Responses of a beaded Arctic stream to short-term N and P fertilisation

JONATHAN P. BENSTEAD,* LINDA A. DEEGAN,* BRUCE J. PETERSON,*
ALEXANDER D. HURYN,[†] WILLIAM B. BOWDEN,[‡] KELLER SUBERKROPP,[†]
KAREN M. BUZBY,* ADRIAN C. GREEN* AND JAY A. VACCA[§]
The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA, U.S.A.
[†]*Department of Biological Sciences, University of Alabama, Tuscaloosa, AL, U.S.A.*
[‡]*School of Natural Resources, University of Vermont, Burlington, VT, U.S.A.*
[§]*Department of Range, Wildlife and Fisheries Management, Texas Tech University, Lubbock, TX, U.S.A.*

SUMMARY

1. Oligotrophic Arctic streams are likely to be sensitive to changes in hydrology and nutrient inputs predicted to occur as a consequence of future climate and land use change. To investigate the potential consequences of nutrient enrichment for low-order Arctic streams, we added ammonium-N and phosphorous to a second-order beaded, tundra stream on Alaska's north slope. We measured responses in nutrient chemistry, chlorophyll *a* standing crop, and in the breakdown and macroinvertebrate colonisation of leaf litter over a 38-day summer period.

2. During the addition, nutrient concentrations immediately downstream of the dripper averaged 6.4 μM ammonium-N and 0.45 μM soluble reactive P. Concentrations upstream of the dripper averaged 0.54 μM ammonium-N and 0.03 μM soluble reactive P. Uptake of both nutrients was rapid. Concentrations were reduced on average to 28% (ammonium-N) and 15% (inorganic P) of maximum values within 1500 m. Standing crops of chlorophyll *a* on standardised samplers were significantly higher by the end of the experiment. Breakdown rates of senescent willow (*Salix* sp.) and sedge (*Carex* sp.) litter and associated fungal biomass were also significantly increased by nutrient addition.

3. Fertilisation resulted in four- to sevenfold higher macroinvertebrate abundance and two- to fourfold higher macroinvertebrate biomass in litter bags, as well as an increase in late-summer body mass of larval *Nemoura* stoneflies.

4. Our results are consistent with those of similar studies of larger streams in the high-Arctic region. Based on our short-term experiment, increased inputs of nutrients into these ecosystems, whether caused by climate change or more local disturbance, are likely to have profound ecological consequences. Longer-term effects of enrichment, and their interaction with other components of future change in climate or land use, are more difficult to assess.

Keywords: Alaska, global climate change, high-latitude streams, leaf litter breakdown, nutrient enrichment

Correspondence: Jonathan P. Benstead, The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543, U.S.A.
E-mail: jbenstead@mbl.edu
Present address: Karen M. Buzby, Civil and Environmental Engineering, West Virginia University, Morgantown, WV 26506, U.S.A.

Introduction

Arctic ecosystems are vulnerable to projected global climate change (IPCC, 2001). The Arctic region will probably experience changes in climate that are more rapid and severe than any other area on Earth. Current general circulation models predict 4–7.5 °C

(summer) and 2.5–14 °C (winter) increases in mean Arctic land temperature by 2080 (IPCC, 2001). Corresponding projected increases in precipitation are 10–20 and 5–80% for summer and winter, respectively. While future climate scenarios are tentative and regional variability will be significant, the Arctic is almost certain to be warmer and wetter in the near future. Even small changes in temperature and precipitation regimes are expected to have significant repercussions for permafrost melting, patterns of run-off and associated nutrient inputs into Arctic streams and rivers (Oswood, Milner & Irons, 1992; Vincent & Hobbie, 2000). Increased temperatures will promote mineralisation of nutrients in the expanded active soil layer, as well as chemical weathering of parent rock material (Rouse *et al.*, 1997). Ultimately, these changes are expected to increase concentrations of nutrients in Arctic streams (Hobbie *et al.*, 1999).

Arctic stream ecosystems are also increasingly vulnerable to local anthropogenic impacts (Walker *et al.*, 1987; Oechel, 1989). Disturbance associated with mining, drilling, road building and construction alters local drainage patterns and promotes thermokarst erosion (i.e. melting of permafrost and subsequent slumping). Local changes in drainage and the melting of surface soil typically increase nutrient inputs into streams (Hobbie *et al.*, 1999). Road dust and fertilisation of roadsides (associated with grass seeding for stabilisation) also contribute toward local nutrient inputs into small tundra streams.

The combined effects of global climate change and localised disturbance are likely to cause nutrient enrichment of naturally oligotrophic Arctic streams. Effects of low-level nutrient enrichment on large (>2nd order), clear-water tundra streams are complex but relatively well understood (Peterson *et al.*, 1985, 1993; Harvey *et al.*, 1998; Slavik *et al.*, 2004). Food webs of these larger streams are based on autotrophic production, despite relatively large inputs of allochthonous carbon (in the form of peat and dissolved organic matter; Peterson *et al.*, 1985; Peterson, Hobbie & Corliss, 1986). The algal base of these large stream food webs is augmented by experimental fertilisation; these increases in primary production typically propagate through the food web (Peterson *et al.*, 1985; Slavik *et al.*, 2004).

In contrast, we know much less about other stream types, including the small streams (<3rd order) that are the tributaries of these larger, better understood rivers. Small streams may receive greater inputs of riparian litter relative to streambed area; relatively high storage is made more likely by higher retention in deep pools and runs choked with willow stems. In addition, models of plant community response to climatic warming predict increases in shrubby vegetation (e.g. Epstein *et al.*, 2000) and such changes have already been documented on the north slope of Alaska, where valley floors appear to be particularly affected (Sturm, Racine & Tape, 2001). Shifts from tussock tundra vegetation towards dominance by shrubs (e.g. dwarf birch *Betula nana* L., willow *Salix* spp. and alder *Alnus* spp.) in riparian areas would have important effects on Arctic small stream ecosystems, including increased shading and inputs of leaf litter. Decomposition of increased terrestrial organic matter inputs is likely to interact with increased nutrient concentrations; however, the paucity of data describing heterotrophic food webs at high latitudes makes prediction of these responses difficult.

In this study, we conducted a short-term, low-concentration N and P enrichment of a 2-km reach of Hershey Creek, a small beaded tundra stream on the north slope of Alaska, U.S.A. that receives relatively large amounts of terrestrial organic matter. We studied the responses of nutrient chemistry, primary producers and breakdown and macroinvertebrate colonisation of leaf litter to the nutrient addition over a single Arctic summer. We use our results to examine, (i) the role of nutrients in controlling trophic structure and function in this small Arctic tundra stream and, (ii) the likely responses of small tundra streams to the low-level increases in nutrient inputs predicted to occur in the future through both local and global processes.

