possible, using McCafferty (1981). Some organisms were missing appendages and/or were physically damaged to the point where identification to family was unreliable. In such cases, they were identified only to order.

Data from both winters (1997–1998 and 1998–1999) were used in comparing the number of organisms in drift samples with and without frazil slush. To determine if there was a difference in the number of insects in the drift when frazil slush was present and when not present, a Mann-Whitney U test was performed since data were not normal (determined with a Lilliefors test). Frazil slush samples collected in 1997–1998 were used to determine invertebrate density trends over the winter in the drift when frazil slush was present. Similarly, the drift samples collected in 1998–1999 were used in determining seasonal trends for drift without frazil slush. To determine these relationships, regression analysis was performed on the abundance of invertebrates per day in the drift when frazil slush was present and when frazil slush was not present. For the purposes of this analysis (and the analysis of invertebrates on the substrate), the earliest day on which samples were first collected in both years, 16 December, was used as the starting date of winter. Since not all relationships between invertebrate abundance and day of winter were linear, the type of regression analysis applied (linear or polynomial) was that which provided the most appropriate degree of fit.

Drift samples with frazil slush were collected in three different locations: at transect #1, 4.9 km downstream from transect #1 and 8.4 km downstream from transect #1. Drift samples without frazil slush were collected at transect #2 (0.6 km downstream from transect #1). There were no barriers to drift in the study area.

Fifty-two substrate (rock) samples (mean = 5 rocks per day) were collected between 16 December 1998 and 8 March 1999 (Table 1). Rocks (mean diameter = 8.68 cm; SD = 3.03) were selected in riffles along transect #1 and transect #2 (approximately 600 m apart) in the Grand River, Ontario. A small dip net (180-micrometer mesh) was used to trap invertebrates that had come loose off the rock when lifted out of the water. Each rock was put into a small container and rinsed with 85% ethanol. Insects on the net were rinsed into the container with 85% ethanol. All of the rock samples were scrubbed with a soft brush and handpicked with forceps to free the invertebrates from the rock surface. The sample was then filtered through the 180-micrometer screen and the material retained was stored in 85% ethanol until identified. The surface area of each rock was estimated by measuring the three largest diameters of the rock (Dall 1978). Both transects were marked so that rock samples and flow measurements could be taken at the same location on subsequent dates. Water velocities (mean and bottom) were measured using a Sigma Doppler flow meter.

At a 5 m^3 s^{-1} discharge rate (approximate winter base flow) transect one had a mean depth of 23 cm (N = 6, SD = 0.06) and mean velocity of 0.21 m s^{-1} (N = 6, SD = 0.11). Transect two had a mean depth of 24 cm (N = 7, SD = 0.10) and mean velocity of 0.68 m s^{-1} (N = 7, SD = 0.45). Substrate in both transects was predominantly large cobble. Since there were no significant differences ($p > 0.05$) between depths or water velocities (Mann-Whitney U test since data were non-normal), data for both transects were grouped. Regression analysis was used to determine if there was a trend in the overall insect abundance on the substrate over the winter. ANCO-

TABLE 1. The number of invertebrate samples taken from the drift and substrate when frazil ice was present or absent in the Grand River, Ontario.

	Number of samples		
Date	Drift with frazil ice	Drift without frazil ice	Substrate samples
21 January 1998	3	-	-
26 January 1998	2	-	-
6 February 1998	3	-	-
16 February 1998	2	-	-
11 March 1998	3	-	-
12 March 1998	4	-	-
13 March 1998	3	-	-
16 March 1998	3	-	-
17 March 1998	3	-	-
16 December 1998	-	1	6
18 December 1998	-	1	6
23 December 1998	-	3	3
31 December 1998	1	-	6
6 January 1999	-	1	3
13 January 1999	-	2	6
20 January 1999	-	2	6
3 February 1999	-	2	6
8 February 1999	-	2	6
21 February 1999	1	-	-
23 February 1999	4	-	5
8 March 1999	-	-	4

VA was used to determine if a consistent relationship existed between the day of the winter and abundance of aquatic invertebrates in both the drift (without frazil slush) and on the substrate.

To determine if the density of invertebrates in the drift was influenced by water discharge, water discharge on sample days when frazil slush was not present was compared to water discharge on days when frazil slush was present. This was done using a Mann-Whitney U test since data were not normal. Subsequently, regression analysis was used to determine if there was any relationship between water discharge and invertebrate density.

