

## The influence of stream age and environmental variables in structuring meiofaunal assemblages in recently deglaciated streams

*A. L. Robertson*

School of Human and Life Sciences, Roehampton University, Holybourne Avenue, London SW15 4JD, United Kingdom

*A. M. Milner*

School of Geography & Environmental Science, University of Birmingham, Edgbaston, Birmingham B15 2TT, United Kingdom

### *Abstract*

The influence of stream age and environmental variables on meiofaunal assemblages were examined for 15 streams across a temporal gradient of 200 yr in Glacier Bay National Park, southeast Alaska. Meiofaunal assemblages were found in all streams but varied in diversity and abundance. Copepod species found had a wide range of habitat affinities and good dispersal abilities; we argue that the observed copepod assemblage in a given Glacier Bay stream is determined by habitat availability rather than dispersal constraints. Two-way indicator species analysis (TWINSPAN) classified the meiofaunal assemblages largely according to stream age. Stepwise multiple regressions were performed on environmental variables and meiofaunal species richness or abundance, and predictors differed between taxa. The sorting coefficient, a measure of the diversity of particle sizes in the sediment, best explained the variation in both total harpacticoid copepod abundance and meiofaunal taxon richness (together with stream gradient). Harpacticoids were more abundant in relatively well-sorted streams and declined as the range of particle sizes within the streams increased; the opposite pattern to that found in the marine environment. The abundance of *Bryocamptus* spp. was best explained by models incorporating stream age and indicators of habitat complexity, whereas abundance of Tardigrada, *Chaetogaster*, and *Moraria affinis* increased with increasing substrate stability. A habitat templet was developed for the meiofaunal assemblages in Glacier Bay streams. Stream age (incorporating stream habitat complexity) formed one axis and the second axis was the sorting coefficient.

Colonization and succession studies of streams and rivers at the spatial scale of entirely new river channels are limited for macroinvertebrates (Fisher 1990) and very rare for meiofauna (although see Gaviria 1998; Robertson and Milner 1999; Milner et al. 2000). Meiofaunal studies that do exist principally focus either on new channels with upstream sources of potential colonizers (e.g., flood alleviation channels; Gaviria 1998) or have examined the relationship between the environmental gradient occurring with increasing distance from a glacier terminus and the hyporheic assemblage in a single river (Malard 2003; Malard et al. 2003) or the larger scale temporal changes (100s to 1000s yr) in lentic assemblages following deglaciation (e.g., Duigan and Birks 2000). In contrast, studies of meiofaunal colonization at the patch-scale are relatively well represented (e.g., Palmer et al. 1992; Schmid-Araya 2000), as are similar studies on macroinvertebrates that may include some members of the temporary meiofauna (young macrofauna that are of meiofaunal size)

(e.g., Matthaei et al. 1997; Gjerlov et al. 2003). In this study, we focus on the permanent meiofauna, organisms remaining within the meiobenthic size category throughout their lifespans (retained by a 63- $\mu$ m sieve but passing through a 1-mm sieve; Giere 1993), and use the spatial gradient of glacial recession in Glacier Bay National Park, Southeast Alaska, to elucidate reach scale comparisons across a temporal gradient of 200 yr. Specifically, we examine large-scale patterns of colonization and primary succession in stream meiofaunal communities following ice recession rather than small-scale patch colonization or rapid colonization from sources within the same watershed (e.g., Boulton et al. 1991; Palmer et al. 1992). As these are new watersheds with no remnants of previous biological communities, colonization involves dispersal from other stream systems and subsequent community development relies on primary successional processes. In contrast with many lotic macroinvertebrates, the permanent meiofauna do not possess winged dispersal stages. There are, however, several ways they could disperse into new stream systems in Glacier Bay, including dormancy and subsequent dispersal by wind, waterfowl, and animals (e.g., Caceres and Soluk 2002; Figuerola and Green 2002).

The development of postglacial streams in coastal Alaska involves complex interactions among the fluvial system, riparian vegetation, and geomorphic processes influencing sediment supply (Sidle and Milner 1989). Increasing stream age is thus linked to changes in many other stream characteristics, such as higher temperatures, greater quantities of coarse particulate organic matter

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(CPOM) derived from the developing riparian zone, and the eventual formation of woody debris dams and increased stream stability (Milner and Petts 1994). These changing characteristics may make a stream more or less suitable for species comprising the meiobenthic assemblage, resulting in succession (Robertson and Milner 1999). An increase in habitat complexity with stream age may be particularly important for meiofaunal assemblage development, as meiofauna are readily displaced downstream during flow events (e.g., Palmer et al. 1992); and several studies have highlighted the importance of areas of low hydraulic stress, such as aggregations of CPOM and woody debris to their survival (Golladay and Hax 1995; Robertson et al. 1995; Robertson and Milner 2001).

Sediment granulometry is an important predictor of marine and hyporheic freshwater meiofaunal distributions (e.g., Hicks and Coull 1983; Strayer et al. 1997; Hunt and Stanley 2003). Although it is rarely measured in studies of epibenthic freshwater meiofaunal assemblages (but see Shiozawa 1986), it is also thought to play a key role in meiofaunal distribution here (Silver et al. 2002).

In order to describe and predict distribution and abundance patterns of organisms, ecologists must first understand the influence of habitat, as this controls community composition by acting as a filter to potential colonists (Poff 1997). Southwood (1988) developed the habitat templet hypothesis as a framework on which to base predictions about characteristics of species and communities. Templet theory depends on extracting some key characteristics from the physical system allowing axes of environmental variation to be specified that may structure biological communities.

