

# Colonization and development of stream communities across a 200-year gradient in Glacier Bay National Park, Alaska, U.S.A.

Alexander M. Milner, E. Eric Knudsen, Chad Soiseth, Anne L. Robertson, Don Schell, Ian T. Phillips, and Katrina Magnusson

**Abstract:** In May 1997, physical and biological variables were studied in 16 streams of different ages and contrasting stages of development following glacial recession in Glacier Bay National Park, southeast Alaska. The number of microcrustacean and macroinvertebrate taxa and juvenile fish abundance and diversity were significantly greater in older streams. Microcrustacean diversity was related to the amount of instream wood and percent pool habitat, while the number of macroinvertebrate taxa was related to bed stability, amount of instream wood, and percent pool habitat. The percent contribution of Ephemeroptera to stream benthic communities increased significantly with stream age and the amount of coarse benthic organic matter. Juvenile Dolly Varden (*Salvelinus malma*) were dominant in the younger streams, but juvenile coho salmon (*Oncorhynchus kisutch*) abundance was greater in older streams associated with increased pool habitat. Upstream lakes significantly influenced channel stability, percent Chironomidae, total macroinvertebrate and meiofaunal abundance, and percent fish cover. Stable isotope analyses indicated nitrogen enrichment from marine sources in macroinvertebrates and juvenile fish in older streams with established salmon runs. The findings are encapsulated in a conceptual summary of stream development that proposes stream assemblages to be determined by direct interactions with the terrestrial, marine, and lake ecosystems.

**Résumé :** En mai 1997, nous avons pu étudier les variables physiques et biologiques de 16 cours d'eau d'âges différents et à des stades divers de leur évolution depuis la récession glaciaire au parc national de Glacier Bay, au sud de l'Alaska. Le nombre de taxons de microcrustacés et de macroinvertébrés ainsi que l'abondance et la diversité de poissons juvéniles se sont avérés significativement plus élevés dans les ruisseaux plus âgés. Il y a une corrélation entre la diversité des microcrustacés et la quantité de bois dans l'eau et le pourcentage d'habitats lénitiques, de même qu'entre le nombre de taxons de macroinvertébrés et la stabilité du lit, la quantité de bois dans l'eau et le pourcentage d'habitats lénitiques. Le pourcentage des Éphéméroptères dans la communauté benthique augmente significativement avec l'âge du cours d'eau et la quantité de matière organique benthique grossière. Les Dolly Varden juvéniles dominent dans les ruisseaux plus jeunes, alors que les Saumons coho juvéniles sont plus abondants dans les ruisseaux plus vieux où les habitats lénitiques prennent plus d'importance. La présence de lacs en amont influence fortement la stabilité du lit, le pourcentage de Chironomidés, l'abondance totale des macroinvertébrés, l'importance la méiofaune, ainsi que le pourcentage du substrat offrant des abris pour les poissons. Des analyses des isotopes stables révèlent un enrichissement en N de source marine chez les macroinvertébrés et poissons juvéniles dans les cours d'eau plus âgés où il y a des migrations de saumons. Ces résultats sont intégrés à un modèle conceptuel qui suggère que les communautés des cours d'eau sont régies par des interactions directes avec les écosystèmes terrestre, marin et lacustre.

[Traduit par la Rédaction]

## Introduction

Macroinvertebrate colonization of streams is influenced by both abiotic and biotic factors (Williams and Smith 1996),

with their relative influence based on the scale of investigation (Downes and Keough 1998). Colonization studies of streams and rivers at the spatial scale of entirely new river channels have been limited (Fisher 1990) and have princi-

Received November 3, 1999. Accepted September 7, 2000.  
J15431

**A.M. Milner.**<sup>1</sup> School of Geography and Environmental Science, University of Birmingham, Edgbaston, Birmingham B15 2TT, U.K., and Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99775, U.S.A.

**E.E. Knudsen.** U.S. Geological Survey, Alaska Biological Science Center, Anchorage, AK 99503, U.S.A.

**C. Soiseth.** National Park Service, Glacier Bay National Park, P.O. Box 140, Gustavus, AK 99826, U.S.A.

**A.L. Robertson.** School of Life Sciences, University of Surrey Roehampton, West Hill, London SW15 3SN, U.K.

**D. Schell.** Institute of Marine Science, University of Alaska, Fairbanks, AK 99775, U.S.A.

**I.T. Phillips and K. Magnusson.** School of Geography and Environmental Science, University of Birmingham, Edgbaston, Birmingham B15 2TT, U.K.

<sup>1</sup>Author to whom all correspondence should be sent at the following address: School of Geography and Environmental Science, University of Birmingham, Edgbaston, Birmingham B15 2TT, U.K. e-mail: a.m.milner@bham.ac.uk

pally involved channel relocation and reconstruction projects where upstream sources of potential drift colonizers enhance colonization rates (e.g., Gore 1982). By using the spatial gradient of glacial recession in Glacier Bay National Park, southeast Alaska, reach-scale comparisons across a temporal gradient of 200 years can be made that increase our understanding of large-scale colonization patterns rather than short-term patch colonization or rapid colonization from sources within the same watershed. As these are entirely new watersheds with no remnants of any previous biological community, colonization must involve dispersal from other stream systems and development invokes primary successional processes (Gore and Milner 1990).

Studies that compared six streams of different ages in Glacier Bay during the late 1970s and early 1980s indicated that community development was influenced principally by abiotic factors, especially water temperature and channel stability (Milner 1987; Sidle and Milner 1989). Postglacial lakes were identified as important hydraulic features for enhancing downstream channel stability by settling coarser sediment and buffering flow variations (Sidle and Milner 1989). Longer term studies of one stream (Wolf Point Creek), with a large feeder lake, indicated that interspecific competition may be an important factor in structuring macroinvertebrate community assemblages in stable channels (Milner 1994; Flory and Milner 1999a, 2000). The importance of riparian vegetation, most notably willow catkins and alder roots, for enhancing the colonization of certain invertebrate species (particularly caddisfly and chironomid taxa) was demonstrated by Flory and Milner (1999b).

Mackay (1992) suggested that the first macroinvertebrate colonizers of new or disturbed systems would be typically Baetidae and Leptophlebiidae (Ephemeroptera), Simuliidae, Orthocladinae (Chironomidae), and Hydropsychidae (Trichoptera). Dolly Varden (*Salvelinus malma*) are the first salmonid colonizers of new streams following deglaciation, since, as bottom dwellers, they are well adapted to the characteristic lack of pools (Milner and Bailey 1989). Coho salmon (*Oncorhynchus kisutch*) also may be relatively early colonizers. In a comparison of two 150-year-old streams, Milner and Bailey (1989) showed that the enhanced channel stability of a lake-influenced stream supported greater densities of juvenile coho salmon than a nonlake system. Where accessible lakes are present, sockeye salmon (*Oncorhynchus nerka*) may rapidly colonize. Pink salmon (*Oncorhynchus gorbuscha*) were found to colonize Wolf Point Creek after these species, following a large run throughout the region (Milner 1997). Colonization of new streams by salmonids provides an important flux of marine-derived nutrients (Kline et al. 1997) and is potentially a key factor influencing their successional development. Wipfli et al. (1998) reported that salmon carcasses enhanced invertebrate densities in experimental channels adjoining a southeast Alaskan stream. However, carcasses need to be retained within the stream if they are to provide a nutrient source (Flory and Milner 1999b).

As terrestrial plant succession proceeds in Glacier Bay watersheds, the amount of coarse woody debris (CWD) in streams will potentially increase and play a significant role in the structure and function of macroinvertebrate assemblages by providing physical habitat diversity (Harmon et al. 1986). CWD is also an important determinant of the carry-

ing capacity for juvenile salmonids (Hicks et al. 1991) and for enhancing salmon carcass retention (Cederholm and Peterson 1985).

With a time gradient of over 200 years of development, Glacier Bay streams provide a unique opportunity to examine community development across different trophic levels as streams age and physicochemical characteristics change. Stable carbon and nitrogen isotope ratios in biological tissues can serve as means for estimation of energy supplied by either terrestrial or aquatic environments (allochthonous versus autochthonous inputs) and across these trophic levels (Kline et al. 1990; Bilby and Fransen 1996). Stream biota attains isotope ratios in proportion to the amount of food derived from these two main sources, thereby allowing discrimination of the food sources for specific organisms (Fry 1999). However, nitrogen fixation, nitrification/denitrification processes, and mineralization of organic matter all contribute to alteration of nitrogen isotopic signatures in the consumers. Similarly, carbon isotope ratios may be responding to such variables as stream flow velocities, free carbon dioxide pool size, algal cell sizes, and respired carbon dioxide in solution and thus adds variability to the observed stream component isotope ratios. If these caveats are considered, determination of stable carbon and nitrogen isotope ratios in biological tissue samples can be a useful tool for discerning successional pathways and community interactions in freshwater and terrestrial ecosystems.

The principal objective of our study was to investigate long-term patterns of biotic community and habitat change by comparing streams representing 200 years of stream development following deglaciation. Four questions were addressed. (i) What is the influence of lakes in different ages of watershed on downstream physical attributes and biological communities? (ii) What is the influence of stream age on physicochemical variables and biological communities? (iii) What is the influence of these variables on the colonization and abundance of invertebrates and fish? (iv) What is the relative importance of marine-derived nutrients from anadromous fish in the growth of riparian vegetation, instream vegetation, macroinvertebrates, and juvenile salmonids in streams of different ages? A final objective was to develop a conceptual summary of stream development that integrates trophic interactions within streams and the influences of other ecosystems (terrestrial, marine, and lake) on community assembly as streams develop.