Methods

Study site

Hershey Creek is a second-order beaded tundra stream that flows into the Kuparuk River, a clearwater tundra river that drains the Arctic foothills and coastal plain regions of Alaska's north slope. Tundra streams differ from other high-latitude stream types (e.g. mountain and spring streams; Craig & McCart, 1975) in having lower alkalinity, pH and conductivity, a higher and more variable temperature and moderate invertebrate abundance and diversity (Craig & McCart, 1975; see Table 1). Beaded streams are a

common type of tundra stream that have a distinctive geomorphology: large (1–35 m^2), roughly circular and deep (up to 2 m) pools are connected by shallow, narrow and steep-sided channels, giving the appearance of a string of beads from above (Oswood, Everett & Schell, 1989; Oswood, Irons & Schell, 1996). Beaded streams are formed through thermal erosion associated with buried ice wedges (Hopkins *et al.*, 1955). Channel substrata are typically soft-bottomed, peaty deposits. Estimated storage of coarse particulate organic matter (CPOM) in Hershey Creek in 2001 was 151 g DM m^{-2} in pools and 58–103 g DM m^{-2} in runs (particles >1 mm; B.J. Peterson, unpubl. data), suggesting that CPOM storage is higher in Hershey Creek than in larger streams such as the Kuparuk River (approximately 35 g AFDM m^{-2} of particles >335 μm and <100 mm; Peterson *et al.*, 1986; Harvey *et al.*, 1997).

The 2-km experimental reach of Hershey Creek is crossed at its upstream and downstream limits by the trans-Alaska oil pipeline and forded at both points by the pipeline's gravel access road (Fig. 1). Catchment vegetation consists of tussock tundra dominated by *Eriophorum vaginatum* L., *B. nana*, *Vaccinium* spp., *Salix* spp. and *Sphagnum* spp. The most common riparian plants in this relatively low-gradient reach are *Salix* spp. and *Carex* spp.; shading of the channel by the dwarfed vegetation is limited to constricted (<0.5 m width) sections of the stream. With the possible exception of Hershey Creek's deepest pools (>1.5 m in depth), its channel is frozen solid from October to May.

Nutrient addition

We began fertilising Hershey Creek with N and P (as NH$_4$Cl and NaH$_2$PO$_4$) on 8 July 2002 at the 625-m point (i.e. 625 m downstream of the upper road crossing; see Fig. 1), using a peristaltic pump. Target concentrations were 5.2 μM N and 0.32 μM P at a nominal discharge of 50 L s^{-1}. For logistical reasons, from 31 July 2002 we added P as KH$_2$PO$_4$. The reach above the dripper served as a reference section. Fertilisation was stopped on 14 August 2002.

Physicochemical parameters

Water temperature and stage height were recorded every 10 min by a Campbell CR-10X data logger located 300 m below the dripper. Discharge was calculated from stage height data using a calibration curve ($R^2 = 0.94$) derived from five manual discharge measurements taken during the experiment. We measured pH, conductivity and nutrient concentrations weekly at three sites in the reference reach and six sites in the fertilised reach. Water samples were filtered in the field (pre-combusted 0.5 μm-pore glass-fibre filters), kept cool and analysed for NH$_4$-N and soluble reactive phosphorous within hours. Frozen samples were subsequently transported to the Marine Biological Laboratory and analysed for NO$_3$-N within 3 months.

Benthic chlorophyll a

We measured responses of benthic chlorophyll *a* standing crop to fertilisation in two ways. First, on three dates (6 July, 17 July and 31 July 2002) we took four core samples (area 5.4 or 11 cm^2, depth approximately 5 cm) in each of four pools in each reach. Cored pools in the reference reach were between 35 m and 345 m upstream of the dripper. Cored pools in the fertilised reach were between 95 m and 175 m downstream of the dripper. Second, we placed artificial substrata (constructed from frayed sisal rope; Finlay & Bowden, 1994) in runs between pools, which were collected on two dates (17 and 31 July 2002; *n* = 10 in each reach on each date). Rope substrata were placed between 25 m and 365 m upstream of the

Table 1 Physicochemical data for Hershey Creek during summers of 1999, 2001 and 2002

Variable	1999	2001	2002
Discharge (L s^{-1})	32.2 (3.4–88.6)	–	12.0 (3.5–112.4)
Temperature (°C)	8.8 (4.1–15.0)	7.1 (3.7–12.9)	8.2 (0.1–15.2)
pH	7.0 (6.4–8.2)	7.1 (6.6–7.3)	7.0 (6.7–7.5)
Conductivity (μS cm^{-1})	65.9 (27.2–92.3)	45.7 (23.0–76.0)	50.7 (20.1–116.6)
Alkalinity (meq L^{-1})	0.53 (0.51–0.54)	0.37 (0.28–0.49)	0.35 (0.15–0.66)
DOC (μM)	416 (344–520)	–	423 (328–529)

Data are means with ranges in parentheses. –, indicates no data. DOC, dissolved organic carbon.
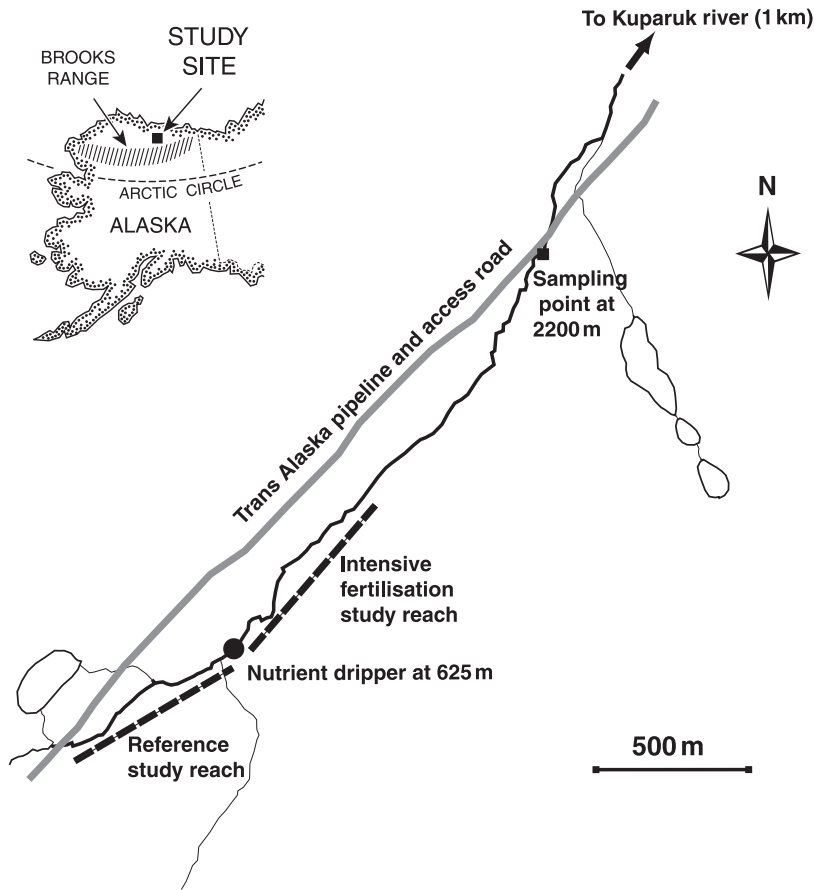
Fig. 1 Map of Hershey Creek experimental reach. Inset shows location of study site on Alaska's north slope.

dripper and between 35 m and 290 m downstream of the dripper. Core samples were homogenised, subsampled and filtered onto glass-fibre filters. Chlorophyll *a* was extracted in buffered 90% acetone in the dark at 4 °C for 48 h and measured fluorometrically (Strickland & Parsons, 1960). Rope substrata were sonicated for 10 min and rinsed. Chlorophyll *a* in resulting slurries was measured as above. Chlorophyll *a* data were analysed using separate *t*-tests for each collection date.