Results

Drift

There was a significantly ($p < 0.05$) larger number of drifting invertebrates on mornings after anchor ice events (mean 118.0 organisms/m^3 drift, SE = 18.6) than when anchor ice events did not occur (mean 4.2 organisms/m^3 drift, SE = 1.8). Both Diptera and Trichoptera were significantly ($p < 0.05$) more abundant when frazil slush was present, but there were no significant ($p > 0.05$) differences in densities of Ephemeroptera and Annelida. Within the order Diptera, there was a significantly ($p < 0.05$) larger number of chironomids in the drift when frazil slush was present (40.5/m^3) than when it was not present (1.8/m^3). There were no significant ($p > 0.05$) differences found in the drift within the families of the order Trichoptera. Nearly all of the Trichoptera in the drift samples were species of the family Hydropsychidae (90%) in 1999 and the family Lepidostomatidae (75%) in 1998. One factor that may have influenced these results is that river discharge was significantly ($p < 0.05$) higher on days when frazil slush was present (mean 9.5 m^3s^{-1}, SD = 7.3, range 1.5–28.0) than when frazil slush was not present (mean 2.4 m^3s^{-1}, SD = 1.5, range 1.6–5.0). However, no significant ($p>0.05$; $r^2 = 0.03$) relationship between water discharge and invertebrate density was found in samples when frazil slush was present.

Total changes over winter in drift

During the winters of 1997–1998 and 1998–1999 the density of animals in the drift decreased significantly ($p < 0.05$) as the seasons progressed, regardless of the presence or absence of frazil slush on each sampling day (Figure 1). In drift samples taken after anchor ice events (1997–1998 field season), both Diptera and Trichoptera (especially Lepidostomatidae) showed significant ($p < 0.05$) negative relationships between drift density and day of the winter. There was no significant ($p > 0.05$) trend in either Annelida (Class Oligochaeta) or Ephemeroptera. No significant ($p > 0.05$) relationships were found among individual taxonomic groups sampled when no anchor ice was present (1998–1999 field season).

Benthos

The total number of insects in the surface layer of substrate declined significantly ($p < 0.05$) as the winter progressed (Figure 2). There was a rebound in numbers following a period when surface ice covered most of the river and anchor ice did not form. Invertebrate densities decreased again when the surface ice cover was gone and nightly anchor ice formations again occurred.

When analyzed by order, only Diptera declined significantly ($p < 0.05$) over the winter (Figure 3). This significant ($p < 0.05$) negative trend was seen in the families Chironomidae and Simuliidae, when analyzed separately, but not in Empididae, Tipulidae, Athericidae or Ephydridae. The relationship between day of winter and insect abundance paralleled the same relationship found between day of winter and insect abundance in the drift (with frazil slush). There was however, no significant ($p > 0.05$) relationship between water temperature and abundance of aquatic invertebrates on the substrate over the winter.

Discussion

There are many variables in the natural riverine environment that influence aquatic invertebrate distribution from year to year. Natural disturbances such as summer flooding, winter freezing and spring thawing, moving ice, and rapidly fluctuating temper-