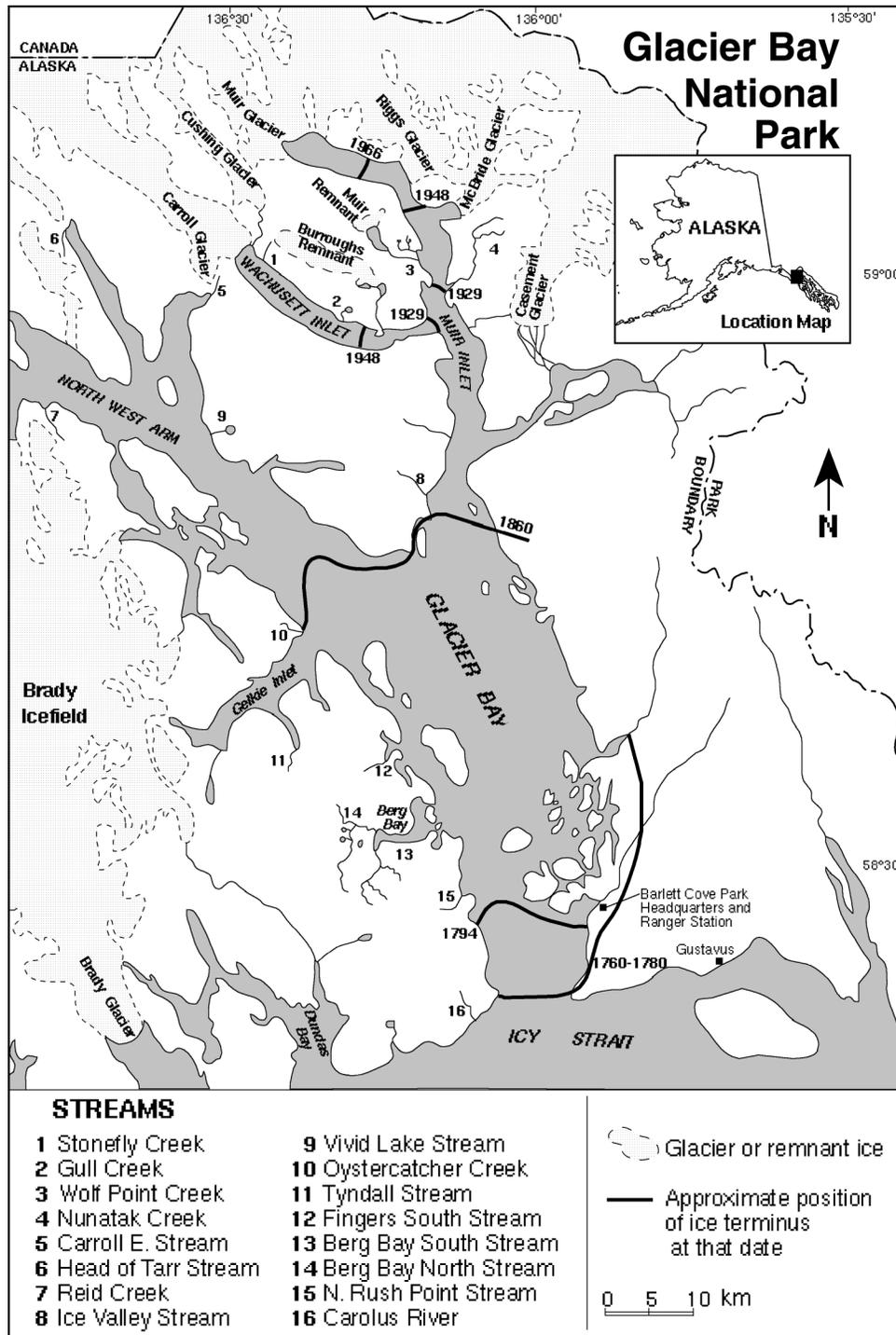
## Materials and methods

### Study site

Glacier Bay National Park and Preserve (11 030 km<sup>2</sup>) in southeast Alaska encompasses a fjord over 100 km long and 20 km wide with two major arms, the northwest arm and Muir Inlet. A Neoglacial ice sheet, which reached its maximum around 1700 AD near the mouth of Glacier Bay, began to recede between 1735 and 1785 (see Fig. 1 for key recession dates). The climate of Glacier Bay is maritime, with a mean annual temperature of 5°C (mean monthly range = -3 to 13°C) and average annual precipitation of 1400 mm.

At least four successional stages of terrestrial vegetation have been documented in Glacier Bay (Chapin et al. 1994). The pioneer community, colonizing recently deglaciated till in the first 15–25 years, typically consists of “black crust” formed of blue-green algae, *Equisetum variegatum*, lichens, liverworts, forbs, *Dryas drummondii*,

Fig. 1. Glacier Bay National Park in southeast Alaska showing the location of the 16 study streams in May 1997.



scattered willows (*Salix* spp.), and cottonwood (*Populus trichocarpa*). Succession gradually leads to a community dominated by *Dryas*, with persistent individuals of woody species also present. *Dryas* typically then disappears, and dense stands of alder form at approximately 50 years following deglaciation. Sitka spruce (*Picea sitchensis*) forests normally become the dominant community after about 100 years, but increasing numbers of western hemlock (*Tsuga heterophylla*) also are evident with further development. Spruce-hemlock forests are sometimes succeeded by *Sphagnum*-dominated muskeg over a period of thousands of years in other areas of southeast Alaska (Chapin et al. 1994).

Soiseth and Milner (1995) identified more than 300 streams within Glacier Bay National Park formed principally as a result of ice recession since the Neoglacial maximum. The majority of these streams occur in small catchments (1–100 km<sup>2</sup>) and are relatively short (<20 km) and steep (average gradient 5–20%). Fifteen of these streams ranging in age from 25 to 200 years since deglaciation were selected for study (Fig. 1). They possessed the following characteristics: gradient <5% in the lower reaches, no barriers to salmonid migration, watershed size ranging from about 10 to 100 km<sup>2</sup>, and either with or without upstream lakes that influence flow regimes and settle coarser sediments. Although not directly

**Table 1.** Summary of major physical watershed features of the 16 study streams used in the May 1997 study in Glacier Bay National Park.

Stream name	Stream age (years)	Lake influence	Basin area (km <sup>2</sup> )	Blue line elevation (m)	Stream length (km)	Stream gradient (%)	Water source <sup>a</sup>	Stream order	Orientation (degrees from true north)
Stonefly Creek	36	Yes	~10.0	91	1.3	7.0	G	1	355
Gull Lake Stream	43	Yes	9.4	366	3.0	12.2	L	2	175
Wolf Point Creek	51	Yes	30.8	183	5.6	3.3	G	2	89
Nunatak Creek	62	No	38.0	793	8.6	9.2	S	3	293
Carrol East Stream	77	No	~10.5	518	3.4	15.2	S	2	226
Head of Tarr Stream	88	No	8.7	579	2.8	20.7	M	1	332
Reid Creek	117	No	17.4	290	6.0	4.8	M	1	321
Head of Tyndall Stream	122	No	5.7	88	2.3	3.8	S	2	2
Vivid Lake Stream	128	No	21.6	442	5.6	7.9	S	2	294
Ice Valley Stream	127	No	18.5	518	8.3	6.2	S	2	160
Oystercatcher Creek	137	No	9.6	476	5.7	8.3	S	2	60
North Fingers South Stream	152	No	17.0	360	8.0	4.5	S	2	56
Berg Bay North Stream	167	Yes	26.8	238	9.0	2.6	L	3	76
Berg Bay South Stream	167	No	18.6	244	7.2	3.4	S	3	340
Rush Point Creek	192	No	22.0	296	6.6	4.5	S	2	112
Carolus River <sup>b</sup>	1377	No	~57.0	271	9.0	3.0	S	3	132

<sup>a</sup>Predominant water sources: G, proglacial lake; L, lake; S, snowmelt and rain; M, glacial meltwater.

<sup>b</sup>Estimate but affected by outwash from neoglacial ice (see text).

influenced by Neoglacial ice, Carolus River (stream 16 on Fig. 1) was also included. Approximately 1400 years old, the Carolus River was almost certainly affected by outwash from Neoglacial ice. Lakes were present in four of the 16 streams, three of which were the youngest streams sampled. From its name, Vivid Lake stream would appear to be a lake system, but since 1994, most of the flow has bypassed the lake due to channel shifting. The lake no longer functions to buffer flow, settle coarse sediment, or influence water temperature. Table 1 summarizes the main physical features of the study streams.

### Stream age and habitat evaluation

Due to insufficient information on relative deglaciation between lowland and upland portions of watersheds, stream age was generally defined as the time since ice recession from stream mouths using historical and aerial photographs, journal articles, and unpublished data. All study reaches were within 0.2–2.8 km of the stream mouth to include at least two pool, riffle, and glide complexes and to be at least 10–14 channel widths in length or include at least one entire sinuous channel wavelength. All streams were studied during May 1997. We placed reference pins on each bank at the lower and upper end of each 100- to 250-m reach to define reach limits and identify locations for mapping cross-sectional profiles. Relative water surface levels were established for each cross section and reach gradient was determined using the difference in water elevations divided by the distance between these cross sections.

Habitats within study reaches were identified as micro-, meso- or macrounits using a hierarchical classification system similar to that of Bryant et al. (1992). We determined a priori a minimum size of >4 m<sup>2</sup> for habitat classification and smaller habitats were aggregated with the habitat unit at the next highest level across the entire reach. Within each habitat classification unit, percent substrate type was visually estimated using bedrock/boulder (>256 mm in diameter), cobble (64–256 mm), gravel (2–64 mm), sand (<2 mm), or fines (silt or clay). We visually estimated (percent) fish cover to include instream wood (rootwads, logs (>30 cm in diameter and >2 m in length), slash (>10 cm but <30 cm in diameter), fine wood (<10 cm in diameter), and debris jams (accumulations of 10 logs or more)), bedrock ledges, boulders, undercut banks, and deep water. We also calculated the percentage of all reach wetted habitat con-

taining any type of fish cover habitat. Spawning substrate included areas dominated by cobble and gravel. Percent instream wood was estimated as the proportion of all wetted habitat in a reach that contained some type of woody debris. The percentage of linear streambank having some type of vegetation (grasses, shrubs, trees) also was estimated visually. The bottom component of the Pfankuch (1975) stability index was used to evaluate substrate stability in each reach, as recommended by Death and Winterbourn (1995). With this index, the lower the value the more stable the stream. Entrenchment ratios were calculated using the approach of Rosgen and Silvey (1996).

### Water chemistry

Water samples were collected at each site and stored as (i) unfiltered and refrigerated, (ii) unfiltered and frozen, or (iii) filtered and frozen prior to analysis for pH, alkalinity, color, total nitrogen, and total phosphorus. Alkalinity was determined by sulphuric acid (0.02 N) titration, and pH was measured using an Orion model 399A ion analyzer. Total phosphorus was measured by the molybdate blue – ascorbic acid method after persulphate digestion. Nitrate and nitrite were determined as nitrite, following cadmium reduction of nitrate, and total ammonia was determined using the phenylhypochlorite procedure. Total Kjeldahl nitrogen was measured as total ammonia following sulphuric acid block digestion. Specific conductance, water temperature, and turbidity were recorded in the field using portable instruments.

### Invertebrates and coarse benthic organic material (CBOM)

Five random samples for invertebrates were collected from riffle areas in a 15-m section within the larger study reaches of each stream using a modified Surber sampler with an 80- $\mu$ m mesh. In the laboratory, macroinvertebrates and meiofauna were sorted from detritus and silt using a dissecting microscope, identified to genus and species where possible, and enumerated. Chironomid head capsules were microdissected and mounted on slides in dimethylhydantoin formaldehyde resin for identification.

Particulate organic carbon collected from sorted invertebrate samples was dried and weighed prior to ashing at 500°C for 40 min. CBOM was calculated as mean ash-free dry weight (g) per area (m<sup>2</sup>).

## Fish

Twenty to 25 minnow traps (40 × 22 cm with 6-mm mesh) baited with salmon eggs were fished continuously in each reach for 1–2 h. Captured fish were identified to species, counted, and returned to the stream after all trapping was completed. No fish were recaptured. Trapping duration was recorded to determine catch per unit trapping effort of 1 h (CPUE).

## Macroinvertebrate, meiofaunal, and fish community metrics

For macroinvertebrates, six groups of metrics were determined: (i)  $\log(x + 1)$  of total abundance (number·m<sup>-2</sup>), (ii) percent Ephemeroptera, percent Plecoptera, percent Trichoptera, and percent Chironomidae, (iii) number of taxa ( $N$ ) and number of Ephemeroptera, Plecoptera, and Trichoptera (EPT) genera, (iv) Shannon index ( $H$ ), where  $H = -\sum p_i \ln p_i$  where  $p_i$  is the proportional abundance of the  $i$ th species =  $n_i/N$ , (v) reciprocal of Simpson's index (1/ $S$ ) where

$$S = \sum \frac{n_i(n_i - 1)}{N(N - 1)}$$

where  $n_i$  is the number of individuals in the  $i$ th species and  $N$  is the total number of individuals, and (vi) the Berger–Parker dominance index ( $D$ ) (Berger and Parker 1970), which is a simple measure of dominance (or evenness) where  $D = N_{\max}/N$  where  $N_{\max}$  is the number of individuals in the most abundant taxa and  $N$  is the total number of individuals collected. Three meiofaunal metrics were used: number of microcrustacean taxa, microcrustacean abundance (number per square metre), and meiofaunal abundance excluding microcrustacean (number per square metre).