Litter breakdown and macroinvertebrates

We measured responses of decomposition processes to fertilisation by measuring breakdown rates and fungal and macroinvertebrate colonisation of senescent litter of the two most common species of riparian plant at the site. Weighed, air-dried litter of *Carex* (sedge; approximately 4 g) and *Salix* sp. (willow; approximately 5 g) in nylon mesh bags (mesh size 8×3 mm; $n = 50$ for each litter species in each reach) were placed in ten successive runs in each reach (five bags of each litter species per run) on 4 July 2002. Litter bags were collected (one of each litter species from each run; $n = 10$ of each species in each reach on each date, except reference reach *Carex* on day 30 where $n = 9$) every 7–9 day. Once transported to the laboratory, contents of litter bags were placed into a container of water and whole leaves and identifiable litter fragments were removed by hand. The water and remaining material were then passed through a 250-µm sieve. Material retained on the sieve was preserved in 4% formaldehyde. Remaining litter fragments were dried (72 h at 55 °C) and weighed. Subsamples of litter were subsequently ashed at 500 °C for ≥1 h to obtain estimates of ash-free dry mass (AFDM) loss over time. Breakdown rates (*k* coefficients) were calculated using linear regression of ln-transformed per cent mass loss data for each species at each collection site (i.e. 10 *k* coefficients for each species in each reach) and analysed by two-way analysis of variance, with nutrient treatment and leaf litter species as factors.

Invertebrates were identified to the lowest practical taxonomic level and their body lengths were measured. Biomass was estimated using family-level length-mass relationships (Benke *et al.*, 1999). Invertebrate assemblage structure and individual biomass were analysed only for 3 August 2002 (day 30). We chose this date because we anticipated that differences in assemblage structure and growth rates would be greatest toward the end of the fertilisation treatment, which coincided with the end of the summer growing season. Only 19 *Carex* litter bags were recovered on this date ($n = 9$ upstream of the dripper, $n = 10$ downstream). To balance the design, we did not include the first litter bag downstream of the dripper (i.e. $n = 9$ in both reaches). We tested the prediction that fertilisation would result in increases in invertebrate abundance and total and individual biomass within each litter type using one-tailed *t*-tests. Larvae of the stonefly *Nemoura* and the crane fly *Tipula* are the primary shredders in Hershey Creek. Therefore, we also tested the more specific prediction that their abundance and total and individual biomass would be greater in the fertilised reach. Litter bags were considered replicates. In addition to testing differences in invertebrate assemblage attributes within litter types, we assessed differences between litter types using two-way ANOVA. Biomass and abundance values were $\ln(x + 1)$ transformed prior to analysis to enhance homogeneity of variance.

Ergosterol extraction and determination

Litter bags were subsampled ($n = 3$ matched pairs of leaf discs of each species in each reach) for ergosterol analysis using a cork borer. One of each pair of leaf discs was preserved in methanol in the dark at 4 °C. The other was dried for 72 h at 50 °C, weighed, ashed and reweighed for estimation of ash-free dry mass. Ergosterol was extracted following the method of Newell, Arsuffi & Fallon (1988) as modified by Suberkropp & Weyers (1996). Leaf discs were refluxed in alcoholic KOH (30 mL) at 80 °C for 30 min. After 10 mL of water was added, ergosterol was partitioned into pentane (3x) and evaporated to dryness under a stream of nitrogen gas. The residue was dissolved in methanol and filtered (0.45 μm Acrodisc). Ergosterol was separated with a Whatman partisphere C-18 column in a high performance liquid chromatograph (Shimadzu) using methanol as the mobile phase

(1 mL min^{-1}) and detected by measuring absorbance at 282 nm. Ergosterol data were analysed using repeated measures ANOVA with treatment (fertilisation) and leaf species as factors. Two dates (third collection, 27 July, and fourth collection, 3 August) had to be excluded from this analysis because of missing replicates. To convert ergosterol concentrations to fungal biomass, an ergosterol concentration of 5.5 μg mg^{-1} of mycelial dry mass was assumed (Gessner & Chauvet, 1993).

Results

Physicochemical parameters

Discharge decreased throughout much of the experiment, from approximately 35 to <4 L s^{-1} by 31 July 2002; subsequent increases in discharge were mostly associated with late-summer snowfall at the end of the study period (Fig. 2). Water temperature was highly variable during the experiment, ranging from 0.1 to 15.2 °C (mean 8.2 °C) and diel changes in water temperature of 2–4 °C were typical (Fig. 2).

Mean NO$_3$-N concentration was relatively high at the upstream end of the experimental reach (>10 μM) and decreased consistently with distance downstream (Fig. 3a). Mean concentration of NH$_4$-N also appeared to be slightly raised at the start of the reference reach (Fig. 3b), decreased over the next 600 m, and increased to >4 μM immediately downstream of the dripper. Mean concentration dropped to 2.9 μM at the 1000-m station. Mean concentration of soluble reactive phosphorus increased to a maximum of 0.31 μM downstream of the dripper and decreased rapidly thereafter (Fig. 3c). High nutrient concentrations were still detectable at the 2200-m station (1575 m below the dripper).

Our target concentrations for the experimental enrichment (5.2 μM N and 0.32 μM P) were slightly exceeded during the course of the experiment (6.4 μM N and 0.45 μM P) because of low discharge. Battery failure caused a 4-day stoppage in fertilisation (4–8 August). This stoppage dramatically lowered nutrient concentrations on 7 August (closed triangles in Fig. 3).

Benthic chlorophyll a

Mean standing crop of chlorophyll *a* in cores remained relatively constant in the reference reach
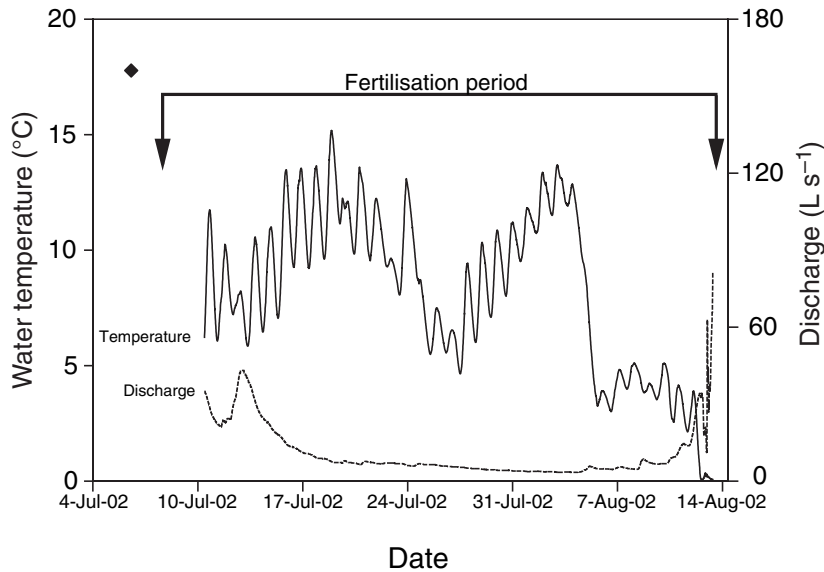
Fig. 2 Water temperature and discharge during fertilisation of Hershey Creek, summer 2002. The data logger was not functioning prior to 11 July 2002; the solid diamond represents a single discharge measurement on 6 July 2002.

(approximately 10 µg cm^{-2}), while that in the fertilised reach increased to approximately 25 µg cm^{-2} (Fig. 4a). However, differences between reference and fertilised reached were not significant on any date (*t*-tests, $P > 0.05$). Differences in chlorophyll *a* standing crop between rope samplers in the two reaches were more dramatic and statistically significant (*t*-tests, $P = 0.0004$ on 17 July and $P = 0.0002$ on 31 July, Fig. 4b). Mean standing crop per sampler remained below 1 mg in the reference reach, but increased to almost 3 mg by day 22 in the fertilised reach (Fig. 4b).

