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Selective feeding of age-0 Arctic grayling in lake-outlet streams of the Northwest Territories, Canada

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Synopsis

A paucity of information exists on the diet of Arctic grayling, *Thymallus arcticus*, particularly for young-of-the-year (YOY). We examined the diet of YOY Arctic grayling in relation to food availability, in the Barrenlands region of the Northwest Territories, Canada, where lake-outlet streams serve as nursery habitat for these fish. Given the small size of YOY grayling and the abundance of lake-derived microcrustacea in the drift of these lake-outlet streams, we anticipated that these prey would make up a major component of the YOY's diet. Food selectivity by YOY grayling, however, was strongly sized-biased; although microcrustacea dominated the drift, YOY primarily consumed larger taxa, especially Chironomidae and Simuliidae. Even among these taxa, grayling tended to select the larger individuals. As they grew, YOY grayling took larger numbers of both large and small prey, particularly the larger invertebrates, although prey size range did not change after mid-July. Selection of pupae and avoidance of Ephemeroptera suggest that prey characteristics other than size also contribute to selectivity by YOY grayling. The relatively limited consumption of terrestrial invertebrates and other large prey may reflect the small sizes of fish in this arctic study, as well as differences in prey availability. Despite the abundance of lake-derived prey, instream production of invertebrates should largely determine the productive capacity of Barrenlands streams as fish habitat.

Introduction

The landscape of the Barrenlands region of the Northwest Territories, Canada, is dominated by innumerable lakes that are connected to each other in chains by relatively short streams. At ice-out, lake-dwelling Arctic grayling, *Thymallus arcticus*, enter these lake-outlet streams to spawn, and return to the lake shortly thereafter, leaving streams to serve primarily as nursery habitat for the young-of-the-year (YOY) grayling (Jones et al. in press). Growth and survival of young fish depend heavily on the availability of suitable prey at the onset of yolk-sac absorption (Braum 1978) and on the ability of YOY to reach sufficient size during their first growing season (Miller et al. 1988). Thus, the productive capacity (sensu DFO 1986) of Barrenlands streams as habitat for Arctic grayling is derived largely from the streams' ability to provide nourishment for the growth of YOY grayling. Hampering our ability to assess productive capacity of these streams, however, is our lack of knowledge of the food requirements of YOY grayling (Armstrong 1986, Northcote 1995).

Grayling appear to feed primarily from the water column. Studies done in other regions indicate that the adult and sub-adult grayling feed primarily on drifting insects in lotic systems, while in lakes, planktivory often prevails (Armstrong 1986, Northcote 1995). Benthic foraging for macroinvertebrates may occasionally become important when invertebrate densities in the water column diminishes (Armstrong 1986), while the significance of terrestrial insects that fall onto the waters' surface is not well known, but may vary with stream size and characteristics of the riparian vegetation, both which would influence the abundance of this prey type (Armstrong 1986). Based on our understanding of fish foraging ecology, however, combined with the nature of Barrenland streams, drifting microcrustacea may be important for YOY grayling in these lotic ecosystems.

Although fish are generally size-selective foragers on invertebrates (Werner 1974), the gapes and swimming abilities of YOY fish can limit the sizes of prey that they can capture and consume (Miller et al. 1988, Schael et al. 1991). Because of their lake-outlet characteristics, Barrenland streams are characterized by high drift densities of lake-derived microcrustacea (Jones et al. in press). A reasonable hypothesis, therefore, would be that YOY Arctic grayling are relatively independent of autochthonous production of macroinvertebrates in Barrenland streams but instead primarily depend on lake-derived microcrustacea for nourishment. Furthermore, a lack of extensive, overhanging vegetation should also limit the importance of terrestrial invertebrates as prey of YOY grayling in these tundra streams. To examine these hypotheses, we quantified the relative importance of lake-derived microcrustacea, terrestrial invertebrates, and benthos-derived drifting invertebrates as food for YOY grayling in Barrenland streams. We also determined the relative abundance of these potential prey types in Barrenland streams, which allowed us to address two additional questions: (i) are YOY grayling selective foragers in terms of prey type, prey size, and per life-history stage? (ii) does grayling size affect the size and types of organisms they consume? By quantifying the diets of YOY grayling in these streams, we should also gain understanding of the factors that contribute to the productive capacity of Barrenland streams as fish habitat.