For fish, four metrics were determined: mean number of juvenile coho salmon CPUE, mean number of juvenile Dolly Varden CPUE, mean number of all juvenile fish species CPUE, and diversity of fish species using the Shannon index.

## Nutrient sources

Biotic material was collected from each stream for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis. New foliage was picked from riparian willows with forceps and stored in plastic sample bags. One sample of stream moss was collected to indicate aquatic in situ primary producers. Invertebrates were collected from stones (two representative genera (typically collectors and grazers) were used for comparison). Three juvenile coho salmon or, when coho were unavailable, three juvenile Dolly Varden captured by minnow trapping were sacrificed and dorsal muscle tissue between the skull and dorsal fin removed for analysis.

These approximately 0.1 g wet weight biotic samples were rinsed with 10% HCl to remove carbonates, rinsed with distilled water, and dried for transfer to the laboratory where they were further dried to a constant weight at 65°C and ground to a fine powder. Isotope ratios of carbon and nitrogen were determined with a continuous-flow Roboprep/Europa 20/20 mass spectrometer system. All samples were run in replicate and reanalyzed if agreement was not within ±0.2%. A peptone working standard and blank were run after each six samples. Results are reported in the standard  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  notation relative to the Pee Dee Belemmite and air references for carbon and nitrogen, respectively. To examine nutrient flow at different trophic levels,  $\delta^{13}\text{C}$  values were plotted against  $\delta^{15}\text{N}$  values.

To assess the relative contributions of marine-derived nitrogen (MDN) among juvenile fish from the study streams, we converted average  $\delta^{15}\text{N}$  values for each stream to percent MDN following the conventions in Kline et al. (1990). We assumed that  $\delta^{15}\text{N}$  reference points described for the mixing model of Kline et al. (1990, fig. 1) were applicable, i.e., that  $\text{N}_2$  based solely on atmospheric sources has a  $\delta^{15}\text{N}$  value of 0, whereas adult salmon returning from the sea

have a  $\delta^{15}\text{N}$  value of  $11.2 \pm 1.0$  (Mathisen et al. 1988). Percent MDN was calculated as

$$\% \text{ MDN} = (\text{OBS} - 6)/7 \times 100$$

where OBS is the observed  $\delta^{15}\text{N}$  value.

Adjustments were made to the observed  $\delta^{15}\text{N}$  for isotopic fractionation (–6) to set the terrestrial end member for juvenile coho and Dolly Varden, the primary carnivores in the mixing model of Kline et al. (1990). The result was then divided by 7, the range of possible  $\delta^{15}\text{N}$  values for primary carnivores in the mixing model, and multiplied by 100 to express  $\delta^{15}\text{N}$  (in terms of MDN) as percent total nitrogen. Although the resulting estimates may be influenced by intrinsic variabilities in assimilation efficiencies and metabolic pathways rather than solely by differences in sources, they serve as an heuristic tool for interpreting source importance (Gannes et al. 1997).

## Data analysis

Based on the field measures described above, we recorded or calculated 26 physicochemical variables and 23 biological variables from the 16 study streams. We used correlation analysis to eliminate highly correlated variables that were potential measures of the same attribute (see Table 2 for a final list of variables used in subsequent analyses) and to document apparent relationships between the remaining variables.

We used  $t$  tests to analyze the effects of presence or absence of upstream lakes on stream water quality, physical features, meiofauna, invertebrates, fish habitat, and fish. Tests for the assumption of normality revealed that data for about half the variables were not normally distributed. Log or square root transformations were applied to the nonnormal variables and the results retested for normality. Effects of lakes for variables found to be nonnormal following transformation were tested with a Wilcoxon signed rank test with alpha set at 0.05 in all tests.

Analysis of covariance was used to test for the effects of independent biotic and abiotic variables on the biotic variables of interest while controlling for the effects of upstream lakes. The general form of the model was

$$Y = aL + bX + c(L \times X)$$

where  $Y$  is the dependent biotic variable,  $L$  is the class variable indicating presence or absence of an upstream lake,  $X$  is the independent biotic or abiotic variable, and  $L \times X$  is the interaction term. When the interaction term was significant, the model was recast by regressing dependent on independent variables separately for streams with and without lakes. Model results for each relationship were evaluated for the best data fit to select (i) analysis of covariance (without the interaction term when it was nonsignificant in the full model), (ii) simple linear regression (i.e., without the lake or interaction terms), or (iii) separate simple linear regressions for streams with lakes and streams without lakes (when the covariance interaction term was significant). Because a large number of physicochemical and biotic variables were evaluated, we report only significant relationships. The Carolus River was not included in the model for stream age due to the uncertainty of its age and how it was influenced during the glacial period; it was included in other models.

Two-way indicator species analysis (TWINSPAN; Hill 1979) was used to classify the 16 stream sites using abundance data for 128 identified macroinvertebrate taxa. Rare taxa were downweighted using the “pseudo-species” facility with abundance cut levels of 0, 2, 5, 10, and 20. Indicator taxa identified by TWINSPAN are reported. Although more taxa than sites were used in this analysis, this approach has been applied elsewhere (e.g., Omerod et al. 1994).

**Table 2.** Comparison of observed mean ( $\pm 1$  SD), type of model (see Materials and methods), and probability of a greater  $t$  value for variables measured in streams with and without upstream lakes.

Variable	Mean ( $\pm 1$ SD)		Model	$p > t$
	Lakes	No lakes		
<b>Stream physical features</b>				
Stream age (years)	74.5 (62.6)	125.3 (38.5)	Untrans	0.08
Gradient (at study site, %)	0.69 (0.44)	0.95 (0.55)	Untrans	0.41
Stream entrenchment	2.04 (0.96)	1.74 (0.73)	log + 1	0.49
Pfankuch bottom stability index	23.2 (8.7)	39.2 (7.2)	Untrans	0.003**
<b>Water quality</b>				
Conductivity ( $\mu\text{mho}\cdot\text{cm}^{-1}$ )	142 (36.3)	133 (43.3)	Untrans	0.74
Alkalinity ( $\text{mg}\cdot\text{L}^{-1}$ )	60.2 (20.7)	58.0 (19.6)	Untrans	0.87
Total nitrogen ( $\mu\text{g}\cdot\text{L}^{-1}$ )	81.7 (33.6)	111.2 (76.4)	log + 1	0.75
Total phosphorus ( $\mu\text{g}\cdot\text{L}^{-1}$ )	20.4 (23.8)	48.2 (72.3)	log + 1	0.61
Temperature ( $^{\circ}\text{C}$ )	3.65 (0.79)	5.04 (1.76)	log + 1	0.17
Turbidity (NTU)	17.2 (23.6)	23.5 (37.6)	log + 1	0.91
<b>Biotic indicators</b>				
CBOM ( $\text{mg}\cdot\text{L}^{-1}$ )	0.48 (0.13)	0.59 (0.39)	Untrans	0.41
% MDN in fish	25.3 (25.8)	19.7 (18.9)	Untrans	0.72
<b>Macroinvertebrates</b>				
% Ephemeroptera/100	0.01 (0.008)	0.46 (0.32)	Wilcoxon	0.003**
% Chironomidae/100	0.84 (0.038)	0.40 (0.31)	Wilcoxon	0.01*
% Trichoptera/100	0.003 (0.002)	0.008 (0.007)	Wilcoxon	0.30
% Plecoptera/100	0.02 (0.02)	0.04 (0.03)	Square root	0.31
Total macroinvertebrate abundance ( $\text{m}^{-2}$ )	4500 (790)	760 (690)	log + 1	0.0001**
No. of EPT genera	4.5 (2.4)	5.8 (3.1)	Untrans	0.46
Shannon index ( $H$ )	0.67 (0.202)	0.60 (0.203)	Untrans	0.58
1/Simpson's index ( $1/S$ )	3.8 (2.08)	3.5 (1.32)	Untrans	0.74
Number of macroinvertebrate taxa ( $N$ )	19.0 (7.62)	15.9 (6.5)	Untrans	0.45
Dominance ( $D$ )	0.36 (0.10)	0.45 (0.15)	Untrans	0.26
<b>Meiofauna</b>				
Number of microcrustacean taxa	2.5 (1.96)	2.4 (1.66)	Untrans	0.67
Total microcrustacean abundance ( $\text{m}^{-2}$ )	488 (444)	141 (194)	Wilcoxon	0.15
Meiofaunal abundance (excluding microcrustaceans) ( $\text{m}^{-2}$ )	573 (372)	95 (73)	log + 1	0.01**
<b>Fish habitat</b>				
% gravel and cobble	70.0 (9.4)	67.1 (14.4)	Wilcoxon	0.73
% fish cover	37.2 (13.4)	20.9 (10.8)	Untrans	0.03*
% instream wood	14.7 (6.6)	11.0 (9.7)	Untrans	0.50
% pool habitat	2.0 (2.5)	4.2 (8.1)	Wilcoxon	1.00
% bank vegetation	68.4 (45.7)	64.2 (27.8)	Wilcoxon	0.64
<b>Juvenile fish</b>				
Fish species diversity	0.31 (0.48)	0.38 (0.34)	Wilcoxon	0.73
All fish CPUE	0.83 (1.39)	0.63 (0.54)	Wilcoxon	0.64
Coho CPUE	0.24 (0.42)	0.28 (0.35)	Wilcoxon	0.95
Dolly Varden CPUE	0.10 (0.12)	0.30 (0.32)	Wilcoxon	0.35

**Note:** Results from the most appropriate model were reported, where Untrans is  $t$  test with untransformed data, log + 1 is  $t$  test with log-transformed data, Square root is  $t$  test with square root transformed data, and Wilcoxon is a Wilcoxon signed rank test. Also represented is a complete list of all variables used in subsequent analyses.

\*Significant; \*\*highly significant.

