

Macroinvertebrate community succession in Wolf Point Creek, Glacier Bay National Park, Alaska

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SUMMARY

1. Macroinvertebrate community development in Wolf Point Creek in Glacier Bay National Park, Alaska formed by ice recession was investigated from 1991 to 1994 as part of a long-term study of colonization now exceeding 20 years. Chironomidae, the first taxon to colonize the stream, still dominated the community comprising 75–95% by number, but species succession was apparent.
2. Species richness in August increased from five species in 1978 to 11 in 1991 and 16 in 1994.
3. *Diamesa* species, abundant in 1978 at densities exceeding 2 750 m⁻², were not collected in 1994, while *Pagastia partica* dominated the community with densities exceeding 10 000 m⁻².
4. Sixteen taxa, never previously collected, colonized the stream between 1991 and 1994 including representatives of Coleoptera, Muscidae, Trichoptera, and the first noninsect taxon, Oligochaeta. Colonization by new taxa was associated with an increase in summer water temperature and the development of riparian vegetation.
5. Inter-specific competition is suggested as a possible factor in species succession and is incorporated into a taxa richness model of community development in postglacial streams incorporating stable and unstable channels.

Keywords macroinvertebrate community succession, species richness, Wolf Point Creek

Introduction

Successional studies of macroinvertebrates in streams frequently address only local patch colonization or seasonal changes as opposed to true site-specific change over time, which remains poorly studied (Minshall, 1988). Site-specific temporal succession reflects a change in the pool of potential colonizers present as larvae or nymphs within a stream channel (Milner, 1994). In addition, few studies have documented primary succession in streams, occurring where invertebrates are not initially present as a colonizing source (Fisher, 1983). Several studies document recovery from disturbances on a spatial scale where recolonization is rapid by survivors that remain at the site (e.g. Death & Winterbourn, 1995). The need

for further research on organism responses to disturbance on larger temporal and spatial scales has been highlighted (Minshall, 1988; Power *et al.*, 1988).

The creation of a new stream, Wolf Point Creek, by glacial recession in Glacier Bay National Park, Alaska, between 1945 and 1960 has provided a unique opportunity to study primary succession of invertebrates in a natural stream system at the catchment scale. Macroinvertebrate studies, which commenced in 1978 (Milner, 1987, 1994, 1997), represent the longest record of primary successional changes in a lotic ecosystem. This paper documents changes in the macroinvertebrate community from 1991 to 1994 in Wolf Point Creek and examines the overall chronosequence of changes from 1978 to 1994 following Milner (1994). The principal variables governing the patterns of colonization and successional changes are examined. Using these data we have developed a conceptual model of macroinvertebrate community development in these postglacial streams.

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Methods

Study site

The mouth of Wolf Point Creek, on the western shore of Muir Inlet in Glacier Bay (Fig. 1), was uncovered around 1940. The lake at its head began to form after 1960 and by 1991 the surface area was 1.35 km² with a

maximum depth of 30 m (Milner, 1994). The stream is 2 km long, ≈ 15 m wide and cuts through a bedrock gorge just below the lake, creating a 30-m fall, which acts as a barrier to fish migration, before flowing over unconsolidated glacial moraine, till and outwash deposits with low gradient to the sea. Much of the remnant ice has melted away, and stream turbidity from suspended glacial sediments ranges from 14 to 30

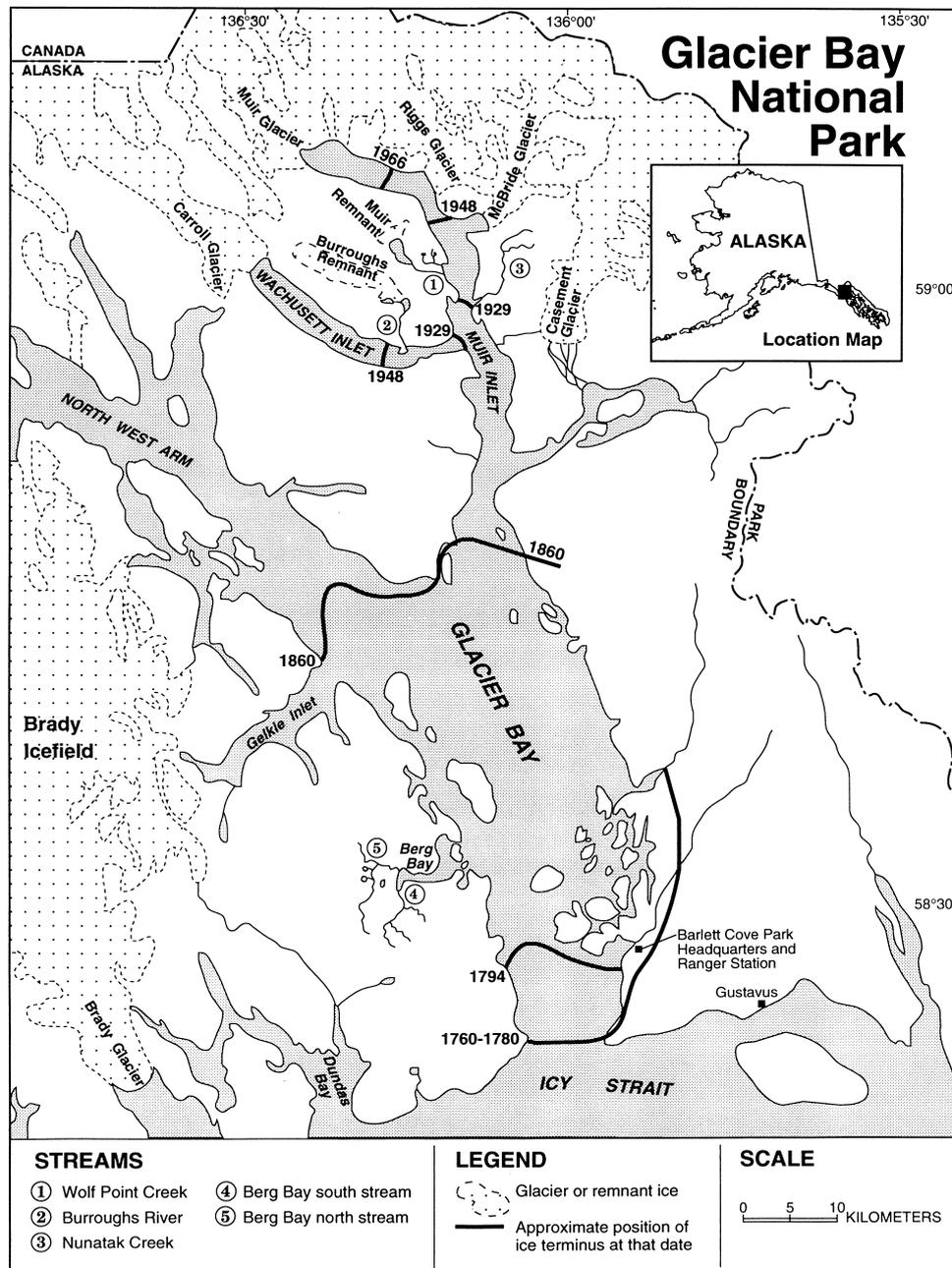


Fig. 1 Map of Glacier Bay National Park in south-east Alaska illustrating the location of Wolf Point Creek and other streams referred to in the text (after Milner, 1994).

NTU. In 1983, upland areas of the floodplain were dominated by alder (*Alnus crispa* Pursch), with isolated clumps, separated by mats of *Dryas*, present on the lower terraces of the originally braided stream channel. By 1996 alders and willows had reached a height of 2.5 m and dominated the floodplain (Milner, 1997).