Materials and methods

The study was centred north of Lac de Gras, ca. 64°45′N, 110°30′W, roughly 100 km north of the tree line. Streams in this region are generally small (bankfull width 2–50 m), and short (length 80–2900 m) lake-outlet systems (Jones et al. in press). Freshet begins in late May and flows (0.1–7.0 $m^3 s^{-1}$) continue until late September, when streams freeze completely. Stream water is circumneutural, stained yellow–brown, and low in turbidity and conductivity (8–19 $\mu s\, cm^{-1}$). The streams support modest densities of benthic invertebrate (17 000 individuals m^{-2}), while upstream lakes provide large numbers of microcrustacea, 10 000 individuals 100 m^{-3}, to the drift (Jones et al. in press).

Fieldwork was conducted in two streams, Polar-Vulture and Pigeon (Table 1). Polar-Vulture contains large substrates and the channel is braided for most of its length. Pigeon has a large amount of fine sediment, particularly sand, and has a single channel for much of its length. The two streams are 10 km apart. The riparian zone of Polar-Vulture is well drained and considerably drier than that of Pigeon. Dwarf heath and scattered low shrub tundra dominates the riparian zone at Polar-Vulture, whereas Pigeon is dominated by sedge tussock.

Young-of-the-year habitat use and foraging behaviour

Stream fish communities are numerically dominated by YOY Arctic grayling, with slimy sculpin, *Cottus cognatus*, and burbot, *Lota lota*, also present. Upon swim-up in early July, grayling are 11–13 mm in length. Foraging begins several days later, often with yolk sacs still visible. Small grayling (<25 mm in length) use marginal habitats along the banks, <25 cm deep and with water velocities <5 cm s^{-1}. As the YOY grow they become territorial, proficient swimmers, and shift to the main channel (depths >40 cm and mean water velocities of ca. 15 cm s^{-1}) (N. Jones, unpublished data). At this stage, grayling use velocity refugia associated with pools or created by large boulders along the thalweg and feed opportunistically on drifting organisms.

Field sampling

We sampled YOY Arctic grayling from Polar-Vulture Creek, two (1998), three (1999) or four (2000) times per summer, between mid-July and late-August, and four times in 2000 from Pigeon Creek. We sampled

Table 1. Physical characteristics of Polar-Vulture and Pigeon streams, Northwest Territories, Canada.

Stream	Length (m)	Slope (%)	Bankfull width (m)	Bankfull depth (m)	Mean velocity ($m\, s^{-1}$)	% fines[a]	% coarse[a]
Polar-Vulture	700	1.4	2.7	0.44	0.13	20	55
Pigeon	2900	0.5	2.4	0.46	0.16	30	58

[a]Fines includes clay, silt, and sand (<2 mm), and coarse includes cobble and boulder (64–256 mm).

grayling after they shifted their habitat use to the main channel (fork length > 25 mm). Grayling were collected primarily with dip nets or with a Smith-Root Model A-12 backpack electrofisher when fish became too dispersed to capture otherwise (late summer). We collected grayling shortly after and downstream of the mid-afternoon drift samples (see below). Upon capture, fish were euthanized (Tricane overdose) and presevered in 90% ethanol. In the laboratory, we measured fish fork length (± 0.5 mm) and removed their stomachs.

We sampled drift from Polar-Vulture in 1999 and 2000 and from Pigeon Creek in 2000, just prior to each fish sampling. We sampled drift simultaneously at two locations within the streams with two tri-net samplers (0.25 mm mesh, Field-Dodgson 1985). Samples were collected either immediately above or below riffles in relatively shallow water (mean depth and velocity, 0.16 m and 0.24 m s^{-1}, respectively) and in close proximity to fish collection areas in order to reflect organisms available to grayling. On each sampling date, we collected drift at dawn, noon, and dusk. Nets were wetted for 30–45 min intervals, depending on flow rates, to filter 3–6 m^3 of water. To determine sample volumes, we measured water velocities at the mouth of each sampler using a Swoffer Model 2100 velocity meter. Drift samples were preserved in 70% ethanol and later identified and counted.

Laboratory analyses

We identified 19 invertebrate taxa in the drift and stomach samples, and subsequently classified taxa as either large or small based on body size (Table 2). Where possible, we also identified insects as larvae, pupae, or adults. Drift samples were subsampled volumetrically in 1999 and 2000, with 63% and 42% of each the sample, on average, examined, respectively. All organisms in the stomach samples were identified and counted. To extend the examination of prey size selection, we measured head capsule widths of the two most commonly consumed invertebrate taxa, Chironomidae and Simuliidae, from random samples of drift and stomachs from each sampling period in 2000. Individuals were measured using a dissecting scope equipped with an ocular micrometer for measurements (± 0.01 mm).

