

APPLIED ISSUES

Recovery of three arctic stream reaches from experimental nutrient enrichment

JONATHAN P. BENSTEAD,* ADRIAN C. GREEN,* LINDA A. DEEGAN,* BRUCE J. PETERSON,* KARIE SLAVIK,* WILLIAM B. BOWDEN[†] AND ANNE E. HERSHEY[‡]

*The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA, U.S.A.

[†]School of Natural Resources, University of Vermont, Burlington, VT, U.S.A.

[‡]Department of Biology, University of North Carolina-Greensboro, Greensboro, NC, U.S.A.

SUMMARY

1. Nutrient enrichment and resulting eutrophication is a widespread anthropogenic influence on freshwater ecosystems, but recovery from nutrient enrichment is poorly understood, especially in stream environments. We examined multi-year patterns in community recovery from experimental low-concentration nutrient enrichment (N + P or P only) in three reaches of two Arctic tundra streams (Kuparuk River and Oksrukuyik Creek) on the North Slope of Alaska (U.S.A.).
2. Rates of recovery varied among community components and depended on duration of enrichment (2–13 consecutive growing seasons). Biomass of epilithic algae returned to reference levels rapidly (within 2 years), regardless of nutrients added or enrichment duration. Aquatic bryophyte cover, which increased greatly in the Kuparuk River only after long-term enrichment (8 years), took 8 years of recovery to approach reference levels, after storms had scoured most remnant moss in the recovering reach.
3. Multi-year persistence of bryophytes in the Kuparuk River appeared to prevent recovery of insect populations that had either been positively (e.g. the mayfly *Ephemerella*, most chironomid midge taxa) or negatively (e.g. the tube-building chironomid *Orthocladius rivulorum*) affected by this shift in dominant primary producer. These lags in recovery (of >3 years) were probably driven by the persistent effect of bryophytes on physical benthic habitat.
4. Summer growth rates of Arctic grayling (both adults and young-of-year) in Oksrukuyik Creek (fertilised for 6 years with no bryophyte colonisation), which were consistently increased by nutrient addition, returned to reference rates within 1–2 years.
5. Rates of recovery of these virtually pristine Arctic stream ecosystems from low-level nutrient enrichment appeared to be controlled largely by duration of enrichment, mediated through physical habitat shifts caused by eventual bryophyte colonisation, and subsequent physical disturbance that removed bryophytes. Nutrient enrichment of oligotrophic Arctic stream ecosystems caused by climate change or local anthropogenic activity may have dramatic and persistent consequences if it results in the colonisation of long-lived primary producers that alter physical habitat.

Keywords: Alaska, before–after control–impact, bryophytes, disturbance, nitrogen, nutrient enrichment, phosphorus, recovery, restoration, rivers

Correspondence: Jonathan P. Benstead, Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487, U.S.A.

E-mail: jbenstead@bama.ua.edu

Present address: Adrian C. Green, United States Geological Survey, Woods Hole, MA 02543, U.S.A.

Present address: Karie Slavik, University of Michigan Biological Station, Ann Arbor, MI 48109, U.S.A.

Introduction

Nutrient enrichment is a significant and pervasive anthropogenic influence on freshwater, estuarine and coastal ecosystems (Carpenter *et al.*, 1998). Inputs of nitrogen and phosphorus, primarily from diffuse sources, are responsible for shifts in plant communities, toxic algal blooms, biodiversity declines, oxygen depletion, fish kills and decreases in the quality of freshwater supplies. In the United States, for example, these impacts make nutrient enrichment a leading cause of ecological impairment of lakes and streams (U.S. EPA [U.S. Environmental Protection Agency], 1996) and the most important form of pollution of estuaries (NRC [National Research Council], 1993).

Clearly, assessing and predicting rates of recovery of aquatic ecosystems from nutrient enrichment are as important as examining the effects of enrichment itself (Cottingham & Carpenter, 1994). Unfortunately, recovery from nutrient enrichment is not well understood, due largely to a lack of experimental tests. Increased understanding of recovery of aquatic ecosystems from nutrient pollution requires experimental studies of the recovery process, conducted in different aquatic ecosystem types. However, recovery studies, experimental or otherwise, are much rarer in the literature than equivalent studies of enrichment effects, especially in stream ecosystems (Kronvang *et al.*, 2005; see Edmondson & Lehman, 1981; Jeppesen *et al.*, 1991; Jeppesen, Jensen & Søndegaard, 2002; O'Brien *et al.*, 2005; Anderson, Jeppesen & Søndegaard, 2005 for relevant lake studies).

Community and ecosystem responses of several Arctic streams to experimental, low-level nutrient addition have been reported in a series of papers (Peterson *et al.*, 1985, 1993; Harvey *et al.*, 1998; Slavik *et al.*, 2004; Benstead *et al.*, 2005). These streams, situated on Alaska's North Slope, also represent ideal sites for studying recovery from nutrient enrichment. First, they are not affected by confounding factors such as land use change. Secondly, they are naturally oligotrophic and show clear responses to nutrient addition (e.g. significant increases in algal standing crops and production). Thirdly, they have relatively simple communities and food web interactions; increases in primary production typically propagate to higher trophic levels. Last, they have been subject to long-term study, so the responses of different trophic levels to nutrient enrichment over multi-year

timescales are relatively well documented and understood (see Harvey *et al.*, 1998; Deegan *et al.*, 1999; Slavik *et al.*, 2004). Moreover, long-term experimental study has allowed the collection of pre-recovery data in both fertilised and reference reaches, strengthening statistical analysis of recovery patterns.

Here, we present data on community recovery (i.e. relative return to reference conditions) from low-level, experimental fertilisation in three Arctic stream reaches created either by successive movement of nutrient addition points downstream from their original locations (Kuparuk River, two reaches) or by complete cessation of experimental nutrient addition (Oksrukuyik Creek). This paper represents the first analysis of community-level recovery from experimental nutrient enrichment of the Kuparuk River and Oksrukuyik Creek. We use our results to (i) examine the effect of nutrient enrichment duration on recovery patterns; (ii) compare how recovery trajectories differ among community components; and (iii) consider general patterns in recovery of oligotrophic stream ecosystems from low-level nutrient enrichment.