Invertebrate samples were collected using a modified Surber sampler (area 0.093 m²; mesh 353 µm) from the representative 15 m long stream section established as a sampling station in 1977. Ten replicate samples of invertebrates were collected approximately every 14 days from July to August 1991 and from June to August 1992–94 and preserved in 90% ethanol. Velocity was recorded at 6/10ths depth at the sample location using a Marsh–McBirney flow meter and depth rod. Substrate sizes and epilithic growth on the substrate were estimated qualitatively for each sample. Stream temperature was recorded at the likely maximum daily temperature (mid-afternoon) using a hand-held digital thermometer, but in 1994 continuous temperature recorders (Hobo Stowaway model STBE02) provided measurements every 2 h.

In the laboratory, invertebrates were sorted from detritus in five samples randomly selected from the 10 collected for each sampling occasion and then identified. Head capsules of chironomid larvae were microdissected and mounted in polyvinyl lactophenol for identification. Keys by Wiederholm (1983) and the assistance of Endre Willassen at the Zoological Museum in Bergen, Norway, provided larval identification to species group in most cases. Comparisons were made with earlier voucher specimens collected by A.M. Milner and stored at the School of Geography and Environmental Science, University of Birmingham to ensure continuity of identification. Sample biovolume was calculated as an alternative nondestructive approach with which to estimate biomass (Smit, Van Heel & Wiersma, 1993). Initially equal amounts of water were added to two 10 mL test tubes. An invertebrate sample was added to one tube and water added to the other using a micropipette until the levels were equal. This additional volume was used as an estimate of biovolume.

The number of species in a sample depends on the total number of organisms collected. As this number varies according to invertebrate abundance, species richness is limited as a comparative index. An alternative is to compare counts of species in samples with equal numbers of organisms using rarefaction

(Hurlbert, 1971) to make such comparisons between sampling dates more valid. The computer program, RAREFRAC.BAS (Ludwig & Reynolds, 1988) was applied to compute the number of species expected ($E(Sn)$) in a sample of n individuals drawn from a population of N total individuals distributed among S species where:

$$E(Sn) = S \left\{ 1 - \left[\left(\frac{N-n_i}{n} \right) / \left(\frac{N}{n} \right) \right] \right\}$$

and

$$\left(\frac{N}{n} \right) = N! / n!(N-n)!$$

and

$$\left(\frac{N-n_i}{n} \right) = (N-n_i)! / n!(N-n_i) - n$$

n_i = number of individuals in the i th sample.

Using the field data collected, the number of species expected to be present $\{E(Sn)\}$ at a range of values of n was calculated and a mean $E(Sn)$ computed for each sampling day. Analysis of variance (ANOVA) was applied to compare mean $E(Sn)$ values and identify significant differences ($P < 0.05$) in species richness between sampling periods.

The method of rarefaction may be extended to estimate the number of species shared by two or more samples (Trueblood, Gallagher & Gould, 1994). The contribution of each species to this measure is determined by the probability that it will appear in a sample of m individuals randomly drawn from two populations (Grassle & Smith, 1976). For small sample sizes, only the most abundant species in both populations are represented, while for large m , less abundant species also contribute. The ideal value of m allows both abundant and rare species to contribute to the estimation, and is intermediate between $m = 1$ and the maximum comparable sample size of the data collected. Here, the abundance of each species ' i ' for sampling period ' k ' was replaced by the probability (P_i) of its occurrence over a range of sample sizes, logarithmically spaced between $m = 1$ and $m = 55$:

$$P_i = \left(\frac{N_i - N_{ik}}{m} \right) / \left(\frac{N_i}{m} \right)$$

expanded as above.

For each m , the probabilities of each species being encountered on a particular sampling period were ranked in order of size and plotted against their rank

number. This enabled a value of $m = 8$ to be chosen as an intermediate sample size for species shared estimation.

Principal components analysis (PCA) was then applied to the mean probabilities at this sample size using the program STATVIEW. Commonly, a large proportion of the variation accounted for by a PCA can be attributed to size differences between samples (Jackson, Somers & Harvey, 1989), but the use of probabilities at a fixed sample size avoids this problem. The eigenvectors, representing species loadings on the first two components, were then plotted. Cluster analysis was used to identify groups of species by measuring the absolute distances between all species probabilities using the program CLUSTER.BAS (Ludwig & Reynolds, 1988). The multivariate distance statistic, Mahalanobis D^2 , was then computed between two clusters using the program SDA.BAS to test for significant differences between the groups formed in the cluster analysis.

Multiple linear regression (MLR) was used to reveal the percentage contribution of each species to the ordination by regressing the sampling unit coordinates derived in the PCA with species probabilities using the program PCREG.BAS, as suggested by Trueblood, Gallagher & Gould (1994). MLR was

then used to identify possible relationships between community composition and environmental changes over time. The sampling unit coordinates from the ordination were regressed with the environmental data for temperature, velocity and depth. Data from August 1978–90 were then added into the analysis for comparison.

Results

The dominant substratum consisted of large cobbles (13–26 cm), average depth was 29–37 cm and mean current velocities for each sampling period ranged from 68 to 73.5 cm s⁻¹. All macroinvertebrate densities are expressed as the average number of individuals 0.1 m⁻² (converted from 0.093 m⁻²) unless otherwise stated. In 1991 invertebrate density was relatively low, typically less than 250 with a mean of 138 (Fig. 2). In 1992 the mean was 350 with densities peaking in late June at 509, while in 1993 the peak was 1197 in early July with a mean of 707. The seasonal peak in 1994 occurred in early August at 865; the mean was 595. Biovolumes did not display similar variations over the 4 years except for 1991 when they were relatively low (Fig. 2).

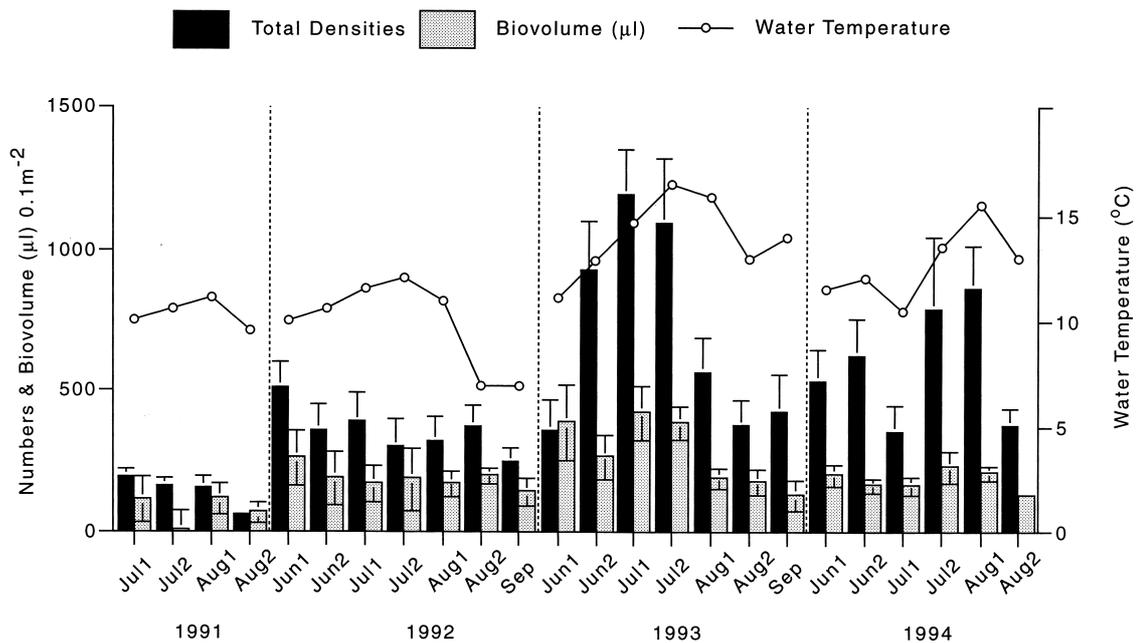


Fig. 2 Total densities and biovolumes of invertebrates (\pm SE) in Wolf Point Creek from 1991 to 1994 with associated maximum daily water temperature (1 = sampled during the first half of the month, 2 = sampled during the second half of the month).