Table 2. Invertebrate taxa identified in the stomachs of YOY Arctic grayling and drift samples collected from Polar-Vulture (1998–2000) and Pigeon (2000) streams. Invertebrates were classified as large or small based on body size. In 2000, Diptera were divided into Chironomidae, Simuliidae, and Culicidae. For some analyses, Cladocera, Copepoda, and Ostracoda were grouped together (as microcrustacea), as were (ETP). Where possible, insects were identified as larvae, pupae, and adult.

Large invertebrates		Small invertebrates	
Diptera	Plecoptera	Cladocera	Oligochaeta
Chironomidae	Hemiptera	Copepoda	Collembola
Simuliidae	Trichoptera	Ostracoda	Tardigrada
Culicidae	Coleoptera	Hydracarina	Coelenterata
Ephemeroptera	Hymenoptera	Nematoda	

Statistical analyses

We excluded invertebrate taxa that did not comprise at least 5% by number of the drift and stomachs on any date from analyses. To keep them above the 5% criteria, Ephemeroptera, Trichoptera, and Plecoptera (ETP) were grouped in 1998 and 1999. Selectivities by YOY Arctic grayling for each prey group were calculated from Polar-Vulture and Pigeon creeks in 2000, using the index of preference D:

$$D_i = \frac{r_i - p_i}{(r_i + p_i) - 2r_i p_i}$$

where D_i is the index of preference for prey group i, p_i is the proportion of individuals belonging to prey group i in the drift, and r_i is the proportion of the prey group in the stomach (Jacobs 1974). Values of D range from -1.0 to 1.0; 0.0 indicates random feeding, while $D > 0.0$ and $D < 0.0$ indicate preference and avoidance, respectively.

We used t-tests to determine if prey selection values differed from zero over the four samplings of 2000. Six prey groups from each stream were tested individually; sample sizes were 120 fish per stream (four samples of 30 fish). To assess if differences in selection strength existed among prey groups, we combined data from both streams and the four sampling periods from 2000 into a general linear model (GLM), following arcsine transformation. Significant GLM results were followed by Tukey multiple comparison tests to identify differences in prey group means. To examine how gape limitation *versus* size-selection affected prey selection as a function of fish size, we used linear regression to determine if the numbers of small (mostly microcrustacea) and large invertebrates (mostly insect larvae) and the proportion of large invertebrates in the diets varied with the size of YOY grayling over of the course of the summer. Mann–Whitney U-tests were used to determine if head capsule widths of Chironomidae and Simuliidae, the predominant large invertebrates, differed between stomachs and drift within each stream for each date. Mann–Whitney tests were also used to determine if there were differences in the relative composition of larvae, pupae, and adult Chironomidae and Simuliidae between the drift and diet. For all statistical tests, we used $\alpha = 0.05$ as a critical level of significance (after performing the Bonferroni adjustment, when that was required, to reduce the experimentwise error rate). We used the Kolmogorov–Smirnov test to examine data for normality and Levene's median test for homogeneity of variances. Proportion data were arcsine transformed and the numbers of small and large invertebrates in the diets of grayling were log-transformed prior to regression analyses.

Results

Composition of drift and diet

Observations of YOY Arctic grayling indicated that they fed almost exclusively from the water column. Rarely, fish made foraging attempts along the bottom of the stream. Very few of the 358 YOY grayling stomachs examined contained sand or algae that would indicate benthic feeding. Disturbed fish quickly returned to their central place and resumed foraging. Based on these observations, we focused on the drift, rather than benthos, as the source of available prey.

Drift was numerically dominated by microcrustaceans, including cladocerans, copepods, and ostracods (Figures 1 and 2). The remaining portion of the drift consisted mostly of dipterans and, to a lesser extent, ETP taxa and mites. In contrast, YOY grayling consumed mainly dipterans, predominantly chironomids and simuliids, but only small numbers of microcrustaceans (Figures 1 and 2). Ephemeropterans were common in the diet in July but diminished by August. Both the diet and drift contained small numbers of adult terrestrial insects, particularly Hymenoptera and Culicidae (<5% by number of the drift and stomachs on any date from analyses). Organic