Litter breakdown and macroinvertebrates

Breakdown rates. Breakdown of *Carex* and *Salix* litter was significantly faster in the fertilised reach than the reference reach (ANOVA, $P < 0.0001$; Fig. 5). There was also a significant difference in breakdown rate between the two litter species (ANOVA, $P < 0.001$); the difference in breakdown rate between leaf species was unaffected by nutrient fertilisation (ANOVA, $P = 0.08$), although there was a trend towards faster relative breakdown in *Salix* (Fig. 5).

Fungal biomass. Initial ergosterol content of *Carex* leaves was more than twice that of *Salix* leaves, suggesting that *Carex* leaves were initially more heavily colonised by fungi in the terrestrial environment than *Salix* (Fig. 6). Ergosterol associated with *Carex* leaves in the control reach declined after approximately 3 weeks in the stream. Ergosterol

concentrations associated with *Salix* leaves in the control reach remained relatively constant throughout the study (Fig. 6). There was a statistically significant effect of leaf species on ergosterol concentration (repeated measures ANOVA, $P = 0.0003$). In the nutrient enriched reach, ergosterol concentrations associated with both types of leaves increased significantly (repeated measures ANOVA, $P = 0.04$) over the values observed in the control reach (Fig. 6). There was no interaction between leaf species and treatment ($P = 0.08$). Maximum values of fungal biomass in the nutrient-enriched reach reached 10.1% of *Carex* leaves and 7.4% of *Salix* leaves after 3 weeks in the stream. Thereafter, ergosterol concentrations levelled off or declined. In the control reach, fungal biomass maxima reached 7.2% of *Carex* and 2.9% of *Salix* leaves.

Macroinvertebrates. Total macroinvertebrate abundance in *Carex* litter bags was higher in the fertilised than in the reference reach [Fig. 7a; 1450 ± 780 versus 197 ± 42 individuals bag^{-1}; $P = 0.004$, one-tailed *t*-test, ln($x + 1$) transformation]. Total macroinvertebrate abundance in *Salix* litter bags also was higher in the fertilised reach (Fig. 7a; 786 ± 234 versus 203 ± 34 individuals bag^{-1}; $P = 0.018$). Compared with total macroinvertebrate abundance, the abundance of *Nemoura* in *Carex* litter bags did not differ between reaches (34 ± 6 and 29 ± 4 individuals bag^{-1} in the fertilised and reference reach, respectively; $P = 0.298$), nor did its abundance in *Salix* litter bags differ between reaches (25 ± 7 versus 30 ± 7 individu-
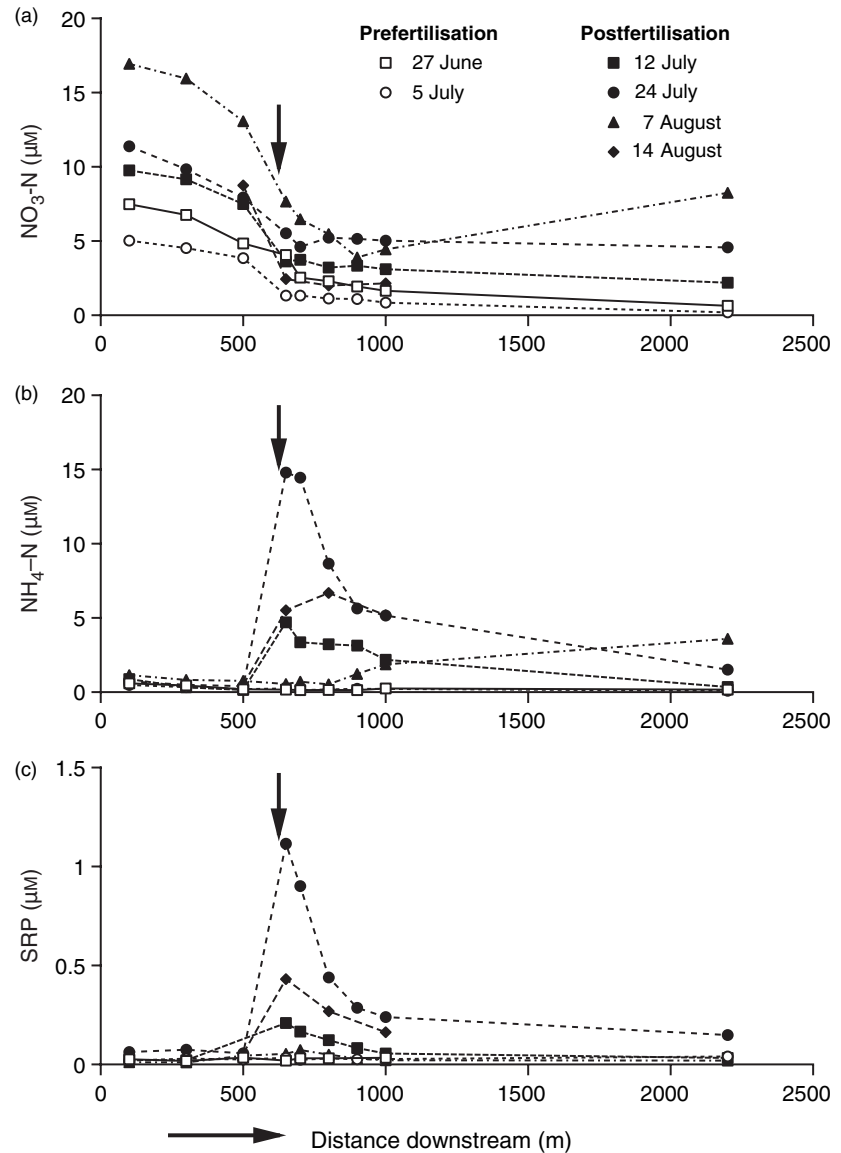
Fig. 3 Mean molar concentrations of (a) NO_3-N, (b) NH_4-N, and (c) soluble reactive phosphorous along the experimental reach of Hershey Creek before and after fertilisation, summer 2002. The arrows indicate the location of the nutrient dripper. The upper road crossing is at 0 m.

als bag^{-1}; $P = 0.185$). As shown for *Nemoura*, the abundance of *Tipula* in *Carex* litter bags did not differ between reaches (approximately 0.5 individual bag^{-1} in both reaches; $P = 0.443$). Patterns of *Tipula* abundance in *Salix* litter bags could not be analysed because only three larvae were collected. Larvae of the Chironomidae, which were responsible for higher total macroinvertebrate abundance in the fertilised reach, contributed 84–89% of individuals in the fertilised reach and 70–77% of individuals in the reference reach regardless of litter type.