## Results

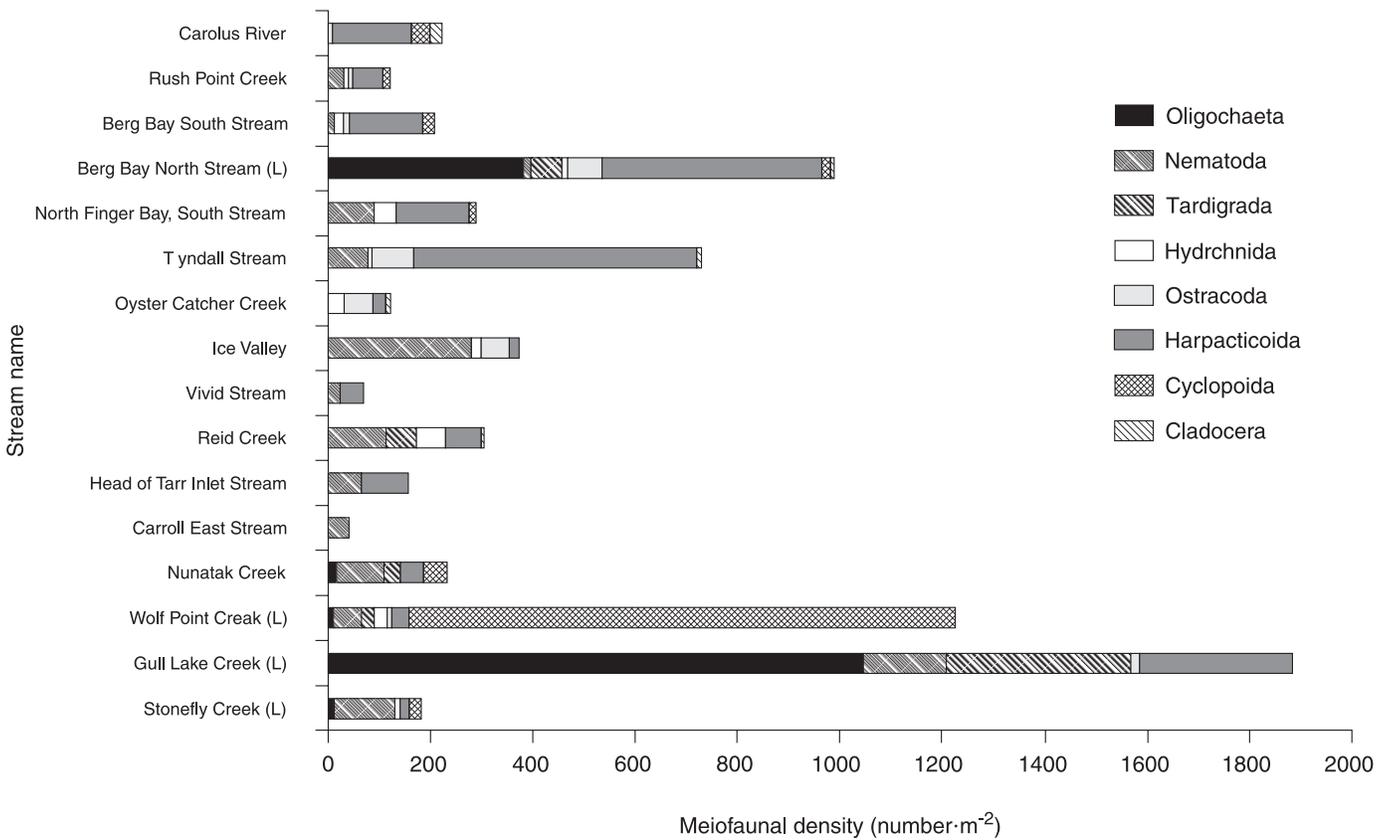
### Influence of lakes on stream habitat and biotic communities

Channel bed stability (as indicated by the Pfankuch stability index) was the only stream habitat variable significantly greater in reaches downstream of lakes than in stream reaches with no upstream lakes (Table 2).

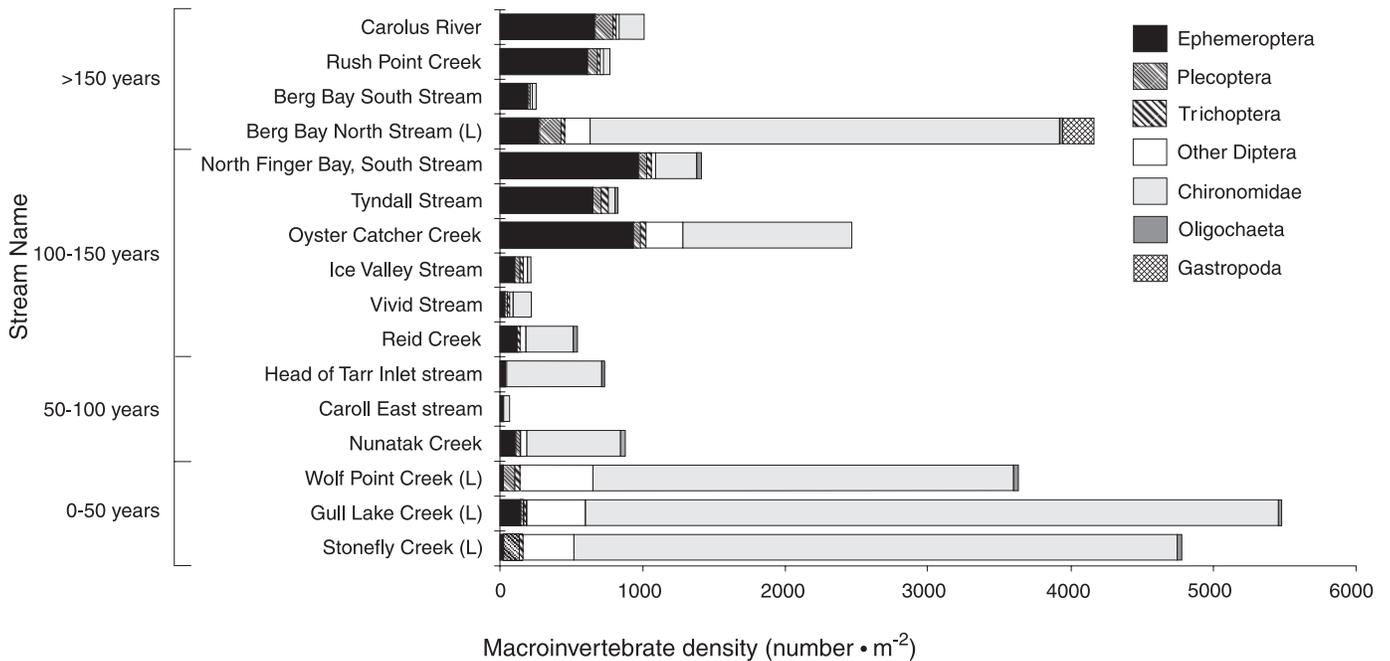
Meiofaunal abundance was significantly greater in chan-

nels downstream from lakes (Table 2) with densities ranging from 179 to 1882·m<sup>-2</sup> compared with 38–730·m<sup>-2</sup> in streams without upstream lakes (Fig. 2). *Chaetogaster* spp. (Oligochaeta), in particular, maintained high densities in such streams in contrast with their low densities or even absence from streams without upstream lakes. Harpacticoid copepods numerically dominated meiofaunal communities in nonlake streams over 140 years old. Chydorid cladocerans were found only in Berg Bay North Stream (an older stream with an upstream

**Fig. 2.** Relative mean densities of the meiofaunal taxonomic groups for the 16 streams sampled in May 1997 (L, lake-influenced system).



**Fig. 3.** Relative mean densities of the principal macroinvertebrate taxonomic groups for the 16 streams sampled in May 1997 (L, lake-influenced system).



lake) and Carolus River (approximately 1400 years old). Macrothricid cladocerans, however, were additionally found in Nunatak Creek (63 years).

Total macroinvertebrate abundance and percent Chironomidae (typically >70%) (Fig. 3) were significantly greater in channels downstream of lakes, while percent Ephemeroptera

**Table 3.** Parameter estimates from analysis of covariance models testing for the effects of stream age on various physicochemical and biotic variables.

Biotic variable	Model $R^2$	Parameter value			
		Intercept	Lakes	Stream age	Interaction
Turbidity	0.27	92.8		-0.55*	
CBOM	0.76	-0.47	0.92**	<0.01**	<0.01**
Streams with no lakes	0.77	-0.47		<0.01**	
Streams with lakes	ns				
No. of EPT genera	0.57	-0.47	1.23	0.05**	
% Chironomidae	0.78	1.21	-0.32	<0.01**	<0.01**
Streams with no lakes	0.65	1.21		<0.01**	
Streams with lakes	ns				
% Ephemeroptera	0.73	-0.33	0.34	<0.01**	<0.01**
Streams with no lakes	0.57	-0.33		<0.01**	
Streams with lakes	ns				
No. of macroinvertebrate taxa	0.44	3.87	7.97*	0.01*	
No. of microcrustacean taxa	0.49	-0.56	2.94*	0.04**	
% pools	0.38	-2.24	1.74	0.03*	
% fish cover	0.71	-2.61	26.73**	0.18**	
% instream wood	0.52	-7.33	11.74*	0.14**	
Fish species diversity	0.55	-0.42	0.26	<0.01**	
All fish CPUE	0.79	-0.58	-0.22	<0.01**	0.01*
Streams with no lakes	0.42	-0.58		<0.01**	
Streams with lakes	0.98	-0.80		0.03*	
Juvenile coho CPUE	0.76	-0.63	0.36*	<0.01**	

**Note:** The results shown are from the analysis of covariance or regression model providing the best fit as described in the Materials and methods. Only significant results are shown (see Table 2 for a complete listing of all variables tested). When the interaction term was significant, the model was recast as separate linear regression models with and without lakes; results are shown only when either of the two recast models was significant. \*Significant ( $p < 0.05$ ); \*\*highly significant ( $p < 0.01$ ); ns, not significant.

was significantly greater in nonlake streams (Table 2). The cumulative abundance of EPT taxa in lake-fed streams was low (Fig. 3). Gastropods were found only in the oldest lake system, Berg Bay North Stream, while oligochaetes were found in nine of the 16 streams including the three youngest streams with lakes (Fig. 3). Total macroinvertebrate densities ranged from 3750 to 5700·m<sup>-2</sup> in lake-influenced streams and from 120 to 2750 m<sup>-2</sup> in non-lake-fed streams.

Percent fish cover was significantly greater in stream reaches downstream of lakes (Table 2), but no other fish habitat, fish abundance, or fish diversity variables were significantly influenced by the presence of upstream lakes.

### Influence of stream age on stream habitat and biotic communities

#### *Stream habitat and physicochemical variables*

Younger streams were significantly more turbid than older streams, but fish habitat development, in terms of the percentage of pools, fish cover habitat, and instream wood, all significantly increased with stream age (Table 3). CBOM was significantly more abundant in older streams lacking lakes. No other physical (e.g., channel stability) or water quality variables were significantly affected by stream age.

#### *Biotic communities*

The number of microcrustacean taxa significantly increased with stream age (Table 3), with a total of 20 taxa collected in the 16 streams. Meiofaunal abundance and stream age were not significantly associated. Distinct patterns of coloniza-

tion were shown within the Harpacticoida. *Maraenobiotus brucei*, *Maraenobiotus isignipes*, *Moraria affinis*, and *Epactophanes richardi* were found in streams under 140 years old. Two species of *Atheyella* (*illinoisensis* and *idahoensis*) co-occurred with these species in streams aged between 140 and 200 years, whereas *Nitocra hibernica* was present only in the Carolus River (age >200 years).

Macroinvertebrates exhibited much greater diversity (128 taxa in the 16 streams) than meiofauna but were less abundant. The number of macroinvertebrate taxa showed a significant positive relationship with stream age (Table 3). However, no significant relationships were apparent between stream age and total invertebrate abundance or the diversity measures (Shannon index and 1/Simpson's index). The number of EPT genera significantly increased with stream age. Relative to other members of EPT genera, percent Ephemeroptera was highly correlated with stream age for streams without lakes. Conversely, Chironomidae were significantly less abundant in older streams lacking lakes.

Fish species diversity and juvenile coho and total fish CPUE were all significantly greater in older streams (Table 3), whereas catches of juvenile Dolly Varden were similar in streams of all ages.