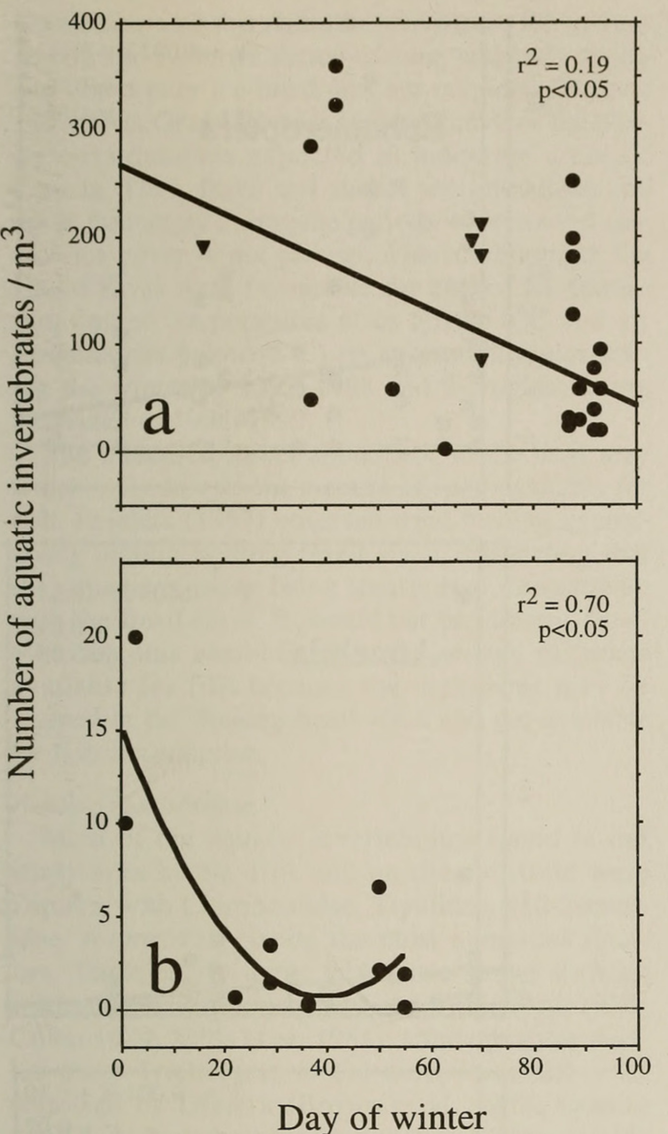

FIGURE 1. (a) Regression plot of the number of aquatic invertebrates collected in the drift on days when frazil ice was present from 21 January to 17 March 1998 and from 31 December 1998 to 23 February 1999 (shown as triangles) in the Grand River, Ontario. The regression analysis includes only data from the first winter. (b) Regression plot of the number of aquatic invertebrates collected in the drift on days when frazil slush was absent from 16 December, 1998 to 8 March 1999 in the Grand River, Ontario. 16 December was designated as Day 1 of the winter for both seasons. Note that the scale of the y axis varies between panels.

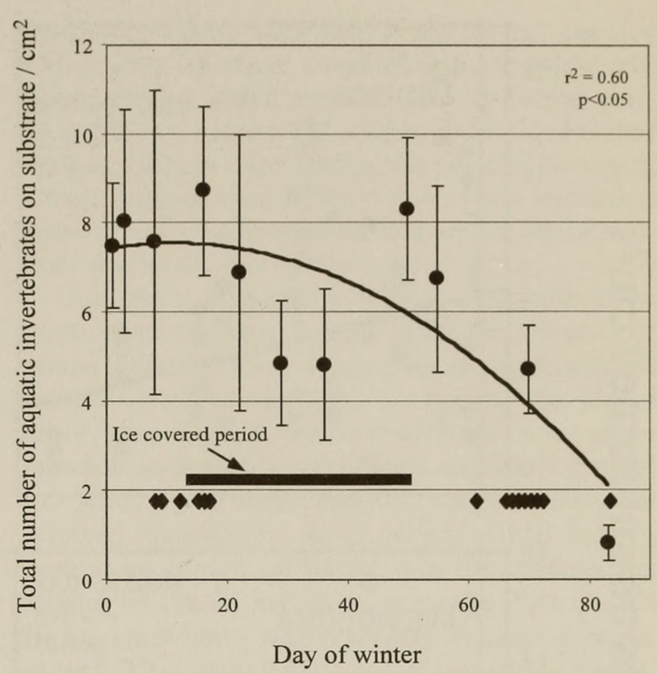

FIGURE 2. Regression plot of mean (± SD) number of aquatic invertebrates found on the substrate (organisms / cm^2) on different days from 16 December 1998 to 8 March 1999 in the Grand River, Ontario. Presence of frazil slush and anchor ice at the sampling site (diamonds) and presence of a surface ice cover (a solid line) in the pool upstream of the sampling site are also indicated.

atures play important roles in the distribution and survival of aquatic invertebrates (Miller and Stout 1989). Anchor ice and frazil slush were the main focus of this study and appear to be important factors in invertebrate dispersal. Since the greatest abundance of immature aquatic insects occurs during the winter season (Maciolek and Needham 1952; Reimers 1957), any conclusions about the dispersal or removal of aquatic invertebrates by anchor ice are important in understanding invertebrate and fish ecology.

Anchor Ice

The importance of anchor ice to benthic organisms is not due to low water temperatures (near 0.0°C) as many aquatic invertebrates are capable of surviving temporary freezing (Olsson 1981; Andrews and Rigler 1985) but due to its mechanical force on the substrate. As frazil ice crystals adhere to the substrate overnight or as the anchor ice releases, benthic organisms are at risk of physical damage and entrapment. Some studies have shown that invertebrates are able to survive entrapment in the ice with little or no mortality (Brown et al. 1953; Benson 1955). We also observed living invertebrates in the melted frazil slush samples. More importantly, our results show that sequential anchor ice events can change the local benthic population density. On days when anchor ice was released from the streambed, the density of invertebrates in the drift was much larger than when no anchor ice was released.