Total macroinvertebrate biomass in *Carex* litter bags was higher in the fertilised than the reference reach [Fig. 7b; 39.8 ± 7.6 versus 12.3 ± 2.0 mg DM bag^{-1};

$P = 0.0002$, one-tailed *t*-test, $\ln(x + 1)$ transformation]. *Tipula* contributed little to total biomass in *Carex* litter bags (<0.1 mg DM bag^{-1}) and showed no response to fertilisation ($P = 0.222$). *Tipula* was excluded from analyses of biomass in *Salix* litter bags because the three specimens collected were relatively large (11.5–73.8 mg DM individual^{-1}) and thus had a disproportionate effect on patterns of biomass between reaches. Macroinvertebrate biomass, excluding *Tipula*, was higher in *Salix* litter bags in the fertilised reach (Fig. 7b, 32.0 ± 5.4 versus 15.0 ± 2.9 mg DM bag^{-1}; $P = 0.010$). *Nemoura* contributed ≥27% to total macroinvertebrate biomass in bags of both litter types in both reaches, but a treatment effect was detected only
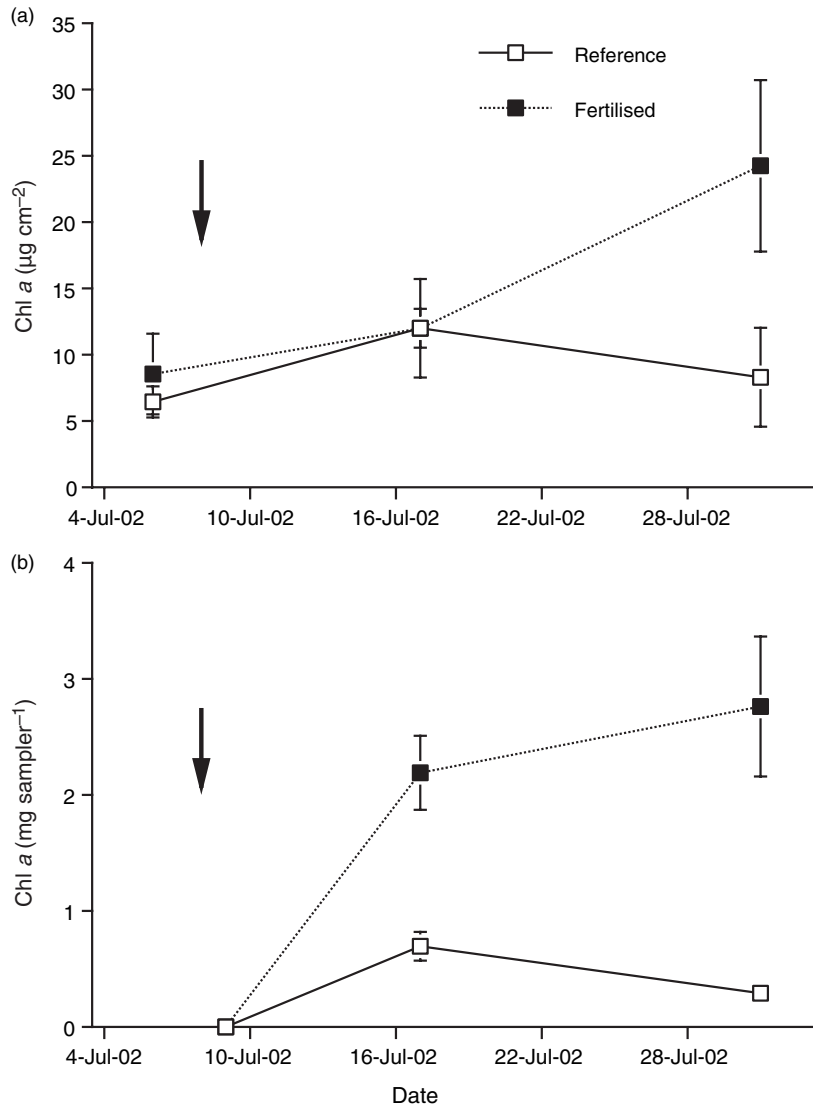
Fig. 4 Mean standing crop (±1 SE) of chlorophyll *a* from (a) core samples from pools and (b) rope substrata in runs of the reference and fertilised reach of Hershey Creek, summer 2002. The arrows indicate the start of fertilisation.

for *Carex* litter bags where litter bags in the fertilised reach had higher biomass than those in the reference reach (11.7 ± 2.3 versus 6.0 ± 1.1 mg DM bag^{-1}; $P = 0.018$).

Individual macroinvertebrate mass for both *Carex* litter bags (fertilised = 0.063 ± 0.013 and reference = 0.074 ± 0.011 mg DM individual^{-1} bag^{-1}) and *Salix* litter bags (*Tipula* excluded) did not differ between reaches (fertilised = 0.064 ± 0.011 and reference = 0.083 ± 0.013 mg DM individual^{-1} bag^{-1}; $P > 0.25$, one-tailed *t*-test). The individual mass of *Nemoura* from *Carex* litter bags, however, was significantly higher in the fertilised reach (Fig. 7c; 0.33 ± 0.02 mg DM individual^{-1} bag^{-1}) than in the reference reach (0.21 ± 0.02 mg DM individual^{-1} bag^{-1}; $P = 0.0002$,

one-tailed *t*-test), as was the individual mass of *Nemoura* from *Salix* litter bags (Fig. 7c; fertilised = 0.32 ± 0.02 and reference = 0.24 ± 0.01 mg DM individual^{-1} bag^{-1}; $P = 0.005$). The individual mass of *Tipula* in *Carex* litter bags was also higher in the fertilised reach (0.09 ± 0.06 versus 0.02 ± 0.01 mg DM individual^{-1} bag^{-1}) but this difference was not significant ($P = 0.117$).

The macroinvertebrate response to the two litter types was essentially identical (Fig. 7). Regardless of treatment (reference versus fertilised), no significant differences were found between *Carex* and *Salix* litter bags for mean total macroinvertebrate abundance and biomass (excluding *Tipula*), *Nemoura* abundance and biomass, total macroinvertebrate individual-mass or
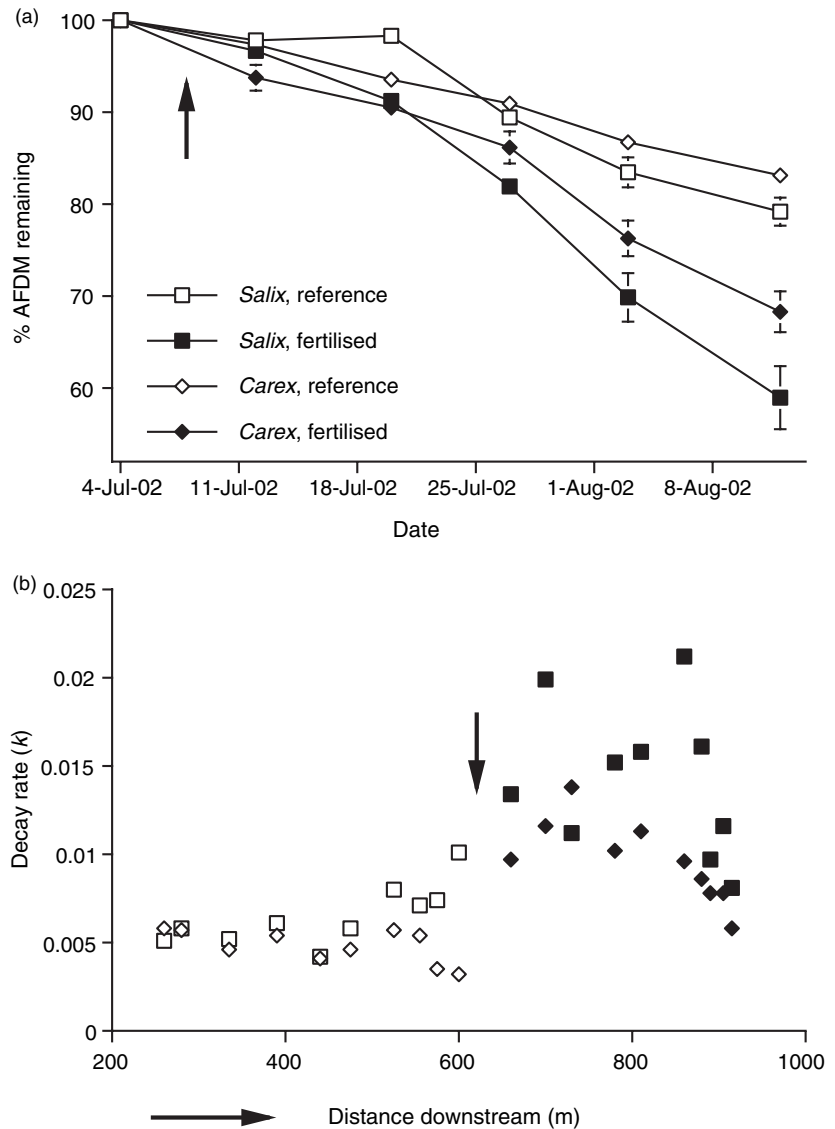
Fig. 5 (a) Mean mass loss (±1 SE) over time and (b) decay coefficients for *Carex* and *Salix* litter along the reference and fertilised reach of Hershey Creek, summer 2002. Some standard errors in (a) were too small to report. The arrows indicate (a) the start of fertilisation or (b) location of the nutrient dripper.

