Productive capacity of an artificial stream in the Canadian Arctic: assessing the effectiveness of fish habitat compensation

Nicholas E. Jones, William M. Tonn, Garry J. Scrimgeour, and Chris Katopodis

Abstract: Few fish habitat compensation projects are assessed with respect to the principle of "no net loss" of productive capacity. Using reference streams as standards against which gains and losses of functions (e.g., production of fish) could be quantified, we examined the effectiveness of a 3.4-km artificial stream in the Northwest Territories, Canada. The artificial stream restored watershed connectivity, allowing fish migration and provided spawning and nursery habitat, particularly for Arctic grayling (Thymallus arcticus). However, the average mass of young-of-the-year (YOY) grayling at the end of summer was lower (57%) in the artificial stream than in natural streams. This difference in growth, in concert with estimates of grayling density, meant that the standing crop produced in the artificial stream averaged 37% of that found in natural streams. A bioenergetics model indicated that cooler water temperatures in the artificial stream had limited influence on growth. Instead, low amounts of autochthonous and allochthonous organic matter and poor physical habitat in the artificial stream appeared to limit the productivity of benthic invertebrates and fish. Our explicit analysis of productive capacity will allow future compensation measures to focus on deficiencies in the artificial stream and on the improvement of its productive capacity as fish habitat.

Introduction

Habitat loss and degradation caused by extraction of natural resources, industrial processing, agriculture, and urbanization threaten the sustainability of fisheries resources. In Canada, the principal legislation for the conservation and management of fisheries and fish habitat is the Fisheries Act. Under this Act, management strategies focus on preventing the harmful alteration, disruption, or destruction (HADD) of habitats that sustain fish productivity. To guide implementation of the Act, the Department of Fisheries and Oceans (DFO) developed a "Policy for the Management of Fish Habitat" (hereafter, the Policy (DFO 1986)). The guiding principle of the Policy is to ensure "no net loss of productive capacity of fish habitats" (NNL; Minns et al. 1996). Productive capacity is defined in the Policy as "the maximum natural capability of habitats to produce healthy fish ... or to support or produce aquatic organisms upon..."
which fish depend” (DFO 1986, p. 28). When developments that will alter fish habitat are proposed and compensation programs are required, HADD and NNL assume the ability to quantify effects on fish production. This, in turn, presumes that the habitat needs of species are understood, that the relationship between habitat and fish production is known or can be assessed, and that there is an undisturbed natural area or time before disturbance that can serve as a reference and provide a measure of the effectiveness of restorative or enhancement measures (Minns 1997). Frequently, however, one or more of these presumptions are not met. For a variety of reasons, most assessments of habitat compensation must rely on rather indirect measures of program effectiveness (Minns 1997).

Despite the overwhelming importance of NNL to fisheries management in Canada, few studies have evaluated the effectiveness of mitigation measures within this framework. Minns et al. (1996) challenged the scientific rigor of habitat compensation programs and suggested that many are rushed within uncharted ecological territory. Rapid compensation action is often seen as more important than carefully examining alternative avenues of compensation and their eventual effectiveness. Ecological restoration is an emerging science and successful restoration is a serious test of our often limited, ecological understanding; as such, efforts will be fraught with mistakes (Bradshaw 1996). A more rigorous approach to compensation is needed, grounded in the principles of the scientific method, including the use of appropriate reference sites. Peer-reviewed examinations of restoration efforts, both successes and failures, need to be published (Bradshaw 1996; Minns et al. 1996), for only then can we begin to learn from our collective experiences.

In 1991, diamonds were discovered in the remote region of the Northwest Territories known as the Barrenlands. In preparation for mineral extraction, two lakes and their tributary streams within a larger chain of lakes were drained. As part of the habitat compensation agreement, a 3.4-km artificial stream was blasted out of Shield rock. Since 1997, water has been diverted around the two lakes, now open-pit mines, through the artificial stream. The objective of the compensation was to restore watershed connectivity for fish migration and provide spawning and nursery habitats, primarily for Arctic grayling (Thymallus arcticus), and thus offset the losses in stream habitat from development.

We based our assessment of this compensation on a hierarchical framework of the specific functions needed by the artificial stream to achieve NNL of productive capacity. Because we lacked an ecological description of the streams lost during development, or even of Barrenland streams in general, the use of natural, undisturbed streams was all the more important for establishing reference conditions and quantifying gains and losses in productive capacity of fish habitat. The relative simplicity of the fish assemblages and the availability of many pristine streams in the region to serve as reference sites provided an unparalleled opportunity to examine the effectiveness of the artificial stream in providing productive fish habitat, as per DFO’s guiding principle of NNL. As part of this examination, the main objectives of our study were to (i) assess the production of young-of-the-year (YOY) grayling in the artificial stream, relative to natural (reference) streams, in terms of density, growth, and condition, and (ii) examine factors that might explain differences in growth between the natural and artificial streams, including water temperature, invertebrate food availability, and physical habitat. We assessed the relative effect of temperature on growth and explored potential effects of food using a bioenergetics model calibrated to field data on YOY Arctic grayling.

**Study system**

The 4000-km² study area is centred around 64°45’N and 110°30’W (see Fig. 1), about 100 km north of the tree line within the southern arctic ecozone. The mean annual temperature is approximately −12 °C, with a summer maximum of 27 °C and a winter minimum of −54 °C (Environment Canada 1991). The climate is semi-arid with 200–300 mm of precipitation annually, 50% of which falls as snow. The region is underlain by granite, gneiss, and schist that form broad, sloping uplands, plateaus, and lowlands. The permafrost layer is continuous. Eskers, kames, and boulder-strewn till plains cover the land. Thin soils in upland areas support dwarf heath and scattered low shrub tundra, whereas lowland and depressional areas near lakes and streams are characterized by sedge tussock and low-tall shrub tundra.

The combination of relatively low topographical relief (~50 m) and extensive glacial activity has molded a landscape covered by about 21% water in the form of numerous chains of lakes and connecting streams. After spring runoff, evaporation from lakes gradually lowers lake levels and stream flows diminish, with many small streams eventually becoming dry. Flows can increase (or resume) in late summer and fall but are frozen solid during the long arctic winter. At ~450 m above sea level (asl), the streams of this area are the headwaters of the Coppermine, Back, and Burnside rivers, which flow north to the Arctic Ocean.