Species richness increased from 11 in July 1991 to 16 in July 1994. The expected number of species in a sample of 500 individuals ($E\{S500\}$) increased from 11 in July 1991 to 13 in June 1992 and 1993 and to 15 in July 1994. Rarefaction revealed that each year, species richness was significantly higher in June or early July ranging from $E\{S500\} = 12\text{--}15$ ($P < 0.05$), declined in late July/early August to $E\{S500\} = 6\text{--}8$ ($P < 0.05$), then increased again in late August to $E\{S500\} = 9\text{--}11$ (not significant $P > 0.05$). P -values are the results of ANOVA comparing species richness for that date with the other dates. The seasonal minima in rarefied species richness typically corresponded to peaks in invertebrate density and vice versa; this was particularly evident for 1993 and 1994 when one species was dominant. The size of E chosen for comparison is limited by the smallest sample size in terms of the number of individuals collected. For the comparison of the 1991 through 1994 data the sample size was 500 but for comparison with the 1978–90 data, the sample size was 50 individuals.

The community was numerically dominated by Chironomidae from 1991 to 1994, typically comprising 75–95%. An exception was *Neaviperla forcipata* (Ricker) which dominated in late July 1991 (Fig. 3). Trichoptera were found in very low densities. Of the Chironomidae, *Pagastia partica* (Roback) dominated between 1992 and 1994 with its abundance increasing tenfold from 1991. *Diamesa sommermani* (Hanson) was not found in 1994 and only a single individual of the *D. davisi* group (Kownacki) was found in late July 1994 and none in August 1992–94. *Paratrichocladius* sp. (previously documented as *Orthocladius* sp. A in Milner, 1983, 1987, 1994) was found in low numbers in 1991 and 1994 but higher densities were collected in 1992 and 1993. *Eukiefferiella gracei* (Kieffer) increased from less than one in August 1991 to 500 in August 1994 and *Tokunagaia* sp. from less than one in 1991 to 80 in 1994. These two species codominated with *P. partica* in August samples. Densities of other chironomids also showed seasonal peaks in abundance; for example *Orthocladius mallochii* (Kieffer) and *Orthocladius manitobensis/obumbratus* (indistinguishable as larvae) but these occurred at different time periods according to year (Fig. 3). Chironomid species collected for the first time between 1991 and 1994 were *Acalcaria* sp., *Brillia* sp., *Chaetocladius vitellinus* (Kieffer), *Orthocladius manitobensis/obumbratus*, *Pseudodiamesa branickii* (Kieffer), *Tanytarsus* sp., *Telmapelopia* sp. and *Tokunagaia* sp.

Eight nonchironomid taxa, never previously found in Wolf Point Creek, were collected between 1991 and 1994. These included the caddis flies *Onocosmoecus* sp., and *Psychoglypha* sp., the empidids *Clinocera* sp. and *Chelifera* sp., the hemipteran *Neocorixa* sp. and unidentified representatives of Muscidae and Oligochaeta. Densities were low, typically less than 5.0 m^{-2} .

The PCA produced a chronological ordering of the samples based on their species composition (Fig. 4a). The first axis (55% of the variation in species probabilities) represented seasonal variation, while the second axis (14% of the variation) reflected interannual variation. The invertebrate communities in 1991, the first half of 1992, and early June 1993, were grouped together indicating strong similarities in species composition. There was a change in the community between late July and early August 1992 and again between early and late June 1993. The seasonal trajectories each year are similar, but in consecutive years the changes occurred earlier. Cluster analysis revealed two distinct groups of communities corresponding to different seasons ($P < 0.001$). No distinction was apparent between communities present in different years (comparing similar months) apart from the separation of the community present in early June 1994.

Several distinct groups of taxa were identified after ordination with PCA that indicated site-specific successional changes (Fig. 4b, axis 1, 55% of the variance, axis 2, 14% of the variance). Taxa clustered in the lower left-hand quadrant of the plot, the *D. davisi* group, *D. sommermani*, *O. mallochii*, *N. forcipata*, and *Baetis* sp. were all more abundant in 1991 or early 1992, but subsequently declined. *Paratrichocladius* sp., which was most abundant in 1992–93, dominated the next quadrant in the plot with *O. manitobensis/obumbratus*. The chironomids *E. gracei*, *E. coerulea* (Kieffer), *E. rectangularis/Toetenia* (indistinguishable) and *P. partica* lie mid-way between the next two quadrants and represent taxa that increased in abundance during 1993–94. At the bottom right quadrant of the plot lies the chironomid *Tokunagaia* sp. which was most abundant in late August of 1993 and 1994.

Multiple linear regression showed that 18 of the 28 taxa contributed more than 1% to the variation in species probabilities. The first axis was negatively correlated with taxa that were more abundant either during 1991–92 or early in the season, particularly