Nemoura individual mass (two-way ANOVA, $P > 0.21$). Nor was there significant interaction (two-way ANOVA, $P > 0.18$).

Discussion

Our short-term, low-concentration N and P enrichment of a small Arctic tundra stream resulted in rapid responses at all trophic levels measured. As predicted by theory and results from other experiments (e.g. Brett & Goldman, 1997), the response by primary producers was most dramatic, with a greater amount of algal cover in the treatment reach being visually apparent by the end of the study. This visual difference was supported by a significantly higher concentration of chlorophyll *a* biomass on artificial substrata in the fertilised reach. Similar to the primary producers, nutrient enrichment resulted in a significant increase in fungal biomass (as indicated by ergosterol concentration) associated with *Salix* and *Carex* leaf litter in the fertilised reach compared with the reference reach. The increase in fungal biomass was associated with a significant increase in litter breakdown rates and, presumably, an increase in detrital food quality.

Breakdown rates of *Salix* and *Carex* litter in the reference reach of Hershey Creek were very similar to those measured in the Kuparuk River under ambient
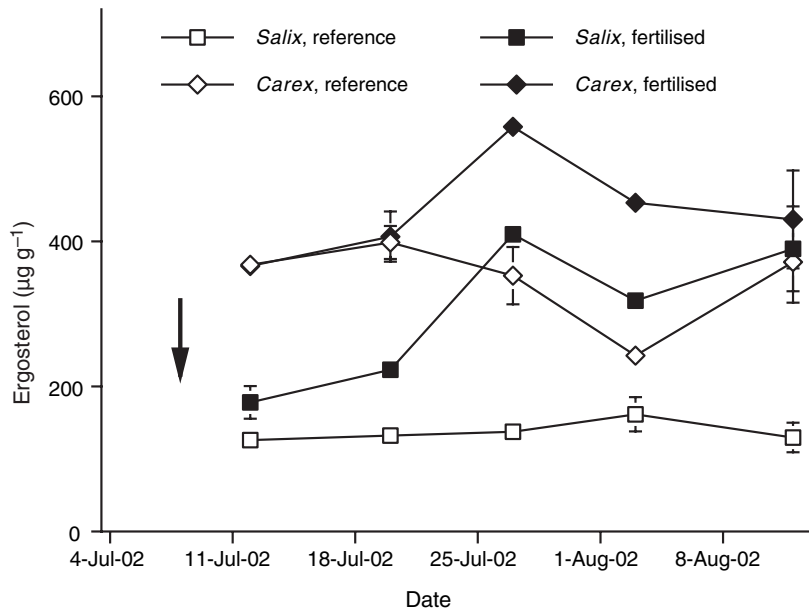
Fig. 6 Mean ergosterol concentrations (±1 SE) associated with *Carex* and *Salix* leaf litter incubated in Hershey Creek, summer 2002. The arrow indicates the start of fertilisation.

nutrient conditions (0.004–0.006 day^{-1}, 0.3-mm mesh; Peterson *et al.*, 1986). Fertilisation of Hershey Creek significantly increased the breakdown rate of both species of riparian litter. In the only comparable study in the Kuparuk River, fertilisation only with phosphorous had no effect on breakdown rate of fresh green *Carex* litter (1-mm mesh; Peterson *et al.*, 1993). However, fertilisation with both nitrogen and phosphorous increased breakdown rate significantly to a value (0.017 day^{-1}) comparable with that we measured in Hershey Creek's fertilised reach (Peterson *et al.*, 1993).

The stimulation of fungal growth associated with increased concentrations of nutrients in the water has been observed previously in temperate streams (Grattan & Suberkropp, 2001; Gulis & Suberkropp, 2003; Stelzer, Heffernan & Likens, 2003). Patterns associated with *Carex* leaves in our study were complex as these leaves contained considerable fungal biomass before they entered the stream. High fungal biomass has been measured in senescent, standing plants in other *Carex* species (Newell *et al.*, 1995). Ergosterol concentration declined in the control reach after *Carex* leaves were introduced into the stream, suggesting that terrestrial fungi were dying. A similar pattern has been observed for tulip poplar (*Liriodendron tulipifera* L.) leaves and assumed to be because of terrestrial fungal colonisation of the leaves prior to entry into streams (Paul & Meyer, 1996). Ergosterol

concentrations in the fertilised reach of Hershey Creek were similar to concentrations that have been observed on leaves decomposing in temperate streams (Gessner & Chauvet, 1994; Suberkropp, 2001). In the control reaches of Hershey Creek, however, particularly on willow leaves, ergosterol concentration was consistently lower than that typical of leaves decomposing in temperate streams.

Macroinvertebrate abundance increased four- to seven-fold, total biomass increased two- to fourfold, and mean body mass of *Nemoura* increased 57% in response to the stimulation of autotrophic and heterotrophic microbial biomass because of fertilisation. The short duration of the experiment coupled with the long life cycles of the macroinvertebrates inhabiting Hershey Creek precluded a numerical response because of enhanced fecundity of recolonising adults. Consequently, the increase in macroinvertebrate abundance, due primarily to an increase in abundance of larval Chironomidae, is attributed to retention of drifting colonisers originating upstream of the fertilised reach, reduced mortality in the fertilised reach, or both. Enhanced food resources in the form of periphyton and microbial production associated with detritus in the fertilised reach may have played a role in either case. A similar response was observed for baetid mayfly larvae following the experimental fertilisation of the nearby Kuparuk River (Hinterleitner-Anderson, Hershey & Schuldt, 1992) as well as for

Fig. 7 (a) Mean number of macroinvertebrates per litter-bag, (b) mean total biomass (mg DM) macroinvertebrates per litter-bag (minus *Tipula* in *Salix* bags) and (c) mean weight (mg DM) of *Nemoura* individuals (estimated on a per litter bag basis) on 3 August 2002 (day 30 of incubation). Open bars refer to reference litter bags, solid bars refer to fertilised litter bags. Error bars are ±1 SE. Note log scales.

chironomids in a neotropical stream (e.g. Costa Rica; Rosemond *et al.*, 2001).