### Influence of habitat variables on invertebrate and fish assemblages

#### *Invertebrates*

Microcrustacean diversity was positively related to fish cover, percent instream wood, and percent pool habitat (Ta-

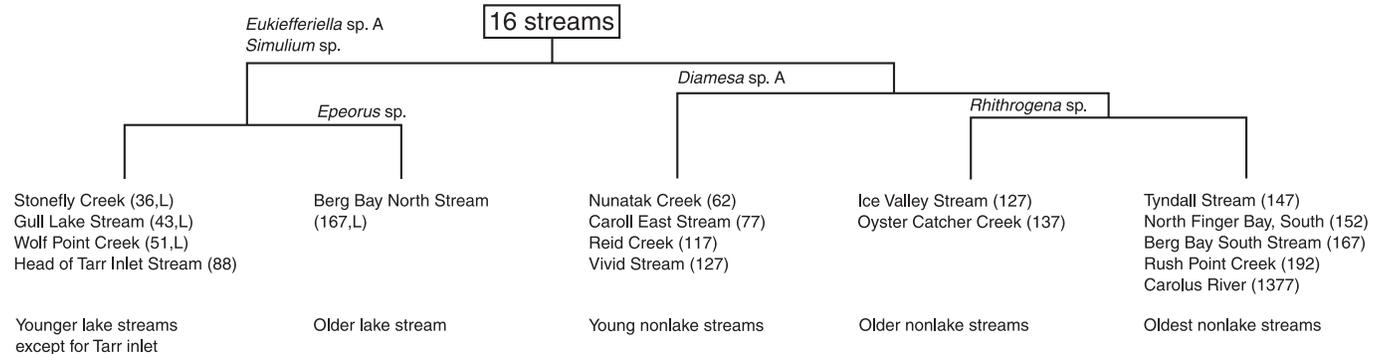
**Table 4.** Parameter estimates from analysis of covariance models testing for the effects of physicochemical variables on stream biotic factors.

Biotic variable	Model $R^2$	Parameter estimate			
		Intercept	Lakes	Physicochemical variable	Interaction
<b>Gradient (at study site, %)</b>					
Total macroinvertebrate abundance	0.91	30.84	540.23**	4 409.82	-21 731.07*
Streams with no lakes	ns				
Streams with lakes	0.94	571.06		-17 321.25*	
Meiofaunal abundance (excluding microcrustaceans)	0.53	768.67	4263.05**	45 102.56	
Dolly varden CPUE	0.25	0.01		28.02*	
<b>Entrenchment</b>					
Total microcrustacean abundance	0.87	-858.37	-1374.92	912.35**	1 391.76**
Streams with no lakes	0.61	-858.37		912.35**	
Streams with lakes	0.94	-2233.28		2 304.12*	
<b>Pfankuch index, bottom component</b>					
Shannon index ( $H$ )	0.44	1.32	-0.21	-0.02*	
No. of macroinvertebrate taxa	0.27	29.04		-0.36*	
1/Simpson's index ( $1/S$ )	0.38	8.60	-1.69	-0.13*	
MDN in fish	0.47	-55.31	116.45*	1.88	-3.42*
Streams with no lakes	0.58	-55.31		1.88*	
Streams with lakes	ns				
<b>Conductivity (<math>\mu\text{mho}\cdot\text{cm}^{-1}</math>)</b>					
Fish species diversity	0.49	-0.53	4.15*	0.15	-0.58*
Streams with no lakes	0.42	-0.53		0.15	
Streams with lakes	ns				
All fish CPUE	0.44	-0.72	9.99*	0.21	-1.32*
Streams with no lakes	0.36	-0.72		0.21*	
Streams with lakes	ns				
Dolly Varden CPUE	0.51	-0.58	-0.40*	0.14**	
<b>Alkalinity (<math>\text{mg}\cdot\text{L}^{-1}</math>)</b>					
Total microcrustacean abundance	0.7	2911.62	2593.82**	-37.66*	
<b>Total nitrogen (<math>\mu\text{g}\cdot\text{L}^{-1}</math>)</b>					
Total macroinvertebrate abundance	0.92	8.21	613.01**	0.61	-2.80*
Streams with no lakes	0.49	8.21		0.61*	
Streams with lakes	ns				
Total microcrustacean abundance	0.48	517.60	2566.19**	1.88	
<b>Total phosphorus (<math>\mu\text{g}\cdot\text{L}^{-1}</math>)</b>					
% Trichoptera	0.37	0.01	-0.006	-0.0001*	
Shannon index ( $H$ )	0.35	0.70	-0.002*		
Number of macroinvertebrate taxa	0.44	19.88	-0.07**		
Dominance ( $D$ )	0.29	0.38	0.001*		
<b>Temperature (<math>^{\circ}\text{C}</math>)</b>					
Total macroinvertebrate abundance	0.9	194.01	343.20**	-23.69*	
Dominance ( $D$ )	0.34	0.21		0.05*	
<b>Turbidity (NTU)</b>					
No. of macroinvertebrate taxa	0.35	17.64	5.47	-0.07*	
No. of microcrustacean taxa	0.37	5.26	1.73	-0.03*	
Total microcrustacean abundance	0.42	965.87	2 124.14*	-11.09	
Meiofaunal abundance (excluding microcrustaceans)	0.74	1721.62	4 964.66**	-24.25**	
<b>CBOM (<math>\text{mg}\cdot\text{L}^{-1}</math>)</b>					
% Ephemeroptera	0.81	0.03	-0.35**	0.69*	
% Chironomidae	0.83	0.82	0.35**	-0.67**	
No. of EPT genera	0.58	1.72	-0.35	6.52**	
% MDN in fish	0.29	39.41		-32.02*	
<b>Fish cover</b>					
Fish species diversity	0.28	0.03	-0.35	0.02*	
All fish CPUE	0.3	-0.17	-0.42	0.03*	
Coho CPUE	0.6	-0.24	-0.43*	0.02**	

**Table 4** (concluded).

Biotic variable	Model $R^2$	Parameter estimate			
		Intercept	Lakes	Physicochemical variable	Interaction
<b>% instream wood</b>					
No. of EPT genera	0.52	3.47	-2.43	0.24**	
No. of macroinvertebrate taxa	0.58	10.20	0.39	0.57**	
No. of microcrustacean taxa	0.45	2.50	-0.03	0.19**	
All fish CPUE	0.55	0.27	-1.97*	0.03**	0.14
Streams with no lakes	0.34	0.27		0.02*	
Streams with lakes	ns				
Juvenile coho CPUE	0.67	-0.08	-0.15	0.03**	
CBOM (mg·L <sup>-1</sup> )	0.28	0.37	-0.18	0.02*	
<b>% pool habitat</b>					
No. of macroinvertebrate taxa	0.55	11.96	3.01	2.01**	
No. of microcrustacean taxa	0.27	4.07		0.19*	
Juvenile coho CPUE	0.34	0.15	0.03	0.03*	
<b>% bank vegetation</b>					
% Trichoptera	0.76	-0.01	0.01*	0.0002*	-0.0003**
Streams with no lakes	0.73	-0.01		0.0002**	
Streams with lakes	ns				

**Note:** The results shown are from the analysis of covariance or regression model providing the best fit as described in the Materials and methods. Only significant results are shown (see Table 2 for a complete listing of all variables tested). When the interaction term was significant, the model was recast as separate linear regression models with and without lakes; results are shown only when either of the two recast models was significant. \*Significant ( $p < 0.05$ ); \*\*highly significant ( $p < 0.01$ ); ns, not significant.

**Fig. 4.** TWINSPLAN classification of the 16 stream sites into five groups using 128 macroinvertebrate taxa collected in May 1997. Indicator taxa for divisions are given.

ble 4). Microcrustaceans were more abundant in streams exhibiting greater entrenchment, reduced alkalinity, and greater total nitrogen. Microcrustacean diversity and abundance and meiofaunal abundance (excluding microcrustaceans) were negatively related to stream turbidity. Meiofaunal abundance (excluding microcrustaceans) was greater in higher gradient streams (Table 4). Meiofaunal community indices did not exhibit significant relationships with CBOM or the Pfankuch stability index.

Total macroinvertebrate abundance was significantly greater in low-gradient streams and in streams with warmer temperatures (Table 4). Macroinvertebrate abundance was significantly related to total nitrogen in streams without lakes. The number of macroinvertebrate taxa was inversely related to total phosphorus and turbidity but positively related to increased channel stability, percent instream wood, and percent pool habitat. Macroinvertebrate diversity (Shannon index) was significantly correlated with the Pfankuch stability

index (Table 4). Species dominance was directly related to total phosphorus and temperature.

The number of EPT genera was directly related to CBOM, fish cover, and percent instream wood but was lower in streams with steeper gradients (Table 4). Percent Trichoptera was highly correlated with total phosphorus and percent bank vegetation in streams lacking lakes. Percent Plecoptera was greater in streams with lower gradients. Percent Ephemeroptera was greater in streams of lower gradient, greater CBOM, and fish cover, whereas percent Chironomidae was greater in streams of higher gradient but less CBOM and fish cover (Table 4).

TWINSPLAN identified two major groups of streams at the first division: the four lake streams and the 12 nonlake streams except Head of Tarr Inlet stream, which was included with the lake-influenced streams (Fig. 4). Indicator taxa for lake streams were primarily Diptera including *Eukiefferiella rectangularis*, *Orthocladius/Cricotopus* sp., and *Simulium* sp.

**Table 5.** Parameter estimates from analysis of covariance models testing for the effects of biotic variables on fish.

Fish community variable	Model $R^2$	Parameter estimate			
		Intercept	Lake effect	Biotic variable	Interaction
<b>% Chironomidae</b>					
All fish CPUE	0.61	1.06	26.42**	-1.12**	-30.33**
Streams with no lakes	0.37	1.06		-1.12*	
Streams with lakes	ns				
<b>% Plecoptera</b>					
% MDN in fish	0.46	23.02	-26.89	-155.14	1410.88*
Streams with no lakes	ns				
Streams with lakes	0.91	-3.87		1255.74*	
<b>No. of EPT genera</b>					
All fish CPUE	0.65	0.29	-2.02*	0.05**	0.52**
Streams with no lakes	ns				
Streams with lakes	0.95	-1.73		0.57*	
Juvenile coho CPUE	0.31	-0.12		0.07*	
<b>Shannon index (<math>H'</math>)</b>					
All fish CPUE	0.64	0.67	-4.42**	-0.11**	6.93**
Streams with no lakes	ns				
Streams with lakes	0.99	-3.74		6.83**	
<b>No. of microcrustacean taxa</b>					
Fish species diversity	0.3	-0.01		0.08*	
All fish CPUE	0.36	-0.20		0.18*	
Juvenile coho CPUE	0.39	-0.15		0.09**	

**Note:** The results shown are from the analysis of covariance or regression model providing the best fit as described in the Materials and methods. Only significant results are shown (see Table 2 for a complete listing of all biotic and fish variables tested). When the interaction term was significant, the model was recast as separate linear regression models with and without lakes; results are shown only when either of the two recast models was significant.

\*Significant ( $p < 0.05$ ); \*\*highly significant ( $p < 0.01$ ); ns, not significant.

The second division separated Berg Bay North, the oldest lake system, from the other lake-influenced streams, with the mayfly *Epeorus* as an indicator taxon. The division for nonlake systems separated the younger streams (<120 years except for Vivid stream) from the older streams, with the chironomid *Diamesa* sp. A the indicator of younger streams. The last division separated older nonlake streams into those 120–140 years and those >140 years using *Rhithrogena* as the indicator taxon (Fig. 4).

Among the Ephemeroptera genera, distinct patterns of colonization were apparent according to stream age. Only *Baetis* was collected in streams <50 years, while *Cinygmula* was added to the fauna in streams between 50 and 100 years. Between 100 and 150 years, *Drunella*, *Epeorus*, and *Rhithrogena* were present, and *Ameletus* also was found in the oldest post-Neoglacial streams examined (150–200 years).