The primary objective of our study was to examine long-term patterns of meiofaunal assemblage change by comparing streams representing 200 yr of stream development following deglaciation. Permanent meiofauna differ from the more commonly studied macroinvertebrates in several respects e.g., small body size, rapid turnover rates, and the absence of a winged dispersal stage; and thus a further objective was to compare the responses of meiofauna and macroinvertebrates to environmental variables in Glacier Bay streams. Our final objective was to develop a habitat templet, as we wished to synthesize our understanding of the factors that structure benthic meiofaunal assemblages in Glacier Bay streams. Specifically, we addressed the following questions: First, what influence does stream age have on meiofaunal assemblages? Second, what is the influence of stream physicochemical variables on meiofaunal abundance and taxon richness? Third, how do the responses of the meiofauna to stream age and physicochemical variables compare with those of the macroinvertebrates? And last, can we develop a habitat templet that explains the variation in the taxonomic composition and abundance of meiofaunal assemblages among Glacier Bay streams?

## 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 (Fig. 1). A Neo-glacial ice sheet, which reached its maximum around A.D. 1700, near the mouth of Glacier Bay began to recede between 1735 and 1785 (see Fig. 1 for approximate position of ice terminus at selected dates). Fifteen streams ranging in age from 25 to 200 yr since deglaciation were selected for study (Fig. 1). They possessed the following characteristics: gradient <5% in the lower reaches, no barriers to salmonid migration, and a watershed ranging in size from 10 to 100 km<sup>2</sup>. Lakes were present in four of the streams, three of which were the youngest streams sampled. Streams were studied in May 1997. Table 1 summarizes the main features of the study streams. See Milner et al. (2000) for further details.

*Stream age and habitat evaluation*—Stream age was defined as the time since ice recession from stream mouths, determined by historical and aerial photographs, published articles, and unpublished data. All study reaches were within 0.2–2.8 km of the stream mouth and were at least 10–14 channel widths in length. Percent instream wood debris (% CWD) was estimated as the proportion of all wetted habitat in a reach that contained some type of woody debris. The bottom component of the Pfankuch (1975) stability index was used to evaluate substrate stability within each reach, as recommended by Death and Winterbourn (1995); this component includes measures of angularity, brightness, substrate consolidation, scouring and deposition, and the extent of aquatic vegetation. Entrenchment ratios were calculated by first determining the elevation of the floodplain area as measured at twice the maximum bankful depth. The floodplain area width at this elevation was then divided by the bankful width (Rosgen and Silvey 1996).

*Sediment granulometry*—A Wolman pebble count was undertaken at each stream. A pebble was selected every 1–2 paces in the stream. This was done by averting eyes and picking up the particle first touched by a pointed vertical finger under the tip of the boot (Bunte and Abt 2001). One hundred pebbles were selected at each stream and the length of the *b*-axis (intermediate axis) measured. These data were then used to provide an approximation of the particle size distribution in each stream by calculating the following parameters: mean ( $\sqrt{D_{16} - D_{84}}$ ), characterizes the central part of the distribution; sorting coefficient ( $\sqrt{D_{84} \div D_{16}}$ ), the standard deviation or width of the distribution;  $D_{95}$ , 95th percentile; 95% of particles are smaller than this value.

*Water chemistry*—A water sample was collected at each stream. Alkalinity (mg L<sup>-1</sup>) was determined by sulfuric acid (0.01 mol L<sup>-1</sup>) titration and pH was measured using an Orion modal 399A ion analyzer. Total phosphorus ( $\mu\text{g L}^{-1}$ ) was measured by the molybdate blue–ascorbic acid method after persulphate digestion. Total Kjeldahl nitrogen ( $\mu\text{g L}^{-1}$ ) was measured as total ammonia following sulfuric acid block digestion. Conductivity ( $\mu\text{mho cm}^{-1}$ ), water temperature (°C), and turbidity (NTU) were