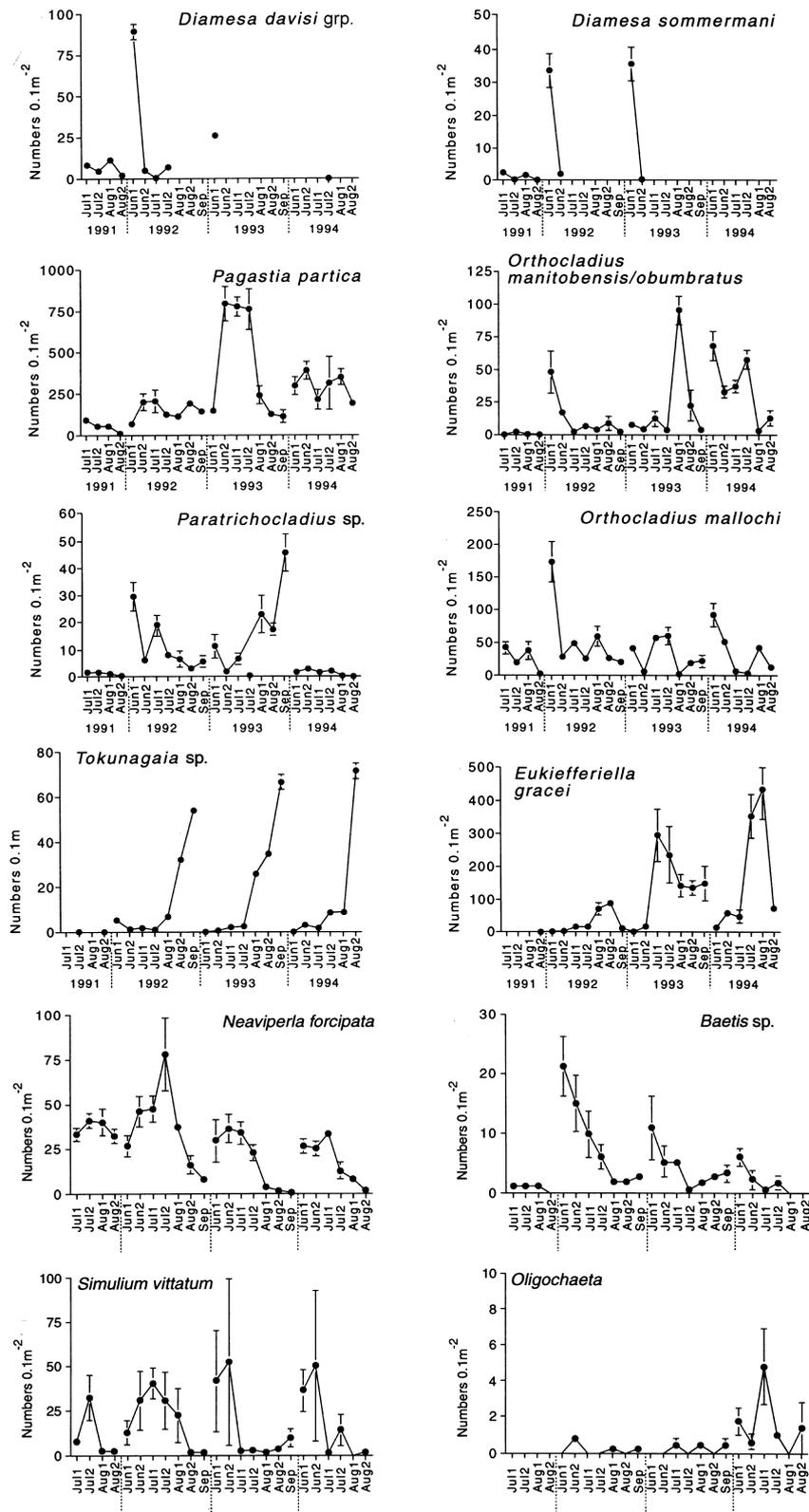


Fig. 3 Mean abundances of key taxa in Wolf Point Creek (\pm SE). Note abundance scales differ between taxa and that where not shown SEs were too small to plot (1 = sampled during the first half of the month, 2 = sampled during the second half of the month).

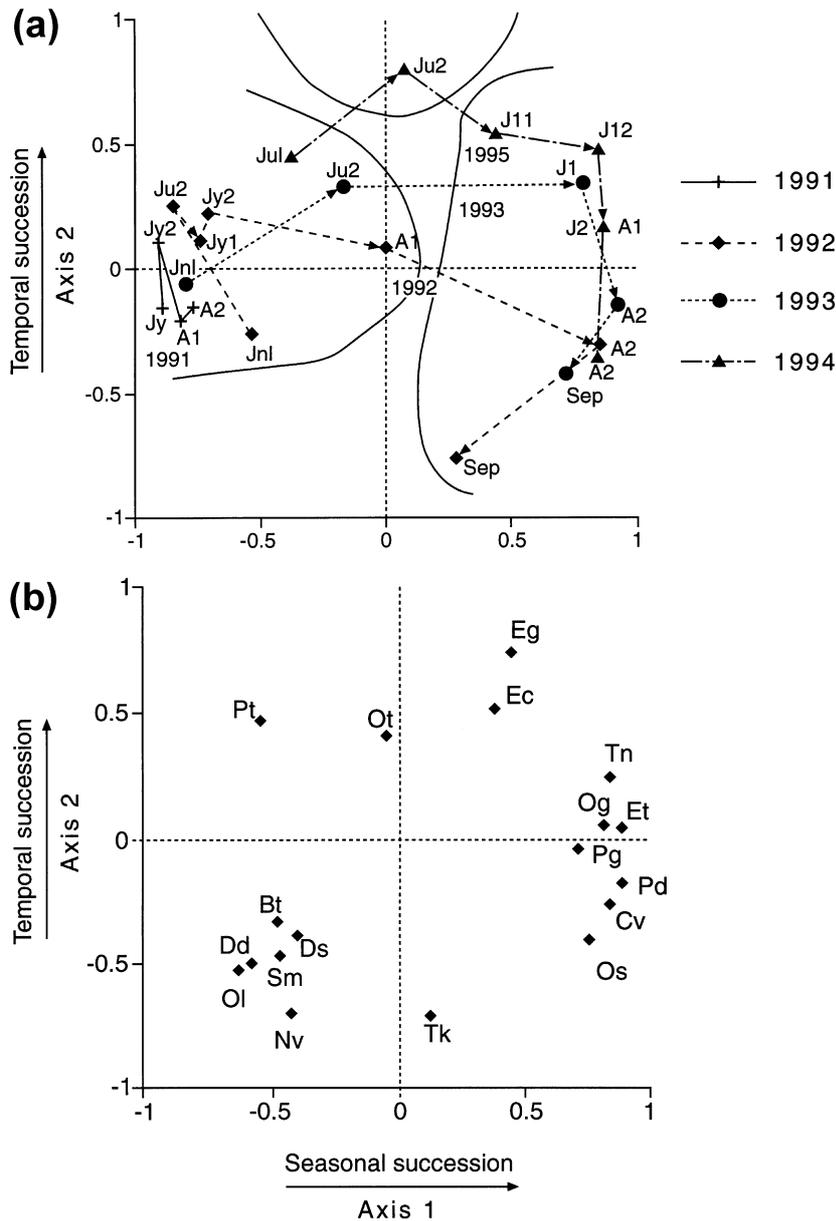


Fig. 4 (a) Ordination of the sample scores in Wolf Point Creek from 1991 to 1994: First two axes of a principal components analysis using the probabilities of each species being present at a fixed sample size (axis 1, 55% of the variance; axis 2, 14%; Jn = June, Jy = July, A = August, Sp = September, 1 = sampled during the first half of the month, 2 = sampled during the second half of the month). Points were separated into three groups by cluster analysis (Mahalanobis $D^2 = 317.164$, $F = 19.26$, $P < 0.001$). (b) First two axes of the species scores from the principal components analysis. Only species that contributed significantly toward the sample ordination pattern are displayed. Bt = *Baetis* sp., Dd = *Diamesa davisii* grp., Ds = *Diamesa sommermani*, Eg = *Eukiefferiella gracei*, Ec = *E. coerulescens*, Et = *E. rectangularis/Tvetenia*, Cv = *Chaetocladius vitellinus*, Nv = *Neaviperla forcipata*, Og = *Oligochaeta*, Os = *Onocosmoecus* sp., Ol = *O. mallochii*, Ot = *Orthocladius manitobensis/obumbratus*, Pg = *Pagastia partica*, Pt = *Paratrichocladius* sp., Pd = *Pseudodiamesa branickii*, Sm = *Simulium vittatum*, Tn = *Tanytarsus* sp., Tk = *Tokunagaia* sp.

the *D. davisii* group and *N. forcipata*, which together accounted for almost 40% of the variation along the first axis (Table 1). Taxa that were positively correlated with the first axis colonized the stream

in 1993 or 1994 or were more abundant later in the season. *Tokunagaia* sp., which was abundant in late summer 1993 and 1994, accounted for almost 40% of the variation along the second axis.

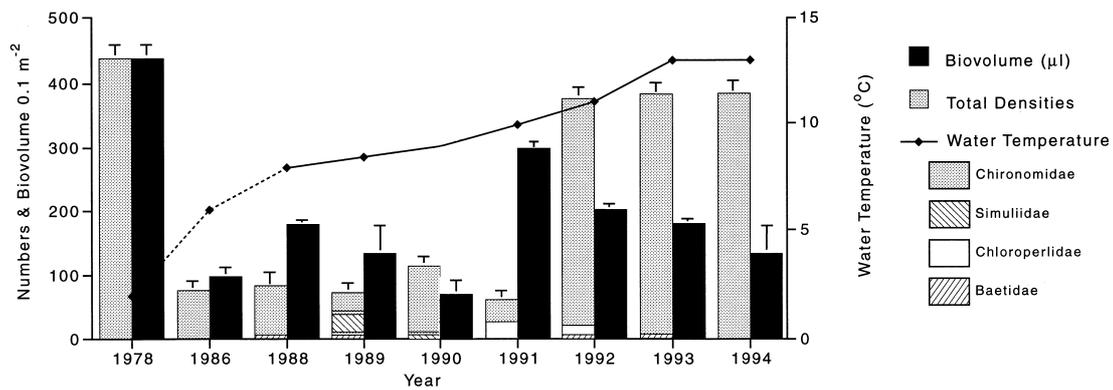


Fig. 5 Total densities and biovolumes (\pm SE) of invertebrates in Wolf Point Creek in August 1978–94 with maximum daily temperature of stream.