Arctic grayling is well represented in the fish communities, which also include slimy sculpin (Cottus cognatus), burbot (Lota lota), round whitefish (Prosopium cylindraceum), lake trout (Salvelinus namaycush), longnose sucker (Catostomus catostomus), ninespine stickleback (Pungitius pungitius), lake chub (Couesius plumbeus), and northern pike (Esox lucius). Most streams support at least one species but commonly contain only three species: Arctic grayling, burbot, and slimy sculpin (Jones et al. 2003a). Streams are used mainly for spawning and subsequently as nursery habitat for YOY grayling, whereas the numerous lakes in the region are used by all ages and species of fish for overwintering. Fish are known to migrate among lakes and streams during the open-water season (N.E. Jones, unpublished data).

**Methods**

**General sampling design**

Data were collected during four summers, 1998 to 2001. Twenty natural streams, distributed throughout the study area and ranging in abiotic and biotic conditions, were surveyed for basic physical characteristics, fish community composition and abundance, and the size of YOY grayling.
just before out-migration (see Jones et al. 2003a). Reference streams were selected based on the presence of visible water in the stream channel during aerial surveys in late July. A subset of nine natural streams, more centrally located around the artificial stream, were also sampled for benthic invertebrates, water chemistry, woody debris volumes, substrate coarse particulate organic matter (CPOM), and epilithon; two of these streams, Polar–Vulture and Pigeon, were subjected to more intensive fisheries and invertebrate drift investigations. Given their remote arctic location, reference streams were assumed to represent the range of natural structure and function (e.g., production of YOY grayling) for streams in this region. As such, we used reference streams to establish standards against which differences of the artificial stream could be compared. The artificial stream was sampled for all of the above parameters.

Basic stream surveys (stream physical characteristics and fish)

Stream geomorphology, including stream length, slope, bankfull width and depth, and substrate composition, were determined from ground surveys, aerial photographs, and topographic maps. Substrate composition and aquatic vegetation cover were quantified along several transects perpendicular to stream flow, with substrates classified as clay and silt (<0.0625 mm), sand (0.0625–2 mm), small gravel (2–32 mm), large gravel (32–64 mm), cobble (64–256 mm), and boulder (>256 mm). Mesohabitat composition (cascade, riffle, run, flat, pool, wetland, boulder garden, and culvert; Ontario Ministry of Natural Resources (OMNR) 1987) was also quantified as percent length of stream.

Arctic grayling fry were first observed 21 to 24 days after spawning (early July). Swim-up dates, determined as the date on which larval grayling were visible along stream margins and captured in larval drift nets, were similar among streams. At this time, young were 11–13 mm in length and 0.01 g in mass (Jones et al. 2003a). During the arctic fall, approximately late August to early September, fish, including YOY grayling, migrate out of streams to overwinter in lakes before streams freeze solid. Hence, by late August, about 50 days after swim-up, YOY grayling mean mass represents a significant percentage of first-year growth.

Fish community composition and the end-of-season size of YOY grayling were determined by electrofishing in late summer (about 23 August), shortly before the out-migration, in one, two, ten, and three natural streams in 1998, 1999, 2000, and 2001, respectively. Captured fish were identified, enumerated, weighed (±0.01 g), and measured (fork length ± 1 mm).

Benthic stream surveys (limnology, woody debris, epilithon, CPOM, and benthic invertebrates)

Three replicate water samples were collected from each stream in late July. Samples were stored in a cold, light-free environment until analysis. In the laboratory, total nitrogen was determined using the persulfate digestion method on a Technicon AutoAnalyzer (Pulse Instrumentation (1992) Ltd., 433 Birch Cres., Saskatoon, SK S7N 2K2). Total phosphorus (±1 µg·L⁻¹) was determined spectroscopically using persulfate-oxidized samples by molybdate blue absorption.

Woody debris volumes were determined by counting all woody debris longer than 10 cm along 40- to 150-m lengths...
of stream channel. We measured the length of each piece and determined the mean diameter by averaging the diameters of each end and converted these dimensions to volume estimates. The surface area of the sampled section was determined by multiplying the transect length by the mean stream width measured at four locations along the stream. Volumes were then standardized to cm$^{-1}$100 m$^{-2}$.

Numbers of shrub stems located within 1 m of the stream bank were counted along transects 40–150 m along each stream bank and converted to mean densities (individuals (ind.)·m$^{-2}$). We also used transects to quantify the amount of grass and shrubs along stream banks as a percentage of the ground covered and similarly determined coverage of the streambed by aquatic macrophytes and bryophytes.

Five replicate samples of substrate CPOM, epilithon, and benthic invertebrates were collected in late July from the same locations in both riffles (mean depth, 0.24 m; mean velocity, 0.25 m·s$^{-1}$) and pools (mean depth, 0.34 m; mean velocity, 0.08 m·s$^{-1}$). CPOM samples were collected by inserting a plastic jar, 90 mm deep × 80 mm diameter, vertically into the substratum. Within 48 h, we washed the refrigerated samples, removing inorganic material and invertebrate cases and exuviae, and sieved them through 1-mm mesh. Filtered organics on the screen were then dried to constant mass at 40 °C (±0.1 mg). Periphyton samples were scraped from the upper surfaces (4.9 or 9.6 cm$^2$) of randomly selected stones. Invertebrates visible without the aid of magnification were removed from scrapings. Samples were stored frozen in the dark for 2–4 weeks before being dried at 40 °C, weighed, ashed at 550 °C, and reweighed for ash-free dry mass determination (±0.1 mg). Benthic invertebrate samples were collected using a 0.093-m$^2$ Surber sampler, fitted with 250-µm mesh. All samples were preserved with 70% ethanol in the field. Invertebrates were identified to genus or species, with the exception of Nematoda, Turbellaria, and terrestrial invertebrates, which were typically identified to family or order. Following enumeration, samples were dried to constant mass at 40 °C and weighed (±0.1 mg).

Intensive stream sampling (temperature, drift, fish growth, biomass, and density)

HOBO temperature loggers synchronously recorded stream water temperature (±0.1 °C) every 4 h from freshet to late August in the artificial (five locations) and Polar–Vulture and Pigeon (two locations each) streams.

The amount and composition of cover available for YOY grayling were visually estimated using transects perpendicular to the axis of the stream. The streams were divided into 10-m sections, and a transect was placed randomly within each section. Cover types, which provide one or a combination of velocity refuge, visual isolation, or overhead cover (sensu Fausch 1993), included depth, turbulence, rock, undercut, aquatic vegetation, and terrestrial vegetation.