Methods

Study sites

Oksrukuyik Creek and the Kuparuk River are clear-water tundra streams (lacking glacial or significant spring inputs) that drain north from the Brooks Range across the Arctic Foothills and Coastal Plain regions of the North Slope of Alaska (U.S.A.) to the Arctic Ocean (Fig. 1). Oksrukuyik Creek is a third-order stream at our study site (mean discharge $\sim 1 \text{ m}^3 \text{ s}^{-1}$), while the Kuparuk River is fourth-order (mean discharge $2.7 \text{ m}^3 \text{ s}^{-1}$). The streams receive 24-h sunlight for much of June–August, with little shading from dwarfed riparian vegetation. Water temperatures are variable annually but average 5–15 °C during the summer. With the possible exception of the streams' deepest pools (>1.5 m in depth), their channels are frozen solid from October to May. Channel substrata are cobble and boulders with some gravel. Precipitation in the region is typically $\sim 15\text{--}30 \text{ cm year}^{-1}$, 30–40% of which falls as snow between September and May. Vegetation in both catchments consists of moist tussock tundra underlain by permafrost (mean August thaw depth $\sim 40 \text{ cm}$). For more detailed site

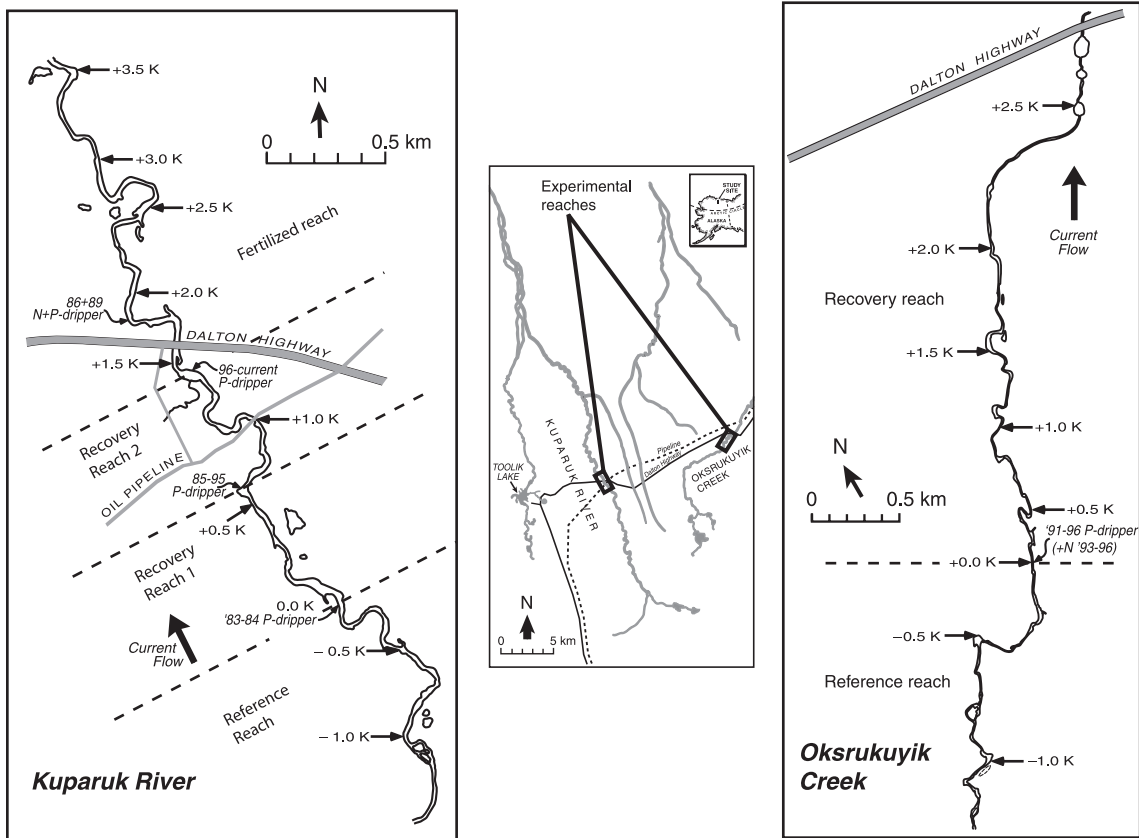


Fig. 1 Maps showing the reference and recovery reaches of the Kuparuk River and Oksrukuyik Creek and the location of the two rivers on Alaska's North Slope. The P-addition site on the Kuparuk River was moved downstream in 1985 and 1996, forming the two recovery reaches.

descriptions, see papers by Harvey *et al.* (1998) and Slavik *et al.* (2004).

Nutrient addition and recovery

Fertilisation of the Kuparuk River with P (added as H_3PO_4 via continuous dripper from mid-June to mid-August, fixed-rate with a target concentration of $0.3 \mu\text{mol L}^{-1}$ at a nominal discharge of $2 \text{ m}^3 \text{ s}^{-1}$) started in the summer of 1983. The H_3PO_4 was added at an arbitrary point called 0.0 km, located 1.6 km upstream of the river crossing at the Dalton Highway (see Peterson *et al.*, 1985 for early results of fertilisation). In subsequent years, all points on the Kuparuk River were referenced relative to this datum (see Fig. 1). In 1985 the P dripper was moved 0.59 km downstream, forming the first Kuparuk recovery reach (enriched for the two previous summers, 1983–1984) between 0.0 km and 0.59 km (Fig. 1). In 1996 the dripper was moved downstream a second time, to 1.4 km below the

original dripper site (Fig. 1). The reach between 0.59 km and 1.4 km became the second Kuparuk recovery reach (enriched for 13 consecutive summers, 1983–1995). See Slavik *et al.* (2004) for a recent overview of the ongoing fertilisation of the Kuparuk River.

The third recovery reach was on Oksrukuyik Creek (Fig. 1). A 2.5 km reach of this stream was fertilised during the summer for six years (1991 to 1996) at 0.0 km (see Harvey *et al.*, 1998 for results of this fertilisation experiment). During the first two summers (1991–1992, mid-June–mid-August), the stream was fertilised with P only (fixed rate, target concentration of $0.3 \mu\text{mol P L}^{-1}$ at $1 \text{ m}^3 \text{ s}^{-1}$). For the last four summers (1993–1996), $\text{NH}_4^+\text{-N}$ was also added as ammonium sulphate to prevent the possibility of severe N-limitation (fixed rate; target concentration of $7 \mu\text{mol N L}^{-1}$ at $1 \text{ m}^3 \text{ s}^{-1}$). Fertilisation of the reach downstream of 0.0 km ceased after the summer of 1996, forming the Oksrukuyik recovery reach (enriched for six consecutive summers).

In this study, 'pre-recovery reach' refers to recovery reaches prior to the downstream movement or cessation of experimental nutrient addition. We used a modified Before-After Control-Impact (BACI) approach in our analysis of most of the data (Stewart-Oaten, Murdoch & Parker, 1986). Our design differs from traditional BACI analyses because the reference (= 'Control') and (pre-)recovery (= 'Impact') reaches were known to differ during the 'Before' period. However, we chose to use our modified BACI design for two reasons. First, we were less interested in divergence from fertilised conditions than we were in convergence of the recovery reach with the reference reach, which has never been fertilised. Secondly, the BACI test is a *t*-test of arithmetic differences between means in the two reaches before and after some manipulation. Consequently, it matters little whether arithmetic differences between means are expected to be zero during the 'Before' or during the 'After' period: the test is neutral in this regard. Assumptions of normality were checked using a Shapiro-Wilk test; violations were either corrected by natural log transformations or tested using non-parametric methods.

Physical and chemical factors

For both the Kugaruk River and Oksrukuyik Creek, stage height was recorded (chart recorder or pressure transducer) and converted to discharge using an annually updated rating curve. Water temperature in the Kugaruk River was measured with a handheld thermometer (1983–1990) or hourly with a thermocouple. Oksrukuyik Creek's water temperature was measured daily with a handheld thermometer from 1989 to 1993 and by a thermocouple thereafter.