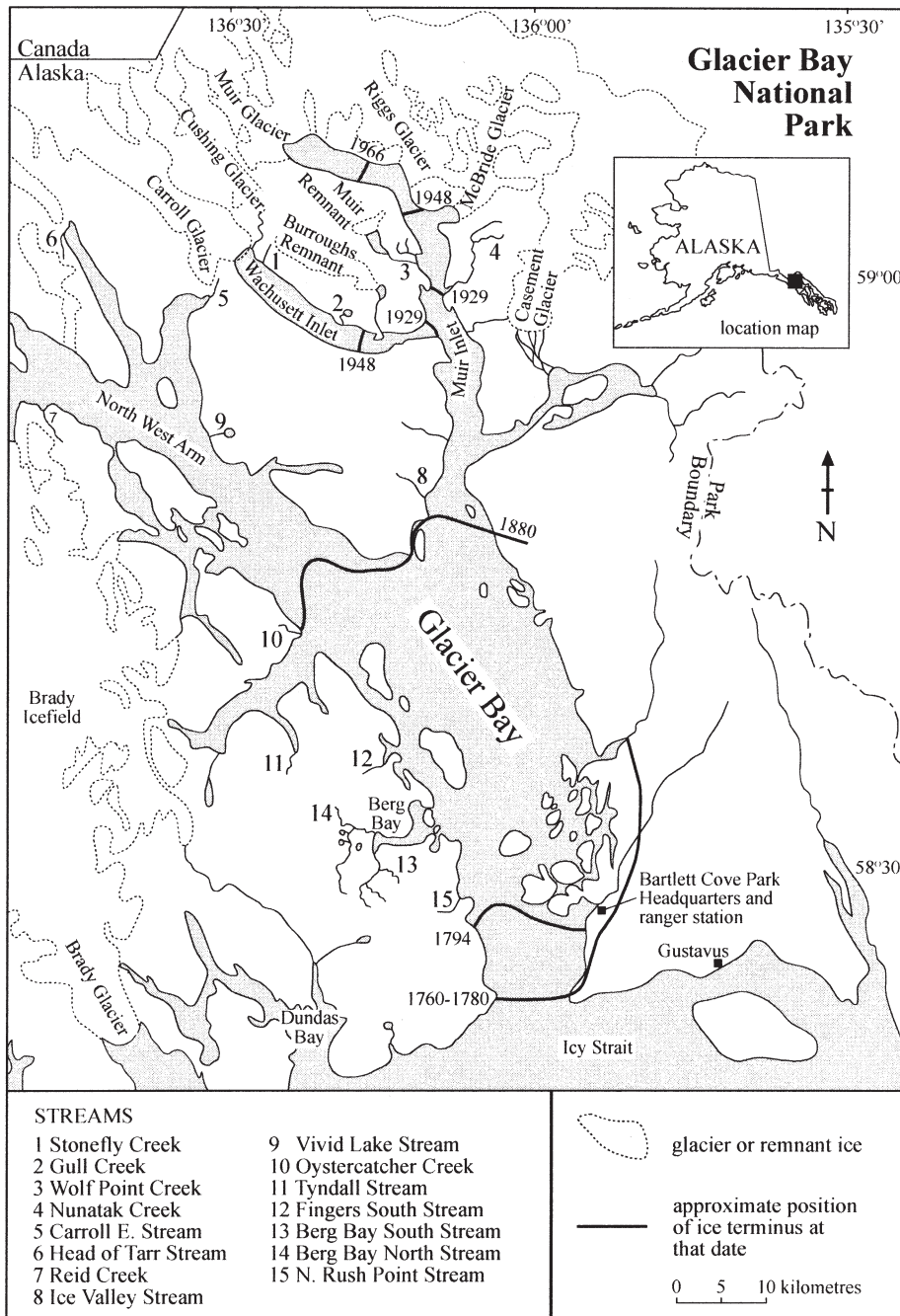


Fig. 1. Glacier Bay National Park in Southeast Alaska showing the location of the 15 study streams in May 1997.

recorded in the field using portable instruments. For further details, see Milner et al. (2000).

*Invertebrates and CPOM*—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 surber sampler with a 63- $\mu$ m mesh. In the laboratory, meiofauna were sorted from detritus using a dissecting microscope, meiofauna were identified to the level of phylum (Nematoda, Tardigrada), class (Ostracoda), or

genus and/or species (*Chaetogaster*, Copepoda, Chydoridae). All were enumerated. CPOM collected from sorted invertebrate samples was dried and weighed prior to ashing at 500°C for 40 min. CPOM was calculated as mean ash-free dry weight (g) per area (m<sup>2</sup>).

*Data analysis*—Two-way indicator species analysis (TWINSPAN; Hill 1979) undertakes the hierarchical classification of community data. It was used to classify 14 streams using log<sub>10</sub>(x + 1) transformed abundance data

Table 1. Summary of major physical watershed features and selected physicochemical variables of the 15 streams in Glacier Bay studied in 1997 (adapted from Milner et al. 2000). SC, Stonefly Creek; GC, Gull Creek; WPC, Wolf Point Creek; NC, Nunatak Creek; CES, Carroll East Stream; HTS, Head of Tarr Stream; RC, Reid Creek; VLS, Vivid Lake Stream; IVS, Ice Valley Stream; OC, Oystercatcher Creek; TS, Tyndall Stream; FSS, Fingers South Stream; BBN, Berg Bay North Stream; BBS, Berg Bay South Stream; NRP, North Rush Point.

Physicochemical variables	SC	GC	WPC	NC	CES	HTS	RC	VLS	IVS	OC	TS	FSS	BBN	BBS	NRP
Stream age (years)	36	43	51	62	77	88	117	127	127	137	147	152	167	167	192
Lake influence	Yes	Yes	Yes	No	No	No	No	No	No	No	No	No	Yes	No	No
Blue line elevation (m)	91	366	183	793	518	579	290	442	518	476	88	360	238	244	296
Stream length (km)	1.3	3.0	5.6	8.6	3.4	2.8	6.0	5.6	8.3	5.7	2.3	8.0	9.0	7.2	6.6
Stream gradient (%)	7.0	12.2	3.3	9.2	15.2	20.7	4.8	7.9	6.2	8.3	3.8	4.5	2.6	3.4	4.5
Water source*	G	L	G	S	S	M	M	S	S	S	S	S	L	S	S
Stream order	1	2	2	3	2	1	1	2	2	2	2	2	3	3	2
Stream temperature (°C)	2.8	3.7	3.4	5.2	5.7	2.7	3.5	6.7	8.4	2.9	3.7	3.4	4.7	6.4	6.2
D <sub>95</sub>	27.6	32.0	29.8	21.3	20.2	19.8	24.6	14.8	27.3	22.0	12.5	28.9	42.0	21.3	35.4
Sorting coefficient	2.7	1.7	2.2	1.8	2.6	1.9	2.2	2.4	2.7	2.3	1.9	2.0	1.9	2.0	2.0
Pfankuch index (bottom component)	26	19	34	33	53	39	29	39	33	32	39	41	14	42	40
Entrenchment	1.3	1.7	3.4	2.3	1.4	2.1	1.0	1.3	1.9	1.0	3.6	1.5	1.7	1.1	1.5
Conductivity ( $\mu\text{mho cm}^{-1}$ )	132	155	101	145	181	126	148	133	206	129	42	110	170	87	170
Total nitrogen ( $\mu\text{g L}^{-1}$ )	71.9	45.9	86.6	77.2	129.9	39.6	63.6	38.8	59.7	263.0	106.9	247.2	112.5	152.8	46.7
Total phosphorous ( $\mu\text{g L}^{-1}$ )	224.8	11.2	47.4	49.9	248.0	33.4	24.8	9.0	6.2	3.9	1.4	53.7	2.5	127.7	3.7
% Coarse woody debris	15.25	14.3	6.6	6.5	1.9	0.8	5.3	5.7	7.7	4.3	16.4	12.2	22.6	14.3	34.5