Drift was sampled simultaneously at two locations within each stream with Field-Dodgson tri-net samplers, fitted with 250-µm nets. On each sampling date (15 and 30 July, 15 and 29 August), drift was collected at dawn, noon, and dusk. Samples were collected from relatively shallow water (mean depth and velocity, 0.16 m and 0.24 m·s$^{-1}$, respectively) in close proximity to fish collection areas to reflect organisms available to grayling. Nets were wetted for 30–45 min, 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 current velocity meter (Swoffer Instruments, Inc., 1048 Industry Drive, Seattle, WA 98188). Drift samples were preserved in 70% ethanol and later identified and counted. After enumeration, samples were dried to constant mass at 40 °C and weighed (±0.1 mg).

Invertebrates in the drift were classified as either large (e.g., insects) or small (e.g., microcrustaceans) based on body mass. Head capsule width (±0.01 mm), an indicator of invertebrate body mass, was measured on Chironomidae and Simuliidae larvae from a random subset of drift samples from each date in year 2000 using a dissecting scope equipped with an ocular micrometer.

In the artificial and Polar–Vulture streams, we estimated total fish density (fish·m$^{-3}$) and biomass (g·m$^{-3}$) in late July 1998–2000 using the three-pass removal method, with habitat stratified as pools and riffles. Captured fish were identified, enumerated, weighed (±0.01 g), and measured (fork length ± 1 mm). Volumes electrofished were determined for each section shortly after being surveyed. Computations for population estimates were made separately for Arctic grayling (juvenile and YOY), slimy sculpin, and burbot. For each section of stream, we estimated total fish biomass per species by multiplying the mean individual mass by the number of fish estimated for that section. Upwards of 75% of the estimated total fish abundance were typically captured in each fished section of stream.

Aside from the estimates of first-year growth of YOY Arctic grayling before out-migration (see Basic stream surveys), the mean mass of YOY grayling was also determined several times from swim-up to shortly before out-migration in the artificial, Polar–Vulture, Pigeon, and Polar–Panda streams.

Finally, the diet of YOY grayling from the artificial stream was determined using methods of Jones et al. (2003b); briefly, 19 invertebrate taxa were identified in the stomachs and subsequently classified as either large or small based on body size. To examine prey size selection, we measured head capsule widths on the two most commonly consumed invertebrate taxa, Chironomidae and Simuliidae, from random subsets of stomach samples from each sampling period in 2000. We used a dissecting scope equipped with an ocular micrometer for measurements (±0.01 mm). We have included some reference stream data from Jones et al. (2003b) for a comparison with the food habits of YOY grayling from the artificial stream.

Bioenergetic model and simulations

We used bioenergetics modelling to assess the relative effects of different water temperatures in artificial and natural streams on observed growth of YOY Arctic grayling (see Ries and Perry 1995; Railsback and Rose 1999). We used the Wisconsin model (Fish bioenergetics 3.0; Hanson et al. 1997), configured for age-0 Arctic grayling (Table 1). Model inputs were average daily temperatures from swim-up to 23 August and the respective mean mass of the YOY grayling on these sampling dates.
Table 1. Physiological parameters used in the bioenergetics model for young-of-the-year Arctic grayling.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Waste losses (eq. 1)(^{a,b})</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FA — egestion</td>
<td>0.15</td>
<td>Hanson et al. (1997)</td>
</tr>
<tr>
<td>UA — excretion</td>
<td>0.1</td>
<td>Hanson et al. (1997)</td>
</tr>
<tr>
<td>Respiration (eq. 2)(^{a,c})</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RA — grams of oxygen (g·g(^{-1})·day(^{-1})) consumed by a 1-g fish at RTO</td>
<td>0.0156</td>
<td>Harrison (1995)</td>
</tr>
<tr>
<td>RB — slope of allometric mass function</td>
<td>-0.287</td>
<td>Harrison (1995)</td>
</tr>
<tr>
<td>RQ — (°C(^{-1})) approximates (Q_{10})</td>
<td>2.1</td>
<td>Harrison (1995)</td>
</tr>
<tr>
<td>RTO — (°C) optimal temperature for respiration</td>
<td>18</td>
<td>Harrison (1995)</td>
</tr>
<tr>
<td>RTM — (°C) maximum lethal temperature</td>
<td>26.4</td>
<td>Harrison (1995)</td>
</tr>
<tr>
<td>SDA — specific dynamic action</td>
<td>0.172</td>
<td>Hanson et al. (1997)</td>
</tr>
<tr>
<td>Activity</td>
<td>1.3</td>
<td>Hanson et al. (1997)</td>
</tr>
<tr>
<td>Consumption (eq. 3)(^{a,c})</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CA — intercept of the mass dependence</td>
<td>0.628</td>
<td>Rand et al. (1993)</td>
</tr>
<tr>
<td>CB — coefficient of the mass dependence</td>
<td>-0.3</td>
<td>Rand et al. (1993)</td>
</tr>
<tr>
<td>CQ — (°C) lower water temperature at which the temperature dependence is a small fraction (CK1) of the maximum consumption rate</td>
<td>5</td>
<td>Rand et al. (1993)</td>
</tr>
<tr>
<td>CK1 — small fraction of the maximum consumption rate</td>
<td>0.33</td>
<td>Rand et al. (1993)</td>
</tr>
<tr>
<td>CTO — (°C) temperature corresponding to 0.98 of the maximum consumption rate</td>
<td>20</td>
<td>Rand et al. (1993)</td>
</tr>
<tr>
<td>CTM — (°C) temperature (≥ CTO) at which dependence is still 0.98 of the maximum consumption rate</td>
<td>20</td>
<td>Rand et al. (1993)</td>
</tr>
<tr>
<td>CTL — (°C) upper water temperature at which temperature dependence is a small fraction (CK4) of the maximum consumption rate</td>
<td>24</td>
<td>Rand et al. (1993)</td>
</tr>
<tr>
<td>CK4 — small fraction of the maximum consumption rate</td>
<td>0.2</td>
<td>Rand et al. (1993)</td>
</tr>
</tbody>
</table>

\(^{a}\)Hanson et al. (1997).
\(^{b}\)Kitchell et al. (1977).
\(^{c}\)Thornton and Lessem (1978).