#### Fish community

Dolly Varden CPUE was greater in streams with steeper gradients and conductivity (Table 4). Fish species diversity and total fish CPUE were positively correlated with conductivity in streams with no lakes but was negatively related to pH in streams with lakes. Juvenile coho and total fish CPUE were positively related to the amount of fish cover habitat and the amount of instream wood. Fish species diversity was also related significantly to the amount of fish cover habitat, while juvenile coho CPUE also was related to the abundance of pool habitat (Table 4). Other physical variables that one might expect to influence juvenile fish diversity and abundance, such as spawning substrate, bank vegetation, gradi-

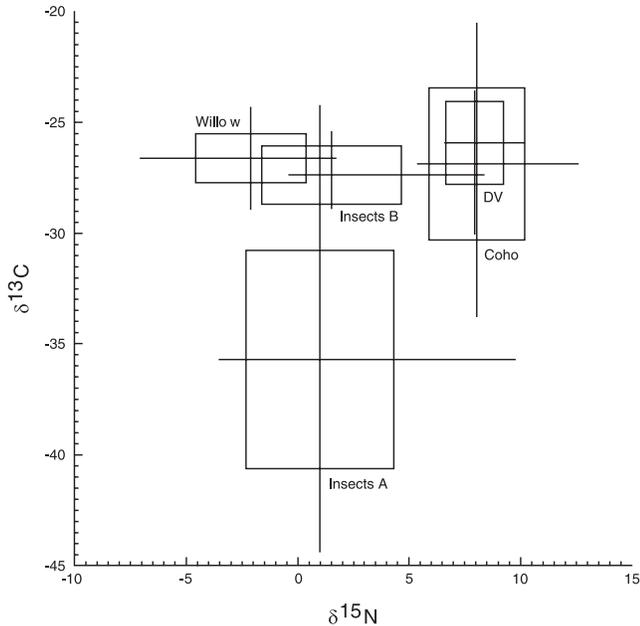
ent, and stream entrenchment, were not significant. MDN in juvenile fish, an indicator of the degree of importance of salmon carcasses in the development of the biotic community, was positively related to the Pfankuch stability index and negatively related to CBOM (Table 4).

All fish CPUE was significantly related to the number of EPT genera in streams with lakes. A similar relationship was found for juvenile coho salmon abundance in all streams (Table 5). All fish CPUE was dependent on the diversity of invertebrates in streams with lakes. Fish species diversity and all fish and juvenile coho CPUE were positively associated with the number of microcrustacean taxa.

#### Isotope analyses

The values of  $\delta^{15}\text{C}$  and  $\delta^{15}\text{N}$  in biological samples from the streams as separated into primary producers (leaves and moss), primary consumers (macroinvertebrates), and secondary consumers (juvenile fish) are summarized in Fig. 5. Carbon isotope ratios of willow leaves ranged from -24 to -29‰, while a single moss sample from Berg Bay North had a value of -41‰. Most insect taxa had  $\delta^{15}\text{C}$  values below -30‰, although values for the caddisflies and stoneflies ranged between -25 and -30‰. Although several juvenile coho salmon were below -30‰, most samples of juvenile Dolly Varden and coho salmon had values in the range -20 to -28‰. Both leaves from riparian vegetation and insects showed a wide range in  $\delta^{15}\text{N}$  values, but most insect values overlapped with those of the leaves and stream moss. The  $\delta^{15}\text{N}$  value of moss, at 4‰, was more enriched than willow leaves, which ranged from -7 to 2‰. Similarly, Chironomidae and

**Fig. 5.** Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (intersection of lines) for willow ( $n = 24$ ), insects A (Baetidae, Chironomidae, Ephemerellidae, Heptageniidae, and Simuliidae;  $n = 37$ ), insects B (Plecoptera and Trichoptera;  $n = 7$ ), Dolly Varden (DV) ( $n = 9$ ), and coho salmon fry ( $n = 15$ ). Boxes represent  $\pm 1$  SD and lines 95% percentiles.



Ephemeroptera from Berg Bay North were enriched relative to samples from several other streams, although most values were below 6‰. Juvenile salmonids, notably from Berg Bay North and Gull Lake, had enriched  $\delta^{15}\text{N}$  values above 7‰. No statistical analyses of the isotope data were undertaken.

## Discussion

### Patterns of meiofaunal colonization

Meiofauna found in all 16 streams sampled in May 1997 had colonized even the youngest stream (Stonefly Creek, 36 years old). Colonization involves dispersal from other stream systems, and, unlike insect members of the macroinvertebrate community, meiofauna do not possess winged dispersal stages. Many meiofaunal taxa, however, have stages in their life cycles that are resistant to adverse environmental conditions such as desiccation and freezing (Kolasa 2000). These organisms may be dispersed between stream systems by wind, waterfowl, and other animals. For example, ectoparasitic Hydrachnidia may be dispersed attached to host adult insects (DiSabatino et al. 2000). Newly deglaciated areas of Glacier Bay also often possess extensive wetlands that are important breeding grounds for Canada geese. High waterfowl densities may play an important role in the initial dispersal of meiofauna to newly formed streams that are close to these wetlands (Robertson and Milner 1999).

Microcrustacean diversity, like macroinvertebrate diversity, increased with stream age due to greater numbers of harpacticoid copepods being present in older streams, confirming an earlier study of five Glacier Bay streams (Robertson and Milner 1999). The lack of a relationship between meiofaunal abundance and diversity with CBOM was surprising, given

the findings of the earlier study (Robertson and Milner 1999) and as most meiofaunal taxa are primary consumers feeding on complex biofilm communities present on CBOM.

The meiofaunal community exhibited significant associations with indicators of habitat complexity (CWD, entrenchment, and percent pools). Meiofauna decline markedly following spates (Palmer et al. 1992; Robertson et al. 1995) but can be resilient to these disturbances depending on the availability of instream flow refugia (Robertson 2000). CWD, an important in-stream refuge during spates (Golladay and Hax 1995), is rare in stable Glacier Bay channels but its accumulation in older stable stream channels may allow the survival of a higher proportion of the community following high flows, thus resulting in a more abundant meiofaunal community. Additionally, stable channels in Glacier Bay develop mats of filamentous algae and moss that may provide small-scale refugia for meiofauna and a food source of trapped fine organic material.

The increase in the number and densities of meiofaunal taxa with increasing percentage of pools is consistent with the findings that lotic meiofauna, particularly cyclopoid copepods and chydorid/macrothricid Cladocera, are characteristically found in slow-water habitats in streams (Vila 1989). Chydorid cladocerans were only found in the two older streams that had highly developed pool habitat. Fine glacial silt may interfere with lotic meiofaunal feeding and account for the lower abundance of meiofaunal indices with higher stream turbidity.

The distinct pattern of harpacticoid copepod colonization was in agreement with the earlier study (Robertson and Milner 1999). Substratum type is known to be an important predictor of harpacticoid copepod community structure in both freshwater and marine environments (Hicks and Coull 1983). Our findings are consistent with the hypothesis that the availability of suitable habitat is important in the successful colonization of harpacticoid copepod taxa.

### Macroinvertebrate assemblages in developing streams

The TWINSPAN classification of the 16 stream reaches showed a distinct division of macroinvertebrate assemblages between lake and nonlake systems (except for Tarr Inlet Stream) substantiating the significant differences found for a number of macroinvertebrate metrics between these two types of system. The classification of the nonlake systems into three distinct groups according to age further indicated distinct changes in macroinvertebrate assemblages with stream development.

The lack of a significant association between stream age and total macroinvertebrate abundance indicates that certain groups rapidly colonize and become abundant in new streams. Although adult Chironomidae are not strong fliers, they are relatively light and have high dispersal capacities. The significant decrease in percent Chironomidae with stream age was related, in part, to the three youngest streams being lake influenced. Streams with lakes were shown to have enhanced chironomid populations due to increased bottom stability but reduced Ephemeroptera abundance. The dominant group of Chironomidae in the young streams with lakes was the Orthocladinae (as predicted by Mackay 1992), but in the nonlake systems, the subfamily Diamesinae was predominant.

At the catchment scale, fluctuating flow regimes may create natural disturbances to benthic invertebrate communities by influencing diversity and limiting biotic interactions (Reice 1985) through their affect on habitat stability. Habitat stability is an important determinant of macroinvertebrate community structure that can enhance species diversity (Death and Winterbourn 1995). Similar trends were evident in this study. Stable channel bottoms are a characteristic of Glacier Bay streams flowing from lakes, and both Chironomidae abundance and total macroinvertebrate abundance were an order of magnitude higher in these than in nonlake systems. Where channel bottoms are stable, what factors favor Chironomidae at the expense of other taxa, particularly Ephemeroptera? In stable Glacier Bay stream channels, autochthonous production is enhanced and dense mats of filamentous algae and (or) moss are present on the streambed that may trap fine organic particles and provide food for collectors like Chironomidae rather than ephemeropteran grazers.

Stream temperature was not related to macroinvertebrate taxon richness, as observed by Robinson and Minshall (1998) in two Idaho streams. Stream temperature was a significant variable in ephemeropteran and plecopteran colonization in the long-term study of Wolf Point Creek (Milner 1994). However, differences in seasonal phenology due to heavy snow loads in the more northerly catchments and limited records may have confounded the effect of temperature in our study. Nevertheless, total macroinvertebrate abundance and dominance were significantly related to spot stream water temperatures.

Aquatic insects have a clear advantage over noninsect taxa for dispersal to, and colonization of, new habitat, although adult insects do not disperse to the same extent. *Baetis* and Simuliidae have been reported to be rapid colonizers of small, disturbed patches where upstream sources of larvae are present (Matthaei et al. 1996). In concord with other studies of macroinvertebrate colonization (Lake and Doeg 1985), *Baetis* were the first ephemeropteran colonizers of the youngest streams, and successional colonization patterns evident within this group indicate the presence of additional taxa with increasing stream age. Moreover, no loss of taxa with increasing stream age was found.

Is the relationship between mayfly colonization and stream age a function of dispersal constraints among different taxa? A number of recent studies have indicated that adult insects do not disperse long distances from their natal stream, typically <100 m (Collier and Smith 1998; Griffith et al. 1998). Chance oviposition by a few female insects can, however, lead to the establishment of dense larval populations (Bunn and Hughes 1997). Also, habitat characteristics may influence the distance traveled, since taxa adapted to predictable habitats with less frequency and severity of disturbance may exhibit more limited dispersal (Williams 1988). *Baetis* has been able to disperse 200 km over the last 220 years, whereas *Ameletus* appears only to have dispersed 20 km. It seems unlikely that such a marked difference between these distances would exist due to different adult dispersal abilities, as they are similar morphologically. We have demonstrated that channel stability had no significant relationship with the number of EPT taxa, and our qualitative observations of periphyton and diatom diversity indicated no marked increase with stream age. The number of EPT taxa did show a significant increase

with the amount of instream wood and CBOM inputs from the maturing forests that develop in the watershed, as suggested by Williams and Smith (1996). Percent Trichoptera in the benthos was significantly correlated with percent bank vegetation, as also found by Harrison et al. (2000) who showed that *Agapetus* larval distribution was closely associated with riparian vegetation, which may be a result of ovipositional cues. Some Trichoptera only disperse within riparian forests (Collier and Smith 1998).