The number of water samples collected for nutrient analyses in each reach depended on the length of each reach and the need to measure uptake of added nutrients in pre-recovery reaches. In the Kugaruk River, water samples were collected from one to three unfertilised stations (i.e. upstream of the original dripper site at 0.0 km), two recovery stations in the first recovery reach (only one station after 1997) and two to three recovery stations in the second recovery reach, during each summer. Water samples in Oksrukuyik Creek were collected at three unfertilised and five to six fertilised stations (three to six stations during recovery in 1997 and 1998). Summer mean nutrient concentrations were calculated using three to

seven weekly measurements per summer. Water samples were filtered in the field through 0.45- μm pore cellulose-acetate filters or pre-combusted glass-fibre filters with a nominal pore size of 0.7 μm . Phosphorus [soluble reactive phosphorus (SRP)], ammonium and nitrate plus nitrite were measured by colourimetric methods (Murphy & Riley, 1962; Solorzano, 1969).

Primary producers

To estimate epilithic algal biomass, chlorophyll *a* was usually measured at least twice each summer (July and August) at the same sites used for nutrient chemistry measurement. Subsamples of epilithic slurry were filtered onto glass-fibre filters; total chlorophyll was extracted in MgCO_3 -buffered 90% acetone in the dark at 4 °C for 24–48 h and measured fluorometrically (Strickland & Parsons, 1960). Chlorophyll *a* data were analysed either by *t*-tests on differences between reach means (raw or log-transformed) before and after nutrient addition ceased (first Kugaruk recovery and Oksrukuyik recovery) or by a Wilcoxon rank-sum test (second Kugaruk recovery). Beginning in 1992, percentage of benthic cover of bryophytes in each reach of the Kugaruk River was estimated using a point transect method (Bowden, Finley & Maloney, 1994). Bryophyte cover data were analysed by a *t*-test on differences between reach means before and after cessation of nutrient addition. Bryophytes did not colonise Oksrukuyik Creek's fertilised reach (Harvey *et al.*, 1998).

Benthic insects

Production of benthic insects during 1985–1986 was compared between the reference and the first Kugaruk recovery reach by Peterson *et al.* (1993). Consequently, in this study we restrict our analysis of recovery of benthic insects to comparison of the Kugaruk River's second (post-1996) recovery reach with its reference reach before and after the downstream movement of nutrient addition. Abundance data for four benthic insect taxa from this reach in 1996 (first year of recovery) were reported by Lee & Hershey (2000). Here, we expand their analysis to compare insect community structure over 3 years of pre-recovery and 3 years of recovery. No benthic insect data were available for the Oksrukuyik Creek recovery reach.

During 1992–1998, benthic insects in the Kuparuk River reaches were sampled on one to two dates (early July to early August) at two to three riffles along each of the reference and recovery reaches. Two replicate samples were collected at each station by scrubbing four cobbles (mean surface area 363 cm²) and collecting insects in a 100- μ m-mesh net. Samples were preserved in 90% ethanol and picked of insects under 6 \times magnification. To examine differences in the Kuparuk River's macroinvertebrate community among years and reaches we used the ordination technique of non-metric multidimensional scaling (MDS; PRIMER Version 6, Plymouth Marine Labs, Plymouth, UK; Clarke and Warwick, 2001). MDS ordination provided a graphical representation of the relationships in a dissimilarity matrix generated by comparing community composition of all sample pairs using the Bray-Curtis coefficient (Bray & Curtis, 1957) which, compared with several commonly used dissimilarity coefficients, has been shown to have the most robust relationship with ecological distance (Faith, Minchin & Belbin, 1987). To ease interpretation of the MDS ordination, we also assessed the responses in abundance of the six macroinvertebrate taxa that dominated the community numerically (Brachycentridae, *Ephemera*, Chironomidae, *Orthocladius rivulorum* Kieffer, Simuliidae and Baetidae).

Fish growth

Summer growth of young-of-year Arctic grayling [*Thymallus arcticus* (Pallas)] has been measured annually in Oksrukuyik Creek since 1990. In each year, young-of-year grayling were captured from a total of five sites (typically \sim 10 fish per site) on one date soon after post-hatching emergence from the gravel (21 June–11 July) and one date in early to mid-August. Young-of-year were captured using dip nets or seines from pools in reference or (pre-)recovery reaches. Fish were transferred live to the laboratory, anaesthetised (Finquel[®], Argent Chemical Laboratories, Redmond, WA, U.S.A.), measured (total length; \pm 0.1 mm), weighed (wet weight; \pm 0.001 g) and returned to their collection point. Specific growth rate (SGR, % day⁻¹) for each annual cohort was calculated for each reach using the following formula:

$$\text{SGR} = 100(\log_e W_2 - \log_e W_1)/(t_2 - t_1),$$

where W_1 is the mean wet weight at first sampling date t_1 and W_2 is the mean wet weight at the last sampling date t_2 (Ricker, 1979). Cohort-specific growth rates were analysed by a t -test on differences between reach means before and after cessation of nutrient addition.

Growth rate data (1990–2001) for adult grayling (>30 cm total length) in Oksrukuyik Creek were also included in our analysis. We did not include comparable data from the Kuparuk River because adults were not sampled in the relatively short recovery reaches situated between the reference and fertilised zones (Fig. 1). Adult grayling were captured by angling in early July and kept in holding pens for >24 h to clear their guts. Fish were subsequently anaesthetised (Finquel[®]), tagged (passive internal transponder), weighed (\pm 0.1 g) and released at the site of capture. Fish were re-captured in early August and processed as above. Specific growth rate for each individual recaptured (SGR, % day⁻¹) was calculated using the same formula as above. Adult grayling demonstrate marked fidelity to summer feeding sites (Buzby & Deegan, 2000) and all fish included in the analysis were recaptured in the reach in which they were captured in early summer.

Adult growth rate data are presented here by plotting the reach-specific mean residual of each year's relationship between initial (early summer) wet weight and specific growth rate for all individuals recaptured. We analysed the data by combining all growth rates in a two-factor analysis of variance model with Reach (reference and recovery) and Phase (before and after nutrient addition stopped) as crossed, fixed factors. Initial weight was not a significant explanatory variable in the pooled growth rate data. A significant Reach \times Phase interaction indicates an effect of cessation of nutrient addition on adult growth that can be investigated further using a Tukey HSD test on the least squares means.