In our bioenergetic simulations, we first adjusted food consumption (\(P\) value) to meet the observed final mass observed in each stream using their respective temperature regimes. We then determined what the final mass for a YOY grayling would be if we substituted the temperature regime in the artificial stream for that observed in the natural stream. Secondly, we asked what the final mass would be if we substituted the \(P\) value observed in the artificial stream for that observed in the natural stream? We estimated the effect of temperature on the growth (\(Growth_T\)), as

\[
Growth_T = \left[ \frac{OBS_{ART} - PRE_{P_0 \& T_{art}}}{OBS_{NAT} - OBS_{ART}} \right] \times 100\%
\]

where \(OBS_{NAT}\) and \(OBS_{ART}\) are the observed mass of YOY grayling on 23 August in the natural and artificial stream, respectively, and \(PRE_{P_0 \& T_{art}}\) is the predicted mass of grayling based on the \(P\) value from the artificial stream (\(P_{art}\)) and the temperature regime from the artificial stream (\(T_{art}\)). We estimated the effect of food availability on the growth (\(Growth_F\)) as

\[
Growth_F = \left[ \frac{OBS_{ART} - PRE_{P_0 \& T_{art}}}{OBS_{NAT} - OBS_{ART}} \right] \times 100\%
\]

where \(OBS_{NAT}\) and \(OBS_{ART}\) are the observed mass of YOY grayling on 23 August in the natural and artificial streams, respectively, and \(PRE_{P_0 \& T_{art}}\) is the estimated mass of grayling based on the \(P\) value from the natural stream (\(P_{nat}\)) and the temperature regime from the artificial stream (\(T_{art}\)).

Our ability to determine the influence of temperature is imperfect in that there is an indirect effect of temperature on \(C_{max}\), the maximum specific feeding rate. However, for the purposes of this study, this indirect effect of temperature is likely small, particularly over the relatively short simulation times used in this study. We also conducted sensitivity analyses for the \(P\) value and activity multiplier by changing these inputs by 25, 50, and 100%.

Statistical analyses

We employed one-sample hypotheses testing (OSH; Sokal and Rohlf 1995), using data from general and benthic stream surveys (e.g., substrate, cover, water chemistry, epilithon, CPOM, benthic invertibrates), for comparisons between the artificial and natural streams. Our interest was in comparing the average value of a measured variable from the artificial stream with the distribution of values among natural streams. When the number of natural streams sampled was limited, we used general linear modelling (GLM) followed by Tukey’s multiple comparison tests for comparisons between the artificial and reference streams (e.g., fish, invertebrate drift, head capsule size). Analysis of covariance (ANCOVA) was used to determine if YOY were of different condition (mass-at-length) among streams and years; mass-length data were square root transformed. We used the Kolmogorov–Smirnov test to examine data for normality and the Levene median test for homogeneity of variances. For all statistical tests, we used \(\alpha = 0.05\) as a critical level of signifi-
The results of these experiments were presented by Dr. Jones at the International Symposium on Fish Ecology and Management. He noted that the artificial stream was significantly different from the natural stream in terms of several physical and chemical parameters. The mean temperature in the artificial stream was 0.7 °C lower than in the natural streams, averaged over the season. This difference was significant (after performing the Bonferroni adjustment, required to reduce the experimentwise error rate).

**Results**

### Physicochemical

Large-scale differences in habitat between the artificial and reference streams include mesohabitat composition and the number of side channels. Although natural streams that drain areas of fine sediment tend to have single, well-defined channels, most natural streams in the Barrenlands are multichannelled, with some streams having more than six side channels. In contrast, the artificial stream was constrained by steep (10–90°) and high (2–10 m) banks, with a single channel throughout its entire length. Natural streams typically contain a diversity of mesohabitat types. Despite its length (3.4 km), however, the artificial stream has a limited number of habitat types, with wetland and boulder garden absent. In addition, the proportions of the habitat types differ from those found in reference streams. For example, natural streams had more riffles (33 vs. 4%) and pools (11 vs. 1%), whereas the artificial stream had more cascades (7 vs. 1%) and flats (55 vs. 18%) (OSH; df = 19, P < 0.05). Cover for YOY grayling in reference streams was nearly double that found in the artificial stream (Table 2). In addition, the cover types available to grayling were more diverse in the natural streams than in the artificial stream, where vegetation (aquatic and terrestrial) was almost entirely absent (Table 2).

Substrate sizes in the artificial stream were significantly smaller than those found in the reference streams. Fine substrates (silt, clay, and sand) dominated 44% of the substrate composition in the artificial stream, whereas in the natural streams, fines composed only 14%; the proportion of sand was significantly greater in the artificial stream (OSH; df = 19, P < 0.05). Moreover, boulders composed only 16% of the substrate in the artificial stream but 56% in natural streams (OSH; df = 19, P < 0.05).

Water chemistry in the artificial stream was similar to that found in natural streams. Total phosphorus in the artificial stream was not significantly different from that measured in natural stream systems (9.85 and 6.92 µg·L⁻¹ ± 0.72 standard error (SE), respectively; OSH; df = 5, P < 0.05). However, total nitrogen was higher in the artificial stream than in the natural stream systems (321.56 and 167.20 µg·L⁻¹ ± 26.7 SE, respectively; OSH; df = 5, P < 0.05). At times, particularly during high flow events (spring and fall), turbidity and suspended solids levels would briefly but dramatically increase in the artificial stream (N.E. Jones, personal observation).

Natural streams accumulated a mean of 351 degree-days from swim-up of YOY Arctic grayling to 31 August (Table 3). Daily water temperatures in the artificial stream averaged 0.9 °C colder than in the natural streams during the growth period (Table 3). This seemingly small difference accumulated to an average deficit of 56 degree-days from swim-up to out-migration in late August.

### Biological

**Vegetation and organic matter**

A major difference between the artificial and reference streams is in the amount of living and dead plant material in the stream channels and adjacent riparian areas. The riparian zones of natural Barrenland streams are generally well vegetated. In well-drained riparian zones, dwarf heath and scattered low shrub tundra dominate, whereas sedge tussock is common in poorly drained areas. In contrast, the riparian
zone of the artificial stream is dominated by a thick layer of blast rock, although willow plugs have been planted to stabilize banks in a few areas. Grasses covered 44% (± 5% SE) of the ground in natural riparian zones, but only 4% in the artificial (OSH; df = 8, P < 0.05). Similarly, cover by shrubs averaged 58% (± 5% SE) in natural riparian zones but only 1% in the artificial stream (OSH; df = 8, P < 0.05). The average density of shrub stems within 1 m of the stream was 0.86·m⁻² (± 0.12 SE) and 0.06·m⁻² in the reference and artificial streams, respectively (OSH; df = 8, P < 0.05).