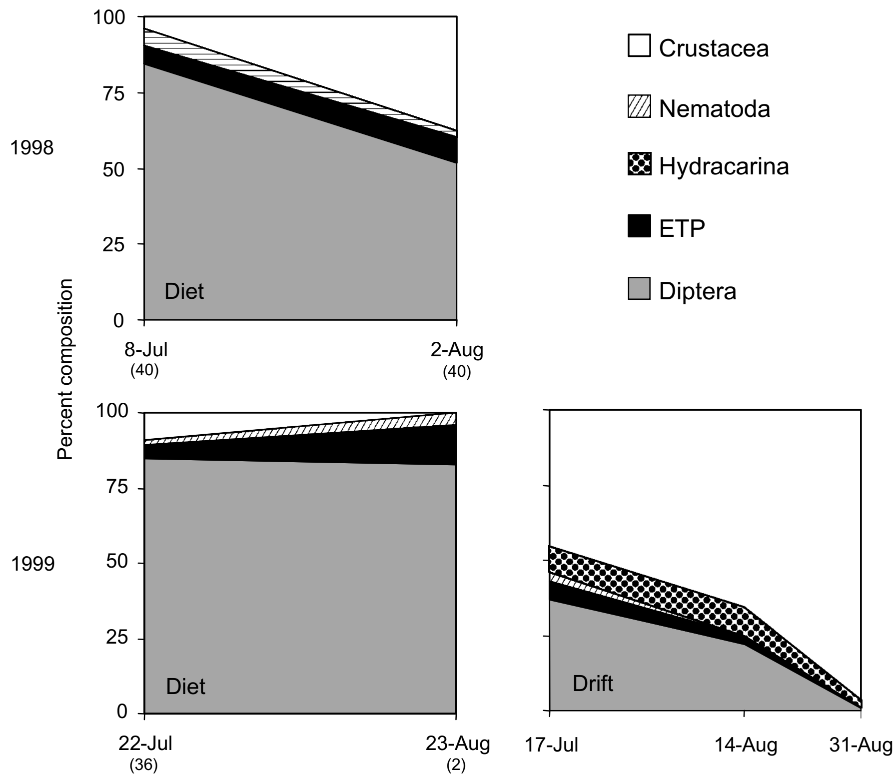

Figure 1. Percentage composition of invertebrates in the drift and diet of YOY Arctic grayling and drift during summers 1998 (upper) and 1999 (lower) in Polar-Vulture Creek. ETP were grouped. Number of stomachs examined for diet analyses are given in parentheses. Eighteen drift samples were collected per date.