Maximum daily water temperature fluctuated seasonally by 2–5 °C, increasing gradually from early July until early August, then declining rapidly (Fig. 2), and also varied over the first 3 years to reach a seasonal maximum of 16.5 °C in July 1993, 5 °C warmer than the 1991 maximum. Total invertebrate densities were positively correlated with maximum daily temperature ($r = 0.71$, $P < 0.01$). Among taxa, changes in *Eukiefferiella* sp. densities showed strongest relationships with water temperature (*E. gracei*, $r = 0.72$, $P < 0.05$; *E. coeruleascens*, $r = 0.71$, $P < 0.05$). Neither the *D. davisi* group nor *P. partica* densities were significantly correlated with water temperature during the period 1991–94. The stream was clear water (< 10 NTU) for the first time in August 1993 and 14 NTU was recorded in August 1994.

Comparison with years 1978–90

Data collected in late August between 1978 and 1990 (Milner, 1994) were available for comparison with recent years. Invertebrate densities and biovolume were relatively high in 1978 (440 0.1 m⁻² and 440 μL),

Table 2 Expected number of species for sample size of 50 for four streams in Glacier Bay from 1978 to 1994

Year	Wolf Point Creek	Nunatak Creek	Berg Bay North	Berg Bay South
1978	4	5	15	12
1986	6			
1988	7			
1989	8	6		
1991	7			
1992	7			
1993	6			
1994	6	10		

but fell to 25% of these values in 1986 (Fig. 5). Densities did not increase again markedly until 1992 when ≈ 400 individuals 0.1 m⁻² were collected. Biovolumes remained around 200 μL in 1992 and 1993, falling to 150 μL in 1994 due to a larger proportion of relatively small species (*E. gracei*, *Tokunagaia* sp. Fig 3). The relatively high biovolume in 1991 was due to the dominance of the large-bodied stonefly *N. forcipata*.

Rarefaction indicated a slow increase from an expected four species in August 1978 to an expected six species in 1986 and rapidly to eight species in 1989 after which there was a steady decline to six species in 1994 (Table 2). The observed number of species was five in 1978 and 13 in 1994, although some rare species may be encountered more frequently in the larger samples (due to increased density) now collected.

Chironomid taxa have dominated the August invertebrate community since 1978, except in 1989 and 1991 when *S. vittatum* and *N. forcipata* dominated, respectively. *S. vittatum* was typically highest in June 1991 and 1992 and during July 1993 and 1994 with values ranging from 30 to 50 (0.1 m⁻²). The *D. davisi* group, which was the most abundant taxon in August 1978 with densities of 275 0.1 m⁻², was not found in August 1992. *P. partica*, first collected in 1986, dominated the community by 1990 (Fig. 6). *E. gracei* was also first apparent in 1986, but remained at low density (< 3) until 1992 (< 130). *Baetis* sp. which colonized in 1986, has remained at low densities (< 3) throughout the study. Another mayfly, *Cinygmula* sp., which was found in 1988, was not collected subsequently; a similar situation applied to *Capnia* sp. (plecoptera) collected in 1986 and 1988. *O. mallochii*,

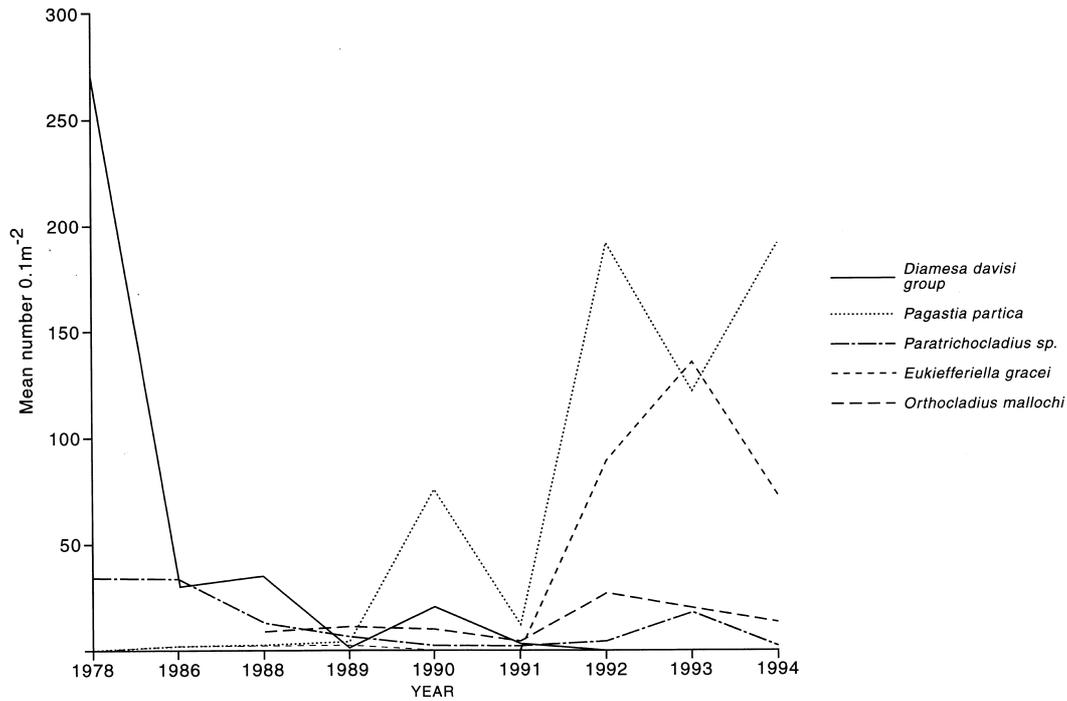


Fig. 6 Changes in August densities of the principal chironomid species in Wolf Point Creek from 1978 to 1994.

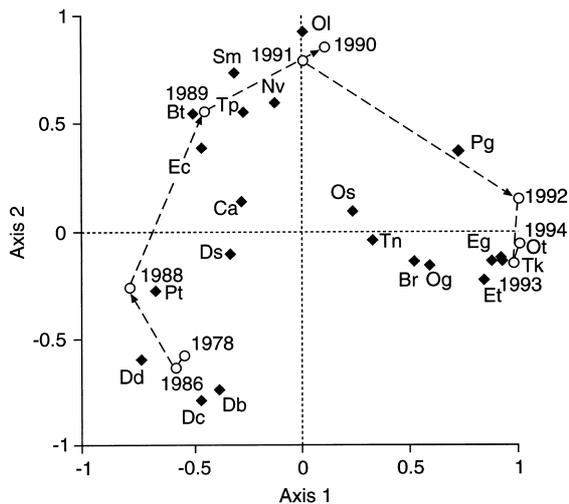


Fig. 7 First two axes of principal components analysis of species probabilities from ordination of the macroinvertebrate succession in Wolf Point Creek in August 1978–94. Points, labelled by year, are joined in chronological order. Ca = *Capnia* sp., Ecl = *Eukiefferiella claripennis*, Bt = *Baetis* sp., Tp = Tipulidae, Sm = *Simulium vittatum*, Nv = *Neaviperla forcipata*, Ol = *Orthocladius mallochi*, Os = *Onocosmoecus* sp., Pg = *Pagastia partica*, Tn = *Tanytarsus* sp., Eg = *E. gracei*, Ot = *O. manitobensis/obumbratus*, Tk = *Tokunagaia* sp., Br = *Brillia* sp., Og = *Oligochaeta*, Et = *E. rectangularis/Tvetenia*, Db = *Diamesa* sp. B, Dc = *Diamesa* sp. C, Dd = *Diamesa davisii* grp., Ds = *Diamesa sommermani*, Pd = *Pseudodiamesa branickii*.