Results

Physical and chemical factors

Mean summer water temperature in the Kuparuk River during the P-addition period ranged from 7 °C to 13 °C from 1983 to 2004 (Table 1) and 10 °C to 13 °C in Oksrukuyik Creek from 1991–1999 (Table 2). Mean daily discharge during the experimental period

Table 1 Mean discharge, water temperature and nutrient concentrations during the summer experimental period for the years 1983–2004 in the Kugaruk River

Year	Mean Q (m ³ s ⁻¹)	Mean temperature (°C)	SRP (µM)			NH ₄ (µM)			NO ₃ (µM)		
			Ref	Rec 1	Rec 2	Ref	Rec 1	Rec 2	Ref	Rec 1	Rec 2
1983	1.2	ND	0.15	0.63	0.64	ND	ND	ND	4.07	3.20	1.71
1984	4.0	ND	0.07	0.39	0.30	0.25	0.29	0.30	0.59	0.62	0.34
1985	2.1	9.0	0.04	0.04	0.93	0.44	0.39	0.49	2.80	2.88	2.39
1986	2.6	9.1	0.12	0.18	0.38	1.52	0.90	0.85	2.15	2.42	2.35
1987	3.5	ND	0.16	0.21	0.39	0.96	1.10	1.10	1.60	1.38	1.82
1988	1.3	8.8	0.06	0.10	0.92	1.40	1.85	1.23	2.02	2.04	1.81
1989	2.7	10.6	0.07	0.05	1.05	0.63	0.66	0.68	1.01	0.98	1.03
1990	0.4	12.9	0.11	0.16	1.36	1.00	1.48	1.97	2.88	4.05	3.09
1991	1.7	9.6	0.00	0.00	0.62	0.15	0.17	0.14	1.07	1.10	0.96
1992	2.3	9.8	0.03	0.02	0.66	0.06	0.12	0.14	0.80	0.81	0.69
1993	2.9	10.1	0.07	0.07	0.83	1.13	1.23	1.05	1.25	1.20	1.10
1994	2.7	10.3	0.16	0.19	0.35	1.15	1.14	1.11	1.08	1.18	0.88
1995	4.2	8.8	0.08	0.07	0.35	0.47	0.52	0.59	0.70	0.77	0.80
1996	2.2	8.2	0.10	0.11	0.10	0.72	0.86	0.74	1.90	1.97	1.86
1997	2.8	9.8	0.23	0.06	0.07	0.25	0.19	0.33	0.32	0.32	0.32
1998	1.3	10.6	0.03	0.03	0.03	0.30	0.45	0.44	1.74	1.73	1.75
1999	3.7	10.3	0.09	0.11	0.08	2.75	2.56	2.69	0.31	0.30	0.34
2000	2.1	8.4	0.03	0.02	0.03	0.18	0.15	0.16	6.43	6.22	6.08
2001	3.5	8.3	0.06	0.04	0.05	0.20	0.19	0.21	1.82	2.45	2.37
2002	2.8	7.6	0.04	0.04	0.04	0.26	0.25	0.28	2.88	3.14	3.13
2003	5.1	6.9	0.03	0.03	0.04	0.06	0.07	0.09	0.98	0.94	1.04
2004	3.5	10.6	0.04	0.04	0.05	0.28	0.30	0.27	2.91	0.80	2.58

Ref, reference reach; Rec 1 = first recovery reach (0–0.59 km); Rec 2 = second recovery reach (0.59–1.4 km); SRP, soluble reactive phosphorus. Bold type indicates recovery conditions. ND indicates no data.

Table 2 Mean discharge, water temperature and nutrient concentrations during the summer experimental period for the years 1991–1999 in Oksrukuyik Creek

Year	Treatment	Mean Q (m ³ s ⁻¹)	Mean temperature (°C)	SRP (µM)		NH ₄ (µM)		NO ₃ (µM)	
				Ref	Rec	Ref	Rec	Ref	Rec
1991	P only	0.6	9.6	0.00	0.44	0.16	0.13	2.35	0.84
1992	P only	1.5	10.5	0.03	0.27	0.06	0.06	1.48	0.54
1993	P + N	0.9	11.2	0.05	0.29	1.46	6.64	2.19	2.31
1994	P + N	1.9	12.8	0.19	0.48	0.64	7.13	0.93	1.41
1995	P + N	1.9	12.9	0.15	0.23	1.55	5.96	0.76	1.04
1996	P + N	0.8	11.3	0.24	0.44	1.70	10.7	1.15	1.16
1997	Recovery	1.0	12.0	0.06	0.08	0.19	0.18	0.51	0.52
1998	Recovery	0.5	13.4	0.01	0.01	0.07	0.13	4.15	3.68
1999	Recovery	1.8	11.7	0.01	0.07	0.16	0.42	3.27	0.25

Ref, reference reach; Rec, recovery reach; SRP, soluble reactive phosphorus. Bold type indicates recovery conditions.

in the Kugaruk River ranged from 0.4 m³ s⁻¹ in 1990 to 5.1 m³ s⁻¹ in 2003 (Table 1), when two large storms occurred during the summer. The long-term mean daily discharge during each summer's fertilisation period in the Kugaruk River from 1983 to 2004 was 2.7 m³ s⁻¹. Mean discharge during fertilisation in Oksrukuyik Creek ranged from 0.5 m³ s⁻¹ in 1998 to

2.0 m³ s⁻¹ in 1994 and 1995 (Table 2). Mean summer discharge in Oksrukuyik Creek from 1991 to 1999 was 1.2 m³ s⁻¹.

Ambient SRP concentrations in both the Kugaruk River and Oksrukuyik Creek are low, typically near the limit of detection (0.05 µmol L⁻¹). Mean SRP was 0.08 µmol L⁻¹ in the reference reach of the Kugaruk

River (1983–2004) and $0.08 \mu\text{mol L}^{-1}$ in Oksrukuyik Creek (1991–1999) during the experimental period (Tables 1 & 2). In the three recovery reaches, P levels returned to ambient concentrations within 1 year. Mean SRP (± 1 SE) in the first recovery reach of the Kugaruk River (entire recovery period) was $0.08 \mu\text{mol L}^{-1}$ (± 0.01), $0.05 \mu\text{mol L}^{-1}$ (± 0.01) in the second recovery reach, and $0.05 \mu\text{mol L}^{-1}$ (± 0.02) in Oksrukuyik Creek's recovery reach (Tables 1 & 2).

Nitrate concentrations in the Kugaruk River recovery reaches did not differ from those of the reference reach. Mean nitrate was $1.9 \mu\text{mol L}^{-1}$ (± 0.3) in the reference reach, $1.8 \mu\text{mol L}^{-1}$ (± 0.3) in the first recovery reach and $2.2 \mu\text{mol L}^{-1}$ (± 0.6) in the second recovery reach. In Oksrukuyik Creek, mean nitrate concentration was $1.9 \mu\text{mol L}^{-1}$ (± 0.4) in the reference reach and $1.4 \mu\text{mol L}^{-1}$ (± 0.8) in the recovery reach (Tables 1 & 2).

Ammonium (NH_4^+) concentrations were near the limit of detection ($0.25 \mu\text{mol L}^{-1}$) in the Kugaruk River and concentrations were similar from year to year in all experimental reaches regardless of treatment. Mean concentration of NH_4^+ in the Kugaruk River was $0.68 \mu\text{mol L}^{-1}$ (± 0.14) in the reference reach, $0.73 \mu\text{mol L}^{-1}$ (± 0.06) in the first recovery reach and $0.58 \mu\text{mol L}^{-1}$ (± 0.05) in the second recovery reach. Mean concentrations in Oksrukuyik Creek were $0.14 \mu\text{mol L}^{-1}$ (± 0.04) in the reference reach (post-fertilisation years only) and $0.24 \mu\text{mol L}^{-1}$ (± 0.09) in the recovery reach (Tables 1 & 2).