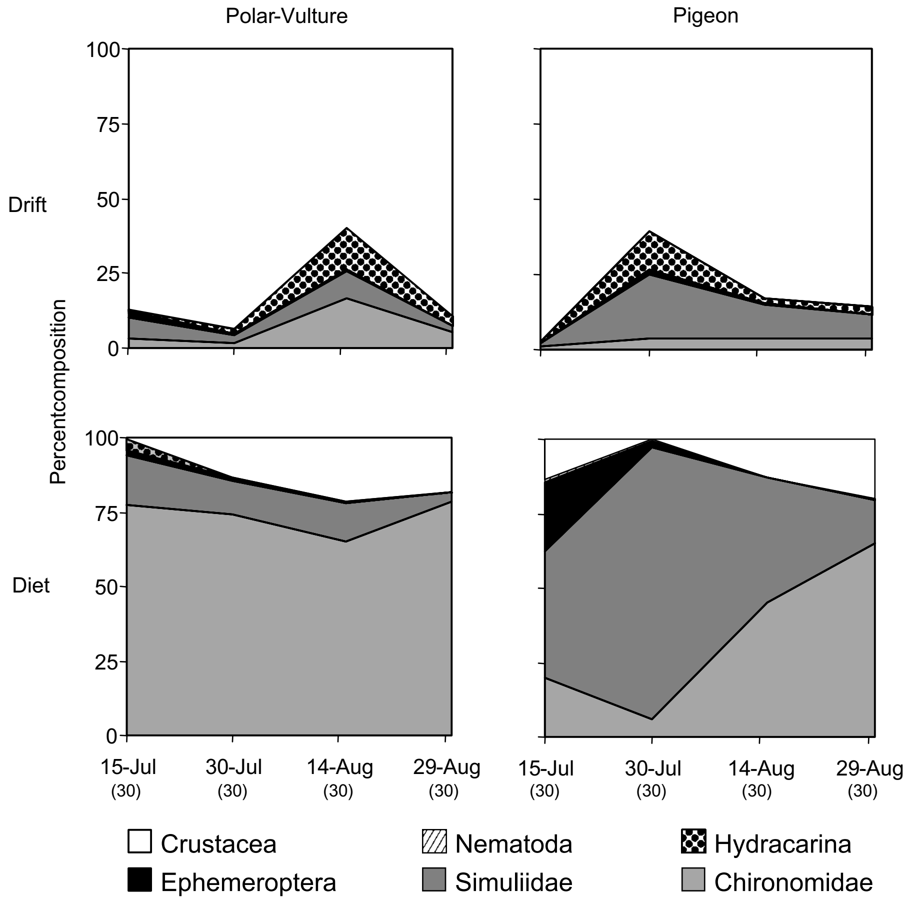

Figure 2. Percentage composition of invertebrates in the diet of YOY Arctic grayling and drift from Polar-Vulture and Pigeon creeks in 2000. Number of stomachs examined for diet analyses is given in parentheses. Eighteen drift samples were collected per date.

debris was present in 7.5–25% of grayling stomachs. All stomachs contained prey items.

Spatiotemporal variation in drift and diet

Although the above pattern was generally consistent among years, the composition of invertebrates in the diet and drift was seasonally variable. For example, dipterans decreased in Polar-Vulture from 37% of the drift to 1% over a 44-day period in 1999 (Figure 1). In that year, which was unusually cold and wet, mites were also more abundant than in other years. In Pigeon Creek (2000), the relative contributions of chironomids and simuliids to the diet increased and decreased, respectively, over the 45-day period (Figure 2). The major difference between the two streams was a higher proportion of simuliids *versus* chironomids in Pigeon Creek, as evident in both the drift and diet (Figure 2).

Prey selection

There was a good relationship between prey preference and prey size. In both streams, YOY grayling displayed strong avoidance (t-tests, $p < 0.05$) of small invertebrates (especially microcrustacea, nematodes, and mites), and preferentially consumed chironomids and simuliids (t-tests, $p < 0.05$; Figure 3). Preferences (D) for each of the six prey groups were significantly different from zero, (t-tests, $p < 0.05$). Mean selection values differed for each prey group except for Hydracarina, Crustacea and Nematoda (GLM followed by Tukey multiple comparisons, $F_{5,1430} = 383$, $p < 0.05$). The general patterns of preference and avoidance among taxa were consistent between streams (GLM, $F_{1,1430} = 0.02$, $p = 0.965$). However, the relative preferences for midges and blackflies switched between streams, and mites were more

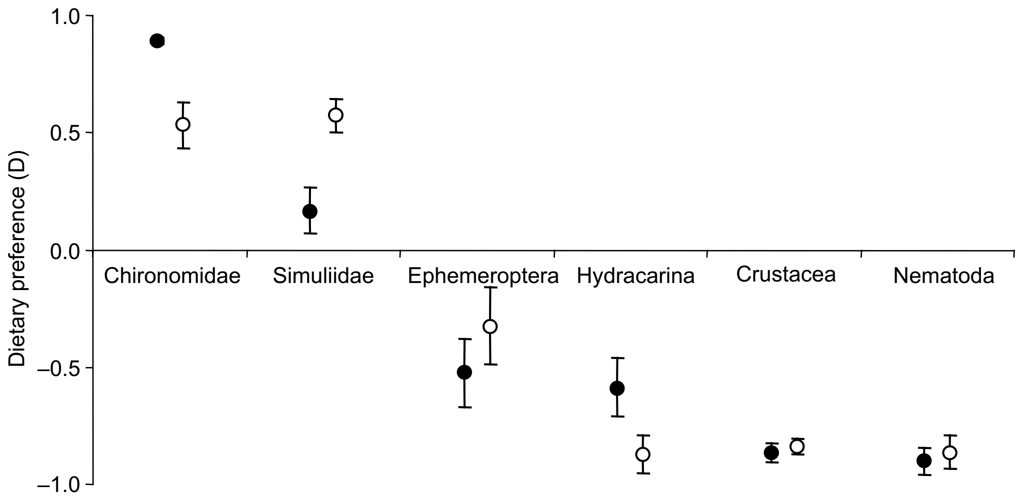

Figure 3. Mean (±95% confidence interval) dietary preference (Jacob's D) by YOY Arctic grayling from Polar-Vulture (●) and Pigeon creeks (○) in 2000. Positive values indicate preference and negative values indicate avoidance. Prey taxa are arranged left to right by decreasing size. Sample size was 120 stomachs per stream (i.e. four samples of 30 fish).