N. forcipata, *Onocosmoecus* sp., and *Simulium vittatum* were first collected in 1988, and *Limnophila* sp. (Tipulidae) in 1989.

From the PCA of invertebrate community structure from 1978 to 1994, the first axis (which accounted for 61% of the total variation among species probabilities)

Table 3 Percentage contribution of species to ordination of 1978–94 data

Species	% Contribution	
	Axis 1	Axis 2
<i>Diamesa davisii</i> grp	- 12.3*	- 8.4*
<i>Neaviperla forcipata</i>	- 0.1	+ 23.8*
<i>Simulium vittatum</i>	- 8.8*	+ 13.5*
<i>D. sommermani</i>	- 1.8	- 2.4
<i>Baetis</i> sp.	- 0.7	+ 5.8*
<i>Orthocladius mallochi</i>	+ 0.8	+ 9.6*
<i>O. manitobensis/obum.</i>	+ 3.2*	- 3.1
<i>Paratrichocladius</i> sp.	- 9.4*	- 5.1*
<i>Eukiefferiella gracei</i>	+ 22.0*	+ 2.2
<i>Eukiefferiella/Tvetenia</i>	+ 4.0	- 1.8
<i>E. claripennis</i>	- 8.1*	+ 1.5
<i>E. coerulescens</i>	+ 3.9*	- 2.2
<i>Pagastia partica</i>	+ 10.8*	+ 6.7*
<i>Tanytarsus</i> sp.	+ 0.8	- 3.6
<i>Tokunagaia</i> sp.	+ 22.0*	- 1.7

Asterisk denotes significance at 5% level with *F* ratio of 555.47 for axis 1 and 522.13 for axis 2; degrees of freedom = 17, 9).

separated the years 1978, 1986 and 1988, from the last three 1992, 1993 and 1994 (Fig. 7). The second axis (39% of the variation) separated these 6 years from a third group 1989, 1990 and 1991. The community was relatively unchanged between 1978 and 1986, but between 1988 and 1989 and between 1991 and 1992 major changes occurred.

Taxa contributing to the ordination fall into three distinct groups (Fig. 7). In the lower left quadrant, the first group consisted of four species of *Diamesa* and *Paratrichocladius* sp. The next stage of succession (1989–91) was characterised by the community comprising *Baetis* sp., *S. vittatum*, *N. forcipata*, another stonefly *Capnia* sp. and *O. mallochii*. The third successional community was dominated by the chironomids *P. partica*, *Eukiefferiella* sp., *Tokunagaia* sp., and *O. manitobensis/obumbratus*. The weightings on the components reflect changes in species abundances.

The first axis in the ordination was most positively associated with *Tokunagaia* sp., *E. gracei* and *P. partica*, which together accounted for over 50% of the variation (Table 3), and negatively associated with the *D. davisi* group, *Paratrichocladius* and *E. claripennis* (Kieffer). The second axis was positively associated with *N. forcipata*,

S. vittatum, and *O. mallochii*, which together accounted for 45% of the variation, and negatively associated with the *D. davisi* group and *Paratrichocladius*. The greatest changes in the community over the 16 years were, therefore, decreases in the *D. davisi* group and *Paratrichocladius* sp. and *E. claripennis*, together with the colonization and increases in *N. forcipata*, *S. vittatum*, *O. mallochii*, *P. partica* and *Baetis* sp. between 1986 and 1989. This was followed by the absence of the *D. davisi* group and *Paratrichocladius* sp. together with the colonization and subsequent increase in *Tokunagaia* sp., *E. gracei* and *E. rectangularis/Tvetenia*, *E. coerulescens* and the further increase of *P. partica* between August 1991 and August 1992.

Stream temperature increased over the 16-year period from $\approx 2^\circ\text{C}$ in August 1978, to 13.5°C in August 1993. The *D. davisi* group and *Paratrichocladius* sp. declined with temperature ($r = 0.94$ and 0.75 , respectively, $P < 0.01$), while *P. partica*, *E. gracei* and *O. mallochii* increased as temperature rose ($r = 0.92$, 0.73 , and 0.84 , respectively, $P < 0.01$). *N. forcipata* and *Baetis* sp. densities showed no significant correlation with water temperature ($r = 0.23$ and 0.22 , respectively).

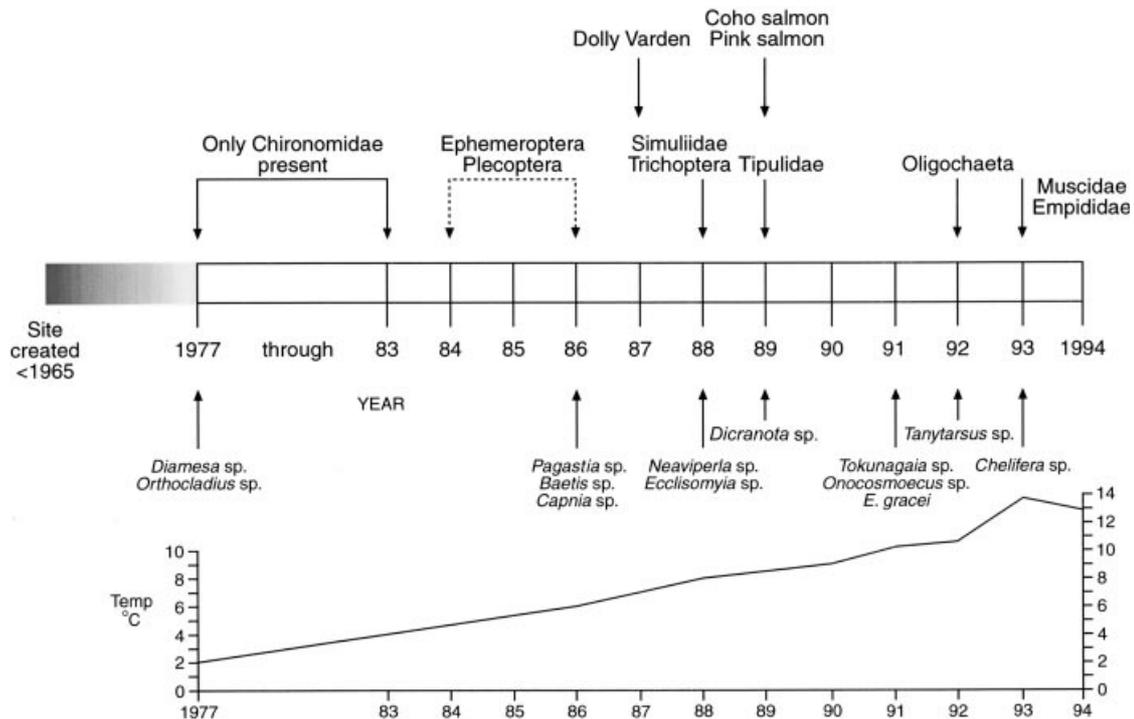


Fig. 8 Chronosequence of first collection of key macroinvertebrate taxa in Wolf Point Creek with associated water temperature from 1978 to 1994.

Discussion

Mechanisms of invertebrate colonization

The dominance of insects in the macroinvertebrate community of Wolf Point Creek 16 years after their presence was first recorded, is attributed to aerial dispersal being the main colonization route since the newly formed stream channel lacked any upstream, downstream, or hyporheic sources for colonization. The high proportion of Chironomidae in the community is a function of the high dispersal ability of their adults (Brundin, 1967; Hardy & Cheng, 1986) and their short life cycles, enabling them to rapidly populate denuded areas (Bruns & Minckley, 1980; Minshall, Andrews & Manuel-Faler, 1983; Cowx, Young & Hellowell, 1984; Molles, 1985).