Primary producers

Once nutrient addition was stopped the shift of algal standing crops to reference levels was consistently rapid among the three recovery reaches, indicating that duration of enrichment (6–13 years) had no effect on recovery rate of algae (Fig. 2). In the Kugaruk River's first recovery reach, the return of chlorophyll *a* standing crop to reference levels after two years of fertilisation was rapid and complete (BACI, $p = 0.005$; Fig. 2a). Similar results were obtained in the Kugaruk River's second recovery reach, despite more muted effects on algal standing crop in the latter years of nutrient addition (1990 onwards; Fig. 2b); BACI analysis indicated complete recovery ($p = 0.002$; Wilcoxon rank-sum test). Lastly, chlorophyll *a* data for Oksrukuyik Creek's recovery period was insufficient to allow meaningful statistical analysis; however, results

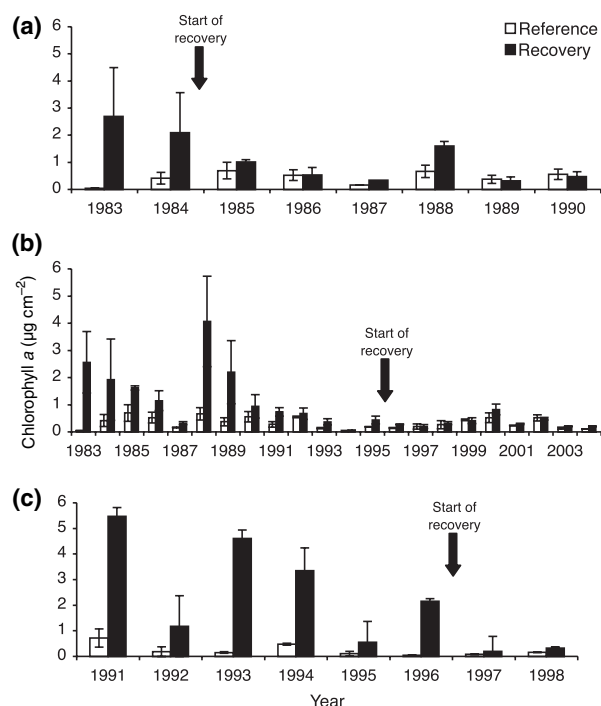


Fig. 2 Mean epilithic chlorophyll *a* standing crop (± 1 SE) in reference and recovery reaches of the (a) Kugaruk River, 1983–1990 (first recovery reach), (b) Kugaruk River, 1983–2003 (second recovery reach), and (c) Oksrukuyik Creek, 1991–1998.

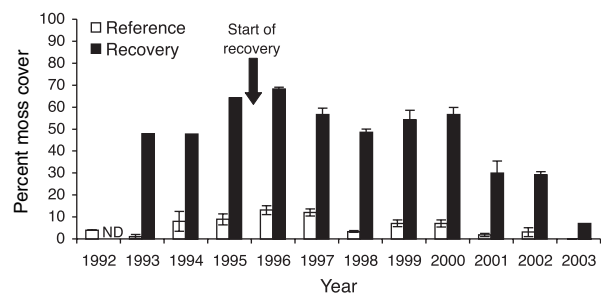


Fig. 3 Mean percent cover of mosses (± 1 SE) on the streambed of the Kugaruk River, 1992–2003. Moss cover was not measured prior to 1992. ND indicates no data.

appeared consistent with the rapid declines in algal standing crop observed in the Kugaruk River (Fig. 2c).

Once fertilisation ceased in 1996, bryophyte cover of $\sim 30\%$ persisted even after 7 years of ambient nutrient concentrations, eventually declining to 7% by 2003 (Fig. 3). Annual decreases in cover were highly variable, with large relative decreases in bryophyte cover occurring only in 2001 and 2003. BACI analysis indicated insignificant recovery of bryophyte cover within the time period analysed ($p = 0.36$).

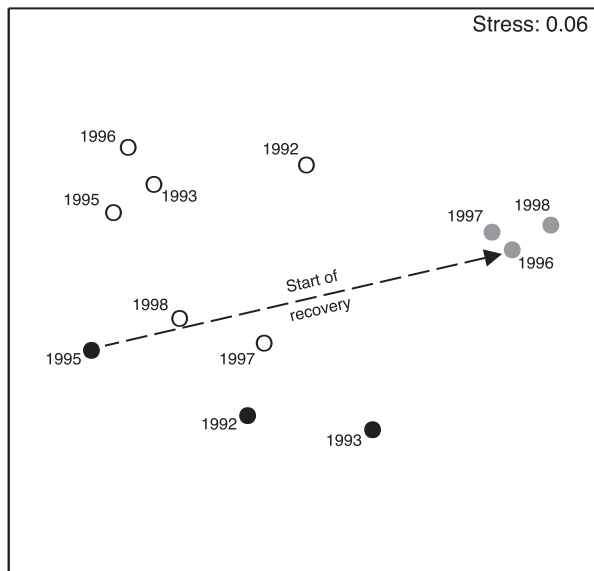


Fig. 4 Non-metric multidimensional scaling ordination plot of benthic macroinvertebrate samples based on Bray-Curtis dissimilarities among untransformed density data. Solid symbols are pre-recovery (fertilised) reach, grey symbols are recovery reach, and open symbols are reference reach. Arrow shows transition from fertilised to recovery conditions. No data were available for 1994. Ordination using log-transformed data showed similar patterns of recovery with an identical stress value.

Benthic insects

The non-metric multidimensional scaling (MDS) ordination plot had a stress value of 0.06, indicating that it provided a good two-dimensional representation of the relationships among the samples (Clarke & Warwick, 2001). Lack of overlap among the plotted samples from each reach showed that the benthic macroinvertebrate samples collected from the Kuparuk River's pre-recovery (fertilised) reach were consistently different in community structure from those collected from the unfertilised reference reach (Fig. 4). The samples from the recovery reach were also different in community structure from both the reference and pre-recovery samples, indicating a departure from fertilised conditions but providing no evidence for a return to reference conditions (Fig. 4).

Density data for the six numerically dominant taxa of benthic insects allowed further interpretation of the MDS ordination plot (Fig. 5). The six taxa could be divided into three groups: taxa that were positively affected by bryophytes (brachycentrid caddisflies, the mayfly *Ephemerella* and most midge taxa); taxa that

were negatively affected (the tube-building midge *Orthocladius rivulorum*) and taxa that showed variable or neutral responses (simuliids and baetid mayflies). Positively moss-affected taxa, including brachycentrids, the grazing mayfly *Ephemerella* and a suite of chironomid midges (mostly Diamesinae and Orthoclaudiinae, excluding *Orthocladius rivulorum*) all continued to show much higher abundances in the recovery reach, even after 3 years of ambient nutrient conditions (Fig. 5a–c).