\* Predominant water sources: G, proglacial lake; L, lake; S, snowmelt and rain; M, glacial meltwater.

for meiofaunal taxa (using PCORD 4). Pseudospecies cut levels of 0, 0.5, 1, 1.5, and 2 were used. Indicator taxa identified by TWINSpan are given. Preliminary analysis indicated that Carroll East stream was an outlier, due to its very impoverished meiofaunal assemblage (Table 2) and it was omitted from this analysis.

We used correlation analysis to eliminate highly correlated ( $p < 0.01$ ) environmental variables that were potential measures of the same attribute (see Table 3). The remainder were entered into a series of stepwise multiple regressions (using SPSS 11.0) to develop models relating environmental variables to harpacticoid copepod and cyclopoid copepod species richness per stream or transformed mean taxon abundances per stream. Meiofaunal abundance data were  $\log_{10}(x + 1)$  transformed to standardize variances and improve normality. Meiofaunal taxa that occurred in fewer than three streams were not analyzed, although they did form part of the data set for species richness.

The environmental variables with the greatest influence on meiofaunal assemblages in Glacier Bay (see Results) formed the axes of the habitat templet. One axis was stream age (partially corresponding to a gradient of stream habitat complexity). Indicators of habitat complexity, e.g., percentage of pools and coarse, woody debris in a reach, increase with increasing stream age and/or increasing substratum stability, and this latter variable is highly correlated with the presence or absence of lakes in a system. The second axis of the habitat templet represented the degree of sorting of the stream substratum (sorting coefficient). Principal components analysis (PCA) was used to distinguish stream groups in Glacier Bay using these variables. A centered PCA (with mean  $\log(x + 1)$  abundances of meiofaunal taxa) examined differences in the composition of meiofaunal assemblages between stream groups.

## Results

Meiofaunal assemblages were found in all streams but varied in taxon richness and abundance. Carroll East Stream contained only nematodes, whereas Berg Bay North Stream supported a relatively taxon rich assemblage of 13 meiofaunal taxa (Table 2).

*Stream age and meiofaunal assemblages*—Harpacticoid copepods were more speciose in older streams (Tables 2 and 4) and harpacticoid assemblages differed with stream age. *Maraenobiotus brucei* and *Moraria affinis* occurred in streams of all ages, whereas *Epactophanes richardi* was only found in younger streams (see also Table 4) and four further species (*Bryocamptus hiemalis*, *B. zschokkei*, *Atheyella illinoisensis*, and *A. idahoensis*) were restricted to streams older than 140 yr (Table 2, and see also Milner et al. 2000). *Maraenobiotus insignipes* was restricted to streams fed largely by glacial meltwater or proglacial lakes (Tables 1 and 2).

TWINSpan identified two major stream groups at the first division, streams less than 140 yr old and those greater than 140 yr old (Fig. 2). Indicator taxa for old streams were primarily *Bryocamptus* spp. The second division separated Berg Bay North, the oldest lake system, from the other older streams with the cyclopoid *Acanthocyclops* sp. as the indicator taxon. The second division for the younger streams separated Gull Creek, Head of Tarr stream, Nunatak Creek, and Vivid Lake stream from the remaining younger streams. The last division separated older streams (120–140 yr), from younger ones.

*Physicochemical variables and meiofaunal assemblages*—The environmental variables that best predicted meiofaunal abundance and taxon richness in the 15 streams differed

Table 2. Mean abundance m<sup>-2</sup> and 1 SE of meiofaunal taxa in 15 Glacier Bay streams. Streams are ordered from youngest (left) to oldest (right). For key to stream abbreviations see Table 1.