strongly avoided in Pigeon Creek (Figure 3). The strength of selection differed among sampling dates, which was primarily driven by a strong selection for ephemeropterans in July followed by little selection in August (GLM, $F_{3,1430} = 18.79$, $p < 0.05$). The number of both small and large prey in the diets ($n = 240$) increased of as the grayling grew (linear regressions, $R^2 = 0.10$, $p < 0.001$, and $R^2 = 0.32$, $p < 0.001$, respectively), the later increasing at a faster rate than the former (t-test, $p < 0.01$). However, the relative proportion of large invertebrates remained fairly constant (mean = 90%, SE = 0.9) as fish increased in fork length from ca. 25 to 90 mm ($R^2 = 0.001$, $p = 0.487$).

Even within the preferred prey groups of chironomidae and simuliidae, YOY grayling tended to select larger individuals from the drift (Figure 4). Interestingly, however, the mean size of chironomids and simuliids consumed and in the drift did not increase uniformly over the summer (Figure 4), perhaps suggesting multiple cohorts or species-specific differences in availability.

The dipterans in both the drift and stomach contents of YOY grayling were dominated by larval stages (Figure 5). However, grayling consistently consumed a disproportionate number of emerging pupal chironomids and simuliids and, in Pigeon, a disproportionate, though still small, number of adult simuliids (Figure 5).

Discussion

Similar to larger and older grayling in streams of British Columbia and Alaska (Stuart & Chislett 1979, Elliott 1982), we found that drifting macroinvertebrates, primarily chironomids and simuliids, are important prey for YOY Arctic grayling in small streams of the Barrenlands. Furthermore, given the relative availability of prey in these lake-outlet streams, we found that grayling prey selectively on these two groups, whereas large numbers of microcrustacea that drift into stream channels from the upstream lake are avoided, as are other small invertebrates. Terrestrial invertebrates were of limited availability and rarely found in the diet.

Efficient feeders that optimize their net energy gain should have greater growth and reproductive output, and therefore increased fitness, than less efficient feeders (Wootton 1990). As a result, foraging theory predicts that, fish should employ the most profitable feeding strategies available to them, within constraints, including selection of certain prey types and sizes (Werner 1974). Studies of stream-dwelling salmonids (e.g., Allan 1981, Bannon & Ringler 1986, Keeley & Grant 1997) have documented selection for larger invertebrate groups and larger individuals within such groups. Consistent with this, we observed that YOY grayling avoided the abundant but small zooplankton, whereas the rarer but larger insects, especially chironomids and simuliids, were consumed preferentially.