Densities of the tube-building midge *Orthocladius rivulorum* were consistently higher in the reference reach relative to the pre-recovery and recovery reach for 3 years, suggesting that this taxon was negatively affected by moss (Fig. 5d). Filter-feeding simuliid larvae and collector-gathering baetids showed recovery responses that were variable or neutral. Densities of simuliid larvae were generally lower in the pre-recovery reach relative to the reference reach. After the start of recovery, densities of simuliids declined slightly in the recovery reach but declined relatively more in the reference reach (Fig. 5e). Baetid abundance was variable within and among years. However, densities were somewhat higher in the reference reach relative to the pre-recovery reach and there was some evidence for a subsequent return to reference levels (Fig. 5f).

Fish growth

Response in young-of-year growth to cessation of fertilisation was clear and immediate with growth rates in the recovery reach subsequently being comparable or lower than those in the reference reach ($p = 0.004$; Fig. 6). Between 1990 and 2001, we obtained summer-time specific growth rates for 169 adult Arctic grayling in Oksrukuyik Creek (mean number of recaptured fish per reach each summer was 7; range 0–26). Comparisons of residuals from annual regressions of initial weight against specific growth rates of individuals showed that growth rates were similar between reaches prior to fertilisation (1990 data in Fig. 7). A significant Reach \times Phase interaction ($P < 0.001$) indicated that the positive fertilisation effect on adult growth did not persist after nutrient addition ceased (Fig. 7); fertilised reach growth rates were significantly higher ($p < 0.05$, Tukey HSD test) than those in the recovery and reference reaches, which did not differ. Although

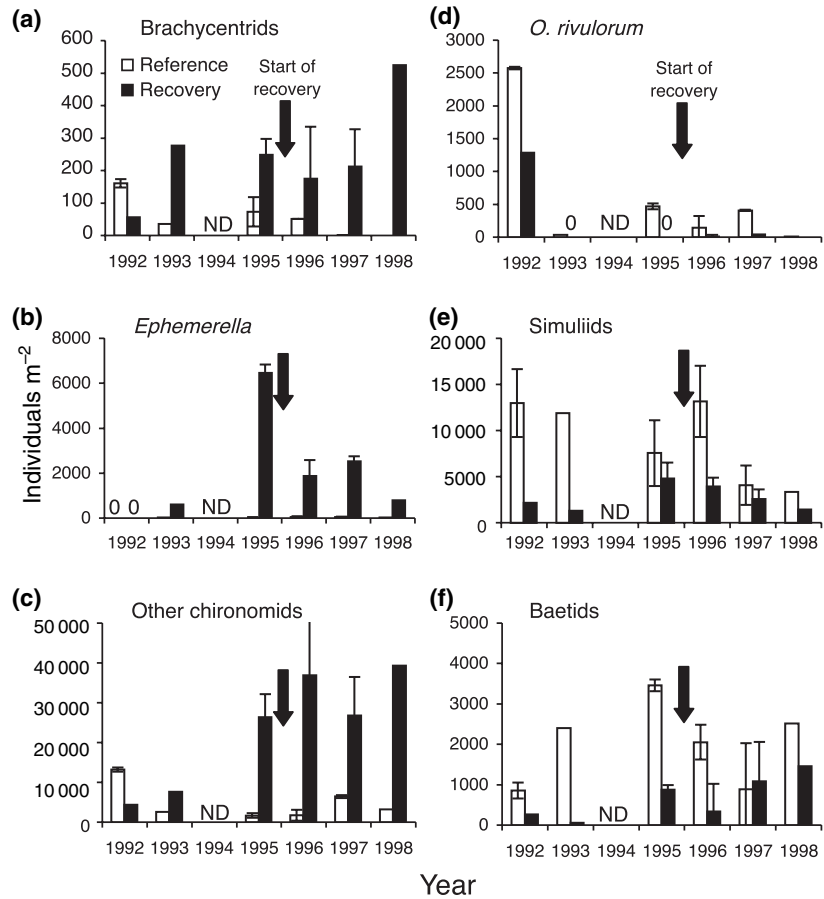


Fig. 5 Mean density (± 1 SE) of six dominant benthic insect groups in the Kuparuk River's reference reach and second recovery reach, 1992–98. ND indicates no data. 0 indicates that the taxon was not found in samples.

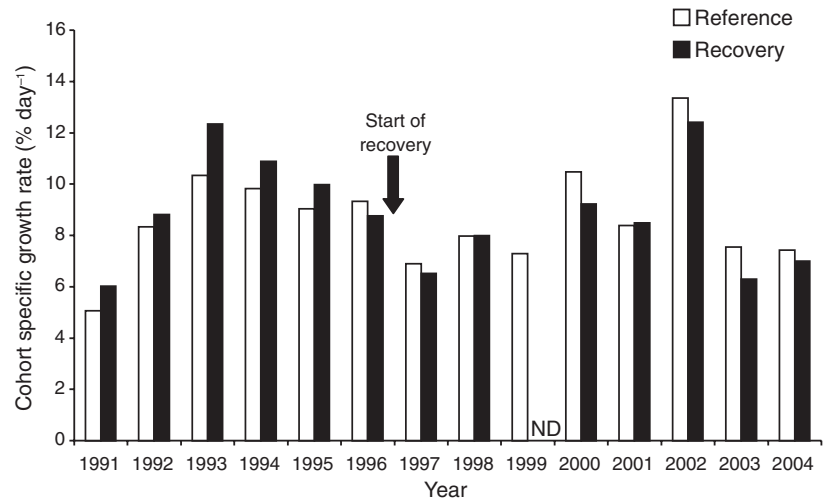


Fig. 6 Cohort-specific growth rate of young-of-year Arctic grayling in Oksrukuyik Creek, 1991–2004. ND indicates no data.

immediate response of adult growth rates to recovery was obscured by low sample size in the reference reach in the first year of recovery, the data suggested that recovery of adult growth rates from nutrient addition was rapid (within 1–2 years).

Discussion

Fertilisation of the Kuparuk River and Oksrukuyik Creek consistently increased epilithic algal standing crops and primary production relative to their reference

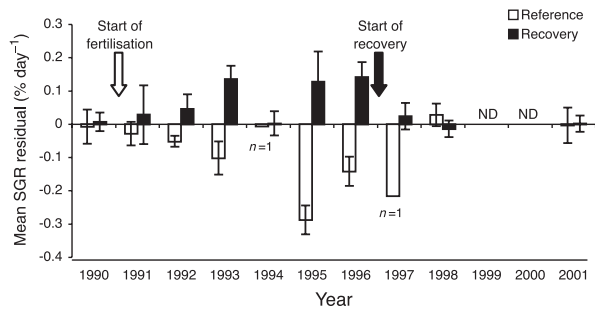


Fig. 7 Mean residuals (± 1 SE) for each reach in the annual relationship between summer-specific growth rates and initial weights for all adult Arctic grayling recaptured in Oksrukuyik Creek, 1990–2001. Residuals were calculated for each year separately (see text). ND indicates no data.

reaches, although the magnitude of the fertilisation effect varied among years (Bowden *et al.*, 1992; Harvey *et al.*, 1998; Arscott, Bowden & Finlay, 1998; Slavik *et al.*, 2004). In all cases, return of epilithic algal biomass to reference levels occurred rapidly after cessation of fertilisation (within 1 year). Rapid shifts in algal standing crop were likely due to high turnover of algal cells combined with a return to P-limited growth after cessation of P addition. Storage of P in algal biomass and recycling within low-biomass epilithic biofilms presumably could not sustain relatively high levels of primary production in these streams following cessation of nutrient enrichment. In support of this, a substantial fraction of the N pool in epilithon turns over relatively rapidly in these Arctic streams (Wollheim *et al.*, 2001). Although we have no data on P regeneration during recovery periods, these streams probably have little capacity for P storage in their mostly mineral sediments.