Meiofaunal taxa	SC	GC	WPC	NC	CES	HTS	RC	VLS	IVS	OC	TC	FSS	BBN	BBS	NRP
Nematoda	121.6	167.2	57.6	96.0	38.4	64.0	112.0	22.4	278.4		76.8	89.6	19.2		32.0
	51.9	97.5	57.6	29.5	19.3	27.2	26.7	13.9	109.8		25.5	27.0	12.8		11.3
Tardigrada		358.4	25.6	32.0			60.8	9.6					60.8	9.6	
		123.4	18.6	11.3			34.4	6.4					29.6	6.4	
Hydrachnidia	12.8		25.6				57.6		22.4	32.0	9.6	44.8	12.8	19.2	9.6
	12.8		18.6				33.7		10.8	11.3	6.4	16.3	9.3	19.2	6.4
Oligochaeta <i>Chaetogaster</i>	6.4	1043	6.4	12.8									377.6	3.2	
	6.4	572.4	6.4	7.8									59.3	3.2	
Ostracoda		12.8	6.4					3.2	51.2	54.4	80.0		64.0	9.6	6.4
		7.8	6.4					3.2	3.2	19.3	60.7		36.4	3.9	6.4
Copepoda Cyclopoida															
<i>Acanthocyclops vernalis</i>			1008	19.2			3.2				6.4	6.4		16.0	12.8
			659.0	19.2			3.2				3.9	6.4		5.0	9.3
<i>Paracyclops poppei</i>			57.6							3.2		3.2	6.4		
			27.5							3.2		3.2	3.9		
<i>Diacyclops</i> sp.	19.2			25.6							3.2			3.2	
	12.8			11.9						3.2				3.2	
<i>Eucyclops agilis</i>														6.4	
														6.4	
Harpacticoida <i>Atheyella</i>												6.4			
<i>illinoisensis</i>												6.4			
<i>Atheyella idahoensis</i>													38.4	9.6	3.2
													16.4	9.6	3.2
<i>Bryocamptus hiemalis</i>											124.8	3.2	358.4	12.8	12.8
											39.6	3.2	243.3	5.9	5.9
<i>Bryocamptus zschokkei</i>											329.6	25.6	9.6	41.6	9.6
											79.1	10.8	6.4	3.9	6.4
<i>Maraenobiotus brucei</i>		115.2	6.4			73.6		32.0	16.0	22.4	105.6	115.2	3.2	83.2	28.8
		48.1	6.4			51.0		14.3	7.16	10.8	21.8	40.9	3.2	34.8	9.3
<i>Maraenobiotus insignipes</i>	19.2					19.2	57.6								
	12.8					11.6	24.0								
<i>Moraria affinis</i>		179.2	25.6	19.2			12.8			6.4			25.6		6.4
		57.7	11.9	7.8			9.3			3.9			17.9		6.4
<i>Parastenocaris</i> sp.			3.2												
			3.2												
<i>Epactophanes richardi</i>		6.4	6.4												
		6.4	6.4												
Branchiopoda															
Macrothricidae				3.2											
				3.2											
Chydoridae <i>Chydorus</i> sp.													6.4		
													3.9		

Table 3. Environmental variables entered into the stepwise regression (left-hand column). Correlated ( $p < 0.01$ ) environmental variables that were not entered into the regression are shown in the right-hand column on the same row.

Environmental variables entered into stepwise regression	Correlated environmental variables ( $p < 0.01$ ) not entered into stepwise regression
Age	CBOM, turbidity
D <sub>95</sub>	Wolmans mean
Pfankuch Index	Wolmans mean, a : f ratio, lakes
% Coarse, woody debris	% pool habitat
Conductivity	Alkalinity
Total phosphorous	Turbidity
Sorting coefficient	
Stream gradient	
Stream temperature	
Total nitrogen	
Entrenchment	

Table 4. Stepwise multiple regression analysis to determine which environmental variables are significant predictors of meiofaunal taxon abundance (mean  $\log(x+1)$  transformed abundance per stream) and taxon richness in 15 streams. The model explaining the largest proportion of the variation is shown. See Table 3 for environmental variables entered into analysis.

	Variable	Parameter estimate (SE)	$r^2$	$p$
Nematoda	Constant	0.533 (0.065)		<0.001
	Total nitrogen	-0.001 (0.001)	0.343	0.022
Tardigrada	Constant	0.619 (0.183)		0.005
	Pfankuch index	-0.012 (0.005)	0.312	0.030
<i>Chaetogaster</i>	Constant	0.711 (0.146)		<0.001
	Pfankuch index	-0.016	0.551	0.002
Ostracoda	Constant	0.104 (0.020)		<0.001
	Total phosphorous	-0.0004 (0.000)	0.282	0.042
Harpacticoida				
Total Harpacticoida	Constant	4.826 (0.849)		<0.001
	Sorting	-1.395 (0.388)	0.499	0.003
<i>Atheyella idahoensis</i>	Constant	-0.623 (0.387)		0.131
	D <sub>95</sub>	0.033 (0.015)	0.283	0.041
<i>Bryocamptus hiemalis</i>	Constant	-0.219 (0.279)		<0.001
	% CWD	0.064 (0.020)	0.448	0.006
<i>Bryocamptus zschokkei</i>	Constant	1.006 (0.433)		0.040
	Age	0.006 (0.002)	0.399	0.012
	Conductivity	-0.011 (0.003)	0.716	0.001
	% CWD	0.033 (0.013)	0.821	<0.001
<i>Maraenobiotus</i> spp.	Constant	4.729 (1.025)		<0.001
	Sorting	-1.640 (0.468)	0.485	0.004
<i>Moraria affinis</i>	Constant	2.394 (0.570)		0.001
	Pfankuch index	-0.051 (0.016)	0.444	0.007
Cyclopoida				
Total Cyclopoida	Constant	1.502 (0.345)		0.001
	Gradient	-0.087 (0.038)	0.288	0.039
<i>Acanthocyclops vernalis</i>	Constant	-0.477 (0.479)		0.337
	Entrenchment	0.598 (0.244)	0.315	0.029
<i>Diacyclops</i> sp.	Constant	-0.621 (0.289)		0.042
	Pfankuch index	0.019 (0.009)	0.395	0.012
	Total phosphorous	0.002 (0.001)	0.567	0.007
Harpacticoid species richness	Constant	8.409 (1.413)		<0.001
	Sorting	-2.774 (0.489)	0.598	<0.001
	Gradient	-0.105 (0.032)	0.787	<0.001
Cyclopoid species richness	Constant	0.796 (0.273)		<0.001
	Gradient	-0.125 (0.027)	0.520	0.001
	Temperature	-0.178 (0.070)	0.664	0.043
Copepoda species richness	Constant	10.734 (2.413)		0.001
	Sorting	-3.386 (0.693)	0.438	<0.001
	Gradient	-0.209 (0.046)	0.796	0.001
Total meiofaunal abundance	Constant	2.969 (0.35)		<0.001
	Pfankuch index	-0.030 (0.007)	0.452	<0.001
	Entrenchment	0.325 (0.083)	0.760	0.002
Total meiofaunal taxon richness	Constant	18.455 (2.095)		<0.001
	Gradient	-0.366 (0.062)	0.522	<0.001
	Sorting	4.411 (0.941)	0.831	<0.001
Total macroinvertebrate abundance	Constant	4.636 (0.508)		<0.001
	Pfankuch index	0.028 (0.008)	0.505	0.005
	Temperature	-0.118 (0.046)	0.692	0.025
	Sorting	-0.556 (0.236)	0.795	0.038
Total macroinvertebrate species richness	Constant	48.447 (6.446)		<0.001
	Pfankuch index	-0.697 (0.182)	0.529	0.002