Aquatic plants, consisting of macrophytes, algae, and bryophytes, were generally abundant in natural streams but were rare in the artificial stream, and those that existed in the latter were mostly planted. Epilithon abundance, particularly Zygnema spp., was significantly greater in the natural streams compared with the artificial stream (OSH; P < 0.05; Fig. 2a). Depositional areas of fine substrate organic matter in natural streams also supported an abundance of aquatic macrophytes (e.g., bur-reed (Sparganium hyperboreum) and mare’s-tail (Hippuris vulgaris)), covering 17% (± 5% SE) of the streambed by mid-July. Macrophytes in the artificial stream consisted of planted Arctic pendant grass, Arctophila fulva, which thinly covered only 1% of the streambed. Bryophytes were common in some natural streams, covering 10% (± 3% SE) of the streambed, but were absent from the artificial stream.

Stemming from a lack of riparian vegetation, the artificial stream contained about one-tenth of the coarse particulate organic matter (CPOM) found in the natural streams (OSH; P < 0.05; Fig. 2b). In the natural streams, many sections of riffle pass through thick growths of dwarf birch and willow, which contribute relatively small pieces of woody debris (mean length and diameter, 370 and 5 mm, respectively) to the channel. Woody debris volume in the artificial stream, 215 cm³·100 m⁻² of streambed, was about fourfold lower than that in the natural streams, 917 ± 350 cm³·100 m⁻².
Overall, all woody debris in the artificial stream were willow plugs added as remediation during 1998–2000.

**Invertebrates**

Although there was considerable variation among streams and years, higher numbers of benthic invertebrates were generally contained in the natural streams than in the artificial stream, especially in riffles (OSH; \( P < 0.05 \); Fig. 2c). Differences were even greater for benthic invertebrate biomass estimates (OSH; \( P < 0.05 \); Fig. 2d), suggesting that the benthic invertebrates in the natural streams were larger. Dipterans were well represented in all streams, contributing about 45% of all individuals and 62% by mass, 19% of which were chironomids.

The numbers of small invertebrates (e.g., microcrustaceans, including cladocerans, copepods, and ostracods) in the drift did not differ between the artificial and natural streams (GLM; \( n = 18 \) per date and stream, \( P > 0.05 \); Fig. 3a). However, there were significantly fewer large organisms (e.g., insect larvae, including chironomids, simuliiids, and ephemeropters) in the drift of the artificial stream on all sampling dates compared with natural streams (GLM; Fig. 3b). Mean drift biomass in the artificial and natural streams was similar in 1999. In 2000, however, drift biomass in natural streams was typically higher (GLM; Fig. 3c). As suggested above, the head capsule widths of drifting larval Chironomidae were larger in the natural streams (Polar–Vulture and Pigeon) than in the artificial stream (GLM; \( df = 223, P < 0.05 \)); however, larval Simuliidae size was similar among streams (GLM; \( df = 252, P = 0.06 \)).

**Fish**

Spawning surveys and radiotelemetry studies indicated that adult and juvenile Arctic grayling were able to migrate successfully through the artificial stream and its three culverts (N.E. Jones, unpublished data). Other species and age-classes, including slimy sculpin and burbot, were unable to ascend a second culvert, 700 m upstream from Kodiak Lake (Fig. 1). Depending on the year, between 200 and 300 grayling were observed migrating into the artificial stream. Although a quantitative estimate of spawning success was not determined, YOY grayling were produced in relatively

© 2003 NRC Canada
large numbers, particularly in the lower end of the stream where most of spawning occurred (N.E. Jones, unpublished data).

Fish communities: density and biomass

Fish community composition in the artificial stream was similar to that in the intensively fished natural stream, Polar–Vulture. Age-0 grayling dominated both communities, numerically and by biomass. Other species in both streams included slimy sculpin and burbot. Total densities of fish in the artificial stream were similar to (1998) or less than (1999, 2000) densities found in Polar–Vulture (GLM; df = 55, \( P < 0.05 \); Fig. 4a). In contrast, fish biomass was consistently and significantly greater in Polar–Vulture on all dates (GLM; df = 55, \( P < 0.05 \); Fig. 4b). Similarly, grayling biomass was generally greater in Polar–Vulture (GLM; df = 55, \( P < 0.05 \); Fig. 4c).

Growth and production of age-0 grayling

Growth varied considerably among years, related to differences in temperature, discharge, and invertebrate densities (Table 4). The two most intensively studied reference streams, Polar–Vulture and Pigeon, produced the slowest- and fastest-growing YOY grayling, respectively, among natural streams. By 23 August, before out-migration, YOY in natural streams averaged 2.74 g ± 0.44 SE, whereas YOY in the artificial stream were only 1.18 g ± 0.14 SE (Table 5). Differences in growth between the artificial and natural streams became more prominent over the course of a summer (Fig. 5a). Analysis of covariance indicated a significant interaction (\( P = 0.003 \)) between the covariate (length) and the independent factor (stream), indicating that the growth rates differed between the artificial and natural streams (Fig. 5a). There appears to be little difference in condition (i.e., mass-at-length) among streams and years (Fig. 5b). Hence, YOY from different streams followed similar allometries but not at the same rate. The large difference in growth, combined with estimates of YOY grayling density, meant that standing crop in the artificial stream averaged 37% of that found in Polar–Vulture (Fig. 4c).

Diet analyses

The composition of invertebrates in the diets of YOY grayling was stream dependent. Grayling stomachs from the artificial stream and Polar–Vulture contained a very similar composition of invertebrates, roughly 75% chironomids and 10% simulids, whereas fish from Pigeon contained 33% chironomids and 46% simulids. The head capsule widths of

Fig. 4. Mean (± standard error) (a) density (ind., individuals) and biomass of (b) all fish and (c) grayling in pool and riffle habitats in the artificial (solid bars) and Polar–Vulture (shaded bars) streams in 1998–2000. Asterisks indicate significant differences (t tests; \( P < 0.05 \)) between streams.