The frequency of frazil and anchor ice formations depend on climate. For these formations to occur, sub-freezing air temperatures are required but a solid surface ice cover must not be present. Freshwater ice cover in Canada is highly variable, from periodic skims in southerly temperature regions to mean thicknesses over 2 m on high-latitude rivers (Prowse

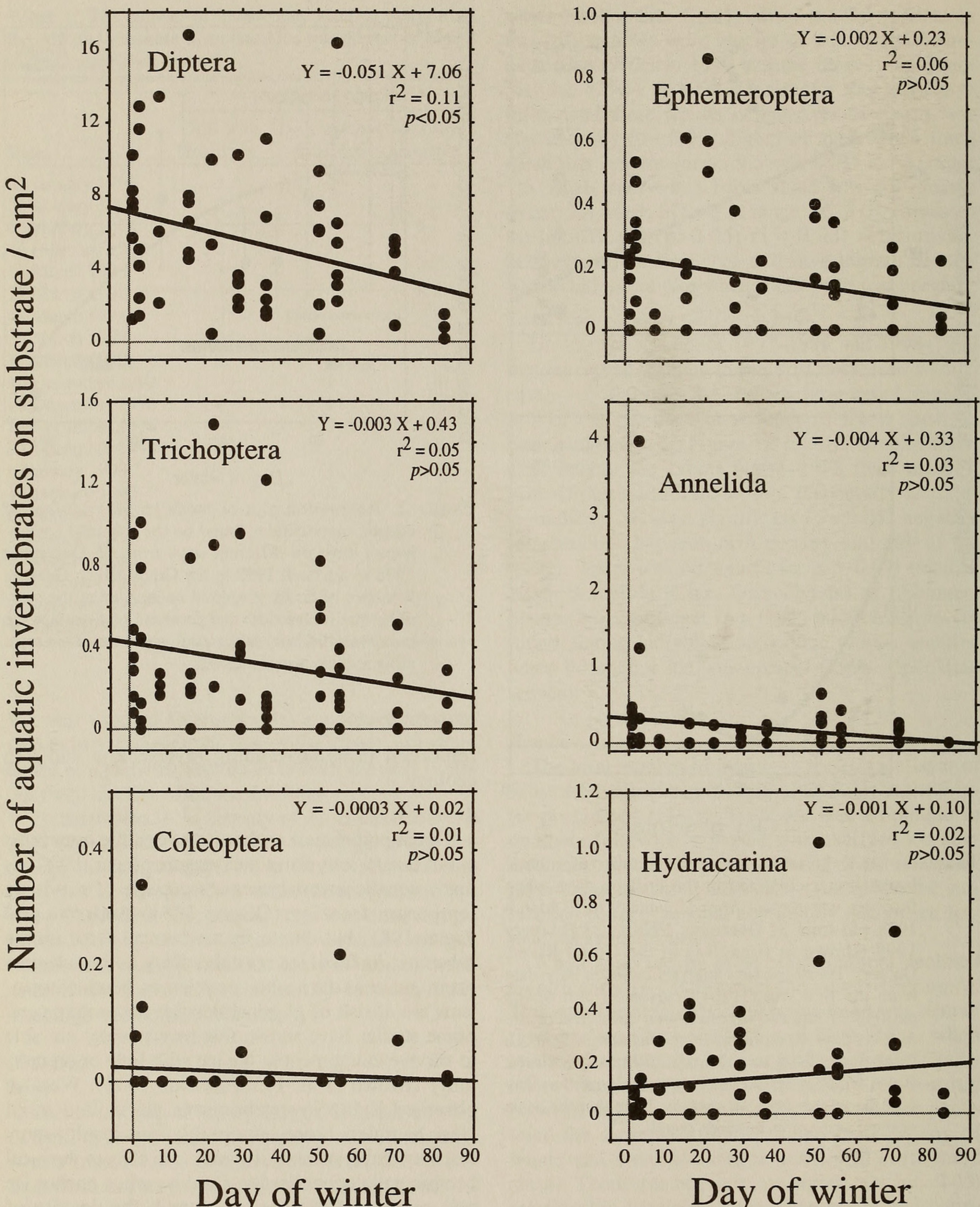

FIGURE 3. Regression plot of the number of aquatic invertebrates in six different orders found on the substrate (organisms / cm^2) on different days from 16 December 1998 to 8 March 1999 in the Grand River, Ontario.