between taxa (Table 4). The abundance of Nematoda and Ostracoda was best predicted by stream nutrient levels (total nitrogen or total phosphorous). The abundance of three taxa (Tardigrada, *Chaetogaster*, and the harpacticoid copepod *Moraria affinis*) was explained most effectively by

the Pfankuch index, abundance rising with increasing substrate stability (Table 4). In contrast, abundance of the cyclopoid copepod *Diacyclops* sp. was best explained by a model incorporating the Pfankuch index and total phosphorous where abundance increased with decreasing

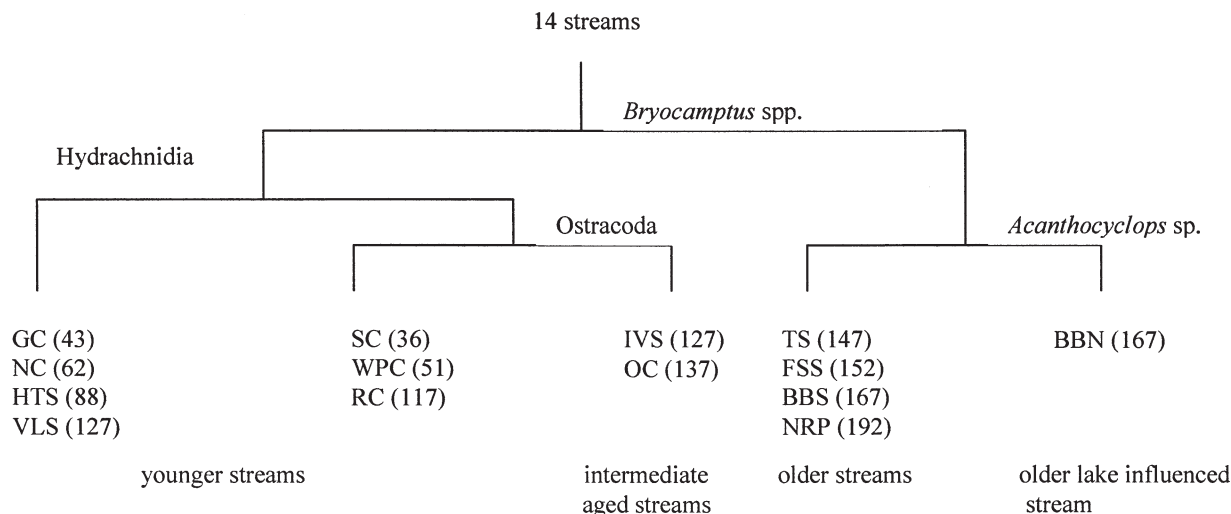


Fig. 2. TWINSpan classification of the 14 stream sites into five groups using meiofaunal taxa collected in May 1997. Indicator taxa for divisions are given. Values in parentheses are stream ages. For key to stream abbreviations, see Table 1.

substrate stability (Table 4). The sorting coefficient best explained the variation in total harpacticoid abundance, a finding largely driven by *Maraenobiotus* spp.; Harpacticoida were more abundant in relatively well-sorted streams; as the range of particle sizes within the stream increased, the abundance declined. The abundance of *Bryocamptus* spp. was described by models incorporating stream age and indicators of habitat complexity. The abundance of the harpacticoid *Atheyella idahoensis* was most effectively described by  $D_{95}$  (94% of the sediment particles were smaller than this value). Streams with higher  $D_{95}$  (i.e., larger substrate sizes) had greater populations of this species. Total cyclopoid abundance was weakly related to stream gradient; abundance declined with increasing gradient. Harpacticoid species richness was best explained by a model incorporating the sorting coefficient and stream gradient; species richness declined as the range of particle sizes within the stream increased and rose with decreasing stream gradient. Cyclopoid species richness was related to stream gradient and temperature; species richness rose with increasing temperature and declined with increasing gradient. Total taxon richness of the meiofaunal assemblage was best explained by a model incorporating stream gradient and the sorting coefficient, whereas total meiofaunal abundance was described by a model incorporating the Pfankuch index and entrenchment; abundance rose with increasing channel stability and entrenchment. There were no significant environmental predictors for *Paracyclops poppei* and *Hydrachnidia* abundance.

*Responses of the macroinvertebrates to stream age and physicochemical variables*—We conducted the same analysis on total macroinvertebrate abundance and species richness in the 15 streams. Macroinvertebrate abundance was best explained by a model incorporating the Pfankuch index, stream temperature, and the sorting coefficient, whereas macroinvertebrate species richness increased with increasing bed stability (Table 4).