© 2003 NRC Canada
Table 4. Annual variation in weather and discharge during June–August and accumulated degree-days from spawning to 23 August in relation to mean (± standard error) epilithon mass and mean (± standard error) benthic invertebrate density for Polar–Vulture, Pikejaw, and Slipper – Lac de Gras streams for 1998–2001.

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>1998</th>
<th>1999</th>
<th>2000</th>
<th>2001</th>
<th>P value and post hoc tests</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abiotic</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Accumulated rainfall (mm)</td>
<td>88</td>
<td>180</td>
<td>118</td>
<td>134</td>
<td></td>
</tr>
<tr>
<td>Mean discharge (m³·s⁻¹)</td>
<td>0.03</td>
<td>0.14</td>
<td>0.13</td>
<td>0.16</td>
<td></td>
</tr>
<tr>
<td>Accumulated mean monthly air temperature (°C)</td>
<td>37</td>
<td>28</td>
<td>34</td>
<td>31</td>
<td></td>
</tr>
<tr>
<td>Mean daily water temperature (°C)</td>
<td>13</td>
<td>12</td>
<td>14</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>No. of degree-days from spawning to 23 August</td>
<td>1137</td>
<td>882</td>
<td>1029</td>
<td>934</td>
<td></td>
</tr>
<tr>
<td>Biotic</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Epilithon (mg·cm⁻²)</td>
<td>1.7 (0.7)</td>
<td>2.0 (0.6)</td>
<td>1.9 (0.4)</td>
<td>—</td>
<td>0.94</td>
</tr>
<tr>
<td>Benthic density (individuals·m⁻²)</td>
<td>31 480 (7541)</td>
<td>3420 (565)</td>
<td>13 720 (1891)</td>
<td>—</td>
<td>0.023 A B A B</td>
</tr>
<tr>
<td>YOY length (mm)</td>
<td>77</td>
<td>57 (0.5)</td>
<td>64 (0.9)</td>
<td>56 (0.47)</td>
<td>&lt;0.01 A B C B</td>
</tr>
<tr>
<td>YOY mass (g)</td>
<td>3.80</td>
<td>1.78 (0.05)</td>
<td>2.55 (0.12)</td>
<td>1.78 (0.04)</td>
<td>&lt;0.01 A B C B</td>
</tr>
</tbody>
</table>

Note: Data on young-of-the-year (YOY) mean size (± standard error) are from Polar–Vulture. For 1998, fish mass on 23 August was estimated based on two prior sampling periods (9 and 30 July). General linear modelling and multiple comparisons were used to assess differences in biotic characteristics among years.

Table 5. Mean mass (g, ± standard error (SE)) and the absolute and relative difference in mass of young-of-the-year Arctic grayling between the artificial and natural streams on 23 August 1998–2001, shortly before out-migration.

<table>
<thead>
<tr>
<th>Year</th>
<th>1998a</th>
<th>1999</th>
<th>2000</th>
<th>2001</th>
<th>Mean</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artificial</td>
<td>1.60</td>
<td>0.99 (0.02)</td>
<td>1.11 (0.09)</td>
<td>1.01 (0.06)</td>
<td>1.18</td>
<td>0.14</td>
</tr>
<tr>
<td>Natural</td>
<td>3.80</td>
<td>2.07 (0.11)</td>
<td>2.91 (0.09)</td>
<td>2.12 (0.2)</td>
<td>2.74</td>
<td>0.44</td>
</tr>
<tr>
<td>Difference</td>
<td>–2.20</td>
<td>–1.08</td>
<td>–1.80</td>
<td>–1.11</td>
<td>–1.55</td>
<td>0.27</td>
</tr>
<tr>
<td>Relative difference (%)</td>
<td>58</td>
<td>48</td>
<td>38</td>
<td>48</td>
<td>57</td>
<td>2.5</td>
</tr>
</tbody>
</table>

Note: Number of natural streams studied per year: 1998, 1; 1999, 2; 2000, 9; 2001, 3.

*aFish mass on 23 August 1998 was estimated based on two prior sampling periods (9 and 30 July).

Chironomidae (GLM; df = 333, P < 0.05) and Simuliidae (GLM; df = 304, P < 0.05) in the diets were larger on 50% of sampling dates in the natural streams (Polar–Vulture and Pigeon) versus the artificial stream.

Bioenergetic simulations

Our simulations estimated that 11% of the difference in the mass of YOY grayling between the artificial and natural streams could be attributed to the cooler temperature of the artificial stream, whereas 80% can be attributed to reduced food consumption. The relative importance of temperature varied by year (Table 6). During cooler summers (e.g., 1999), temperature had more of an influence on growth, but during warm summers (e.g., 2000), temperature had little bearing on differences in growth (Table 6).

Our sensitivity analysis of the bioenergetics model indicated that a 50% increase in the P value resulted in a four-fold increase in body mass, and a 100% increase resulted in
a 13-fold increase in body mass and thus could contribute to the observed differences in growth between the artificial and natural streams. The bioenergetic model was less sensitive to changes in the activity multiplier. A 50% increase in activity resulted in approximately a twofold reduction in body mass, and a 100% increase resulted in a sevenfold reduction in body mass.

Discussion

Assessing the artificial stream as productive fish habitat

Our assessment of the artificial stream is based on a hierarchical framework of stream functions focused on the production of YOY Arctic grayling: can grayling successfully migrate through the channel, do the grayling spawn in the channel, do the eggs hatch, and do the young grayling grow to a sufficient size? Each function is needed if the artificial stream is to compensate for lost habitat and result in NNL of productive capacity. Reference streams provided standards and therefore enabled us to measure effectiveness.

The artificial stream met or approached our expectations for some of these functions. Although not quantified in this study, we observed that watershed connectivity was at least partially restored and this allowed adult grayling and lake trout to migrate throughout the drainage basin, i.e., the artificial stream restored landscape-scale habitat use (N.E. Jones, unpublished data). Because Barrenlands grayling, with their adfluvial life history, migrate among the chains of lakes and streams in the watershed, its fragmentation would mean the loss of habitat availability at this scale, which could have significant population-level consequences (Kentaro and Rose 1999). Although the growth of YOY salmonids in Barrenlands was not directly related to temperature (Railsback and Rose 1999). Although the growth of YOY salmonids in streams can be affected by temperature, particularly when it affects emergence times and thus the length of the growing season (Holtby 1988), emergence in the artificial stream was unaffected.