Nemoura is the most abundant shredder in tundra streams of Alaska's north slope, and the enhancement of detritus food-quality as a consequence of fertilisation was specifically predicted to result in an increase in its abundance and biomass. Unlike the Chironomidae, however, fertilisation had no effect on its abundance, which is explained by the lack of an intergenerational response (*Nemoura* has a 2-year life cycle in Hershey Creek) coupled with an apparently low rate of movement between stream reaches. Differences in apparent movement patterns between taxa may be related to differences in the availability of primary production and detritus. For example, populations of macroinvertebrates feeding on periphyton in Arctic streams may be more prone to food limitation and thus emigration (e.g. Baetidae; Hinterleitner-Anderson *et al.*, 1992) than are shredders.

Larvae of the Nemouridae have been documented to be shredders in north slope streams by gut-content analysis (S.M. Parker, University of Alabama, unpubl. data). However, nemourids are also known to consume biofilms (Ledger & Hildrew, 2000, 2001). Consequently, it is by no means clear if the observed increase in growth rate by *Nemoura* in the fertilised reach of Hershey Creek can be attributed to an increase in detritus quality, to an increase in algae-dominated biofilms associated with the detritus, or both. Nevertheless, fertilisation had a strong effect on the growth rates of this important Arctic shredder. This response is similar to that reported for *Tallaperla* (Plecoptera: Peltoperlidae), a stonefly shredder that reached larger individual masses in a North Carolina stream with high concentrations of nitrate-N compared with a population in a more nutrient-poor stream (O'Hop, Wallace & Haefner, 1984). Given the positive relationship between fecundity and body size that has been shown for many insects (Vannote & Sweeney, 1980), fertilisation over successive summers could have a large effect on population dynamics of this species.

We attempted to include the growth response of juvenile Arctic grayling (*Thymallus arcticus* Pallas) to nutrient addition in our experiment, but low recapture rates in the reference reach made statistical analysis problematic. However, the three grayling recaptured from the fertilised reach had the highest mean growth rate recorded over three summers of

data collection from Hershey Creek ($n = 14$ grayling). High growth rates are consistent with those from previous stream fertilisation studies on Alaska's north slope and elsewhere (Johnston *et al.*, 1990; Deegan & Peterson, 1992; Golden & Deegan, 1998; Harvey *et al.*, 1998; Deegan *et al.*, 1999). In these experiments, faster growth of fish under fertilised conditions has been posited as a response to release from food limitation. This is logical given the increases in potential prey species observed in these studies, assuming that fish populations are food-limited under ambient nutrient conditions. Fertilisation of Hershey Creek resulted in higher macroinvertebrate abundance and biomass, as well as higher mean body size of some prey species (e.g. larval *Nemoura*). Regardless of the potential mechanisms, faster growth rates of grayling in Hershey Creek's fertilised reach would suggest that the effects of nutrient enrichment were transmitted to the top of the stream's food web during the course of a single Arctic summer.

As a consequence of a point source of nutrient input above the reference reach of Hershey Creek, we were able to assess the potential for N and P limitation of stream ecological processes. Water chemistry data indicated that the reference reach had a relatively high concentration of nitrate-N. Presumably the source of this nitrate-N was the road crossing upstream of the reference reach, as nitrate concentration declined rapidly downstream from this location. There was no evidence for inputs of inorganic P from the road crossing. Chlorophyll *a* biomass, ergosterol concentration and litter breakdown rate showed no response to road-associated nitrate-N in the reference reach, suggesting that primary producers and decomposers are primarily P-limited in this small Arctic stream. This result is in agreement with other studies of nutrient limitation on nearby but higher-order streams (Peterson, Hobbie & Corliss, 1983).

In summary, we observed rapid responses to relatively low-level nitrogen and phosphorous enrichment in both autotrophic and heterotrophic components of the food web of a small, beaded Arctic stream. Every trophic level that we measured was affected by the enrichment. Our results are consistent with those of similar studies on larger high-Arctic streams. In combination, fertilisation experiments indicate that Arctic tundra streams are extremely sensitive to the increased inputs of nutrients – particularly phosphorous – that are predicted to result from local disturbance and Arctic climate change. However, we caution that our study is based on data from a single summer. Research to date illustrates the difficulty in forecasting long-term consequences of fertilisation on the basis of short-term studies. For example, the Kuparuk River's fertilised reach underwent a dramatic and unforeseen state change after 8 years of enrichment when an aquatic bryophyte replaced epilithic algae as the dominant primary producer (Bowden, Finlay & Maloney, 1994; Slavik *et al.*, 2004). Long-term responses of small peat-bottomed streams to increased nutrient concentration may diverge from the pattern of succession seen in the Kuparuk River.

Understanding of clear-water tundra streams, such as Hershey Creek and the Kuparuk River, has increased greatly in recent decades. However, the Arctic region supports a remarkable diversity of stream types (i.e. mountain, spring and glacier streams), which are known to differ greatly in community structure and controls on productivity (Craig & McCart, 1975; A.D. Huryn, University of Alabama, unpubl. data). Consequently, extrapolation of our short-term results to other (non-tundra) Arctic stream types should be approached with caution. Finally, many stream ecosystem responses to increased nutrient inputs are likely to interact with other components of climate change (e.g. temperature and precipitation). Such interactions will be difficult to predict and represent a challenge for future research.

Acknowledgments

References

Benke A.C., Huryn A.D., Smock L.A. & Wallace J.B. (1999) Length-mass relationships for freshwater macroinvertebrates in North America with particular

reference to the southeastern United States. *Journal of the North American Benthological Society*, **18**, 308–343.

Bowden W.B., Finlay J.C & Maloney P.E. (1994) Long-term effects of PO_4 fertilization on the distribution of bryophytes in an Arctic stream. *Freshwater Biology*, **32**, 445–454.

Brett M.T. & Goldman C.T. (1997) Consumer versus resource control in freshwater pelagic food webs. *Science*, **275**, 384–386.

Craig P.C. & McCart P.J. (1975) Classification of stream types in Beaufort Sea drainages between Prudhoe Bay, Alaska, and the Mackenzie Delta, N.W.T, Canada. *Arctic and Alpine Research*, **7**, 183–198.

Deegan L.A. & Peterson B.J. (1992) Whole-river fertilization stimulates fish production in an Arctic tundra river. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 1890–1901.

Deegan L.A., Golden H.E., Harvey C.J. & Peterson B.J. (1999) Influence of environmental variability on the growth of age-0 and adult Arctic grayling. *Transactions of the American Fisheries Society*, **128**, 1163–1175.

Epstein H.E., Walker M.D., Chapin III F.S. & Starfield A.M. (2000) A transient, nutrient-based model of Arctic plant community response to climatic warming. *Ecological Applications*, **10**, 824–841.

Finlay J.C. & Bowden W.B. (1994) Controls on production of bryophytes in an Arctic tundra stream. *Freshwater Biology*, **32**, 455–465.

Gessner M.O. & Chauvet E. (1993) Ergosterol-to-biomass conversion factors for aquatic hyphomycetes. *Applied and Environmental Microbiology*, **59**, 502–507.

Gessner M.O. & Chauvet E. (1994) Importance of stream microfungi in controlling breakdown rates of leaf litter. *Ecology*, **75**, 1807–1817.

Golden H.E. & Deegan L.A. (1998) The trophic interactions of young Arctic grayling (*Thymallus arcticus*) in an Arctic tundra stream. *Freshwater Biology*, **39**, 637–648.