*The meiofaunal habitat templet for Glacier Bay streams*—A PCA performed on the 15 streams using measures of age, indicators of habitat complexity (% CWD, % pools), the sorting coefficient, and substratum stability (Pfankuch index) distinguished three stream groups in Glacier Bay (Fig. 3). Group I (Berg Bay North stream, Tyndall stream, North Fingers stream, Berg Bay South stream, and Rush Point stream) contained the oldest streams, with the highest habitat complexity and relatively well-sorted substrates

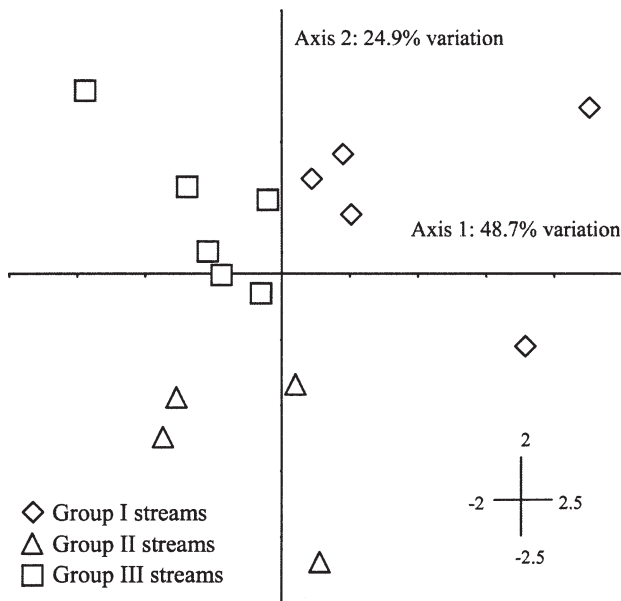


Fig. 3. A plot of factorial scores for the 15 streams from a principal components analysis used to distinguish the three stream groups in Glacier Bay. The environmental variables entered into the analysis were stream age, indicators of habitat complexity (% of pools, % CWD), the sorting coefficient, and a measure of substratum stability (the bottom component of the Pfankuch index). See text and Table 5 for details of the stream groups.

Table 5. Stream age, sorting coefficient, Pfankuch index (bed stability), and % CWD (an indicator of habitat complexity) in the three stream groups identified in Glacier Bay. Values are means  $\pm$  1 SE. The Pfankuch index decreases with increasing substrate stability, the sorting coefficient decreases with increased substrate sorting.

	Stream age	Sorting coefficient	Pfankuch index	% CWD
Group I	165 $\pm$ 7.8	1.96 $\pm$ 0.03	35.2 $\pm$ 5.3	19.9 $\pm$ 4.0
Group II	40 $\pm$ 9.5	2.1 $\pm$ 0.2	28.0 $\pm$ 3.4	10.6 $\pm$ 2.3
Group III	112 $\pm$ 4.0	2.37 $\pm$ 0.04	37.5 $\pm$ 1.45	4.3 $\pm$ 0.4

(Table 5). Group II (Nunatak Creek, Wolf Point Creek, Gull Creek, and Stonefly Creek) possessed the youngest streams, with lower habitat complexity than group I (Table 5) but higher habitat complexity and substratum stability than group III. They were relatively well sorted. Group III (Carroll East Stream, Head of Tarr stream, Reid Creek, Vivid Lake stream, Ice Valley stream, and Oystercatcher creek) were intermediate in age with low habitat complexity. Their substrata were relatively poorly sorted, with lower stability than groups I or II (Table 5).

There was a clear decreasing gradient of taxonomic richness in meiofaunal assemblages among stream groups (Fig. 4A). Taxonomic richness was highest in old streams with high habitat complexity that were relatively well sorted (group I) and lowest in streams with minimal complexity that were relatively poorly sorted (group III). Meiofaunal abundance was highest in group II streams, but otherwise followed a similar pattern to taxonomic richness (Fig. 4B).

The centered PCA, used to examine differences in the composition of meiofaunal assemblages between stream groups, showed that their centroids were separated along the first and second axes of the PCA (Fig. 5A). Group I streams contained assemblages characterized by two genera of harpacticoid copepods (*Bryocamptus* spp. and *Atheyella* spp.), ostracods, and the cyclopoid copepod *Eucyclops agilis* (Fig. 5B). Group II streams were characterized by nonmicrocrustacean meiofauna (*Chaetogaster*, Tardigrada) and also the harpacticoid copepods *Moraria* and *Epactophanes* (Fig. 5B). Group III streams were characterized by the cyclopoid copepod *Diaicyclops* (Fig. 5B).

## Discussion

This is the first study to examine in detail the responses of benthic meiofaunal assemblages to glacial retreat by making reach scale comparisons of 15 streams across a temporal gradient of 200 yr. The copepod assemblages of these Glacier Bay streams comprised species that typically possess widespread distributions (although see Reid 1998). The cyclopoid copepods *Acanthocyclops vernalis* and *Paracyclops poppei*, for example, are cosmopolites, as is the harpacticoid copepod *Epactophanes richardi* (Dussart 1969). Many of the species found are also eurytopic, for example, *Epactophanes richardi* has been found in moist soils in addition to the benthos of streams and rivers (Reid 2001). *Maraenobiotus insignipes*, in contrast, is restricted to the border zone of glaciers (Husmann 1975), a finding supported by this study. Many species also possessed characteristics that suggested good dispersal abilities, as might be expected from their presence in streams less than 200 yr old. Desiccation-resistant eggs or resting stages capable of dispersal between systems by wind, waterfowl, and animals (e.g., Caceres and Soluk 2002; Figuerola and Green 2002) are produced by several genera (*Acanthocyclops*, *Eucyclops*, *Diaicyclops*, *Bryocamptus*) and the species *Epactophanes richardi* (Dahms 1995; Fryer 1996). The harpacticoid copepod genus *Mesochra* is euryhaline and could disperse into stream systems from the adjacent marine environment.