1990). Mean freeze-over dates, mean ice thickness, and mean ice-free dates are provided by Allen (1977) and reviewed by Prowse (1990). In many of the colder parts of Canada, streams have a short freeze-up period followed by a fairly stable period of surface ice cover until spring break-up (Prowse 1995). This occurs in the northern part of the country, and much of the prairie provinces (Beltaos 1997). In more moderate areas of Canada, such as the southern parts of Ontario, Quebec, and British

Columbia, and the Atlantic provinces, ice covers remain for a shorter period of time and both spring and mid-winter ice break-ups are common (Beltaos 1997). The Grand River is representative of the winter environments expected in moderate areas of Canada. Thus, frazil and anchor ice formations can occur frequently during the periods when a solid surface ice cover is not present. The conditions in the Grand River were favourable for anchor ice formation (water temperatures at or near 0.0°C and air temperatures below -5°C) on at least 42 nights during the winter of 1997–1998 and 57 nights during the winter of 1998–1999.

The increased insect abundance in the drift may temporarily elevate the amount of food available for fish. Reimers (1957) observed trout feeding aggressively among floating frazil slush, suggesting that the organisms were being transported downstream with the frazil slush. It should not be inferred, however, that this would increase the amount of forage available for fish because the organisms may be trapped in the floating frazil slush and not available for fish consumption.

Benthic composition

Most of the aquatic invertebrates found in our study area in the drift and on the substrate were Diptera, with Chironomidae, Tipulidae, and Simuliidae, respectively, being the most numerous families. These results agree with other winter findings in temperate streams and rivers (Clifford 1978; Colbo 1979; Mills et al. 1981), although some studies show Trichoptera as the most abundant order followed by Diptera (Brown et al. 1953; Benson 1955). In Newfoundland streams, Colbo (1979) observed that simuliid population density in a stream normally increases between December and April. However, in our study, the number of simuliids on the substrate decreased as the winter progressed. Colbo (1950) also noted that certain Simuliidae larvae were absent or rare in zones where anchor ice occurs. This would compare favourably with our observations that the release of anchor ice removed larvae from the streambed and increased the number in the drift on days when frazil slush was present.

In comparison, densities of Chironomidae, (another common family of the order Diptera) may be highest in December and January, then gradually decrease until May (Clifford 1978). Conversely, our results show that the number of Chironomidae decreased in the substrate throughout December and January. Although Clifford (1978) suggests that population density trends can be attributed to various phenomena such as the appearance of new generations, delayed hatching, overlapping generations and available habitat, our observations indicate that this decrease in Chironomidae may be exacerbated by anchor ice. If so, this abrupt change in drifting density could be very important to fish species which prey on these invertebrates, particularly Chironomidae, which normally show a distinct periodic drifting pattern (McCafferty 1981). Further work to confirm these findings is advised, however, since a large amount of influence on the regression is due to the low invertebrate abundance on the substrate during the last winter sample.

This study provides evidence that anchor ice events correlate with changes in the local density of stream invertebrates and may play an important role in the dispersal of aquatic invertebrates in the Grand River. Our finding that invertebrates were more abundant in the drift when frazil slush was present than when it was absent suggests that the anchor ice removed invertebrates from the streambed causing them to be carried off by the drift. In addition, the number of stream invertebrates in the drift and on the stream bottom was gradually reduced over the winter. This effect may not occur in all rivers. Anchor ice forms in turbulent areas which are not readily covered by surface ice. If such areas are distributed along a river, invertebrates dislodged will resettle downstream and the overall effect on the stream benthos will be minimal. The largest impact from the removal of invertebrates may be areas directly below reservoirs, where invertebrates fall from the drift, preventing recolonization of areas which are depopulated by anchor ice. Warm water discharged from the dam precludes formation of anchor ice for a short distance downstream (depending on air temperatures) reducing the supply of replacement organisms. Depletion of the benthic fauna over the course of the winter may be a fairly widespread phenomenon as most rivers throughout the world have impoundments.

In future studies, it is recommended that invertebrate densities and distribution in the substrate be sampled prior to the formation and immediately after the release of anchor ice. This type of disturbance study (Underwood 1994) may provide more insight into the immediate influence of anchor ice.

Additionally, the restrictions of winter sampling make it difficult to control each of the variables that usually influence invertebrate density. Comparative sampling of neighbouring streams, one with anchor ice and one without anchor ice (possibly below a hydroelectric dam) which have similar structure, flow, temperature, etc., would be advantageous. One ecological condition that has not been considered during this research, but that may prove significant, is how feeding habits of fish change in association with anchor ice events or throughout the winter. Feeding habits of fish could be monitored and any analogous changes in benthic composition could be identified. During winter, aquatic invertebrates are clearly exposed to highly variable environments which may have large impacts on their population densities. Thus this area of ecology deserves much more research.

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