The continued dominance of chironomids is also linked to the limitations of other taxa to disperse to and colonize the stream. In other stream colonization studies, larger, heavier taxa, such as Ephemeroptera and Plecoptera, generally arrive only days to weeks after chironomids (e.g. Williams, 1981). However, these groups first appeared in Wolf Point Creek at least seven years after Chironomidae, and 11 years elapsed before the first Trichoptera were collected (see Fig. 8 for chronosequence summary of colonization). Anderson (1992), Wallace (1990) and Hemphill & Cooper (1983) all documented markedly faster rates of community development involving aerial dispersal. Species replacement of chironomids was observed after only 35 days in artificial stream channels in the south of England (Ladle *et al.*, 1985). Even among chironomid species, Wolf Point Creek showed negligible change 5 years after it was first studied in 1978 (Milner, 1994).

According to island biogeography theory (MacArthur & Wilson, 1967) the size of the potential species pool of immigrants will influence colonization rates. Potential colonization sources such as streams in Berg Bay, 75 km away, are 200 years older than Wolf Point Creek, but still contain less than 50 macroinvertebrate taxa (Milner, 1983), thereby limiting the size of the potential colonizing pool. Moreover, Alaskan systems in general exhibit lower species richness than those in temperate regions (Oswood, Irons & Milner, 1995), most probably due to the lower temperatures that may ultimately limit colonization rates.

Despite the relative isolation of the stream from

local colonization sources, it is unlikely that variable dispersal times among taxa can account for the long delays between the establishment of these orders. Firstly, wind is frequently a random carrier in terms of direction and speed and as such is unlikely to discriminate between different species of chironomid which frequently vary little in size (Armitage, 1995). Secondly, taxa which did not colonize the stream until 1986, such as *P. partica*, *Baetis* sp. and *N. forcipata*, were present only 2 km away at Nunatak Creek (see Fig. 1) in 1978 (Milner, 1987).

Non-insect taxa are commonly among the last to colonize denuded areas owing to their slower dispersal rates (Cairns, Dickson & Hendricks, 1977; Wallace, 1990). The first noninsect group of the Wolf Point Creek community, Oligochaeta, was collected in 1992, 30 years after stream formation. Individuals of this group were found 75 km away in 1978 (Milner, 1987) but they would have had to rely on passive dispersal mechanisms such as birds (Talling, 1951) or wind (Malmqvist, Meisch & Nilsson, 1997) to cross the barriers posed by saltwater, mountains and poorly vegetated terrain to reach Wolf Point Creek. While such barriers may have delayed colonization to some extent, they are unlikely to have inhibited dispersal for 30 years.

Successful colonization and establishment in a stream not only depends on dispersal mechanisms and rates, but on the suitability of the habitat upon arrival (Williams & Hynes, 1976). Site characteristics were, therefore, probably important in determining the successional sequence of community establishment and development.

Early dominance of Diamesa taxa and their subsequent decline

The dominance of *Diamesa* chironomids in the Wolf Point Creek invertebrate community from 1978 to 1986 may have been partially due to their ability to withstand the prevailing habitat conditions at that time. Stream temperature was 2 °C in August 1978 and velocities typically exceeded 70 cm s⁻¹ (Milner, 1987).

Species of *Diamesa*, including those of the *D. davisii* group, are the sole inhabitants of the uppermost reaches of glacial streams in Swedish Lapland, Norway, Hudson Strait, Greenland (Saether, 1968) and the European Alps (Milner & Petts, 1994). Two species from the *D. davisii* group have been collected from Wolf

Point Creek, *D. alpina* and *D. lupus*, but their larvae are indistinguishable (Willassen, 1985). Such habitat is characterized by water temperatures below 2 °C, highly unstable substrates (Steffan, 1971), high current velocities (Rothlisberger & Lang, 1987), and a high suspended sediment load (exceeding 30 NTU, Milner & Petts, 1994). Specific adaptations to such conditions for *Diamesa* species include elongated posterior prolegs and procerci enabling them to firmly grip the substrate in glacial torrents (Saether, 1968), and their apparent ability to subsist solely on allochthonous particles washed into the stream (Steffan, 1971).

Nolte (1991) described the *D. davisi* group as cold stenothermic taxa, but Rossaro (1991) concluded that thermal tolerance alone could not explain the confinement of the closely related *Diamesa steinboeckii* to glacial streams. Saether (1968) suggested competition was responsible for turnover among *Diamesa* species in a glacier-fed stream in Norway.

The strong negative correlation between *Diamesa* densities and water temperature found in Wolf Point Creek might suggest intolerance of increasing temperature (above 4 °C) is responsible for their decline in abundance during summer. However, in Nunatak Creek across the fjord (Fig. 1), the *D. davisi* group has remained dominant in the community at a water temperature of 10–12 °C (Milner, 1997) which may result from the effect of different channel habitats on biotic interactions. While Wolf Point Creek achieved channel stability prior to 1978 due to the presence of a flow-buffering lake upstream, Nunatak Creek is characterized by highly unstable flow. Frequent disturbances in Nunatak Creek may prevent other taxa from becoming established and competitively eliminating chironomids of the *D. davisi* group. Milner (1994) suggested that the *D. davisi* group were fugitive species, persisting in habitats unsuitable for most taxa but are competitively displaced when favourable conditions allow colonization by other species (e.g. *P. partica*). Preliminary experimental information supports this suggestion (Flory & Milner, 1999a).

Colonization by taxa other than *Diamesa*

Colonization of Wolf Point Creek by taxa other than *Diamesa* was related to changes in the stream environment associated with the reduced influence of remnant ice and an increase in the surface area of the lake feeding the stream. Stream temperature in the

summer increased while sediment load and turbidity declined, thereby improving conditions for invertebrate colonization. Species that may have successfully dispersed to the drainage earlier, but were unable to establish a viable population could now do so. Sixteen taxa not previously collected in Wolf Point Creek in August were found between 1991 and 1994. However, eight of these taxa were collected at other times than August when most of the pre-1991 samples were collected, and many of these records represented one specimen in a 0.1-m² sample.

Increase in stream temperature is believed to have induced community changes in Wolf Point Creek by facilitating the establishment of many of the chironomid species, *Baetis*, and *N. forcipata*, which were not found until temperatures increased above 2 °C. There are similar observations in the literature. Markosova (1974 in Davies, 1976) found increased temperature increased the colonization rate of Chironomidae on artificial substrates in winter. In Scandinavian streams where water temperature exceeded 2 °C, species of *Eukiefferiella* and larvae of Simuliidae, Ephemeroptera and Trichoptera have been found in association with *Diamesa* sp. (Steffan, 1971). In addition *Baetis* spp. apparently prefer temperatures above 3 °C (Ward, 1992). From the Wolf Point Creek data, some chironomid densities were highly correlated to increasing temperature, particularly *P. partica*.

A factor other than temperature may have influenced the colonization of simuliid larvae in Wolf Point Creek. Simuliids have been found at 4 °C in streams (Steffan, 1971), but were not collected in Wolf Point Creek until 8 °C was reached in 1988. Being good dispersers and able to withstand disturbances, Simuliidae are frequently early colonizers of new stream reaches (Hemphill & Cooper, 1983; Malmqvist *et al.*, 1991), but a continual food supply of fine particulate organic matter strongly influences their colonization (Pinder, 1992; Gislason, Hrafnisdottir & Gardarsson, 1994). This material was available in Wolf Point Creek, particularly with a lake as its source and the delay in Simuliidae colonization may have been due to the previous lack of oviposition cues from riparian vegetation. Timm (1994) found that adult *Simulium vernum* only laid eggs in shaded forest reaches, where the larvae are subsequently found, and avoided open areas.