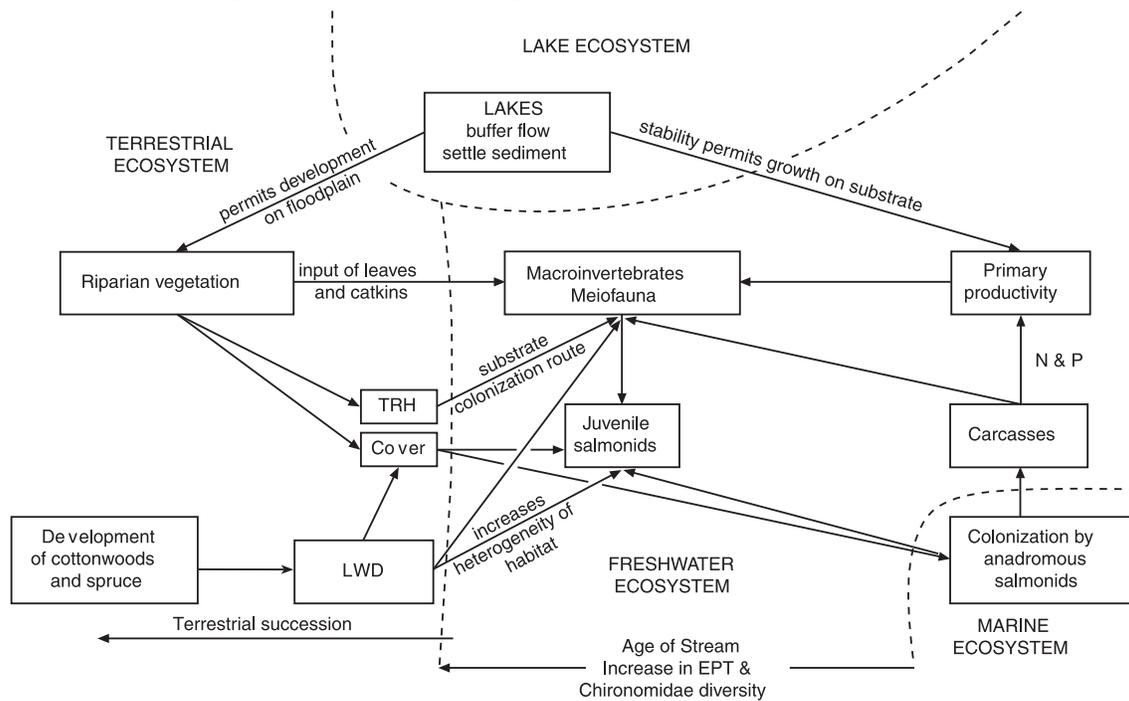
### Colonization by anadromous salmonids

Our results indicate that the colonization and succession of the fish community (abundance and diversity) were strongly related to stream age. More importantly, fish abundance and diversity may be dependent on stream habitat complexity and stability, as indicated by variables such as instream wood, pools, and fish cover. Salmonids were captured in young, recently deglaciated streams, indicating that they are relatively rapid colonizers of newly available habitat. Juvenile coho salmon were captured in 10 of the 16 streams, the youngest an estimated 43 years old. In spite of their well-known tendency to home to their natal streams, straying to other streams is a natural characteristic of salmon (Quinn 1993) to avoid adverse or detrimental local conditions (Pascual et al. 1995), thereby facilitating the colonization and establishment of new populations.

As Dolly Varden were captured in all but three of the 16 streams, including three of the youngest streams, their distribution and abundance among streams were not related to stream age. These findings supports the conclusion of Milner and Bailey (1989) that Dolly Varden are typically the first salmonid colonizers of new streams and that their densities may not be dependent on stream habitat complexity. Armstrong (1974) documented considerable Dolly Varden movement among adjacent stream systems within southeast Alaska that may enhance their colonization rates in adjacent streams relative to other salmonid species. Milner and Bailey (1989) captured no salmonids in Wolf Point Creek in seven samplings from 1977 to 1985, approximately 31–39 years after the mouth was deglaciated. We captured both juvenile coho salmon and Dolly Varden in Wolf Point Creek. Juvenile coho salmon association with pool habitat and instream wood reflects their preference of pools for surface feeding and wood for cover (Nielsen 1992).

Our work provided new opportunities to explore some of the physicochemical variables that influence fish abundance and diversity. The influence of upstream lakes on the amount of fish cover habitat results from the stabilizing effects of lakes. Flooding or severe drought is less frequent downstream of these lakes, allowing more complex habitat features to establish. Fish species diversity was positively related to conductivity. As expected, the availability of prey items influenced fish abundance and diversity. Fish were more abundant where there were more EPT genera and higher macroinvertebrate diversity in streams with lakes, and there was increased fish species diversity when a greater number of microcrustacean taxa occurred. The importance of stream invertebrates indicates a further successional synergism between the development of stream habitat complexity, macroinvertebrate and meiofaunal assemblages, and the fish community.

**Fig. 6.** Conceptual summary showing the proposed linkages between the different ecosystems as stream development proceeds following glacial recession. TRH, trailing riparian habitat; LWD, large woody debris.



### Role of terrestrial- and marine-derived nutrients

As no corrections for trophic enrichment of carbon or alterations of  $\delta^{15}\text{N}$  from nitrification/denitrification have been applied to our stable nitrogen and carbon ratio data, the approximations of marine nitrogen content may be an overestimate. Nevertheless, the marked enrichment in Berg Bay North Stream over most other streams with little or no salmon runs implies that the effect of salmon colonization on the stream and streamside biota follows quickly after colonization. Other streams showed intermediate values that may have resulted from minor inputs of marine nitrogen.

Nitrogen isotope ratios reflect both food source and the trophic status of the consumer (Hobson and Welch 1992). As nitrogen in food is assimilated, the heavy isotope is enriched by approximately 3‰ with accompanying loss of the lighter isotope through excretion. Enrichment occurs with each trophic step and allows the testing of conceptual models about food webs and the assignment of trophic status to species for which dietary data are sparse. Using the mixing model of Kline et al. (1990) from southeast Alaska, primary producers would have a range of 0‰ (0% MDN) to 6.5‰ (100% MDN) and herbivorous insects 3 to 9.5‰. Willow leaf samples from riparian vegetation ranged from -7 to 1.7‰, with the highest value being from Berg Bay North, which supported the largest salmon runs, and implying uptake of MDN from decaying salmon. Ben-David et al. (1998) reported pronounced enrichment in vegetation up to 50 m from streams on Chicagof Island in southeast Alaska. The  $\delta^{15}\text{N}$  value of the one moss sample from Berg Bay North, at 3.5‰, was more enriched than willow samples from the same stream. Similarly, Chironomidae and Ephemeroptera (insects A) from Berg Bay North Stream were enriched relative to samples from other creeks sampled with values of 2.7

and 4.6‰. Subsequent investigations in the spring of 1998 following a very large run of pink salmon in 1997 gave average values for this group of insects of 5.3‰ (D. Schell and A.M. Milner, unpublished data). Most other insects from group A had  $\delta^{15}\text{N}$  values in the negative range, as would be expected from purely terrestrial sources of nitrogen. Kline et al. (1990) suggested a range of 6.5 to 12.5‰ for primary carnivores like juvenile salmonids. Juvenile coho salmon from Berg Bay North at 7.4‰ and from Vivid Lake stream at 7.9‰ clearly indicated some marine enrichment. In 1998, average values for juvenile coho salmon from Berg Bay North were 10.2‰ (D. Schell and A.M. Milner, unpublished data). These data from spring 1998 substantiated the findings from the May 1997 study.

It can be postulated that the natural stable isotope levels of stream biota will shift because of changes in trophic level, food web structure, and primary productivity in stream ecosystems as salmon runs become more abundant. In streams essentially devoid of biota only decades ago, isotopic tracers indicated that allochthonous detritus, potentially autochthonous primary production, and marine-derived nutrients are contributing to the support of instream biota. Carbon isotope ratios of terrestrial vegetation samples reflect the typical  $\delta^{13}\text{C}$  values ranging from -24 to -29‰ and the one moss sample from Berg Bay North indicating the much more  $^{13}\text{C}$ -depleted aquatic primary producers with a  $\delta^{13}\text{C}$  of -41‰. Most insect taxa showed  $\delta^{13}\text{C}$  values below -30‰, indicating that autochthonous primary production was driving much of the system. Peterson et al. (1993) found values of -30 to -32‰ for *Baetis* and -27 to 28‰ for *Brachycentrus* (Trichoptera) in the Kuparuk River, northern Alaska. These authors ascribed the *Baetis* values to feeding on epilithic algae and those of the caddisflies to filter feeding on fine particulate organic

matter derived from allochthonous organic matter. Our own data on caddisflies and stoneflies also show a strong dependence on allochthonous production with  $\delta^{13}\text{C}$  values typical of terrestrial vegetation, although some diatoms have similar values (France 1996). The  $\delta^{13}\text{C}$  values for fish showed a mix of carbon sources. Although several juvenile coho salmon were below  $-30\text{‰}$ , indicating a composition derived from freshwater insects, the range of  $-20$  to  $-28\text{‰}$  for most Dolly Varden and coho fry indicates a mixture of marine carbon derived from ingested salmon spawn or tissue (greater than  $-21\text{‰}$ ) and freshwater-derived food.

### Conceptual summary of stream development

From the information gained during this study, we have constructed a conceptual summary of the linkages between major ecosystems: lake, stream, terrestrial, and marine (Fig. 6). Previous studies have made it clear that major lakes buffer flows and permit terrestrial vegetation development on the floodplain earlier than might otherwise be expected (Milner 1997). This vegetation provides a positive feedback by intercepting runoff, thereby further enhancing channel stability, and provides inputs of leaves and catkins that are important food sources for a number of macroinvertebrate taxa (Flory and Milner 1999b). Trailing roots from a close border of riparian vegetation may act as a route to colonization of the benthos by certain taxa, particularly stoneflies, and provide cover for juvenile salmon and adult spawning fish. The accumulation of CBOM and instream wood may be essential for colonization by many EPT taxa. Riparian vegetation also provides cover for rearing juvenile salmon and adult spawning fish. As terrestrial succession proceeds and mixed stands of cottonwoods and Sitka spruce develop, increased inputs of CWD will provide greater habitat diversity (riffles, runs, and pools) and enhance fish species diversity and juvenile coho salmon abundance. CWD also will potentially increase channel stability and provide habitat for macroinvertebrates. As stream channel stability increases, particularly where lakes are present, the number of spawning salmon and juvenile salmon will increase. Salmon carcasses will, in turn, provide an influx of nutrients from the marine ecosystem, which become incorporated into both primary and secondary producers (invertebrates and juvenile fish) within the stream and potentially into vegetation along the stream margins. Further evaluation of the relationships within this conceptual summary will provide for more informed decisions about stream management, both for protecting pristine streams and for rehabilitating streams in watersheds that have been degraded.

### Acknowledgements

We thank Carol Woody, Kevin Sage, John Sargent, Robert Schmech, and Kim Scribner for assistance in the field and laboratory. Norma Haubensstock performed the isotope ratio mass spectrometry. We are grateful to the National Park Service for supplying the MV *Stellar* and to her captain Dan Foley and first mate Rocky Wood for putting us at the stream estuaries with good cheer. Greg Streveler provided most of the dates for stream deglaciation. We thank Profs. Ken Stewart and Glenn Wiggins for assistance in the identification of the caddisflies and stoneflies and Dr. Steve Burian for iden-

tification of the mayflies. Dr. Endre Willassen examined the chironomids. We are particularly grateful to the Alaska Department of Fish and Game Limnology Laboratory in Soldotna, particularly Ginny Litchfield and Jim Edmundson, for analysis of the water samples. Comments by Dr. Chris Robinson, Prof. Mike Winterbourn, and two anonymous reviewers significantly improved the manuscript. A.M.M. and A.L.R. acknowledge the support of the National Environment Research Council of the United Kingdom (grant GR9/2913) for funding towards this research.