Growth of YOY Arctic grayling

Temperature

Water temperature influences the growth of fish both directly, through physiological processes, and indirectly by affecting rates of energy flow and nutrient dynamics. Water temperature in the artificial stream is, on average, 1 °C colder than that observed in natural streams. The cooler temperatures likely result from less direct sunlight reaching the artificial stream because of steep and high stream banks and because the streambed penetrates deep into permafrost. In contrast, natural Barrenland streams flow through wide shallow valleys and tend to spread laterally. Thus, even with the lower angle of incidence of sunlight characteristic of high latitudes, natural streams are almost always well lit throughout the long summer days of the Arctic.

Our bioenergetics simulations nevertheless suggest that summer water temperatures had little influence on the differences in growth. On average, only 11% of the difference in the mass of YOY grayling can be attributed to the cooler temperature of the artificial stream. Other factors, namely food availability and possibly physical habitat, are clearly more important than temperature. Similarly, summer growth of rainbow trout (Oncorhynchus mykiss) in the Sierra Nevadas was not directly related to temperature (Railsback and Rose 1999). Although the growth of YOY salmonids in streams can be affected by temperature, particularly when it affects emergence times and thus the length of the growing season (Holtby 1988), emergence in the artificial stream was unaffected.

Nutrients and energy resources

In contrast to the limited effect of temperature, our bioenergetic simulations indicated that differences in food consumption could explain about 80% of the difference in growth of YOY grayling between the artificial and natural streams, suggesting that food availability differed. The well-vegetated banks of natural streams contrast sharply to the waste rock used to line the channel and riparian zone of the artificial stream. Although concentrations of commonly limiting nutrients (phosphorus and nitrogen) in the artificial stream are similar to or greater than those measured in natural streams, the waste rock in the artificial stream supports little algal growth. The artificial stream is also lacking the large amounts of aquatic macrophytes found in natural streams. It seems likely that this paucity of sources of


<table>
<thead>
<tr>
<th></th>
<th>1998</th>
<th>1999</th>
<th>2000</th>
<th>2001</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artificial vs.</td>
<td>PV</td>
<td>PV</td>
<td>PV</td>
<td>PV</td>
</tr>
<tr>
<td>Temperature</td>
<td>13</td>
<td>19</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Food</td>
<td>81</td>
<td>69</td>
<td>81</td>
<td>93</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td></td>
<td>84</td>
<td>80</td>
</tr>
</tbody>
</table>

Note: Relative influence of temperature and food on young-of-the-year Arctic grayling growth as estimated from the simulations. Natural streams are Polar–Vulture (PV) and Pigeon (PG).

© 2003 NRC Canada
allogrowth and autochthonous organic matter is ultimately a major contributor to the reduced growth and production of YOY grayling in the artificial stream. Moreover, it is likely that the habitat needed by terrestrial and aquatic plants is not currently available and that successional processes are required for their persistence, even if they would be manually introduced. In addition, high flows in the spring and fall result in heavy scour and erosion, further hampering plant colonization and growth (Waters 1995).

In turn, the lack of terrestrial and aquatic plant growth leads to low amounts of particulate organic matter and woody debris. Unlike alluvial streams, where channel migration plays an important role in woody debris recruitment, stream channels in Barrenland streams are generally stable, permafrost-bound, and boulder-dominated colluvial systems, i.e., fluvial process are relatively ineffective at removing material deposited on the valley floor. Natural processes that recruit CPOM and woody debris in natural Barrenland streams include fluvial transport of floodplain organic matter, leaf fall, and Barrenland caribou (Rangifer tarandus) that when migrating across the streams trample the riparian shrubs and kick pieces into the stream (Jones et al. 2003a). However, the floodplain, and its crossing by caribou, in the artificial stream is extremely limited because of its deeply incised channel design.

The importance of plants and organic matter as food and substrate for stream invertebrates is well known (Egglishaw 1964; Reice 1980; Flory and Milner 1999). The density and biomass of benthic invertebrates were much reduced in the artificial stream, leading to low drift densities of macroinvertebrates. In addition, the head capsules of chironomids were often smaller in the artificial stream, suggesting food limitation at this trophic level. Successful colonization and growth of invertebrates will also depend on the development of suitable habitat; unassisted, this process will likely require many years before the benthic invertebrate community resembles that in natural streams (Milner et al. 2000). Also, heavy sediment pulses and bed scouring likely damage invertebrate assemblages and hamper invertebrate establishment and growth (Waters 1995; Shaw and Richardson 2001).

Young-of-the-year Arctic grayling in natural Barrenland streams selected aquatic insect larvae, particularly chironomids and simulids, as primary prey, whereas smaller microcrustacea, nematodes, and mites were strongly avoided (Jones et al. 2003b). Further, the sizes of chironomids and simulids in the stomachs of grayling were frequently larger than those available in the drift, indicating a strong size-based foraging strategy. These forage preferences, and the reduced numbers of large-sized prey available in the drift of the artificial stream, support the hypothesis that the forage base for grayling is limiting their growth in the artificial stream.

Annual variability in temperature and production

Invertebrate drift and benthic invertebrate density and biomass varied considerably among the four study years in relation to air and water temperature, rainfall, and discharge. Correspondingly, YOY grayling were larger in the warm, dry year (1998) when food (i.e., macroinvertebrates) was plentiful. Conversely, epilithon abundance was low, perhaps because of high invertebrate numbers. The opposite pattern was observed in the cool, wet year (1999). These relationships are consistent with those observed recently among discharge, water temperature, and growth of YOY grayling in Alaska (Deegan et al. 1999).

The importance of climate in relation to stream productivity and fish growth is evident from the strong relationship between growing degree-days and end-of-season fish mass in Polar–Vulture stream (Fig. 6). The strength of the relationship suggests that fish growth is affected more by climatic factors controlling annual productivity than by the direct effects of temperature on fish physiology. In the artificial stream, however, the relationship between grayling growth and climate is greatly muted. We suggest that food limitation, based ultimately on a paucity of organic matter and suitable habitat for invertebrates, masks the influence of climate in the artificial stream; i.e., the system is unable to respond to the more favourable conditions of a warm, dry year by producing larger YOY fish.