Bryophytes became the dominant primary producer in the Kuparuk River's fertilised reach only after long-term nutrient addition (>7 years; Bowden, Finlay & Maloney, 1994). The taxon largely responsible for the increase in bryophyte biomass, *Hygrohypnum* spp., has been shown to be strongly P-limited under ambient nutrient conditions in the Kuparuk River (Bowden *et al.*, 1994; Finlay & Bowden, 1994). Although nutrient limitation was relieved by P addition, the speed with which *Hygrohypnum* was able to colonise the P-fertilised reach was presumably limited by the dispersal of vegetative fragments (or spores) from distant source populations such as headwater springs (Bowden *et al.*, 1994; Stream Bryophyte Group, 1999).

Once established, *Hygrohypnum* spp. formed persistent biomass that only decreased to reference levels after eight years of ambient nutrient concentrations. This persistence was presumably related to the longevity of individual bryophyte plants combined with secure attachment to cobbles and boulders by tough rhizoids (Stream Bryophyte Group, 1999). It seems likely that the gradual attrition of *Hygrohypnum* cover that we observed was driven by senescence of individual plants stressed by increasing nutrient limitation. Declines in bryophyte cover during recovery were variable among years; however, large annual decreases in bryophyte cover occurred in 2001 and 2003. These larger relative decreases were likely caused by an interaction between storm-associated scour and moss senescence. The decrease in bryophyte cover in 2003 was clearly related to a particularly large storm in mid-August 2002 (>100 m³ s⁻¹), which disturbed a large proportion of the Kuparuk's streambed. Decreases in bryophyte cover during this event were caused both by scouring and by overturning of large, formerly stable substrata (J.P. Benstead, personal observation).

Recovery of the six dominant insect taxa was relatively slow in the Kuparuk River's second, moss-dominated recovery reach. This slow rate of return to reference levels of insect abundance contrasted with the relatively rapid return to reference levels of secondary production (<2 years) that was observed in four of these benthic insect taxa in the Kuparuk River's first recovery reach, which did not develop thick bryophyte cover (Peterson *et al.*, 1993). Changes in the insect community in the Kuparuk River's second recovery reach was correlated with the correspondingly slow attrition of bryophyte cover, so it appears that bryophyte colonisation and its physical effect on benthic habitat very likely drove the differences in recovery trajectories between the Kuparuk's first and second recovery reaches.

Competition for space with lush growth of the dominant bryophyte taxon (*Hygrohypnum* spp.) negatively affected *Orthocladius rivulorum*, as this chironomid species requires bare rock substrate for tube attachment (Hershey *et al.*, 1988; Slavik *et al.*, 2004). Persistence of bryophytes would presumably continue to affect *Orthocladius* negatively until bryophyte cover returned to reference levels. Taxa that were positively affected by bryophytes were also likely responding to physical changes in habitat. During the

first year of recovery in 1996, Lee & Hershey (2000) used a combination of benthic samples and enclosure experiments to study the effect of bryophytes on the distributions and densities of four insect taxa in the Kuparuk River's reference, second recovery and fertilised reaches (brachycentrids were not included in their analysis). Chironomid midges and the mayfly *Ephemerella* responded largely to the increased habitat complexity created by bryophytes, rather than the augmented food supply resulting from P fertilisation. These two taxa (and brachycentrids) showed little to no recovery in our 3-year post-recovery data set. Baetids showed relatively depressed densities in the pre-recovery (i.e. fertilised) reach and subsequently increased somewhat after nutrient addition ceased. Any increase in baetid density after nutrient addition ceased would not be consistent with a mechanism controlled by an algal food supply, which decreased during recovery. The mechanism behind any potential baetid response is therefore unclear.

Reductions in densities of simuliid larvae in the Kuparuk's fertilised zone are thought to have been caused by negative interactions with brachycentrid caddisfly larvae (Hershey & Hiltner, 1988). Simuliids showed no post-recovery increase in density during the recovery period. It is possible that persistence of brachycentrids in the recovery reach resulted in the continuation of this negative interaction between the two taxa.

Growth rates of adult and young-of-year Arctic grayling showed clear positive responses to N and P addition in Oksrukuyik Creek, presumably because of the observed increases in availability of important prey taxa (Harvey *et al.*, 1998). Growth of both age-classes returned to reference values rapidly (within 1–2 years) after nutrient addition ceased. Arctic grayling feed predominantly on drifting benthic insects (Deegan & Peterson, 1992), so it is likely that rapid return of grayling growth to reference rates was linked to correspondingly fast return of important prey taxa to lower levels of availability. Unfortunately, no insect drift data are available for Oksrukuyik Creek.

Differences in recovery from nutrient enrichment among the three Arctic stream reaches were driven by the duration of nutrient enrichment and by the effects of bryophyte colonisation. Short-term nutrient enrichment of the Kuparuk's first recovery reach (2 years) and Oksrukuyik Creek (6 years) did not result in bryophyte colonisation. These two reaches showed

rapid community-wide return to reference levels of biomass and biological activity. The main effect of bryophyte colonisation on recovery patterns was the establishment of a high-biomass and physically complex benthic environment that was more stable, relatively resistant to scouring and consequently persistent in the long term (Stream Bryophyte Group, 1999). In turn, this allowed some dominant 'moss-loving' primary consumer taxa to remain at high levels relative to the moss-free reference reach. It is possible that some of the differences in recovery patterns between the two streams were caused by differences in the original experimental treatment (i.e. Oksrukuyik Creek was fertilised with N, as well as P). However, it is impossible to tease apart the potential effects of combined N and P addition from the many other differences between the two experiments.

In conclusion, our results show that the Arctic streams that we studied could recover rapidly from short-term, low-concentration nutrient enrichment, as has been seen in studies of many different perturbations to stream ecosystems (Niemi *et al.*, 1990). Longer enrichment led to shifts in the primary producer community, however, with persistent effects on benthic habitat and community recovery. Similar responses to low-level enrichment may be common to oligotrophic freshwater ecosystems; unfortunately, long-term data from comparable studies are lacking. Long-term nutrient enrichment of oligotrophic Arctic stream ecosystems is likely to increase in the future due to permafrost thawing associated with climate change, as well as local anthropogenic impacts such as mining and drilling (Benstead *et al.*, 2005). Such nutrient enrichment, even at low concentrations, may have dramatic and persistent consequences if it results in the colonisation of long-lived primary producers that eventually alter physical habitat.