The establishment of deciduous riparian vegetation influences invertebrate colonization of streams for

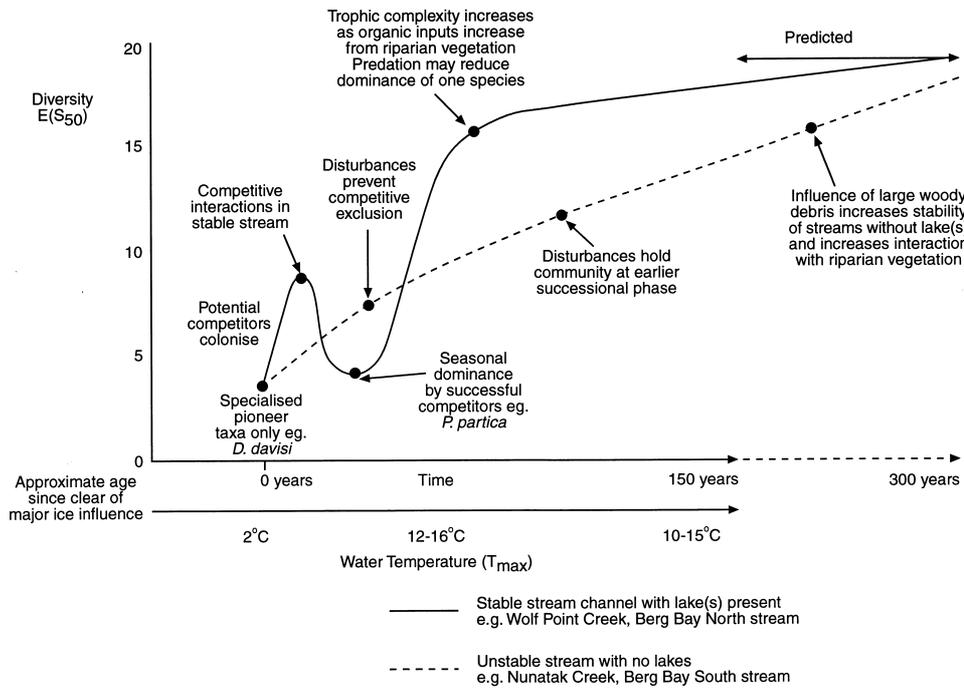


Fig. 9 Conceptual model of macroinvertebrate community development for streams in Glacier Bay, incorporating the influence of biotic interactions and disturbance.

other reasons, particularly by Trichoptera (Anderson, 1992). Associated leaves are an important potential food source for obligate and facultative shredding organisms (e.g. Benke *et al.*, 1988). Certain taxa, absent from the benthos of Wolf Point Creek, were associated with willow catkins and willow leaves, including *Brillia*, *Dicranota* and Limnephilidae caddis flies. Riparian willow development was found to be important for the establishment of these taxa (Flory & Milner, 1999b).

The sequence in which functional feeding groups colonized Wolf Point Creek does not follow the typical sequence outlined by Gore (1982), in which predators are the last group to colonize. *N. forcipata* is predatory (direct observations of consumption of *P. partica*) and thus predators colonized before shredders. This finding reflects the time required for sufficient development of riparian vegetation to facilitate establishment of shredders and associated groups.

A diversity model of invertebrate community development and succession in new streams following glacial recession.

Rapid recession of glaciers (particularly those with tidewater termini) may leave remnant ice sheets in

valleys. Meltwater from remnant ice may form new streams that subsequently become colonized by biotic communities (Milner, 1997). As the ice ablates, these streams may eventually become clear water, fed by snowmelt and rainfall in the valley.

Based on recent findings, we outline a conceptual model suggesting the pathways followed in the development of macroinvertebrate communities in these new streams (Fig. 9) which updates a model presented in Milner (1987). Observed changes in the expected species number, at a fixed sample size of 50 individuals for a number of streams, were used to construct the species richness axis. Information related to water temperature and allochthonous inputs to Wolf Point Creek and data from older streams in the region were used to predict future changes in invertebrate diversity along the time axis. Increased biomass would also be expected along the *y*-axis.

Species richness is initially low in newly emergent streams due to low water temperature associated with remnant ice restricting species richness to a few specialized taxa (e.g. the *D. davisii* group). This low richness may persist for a long period of time (> 30 years) where remnant ice sheets are large and

maintain a significant influence on stream flow (e.g. the Burroughs River in Wachusett Inlet; Fig. 1). Where stream temperature increases with remnant ice ablation, other taxa colonize and overall species diversity increases. The trophic complexity of the community will increase with the input of allochthonous material that accumulates as riparian vegetation develops.

A major factor in stream development is whether a lake forms in the system that is capable of depositing coarser sediment and buffering flow regimes, thereby enhancing channel stability downstream. In stable channels (e.g. Wolf Point Creek and Berg Bay north stream) densities of certain taxa may reach levels that potentially result in competitive exclusion of earlier colonizers (e.g. the *D. davisi* group) and seasonal dominance of one taxon may occur (e.g. *P. partica*). Flow disturbances in unstable stream channels without lakes (e.g. Nunatak Creek and Berg Bay south stream) inhibit the establishment and densities of taxa, even though water temperature may be more suitable for colonization, thereby restricting competitive interactions. In both stream types, predation (e.g. by juvenile coho salmon [*Onchoryhnchus kisutch* Walbaum] or stoneflies) may promote species evenness by preventing any one prey species from dominating the community (Lake, 1990). Ultimately, seasonal richness may be higher in unstable channels than stable channels since seasonal dominance is prevented. For example, Nunatak Creek exhibited a greater expected number of species than Wolf Point Creek in 1994.

In the long-term (> 100 years), we suggest that species richness and macroinvertebrate biomass will be higher in a stream with a flow buffering lake than in a stream of similar age without lakes. This is demonstrated by two streams in Berg Bay (a north stream with a series of lakes and a south stream without lakes) that have both been free from ice for \approx 150 years. At similar sites the stable Berg Bay North stream exhibited higher species richness compared to the unstable Berg Bay South stream (26 and 16 taxa, respectively, Milner, 1983), although the stable stream exhibited lower species evenness due to dominance by *P. partica* (Milner, 1987).

Species richness is predicted to increase in both stream types due to the maintenance of optimal temperatures for a wide range of species by shading from riparian vegetation (cottonwood *Populus trichocarpa* Torr and Carr and Sitka spruce *Picea sitchensis* Carr) and the establishment of taxa associated with

increased allochthonous inputs. Over time, timber fall will increase and large woody debris (LWD) will potentially confer increased stability to streams without lakes by diversifying flow patterns and routing sediment (Murphy & Milner, 1997). Murphy & Koski (1989) estimated that LWD levels in south-east Alaska would take 250 years to return to their former value following clear-cut logging and input of wood depended upon forest regrowth. However, this regrowth assumes developed soils are present, unlike Glacier Bay where soils must first be established following deglaciation. We predict therefore that diversity and biomass of communities in the two stream types will be more similar after 300 years as the influence of LWD increases.

Acknowledgments

This work was carried out while E.A.F. was in receipt of a NERC studentship. Donald McLusky and other staff at the University of Stirling, provided a supportive environment. Additional funding was received from the United States Environmental Protection Agency. Many thanks to the National Park Service in Glacier Bay, Alaska, in particular Chad Soiseth and Mary Beth Moss, and to Captain J.F. Luthy of the m.v. *Nunatak* for invaluable logistic assistance and loan of equipment. We also thank Dr Endre Willassen of the Natural History Museum, Bergen, Norway for assistance in chironomid identification and to Professor Ken Stewart for identifying stoneflies. We acknowledge Colin Bull, Mike Dauber, Steve Mackinson, Calum MacNeil, Olaf Olafsson, Mark Porter, and Sarah Roberts for assistance with the collection of field data and Calum MacNeil for helping to identify the 1991 samples. We thank Mike Winterbourn and two anonymous reviewers for constructive criticism of earlier drafts of this manuscript.

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(Manuscript accepted 14 December 1999)