### References

- Armstrong, R.H. 1974. Migration of anadromous Dolly Varden (*Salvelinus malma*) in Southeastern Alaska. *J. Fish. Res. Board Can.* **31**: 435–444.
- Ben-David, M., Hanley, T.A., and Schell, D.M. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. *Oikos*, **83**: 47–55.
- Berger, W.H., and Parker, F.L. 1970. Diversity of planktonic Foraminifera in deep sea sediments. *Science (Washington, D.C.)*, **168**: 1345–1347.
- Bilby, R.E., and Fransen, B.R. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Can. J. Fish. Aquat. Sci.* **53**: 164–173.
- Bryant, M.D., Wright, B.E., and Davies, B.J. 1992. Application of a hierarchical habitat unit classification system: stream habitat and salmonid distribution in Ward Creek, Southeast Alaska. *USDA For. Serv. Pac. NW Res. Stn. Res. Note PNW-RN-508*.
- Bunn, S.E., and Hughes, J.M. 1997. Dispersal and recruitment in streams: evidence from genetic studies. *J. North Am. Benthol. Soc.* **16**: 338–346.
- Cederholm, C.J., and Peterson, N.P. 1985. The retention of coho salmon (*Oncorhynchus kisutch*) carcasses by organic debris in small streams. *Can. J. Fish. Aquat. Sci.* **42**: 1222–1225.
- Chapin, F.S., III, Walker, L.R., Fastie, C.L., and Sharman, L.C. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecol. Monogr.* **64**: 149–175.
- Collier, K.J., and Smith, B.J. 1998. Dispersal of adult caddisflies (Trichoptera) into forests alongside three New Zealand streams. *Hydrobiologia*, **361**: 53–65.
- Death, R.G., and Winterbourn, M.J. 1995. Diversity patterns in stream benthic invertebrates: the influence of habitat stability. *Ecology*, **76**: 1446–1460.
- DiSabatino, A., Gerecke, R., and Martin, P. 2000. Lotic meiofauna IV. Hydracarina. *Freshwater Biol.* **44**: 47–62.
- Downes, B.J., and Keough, M.J. 1998. Scaling of colonization processes in streams: parallels and lessons from marine hard substrata. *Aust. J. Ecol.* **23**: 8–26.
- Fisher, S.G. 1990. Recovery processes in lotic ecosystems. *Environ. Manage.* **14**: 725–736.
- Flory, E.A., and Milner, A.M. 1999a. The role of competition in invertebrate community development in a recently formed stream in Glacier Bay National Park, Alaska. *Aquat. Ecol.* **33**: 175–184.
- Flory, E.A., and Milner, A.M. 1999b. Influence of riparian vegetation on invertebrate assemblages in a recently formed stream in Glacier Bay National Park, Alaska. *J. North Am. Benthol. Soc.* **18**: 261–273.
- Flory, E.A., and Milner, A.M. 2000. Macroinvertebrate community succession in Wolf Point Creek, Glacier Bay National Park, Alaska, U.S.A. *Freshwater Biol.* **44**: 465–480.

- France, R.L. 1996. Scope for the use of stable carbon isotopes in discerning the incorporation of forest detritus into aquatic food-webs. *Hydrobiologia*, **325**: 219–222.
- Fry, B. 1999. Using stable isotopes to monitor watershed influences on aquatic trophodynamics. *Can. J. Fish. Aquat. Sci.* **56**: 2167–2171.
- Gannes, L.Z., O'Brien, D.M., and del Rio, C.M. 1997. Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. *Ecology*, **78**: 1271–1276.
- Golladay, S.W., and Hax, C.L. 1995. Effects of an engineered flow disturbance on meiofauna in a north Texas prairie stream. *J. North Am. Benthol. Soc.* **14**: 737–753.
- Gore, J.A. 1982. Benthic invertebrate colonization: source distance effects on community composition. *Hydrobiologia*, **94**: 183–193.
- Gore, J.A., and Milner, A.M. 1990. Island biogeographical theory: can it be used to predict lotic recovery rates? *Environ. Manage.* **14**: 737–753.
- Griffith, M.B., Barrows, E.M., and Perry, S.A. 1998. Lateral dispersal of adult aquatic insects (Plecoptera, Trichoptera) following emergence from headwater streams in forested Appalachian catchments. *Ann. Entomol. Soc. Am.* **91**: 195–201.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* **15**: 133–302.
- Harrison, S., Harris, I., Croeze, A., and Wiggers, R. 2000. The influence of bankside vegetation on the distribution of aquatic insects. *Verh. Int. Ver. Limnol.* In press.
- Hicks, B.J., Hall, J.D., Bisson, P.A., and Sedell, J.R. 1991. Response of salmonids to habitat changes. *Am. Fish. Soc. Spec. Publ.* **19**: 83–138.
- Hicks, G.R.F., and Coull, B.C. 1983. The ecology of marine meiobenthic harpacticoid copepods. *Oceanogr. Mar. Biol. Annu. Rev.* **21**: 67–175.
- Hill, M.O. 1979. TWINSPAN — a Fortran programme for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. *Ecology and Systematics*, Cornell University, Ithaca, N.Y.
- Hobson, K.A., and Welch, H.E. 1992. Determination of trophic relationships within a high Arctic marine food web using stable-isotope analysis. *Mar. Ecol. Prog. Ser.* **84**: 9–18.
- Kline, T.C., Jr., Goering, J.J., Mathisen, O.A., Poe, N.P.H., and Parker, P.L. 1990. Recycling of elements transported upstream by runs of Pacific salmon: I.  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  evidence in Sashin Creek, southeastern Alaska. *Can. J. Fish. Aquat. Sci.* **47**: 136–144.
- Kline, T.C., Jr., Goering, J.J., and Piorkowski, R.J. 1997. The effect of salmon carcasses on Alaskan freshwaters. *In Freshwaters of Alaska: ecological syntheses. Edited by A.M. Milner and M.W. Oswood.* Springer-Verlag, New York. pp. 179–204.
- Kolasa, J. 2000. Lotic meiofauna VI. Microturbellaria. *Freshwater Biol.* **44**: 5–14.
- Lake, P.S., and Doeg, T.J. 1985. Macroinvertebrate colonization of stones in two upland southern Australian streams. *Hydrobiologia*, **126**: 199–211.
- Mackay, R.J. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. *Can. J. Fish. Aquat. Sci.* **49**: 617–628.
- Mathisen, O.A., Parker, P.L., Goering, J.J., Kline, T.C., Poe, P.H., and Scanlan, R.S. 1988. Recycling of marine elements transported into freshwater by anadromous salmon. *Verh. Int. Ver. Limnol.* **23**: 2249–2258.
- Matthaei, C.D., Uehlinger, U.R., Meyer, E.I., and Frutiger, A. 1996. Recolonization by benthic invertebrates after experimental disturbance in a Swiss prealpine river. *Freshwater Biol.* **35**: 233–248.
- Milner, A.M. 1987. Colonization and ecological development of new streams in Glacier Bay National Park, Alaska. *Freshwater Biol.* **18**: 53–70.
- Milner, A.M. 1994. Invertebrate colonization and succession in a new stream in Glacier Bay National Park, Alaska. *Freshwater Biol.* **32**: 387–400.
- Milner, A.M. 1997. Glacial recession and freshwater ecosystems in coastal Alaska. *In Freshwaters of Alaska: ecological syntheses. Edited by A.M. Milner and M.W. Oswood.* Springer-Verlag, New York. pp. 303–330.
- Milner, A.M., and Bailey, R.G. 1989. Salmonid colonization of new streams in Glacier Bay, Alaska. *Aquacult. Fish. Manage.* **20**: 179–192.
- Nielsen, J.L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. *Trans. Am. Fish. Soc.* **121**: 617–634.
- Omerod, S.J., Rundle, S.D., Wilkinson, S.M., Daly, G.P., Dale, K.M., and Juttner, I. 1994. Altitudinal trends in the diatoms, bryophytes, macroinvertebrates and fish of a Nepalese river system. *Freshwater Biol.* **32**: 309–322.
- Palmer, M.A., Bely, A.E., and Berg, K.E. 1992. Response of invertebrates to lotic disturbances: a test of the hyporheic refuge hypothesis. *Oecologia*, **89**: 182–194.
- Pascual, M.A., Quinn, T.P., and Fuss, H. 1995. Factors affecting the homing of fall chinook salmon from Columbia River hatcheries. *Trans. Am. Fish. Soc.* **124**: 308–320.
- Peterson, B., Fry, B., Deegan, L., and Hershey, A. 1993. The trophic significance of epilithic algal production in a fertilized tundra river ecosystem. *Limnol. Oceanogr.* **38**: 872–878.
- Pfankuch, D.J. 1975. Stream reach inventory and channel stability evaluation. USDA Forest Service, Region 1, Missoula, Mont.
- Quinn, T.P. 1993. A review of homing and straying of wild and hatchery-produced salmon. *Fish. Res.* **18**: 29–44.
- Reice, S.R. 1985. Experimental disturbance and the maintenance of species diversity in a stream community. *Oecologia*, **67**: 90–97.
- Robertson, A.L. 2000. Lotic meiofauna community dynamics: colonisation, resilience and persistence in a spatially and temporally heterogeneous environment. *Freshwater Biol.* **44**: 135–147.
- Robertson, A.L., and Milner, A.M. 1999. Meiobenthic arthropods in new streams in Glacier Bay National Park, Alaska. *Hydrobiologia*, **397**: 197–209.
- Robertson, A.L., Lancaster, J., and Hildrew, A.G. 1995. Stream hydraulics and the distribution of microcrustacea: a role for refugia? *Freshwater Biol.* **33**: 469–484.
- Robinson, C.T., and Minshall, G.W. 1998. Macroinvertebrate communities, secondary production and life history patterns in two adjacent streams in Idaho, U.S.A. *Arch. Hydrobiol.* **142**: 257–281.
- Rosgen, D.L., and Silvey, H.L. 1996. Applied river morphology. *Wildland Hydrology*, Pagosa Springs, Co.
- Sidle, R.C., and Milner, A.M. 1989. Stream development in Glacier Bay National Park, Alaska, U.S.A. *Arct. Alp. Res.* **21**: 350–363.
- Soiseth, C.R., and Milner, A.M. 1995. Predicting salmonid occurrence from physical characteristics of streams in Glacier Bay National Park and Preserve. *In Proceedings of the Third Glacier Bay Science Symposium, 1993. Edited by D.R. Engstrom.* National Park Service, Alaska System Support Office, Anchorage, Alaska. pp. 174–183.
- Vila, P.B. 1989. The occurrence and significance of Cladocera (Crustacea) in some streams in central Indiana, U.S.A. *Hydrobiologia*, **171**: 201–214.
- Williams, D.D., and Smith, M.R. 1996. Colonization dynamics of

- river benthos in response to local changes in bed characteristics. *Freshwater Biol.* **36**: 237–248.
- Williams, W.D. 1988. Limnological imbalances: an antipodean viewpoint. *Freshwater Biol.* **20**: 407–420.
- Wipfli, M.S., Hudson, J., and Caouette, J. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. *Can. J. Fish. Aquat. Sci.* **55**: 1503–1511.