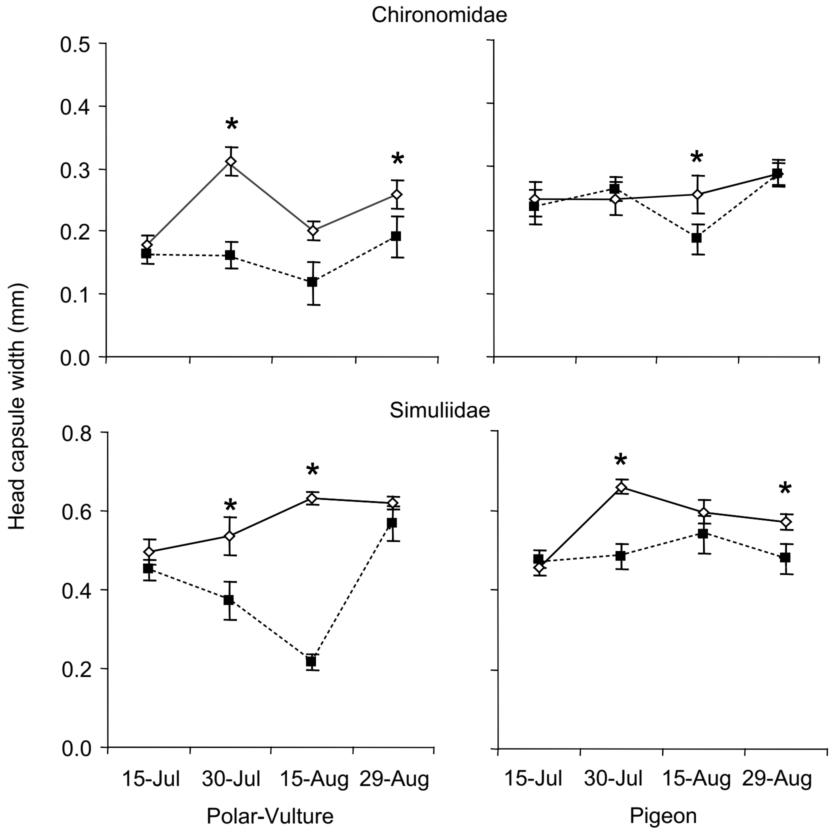

Figure 4. Mean (±SE) head capsule widths of larval chironomidae (upper) and simuliidae (lower) in the drift (■) and diet of YOY Arctic grayling (◇) in Polar-Vulture (left) and Pigeon creeks (right), July–August 2000. Significant differences (Mann–Whitney tests, $P < 0.05$; with Bonferroni adjustment) are indicated with an asterisk. Average sample size per date is 22.

Moreover, we found that grayling tended to select the larger dipterans from the drift. It is unlikely that the zooplankton are too small to be seen or retained by gill rakers of YOY (Wankowski 1979); large adult Arctic grayling readily consume *Daphnia* (O'Brien et al. 2001). It is possible, however, that zooplankton are less detectable than the larger and more darkly colored dipterans. Despite the almost 9-fold difference in the abundance of zooplankton relative to dipterans, the dominance of dipterans in the diet of YOY suggests strongly that such selective foraging results in a greater net energy gain than feeding on microcrustaceans.

Typically, fish ingest larger prey (Wankowski 1979, Werner & Gilliam 1984, Keeley & Grant 1997) and increase diet breadth (Allen 1941, Cadwallader 1975) with increasing body size. However, we found that prey size of YOY grayling varied relatively little over a season. This is likely because the size range of invertebrates available for consumption in these Barrenlands streams was rather restricted, as was the size of fish (YOY from ca. 25 to 90 mm in length). Organisms larger than chironomids and simuliids (e.g., Acrididae and Coleoptera) were rarely found and were generally very large (ca. 30–40 mm in length and quite wide) such that they probably could not be consumed by YOY grayling due to gape limitation (Schael et al. 1991).

Similarly, the diversity of available prey in our study streams was fairly limited, resulting in YOY grayling having a limited and relatively invariant diet of chironomids and simuliids throughout the summer. Terrestrial prey, in particular, was notably unimportant as food for our YOY Arctic grayling. In 1999, however, a wet and cool summer, mosquitoes were abundant in riparian areas, and were disproportionately more abundant in YOY stomachs (15% by number) compared to that in the drift (7% of all individuals). Otherwise, terrestrial insects were not often consumed, nor readily available, even though they are often an important food elsewhere, particularly in small streams with dense riparian vegetation (Armstrong 1986).