Grattan R.M. & Suberkropp K. (2001) Effects of nutrient enrichment on yellow poplar leaf decomposition and fungal activity in streams. *Journal of the North American Benthological Society*, **20**, 33–43.

Gulis V. & Suberkropp K. (2003) Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. *Freshwater Biology*, **48**, 123–134.

Harvey C.J., Peterson B.J., Bowden W.B., Deegan L.A., Finlay J.C., Hershey A.E. & Miller M.C. (1997) Organic matter dynamics in the Kuparuk River, a tundra river in Alaska, USA. In: *Stream Organic Matter Budgets* (Eds J.R. Webster & J.L. Meyer), pp. 18–23. *Journal of the North American Benthological Society*, 16, 3–161.

Harvey C.J., Peterson B.J., Bowden W.B., Hershey A.E., Miller M.C., Deegan L.A. & Finlay J.C. (1998) Biologi-cal responses to fertilization of Oksrukuyik Creek, a tundra stream. *Journal of the North American Benthological Society*, **17**, 190–209.

Hinterleitner-Anderson D., Hershey A.E. & Schuldt J.A. (1992) The effects of river fertilization on mayfly (*Baetis* sp.) drift patterns and population density in an arctic river. *Hydrobiologia*, **240**, 247–258.

Hobbie J.E., Peterson B.J., Bettez N., Deegan L., O'Brien W.J., Kling G.W., Kipphut G.W., Bowden W.B. & Hershey A.E. (1999) Impact of global change on the biogeochemistry and ecology of an Arctic freshwater system. *Polar Research*, **18**, 207–214.

Hopkins D.M., Karlstrom T.N.V., Black R.F., Williams J.R., Péwé T.R., Fernald A.T. & Muller E.H. (1955) *Permafrost and Ground Water in Alaska*. United States Geological Survey Professional Paper 264-F. United States Government Printing Office, Washington, DC, U.S.A.

IPCC (2001) Climate change 2001: impacts, adaptation, and vulnerability. In: *Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (Eds J.J. McCarthy, O.F. Canziani, N.A. Leary, D.J. Dokken & K.S. White), Cambridge University Press, Cambridge, U.K.

Johnston N.T., Perrin C.J., Slaney P.A. & Ward B.R. (1990) Increased juvenile salmonid growth by whole-river fertilization. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 862–872.

Ledger M.E. & Hildrew A.G. (2000) Herbivory in an acid stream. *Freshwater Biology*, **43**, 545–556.

Ledger M.E. & Hildrew A.G. (2001) Growth of an acid-tolerant stonefly on epilithic biofilm from streams of contrasting pH. *Freshwater Biology*, **46**, 1457–1470.

Newell S.Y., Arsuffi T.L. & Fallon R.D. (1988) Fundamental procedures for determining ergosterol content of decaying plant material by liquid chromatography. *Applied and Environmental Microbiology*, **54**, 1876–1879.

Newell S.Y., Moran M.A., Wicks R. & Hodson R.E. (1995) Productivities of microbial decomposers during early stages of decomposition of leaves of a freshwater sedge. *Freshwater Biology*, **34**, 135–148.

O'Hop J., Wallace J.B. & Haefner J.D. (1984) Production of a stream shredder, *Peltoperla maria* (Plecoptera: Peltoperlidae) in disturbed and undisturbed hard-wood catchments. *Freshwater Biology*, **14**, 13–21.

Oechel W.C. (1989) Nutrient and water flux in a small arctic watershed: an overview. *Holarctic Ecology*, **12**, 229–237.

Oswood M.W., Everett K.R. & Schell D.M. (1989) Some physical and chemical characteristics of an arctic beaded stream. *Holarctic Ecology*, **12**, 290–295.

Oswood M.W., Irons III J.G. & Schell D.M. (1996) Dynamics of dissolved and particulate carbon in an

Arctic stream. In: *Landscape Function and Disturbance in Arctic Tundra* (Eds J.F. Reynolds & J.D. Tenhunen), pp. 275–289. *Ecological Studies*, 120. Springer-Verlag, Berlin.

Oswood M.W., Milner A.M. & Irons J.G. III (1992) Climate change and Alaskan rivers and streams. In: *Global Climate Change and Freshwater Ecosystems* (Eds P. Firth & S.G. Fisher), pp. 192–210. Springer-Verlag, Berlin.

Paul M.J. & Meyer J.L. (1996) Fungal biomass of 3 leaf litter species during decay in an Appalachian stream. *Journal of the North American Benthological Society*, **15**, 421–432.

Peterson B.J., Hobbie J.E. & Corliss T.L. (1983) A continuous flow periphyton bioassay: tests of nutrient limitation in a tundra stream. *Limnology and Oceanography*, **28**, 583–591.

Peterson B.J., Hobbie J.E. & Corliss T.L. (1986) Carbon flow in a tundra stream ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1259–1270.

Peterson B.J., Hobbie J.E., Hershey A., Lock M., Ford T., Vestal R., Hullar M., Ventullo R. & Volk G. (1985) Transformation of a tundra river from heterotrophy to autotrophy by addition of phosphorus. *Science*, **229**, 1383–1386.

Peterson B.J., Deegan L.A., Helfrich J. *et al.* (1993) Biological responses of a tundra river to fertilization. *Ecology*, **74**, 653–672.

Rosemond A.D., Pringle C.M., Ramírez A. & Paul M.J. (2001) A test of top-down and bottom-up control in a detritus-based food web. *Ecology*, **82**, 2279–2293.

Rouse W.R., Douglas M.S.V., Hecky R.E. *et al.* (1997) Effects of climate change on the freshwaters of Arctic and Subarctic North America. *Hydrological Processes*, **11**, 873–902.

Slavik K., Peterson B.J., Deegan L.A., Bowden W.B., Hershey A.E. & Hobbie J.E. (2004) Long-term responses of the Kuparuk River ecosystem to phosphorus fertilization. *Ecology*, **85**, 939–954.

Stelzer R.S., Heffernan J. & Likens G.E. (2003) The influence of dissolved nutrients and particulate organic matter quality on microbial respiration and biomass in a forest stream. *Freshwater Biology*, **48**, 1925–1937.

Strickland J.D.H. & Parsons T.R. (1960) A manual of sea water analysis. *Bulletin of the Fisheries Research Board of Canada*, **125**, 1–185.

Sturm M., Racine C. & Tape K. (2001) Increasing shrub abundance in the Arctic. *Nature*, **411**, 546–547.

Suberkropp K. (2001) Fungal growth, production and sporulation during leaf decomposition in two streams. *Applied and Environmental Microbiology*, **67**, 5063–5068.

Suberkropp K. & Weyers H.S. (1996) Application of fungal and bacterial production methodologies to decomposing leaves in streams. *Applied and Environmental Microbiology*, **62**, 1610–1615.

Vannote R.L. & Sweeney B.W. (1980) Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *American Naturalist*, **115**, 667–695.

Vincent W.F. & Hobbie J.E. (2000) Ecology of Arctic lakes and rivers. In: *The Arctic* (Eds M. Nuttall & T.V. Callaghan), pp. 197–232. Harwood Academic, U.K.

Walker D.A., Webber P.J., Binnian E.F., Everett K.R., Lederer N.D., Nordstrand E.A. & Walker M.D. (1987) Cumulative impacts of oil fields on northern Alaskan landscapes. *Science*, **238**, 757–761.