**Physical habitat**

Relative to the reference streams, habitat complexity at small and large scales was considerably reduced in the artificial stream. The artificial stream had only one fairly straight channel and was deficient in or lacked several mesohabitat types, comparable with many perturbed rivers that have lost channel structure, complex banks, and important snag habitat (Sedell and Froggatt 1984; Benke et al. 1985; Mitro and Zale 2002). At small scales, the artificial stream lacked large substrates, woody debris, and aquatic and terrestrial vegetation, which can create hydraulically complex flows, including flow refuges that provide habitat for YOY grayling.
invertebrates, and other aquatic life. Large substrates also provide a stable surface area and interstitial space for invertebrates relative to small substrates; as such, they frequently harbour greater numbers and biomass and a diversity of benthic invertebrates (e.g., McElhone and Davies 1983). The effects of fine sediment on invertebrate production can be dramatic and can cascade to higher trophic levels. For example, the introduction of sand into Hunt Creek, Michigan, resulted in stream aggradation, the replacement of pool and riffles series with continuous run habitat, a large reduction in food for brook trout (Salvelinus fontinalis), and a 50% reduction in their numbers (Alexander and Hansen 1986).

Complex habitats often support greater standing crops and production (e.g., Murphy et al. 1984; McMahon and Hartman 1989; Fauch and Northcote 1992) and enhance the growth and survival of stream-dwelling fishes (e.g., Quinn and Peterson 1996; Sundbaum and Näslund 1998). Observational studies indicate that salmonids seek optimal conditions of depth and velocity for foraging, within the constraints of competition (Fausch 1984) and predation (Lima and Dill 1990). Experimental evidence (Fausch (1993) and references therein) suggests that habitat structures provide three main features related to the tradeoffs between foraging and predation risk: (i) velocity refuge, (ii) visual isolation, and (iii) overhead cover. Structures that provide visual isolation from other fish reduce energetically costly agonistic behaviour (Sundbaum and Näslund 1998), and overhead cover such as riparian vegetation can reduce the degree of predator vigilance. Physical habitats that provide velocity refuge, such as boulders, allow fish to hold low-velocity positions adjacent to faster water currents and thus maximize their energy intake from drifting food items while minimizing the cost of swimming to maintain position (Fausch and White 1981; Fausch 1984; McLaughlin and Noakes 1998).

Interestingly, the size and composition of invertebrates in the diets of YOY grayling in the natural and artificial streams reveal little if any difference, despite poor growth in the artificial stream. This similarity of stomach contents contrasts with the differences in the invertebrate prey base and suggests that grayling in the artificial stream may have to expend more energy in obtaining their food requirements, ultimately resulting in a lower net gain in energy and poor growth. Our sensitivity analyses of the bioenergetics model indicated that a 50% increase in the activity multiplier resulted in a twofold reduction in body mass and suggests that increased swimming costs could contribute to the observed differences in growth between the artificial and natural streams. Still, the model was almost twice as sensitive to changes in food consumption ($P$ value).

Perspective

The compensation of habitat in the artificial stream has been neither a success nor a failure; instead, there has been a progression of successes necessary for compensation. In this hierarchical framework, the artificial stream allows grayling to migrate through and spawn in it and the eggs to hatch; however, as nursery habitat, it offers cooler temperatures, low invertebrate production, and physically simple habitat and as a result produces relatively small YOY, even though fish densities in the artificial stream are lower than those observed in natural streams. Temperature effects appear limited, and although habitat complexity may have an influence on the overall productivity, it is doubtful that grayling growth would achieve the levels observed in reference streams if complexity alone were increased in the artificial stream. Rather, we suggest that the scarcity of organic matter in the artificial stream is primarily limiting the overall growth and productivity of benthic invertebrates, ultimately leading to poor growth and production of YOY Arctic grayling. Importantly, DFO’s (1986, p. 28) definition of productive capacity explicitly acknowledges the importance of food and trophic interactions. This differs from many traditional stream habitat management plans in which managers typically focus on modification of the physical structure of streams via instream habitat structures, without much consideration of the flow of energy and nutrients. We strongly urge habitat managers to use all available knowledge to design compensation programs, not just a physical perspective. Some of the problems associated with the artificial stream most likely could have been predicted from an understanding of stream ecosystem ecology.

The growth of young fish can have significant implications at the population level and thus directly affect the productive capacity of an ecosystem (Holby 1988). Size-dependent mortality, stemming from overwinter starvation (Post and Evans 1989) and predation (Post et al. 1999), is frequently observed in cohorts of young fish (Miller et al. 1988; Post and Parkinson 2001). For young fish, the chances of an individual surviving a period of low food availability, such as the long arctic winter, is largely based on their energy reserves and the rate at which they are used metabolically. It is thus reasonable to suggest that age-0 grayling in the artificial stream, which have reached an end-of-summer mass approximately half that observed in natural streams, may experience reduced survival during their first winter. In turn, recruitment into the breeding population may be impaire.

As a result of our assessment of fish production and the productive capacity of the artificial stream, managers can begin to make defensible decisions and guide the subsequent work that will be required for compensation. The objectives of future studies will need to consider a number of important questions such as (i) what can be done to improve the growth of grayling while continuing to learn about the relative roles of food production, physical habitat, and temperature, (ii) at what point will grayling have reached an acceptable rate of growth, (iii) because the artificial stream is a completely new ecosystem and ecological succession in the Arctic is slow, how can we speed up the successional process, and (iv) how long should compensation take? These questions are challenging, but the characteristics of this ecosystem and the information that our studies have provided offer an unparalleled opportunity to advance the study of fish habitat compensation and stream restoration ecology.

Acknowledgments

This research was made possible through a grant and in-kind support from BHP Billiton Diamonds Inc. (BHPB). Additional financial support came from the Canadian Circumpolar Institute (Northern Science Training Program and
Circumpolar/Boreal Alberta Research), a Natural Sciences and Engineering Research Council of Canada (NSERC) industrial scholarship (with support from BHPB) to N.E.J.; an NSERC research grant to W.M.T., and support for C.K. from the Department of Fisheries and Oceans. The Alberta Research Council kindly provided some field equipment. Finally, we sincerely thank all of the hard-working field crew members.

References


Department of Fisheries and Oceans. 1986. The Department of Fisheries and Oceans policy for the management of fish habitat. Communications Directorate, Fisheries and Oceans Canada, Ottawa, Ont.


Quinn, T.P., and Peterson, P.N. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of indi-