Acknowledgments

This material is based upon work supported by the National Science Foundation under DEB-LTER 9810222, OPP-9911278 and preceding grants. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. Many people contributed to the long-term data set on which this paper is based. We thank them for their hard work in the field

and laboratory. Finally, we are grateful to John Hobbie, Alex Huryn and two anonymous reviewers for comments that improved the manuscript.

References

- Anderson N.J., Jeppesen E. & Søndegaard M. (2005) Ecological effects of reduced nutrient loading (oligotrophication) on lakes: an introduction. *Freshwater Biology*, **50**, 1589–1593.
- Arcscott D.B., Bowden W.B. & Finlay J.C. (1998) Comparison of epilithic algal and bryophyte metabolism in an arctic tundra stream, Alaska. *Journal of the North American Benthological Society*, **17**, 210–227.
- Benstead J.P., Deegan L.A., Peterson B.J., Huryn A.D., Bowden W.B., Suberkropp K., Buzby K.M., Green A.C. & Vacca J.A. (2005) Responses of a beaded Arctic stream to short-term N and P fertilisation. *Freshwater Biology*, **50**, 277–290.
- Bowden W.B., Finlay J.C. & Maloney P.E. (1994) Long-term effects of PO₄ fertilization on the distribution of bryophytes in an arctic river. *Freshwater Biology*, **32**, 445–454.
- Bowden W.B., Peterson B.J., Finlay J.C. & Tucker J. (1992) Epilithic chlorophyll *a*, photosynthesis, and respiration in control and fertilized reaches of a tundra stream. *Hydrobiologia*, **240**, 121–131.
- Bray J.R. & Curtis J.T. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, **27**, 325–349.
- Buzby K.M. & Deegan L.A. (2000) Inter-annual fidelity to summer feeding sites in Arctic grayling. *Environmental Biology of Fishes*, **59**, 319–327.
- Carpenter S.R., Caraco N.F., Correll D.L., Howarth R.W., Sharpley A.N. & Smith V.H. (1998) Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications*, **8**, 559–568.
- Cottingham K.L. & Carpenter S.R. (1994) Predictive indices of ecosystem resilience in models of north temperate lakes. *Ecology*, **75**, 2127–2138.
- Clarke K.R. & Warwick R.M. (2001) *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation*, 2nd edition. PRIMER-E Ltd, Plymouth, UK.
- 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.
- Edmondson W.T. & Lehman J.T. (1981) The effect of changes in the nutrient income on the condition of Lake Washington. *Limnology and Oceanography*, **26**, 1–29.
- Faith D.P., Minchin P.R. & Belbin L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, **69**, 57–68.
- Finlay J.C. & Bowden W.B. (1994) Controls on production of bryophytes in an arctic tundra stream. *Freshwater Biology*, **32**, 455–466.
- Harvey C.J., Peterson B.J., Bowden W.B., Hershey A.E., Miller M.C., Deegan L.A. & Finlay J.C. (1998) Biological responses to fertilization of Oksrukuyik Creek, a tundra stream. *Journal of the North American Benthological Society*, **17**, 190–209.
- Hershey A.E. & Hiltner A.L. (1988) Effect of a caddisfly on black fly density: interspecific interactions limit black flies in an arctic river. *Journal of the North American Benthological Society*, **7**, 188–196.
- Hershey A.E., Hiltner A.L., Hullar M.A.J., Miller M.C., Vestal J.R., Lock M.A., Rundle S. & Peterson B.J. (1988) Nutrient influence on a stream grazer: *Orthocladius* microcommunities respond to nutrient input. *Ecology*, **69**, 1383–1392.
- Jeppesen E., Jensen J.P. & Søndegaard M. (2002) Response of phytoplankton, zooplankton and fish to re-oligotrophication: an 11-year study of 23 Danish lakes. *Aquatic Ecosystem Health and Management*, **5**, 31–43.
- Jeppesen E., Kristensen P., Jensen J.P., Søndegaard M., Mortenson E. & Lauridsen T. (1991) Recovery resilience following a reduction in external phosphorus loading of shallow eutrophic Danish lakes: duration, regulating factors and methods for overcoming resilience. *Memorie dell'Istituto Italiano di Idrobiologia*, **48**, 127–148.
- Kronvang B., Jeppesen E., Conley D.J., Søndegaard M., Larsen S.E., Ovesen N.B. & Carstensen J. (2005) Nutrient pressures and ecological responses to nutrient loading reductions in Danish streams, lakes and coastal waters. *Journal of Hydrology*, **304**, 274–288.
- Lee J.O. & Hershey A.E. (2000) Effects of aquatic bryophytes and long-term fertilization on arctic stream insects. *Journal of the North American Benthological Society*, **19**, 697–708.
- Murphy J. & Riley G. (1962) A modified single solution method for the determination of phosphate in natural waters. *Analytica et Chimica Acta*, **27**, 31–36.
- Niemi G.J., DeVore P., Detenbeck N., Taylor D., Lima A., Pastor J., Yount J.D. & Naiman R.J. (1990) Overview of case studies on recovery of aquatic systems from disturbance. *Environmental Management*, **14**, 571–587.

- NRC (National Research Council) (1993) *Managing wastewater in coastal urban waters*. National Academy Press, Washington, D.C., U.S.A..
- O'Brien W.J., Barfield M., Bettez N., Hershey A.E., Hobbie J.E., Kipphut G., Kling G. & Miller M.C. (2005) Long-term response and recovery to nutrient addition of a partitioned arctic lake. *Freshwater Biology*, **50**, 731–741.
- 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.
- Ricker W.E. (1979) Growth rates and models. In: *Fish Physiology* (Eds W.S. Hoar, D.J. Randall & J.R. Brett), pp. 677–743. Academic Press, New York, U.S.A..
- 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.
- Solorzano L. (1969) Determination of ammonia in natural waters by the phenylhypochlorite method. *Limnology and Oceanography*, **14**, 799–801.
- Stewart-Oaten A., Murdoch W.W. & Parker K.R. (1986) Environmental impact assessment: "pseudoreplication" in time? *Ecology*, **67**, 929–940.
- Stream Bryophyte Group (1999) Roles of bryophytes in stream ecosystems. *Journal of the North American Benthological Society*, **18**, 151–184.
- 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.
- U.S. EPA (U.S. Environmental Protection Agency). (1996) *Environmental indicators of water quality in the United States*. EPA 841-R-96-002. USEPA, Office of Water (4503F). U.S. Government Printing Office, Washington, D.C., U.S.A..
- Wollheim W.M., Peterson B.J., Deegan L.A., Hobbie J.E., Hooker B., Bowden W.B., Edwardson K.J., Arscott D.B., Hershey A.E. & Finlay J.C. (2001) Influence of stream size on ammonium and suspended particulate nitrogen processing. *Limnology and Oceanography*, **46**, 1–13.

(Manuscript accepted 12 December 2006)