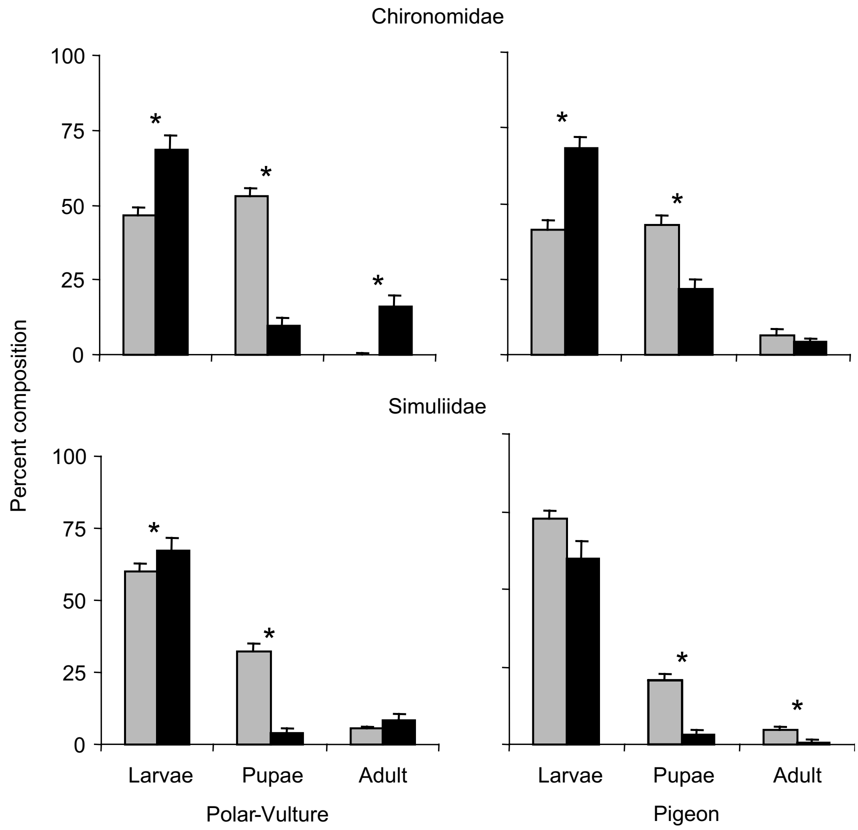

Figure 5. Mean (±SE) percentage composition of different life history stages of chironomidae (upper) and simuliidae (lower) in the diet of YOY Arctic grayling (grey) and drift (black) from Polar-Vulture and Pigeon creeks during July–August, 2000. Significant differences (Mann–Whitney tests, $p < 0.05$; with Bonferroni adjustment) are indicated with an asterisk. Sample sizes for Polar-Vulture are 72 and 120, and for Pigeon are 66 and 123, for drift and stomach samples, respectively.

Elliott (1982) found that diet diversity increased among older and larger grayling, including the consumption of terrestrial prey, while YOY largely concentrated on aquatic organisms. This was also found in a seasonal analysis of the diet and feeding dynamics of brown trout, *Salmo trutta*, in the Owenddoher Stream, Ireland (Kelly-Quinn & Bracken 1990). In fact, Elliott (1982) found that the number of terrestrial insects in the diet surpassed the number of aquatics in some streams. Elliott (1982) suggested that the trend of increasing diet diversity is a function of several factors, including more prey becoming available as fish grow and are able to consume larger prey organisms and because larger fish are able to use a broader range of stream habitats as they grow and become stronger swimmers. Thus, the paucity of terrestrial and other large prey consumed by YOY grayling in Barrenlands streams may also reflect their small size, rather than (or in addition to) differences in prey availability and preference.

Ephemeropterans, although comparable in size to chironomids and simuliids, were not preferentially selected. Because ephemeropterans were much lower in abundance compared to chironomids and simuliids, grayling were perhaps more familiar with the shape and drifting behavior of these dipterans and thus may have developed a 'training bias' (sensu Dill 1983). The low predation intensity on ephemeropterans could also be the result of decreased catchability and increased handling time required to consume a more motile and behaviorally responsive insect group (Scrimgeour et al. 1994). Though perhaps not as important in the Arctic summer, mayflies are also well known to reduce the risk of predation by drifting at night when predatory fishes would be less likely to detect their presence (Flecker 1992).

The Arctic grayling in our study displayed a sit-and-wait, central-place mode of foraging (Fausch 1984, Grant et al. 1989). This mode is well suited for preying on drifting insect larvae, emerging pupae, and surface oriented adults, but not cryptic, stationary benthic prey. Relative to the abundances of the three insect stages, pupae were selected preferentially. Pupation emergence is a vulnerable time in the life cycle of an aquatic insect (LaFontaine 1981).

Individual variation among trout is frequently noted in diet studies (Allan 1981, Ringler 1983). Although rare, we found some grayling consumed high numbers of certain prey, including crustacea, mayflies, wasps, and mosquitoes, that were normally taken in low numbers. Such variation may be related to individual hunger level, past feeding experience or represent opportunistic feeding such as when wind-downed insects become available or when migrating caribou cause catastrophic drift by the benthic invertebrate community (Jones et al. in press). Discovering the mechanism(s) behind this individuality is an interesting challenge, however, such variation was inherently exceptional in our study streams and most grayling mainly consumed chironomids and simuliids in a truly selective manner.

Our understanding about northern aquatic resources remains very much incomplete (Schindler 2001, NSERC 2000), yet is critical for the protection and management of those resources. This study contributes to our understanding of the food habits of YOY Arctic grayling, an economically and culturally important, yet poorly understood, fish species in Canada's North. As well, our study demonstrates clearly that despite the abundance of lake-derived zooplankton in the lake-outlet streams of the Barrenlands, productive capacity of these streams will likely remain dependent on instream production of invertebrates. As resource exploitation increases in the Arctic regions of the world so to will the unavoidable alteration, disruption, and destruction of fish habitat (sensu DFO 1986). Habitat compensation efforts will need to provide more than just suitable physical habitat for fish, but must also consider autochthonous invertebrate production.

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