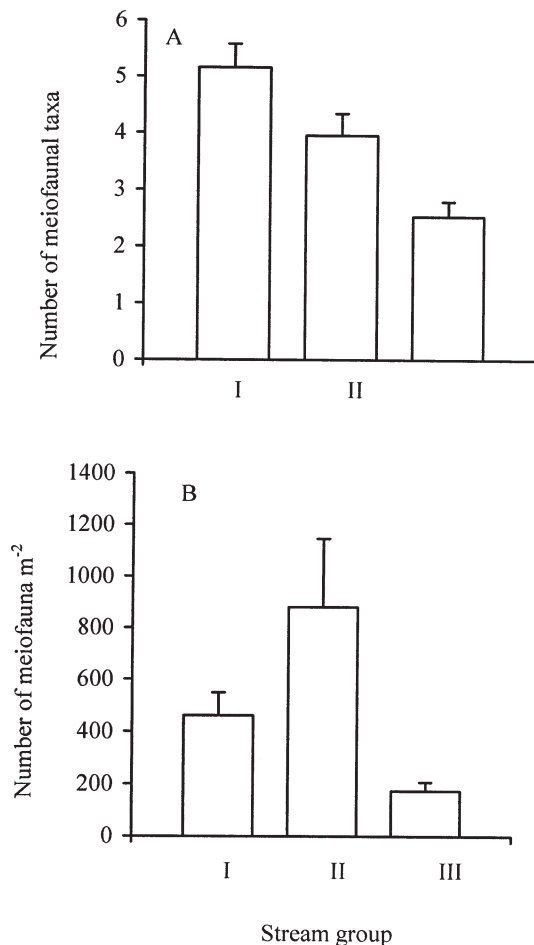


Fig. 4. (A) Mean ( $\pm$  1 SE) taxonomic richness and (B) mean density ( $\pm$  1 SE) of meiofaunal assemblages in three stream groups in Glacier Bay. See text and Table 5 for definition of stream groups.

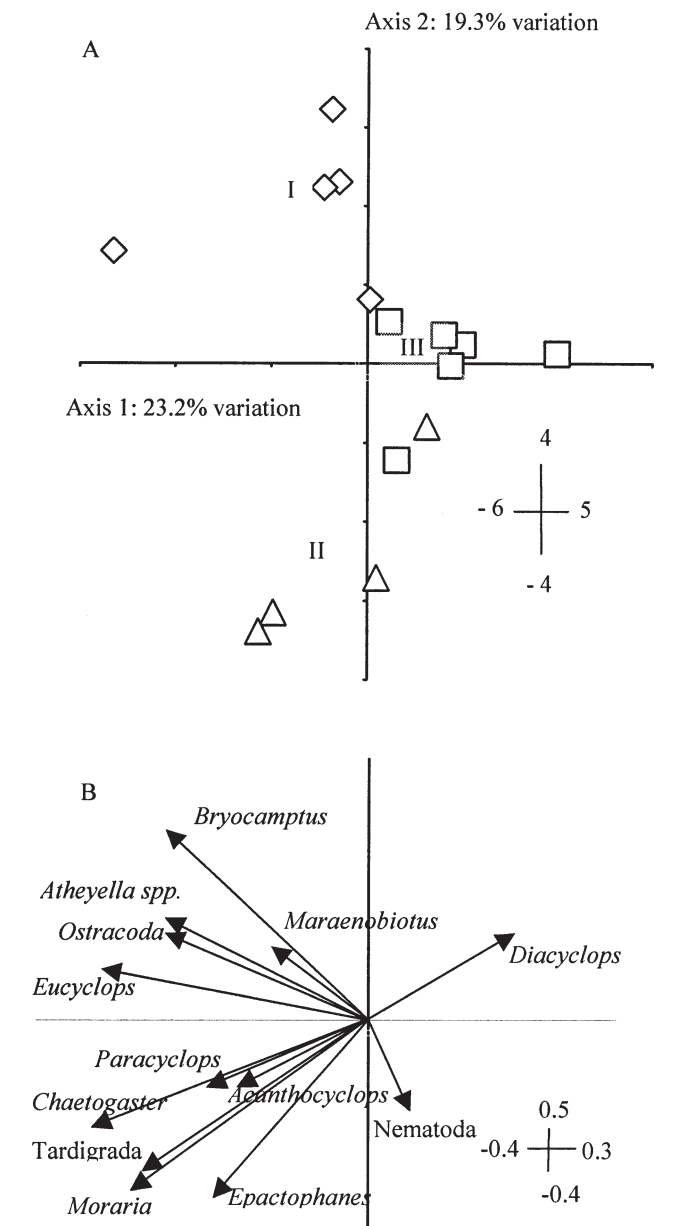


Fig. 5. Differences in the composition of meiofaunal assemblages among three stream groups in Glacier Bay. (A) Plot of factorial scores of streams I, II, and III correspond to the centers of gravity of the three stream groups. (B) Plot of factorial scores of meiofaunal taxa along the first two axes of the principal components analysis. See text and Table 5 for the definition of stream groups.

**Stream age and meiofaunal assemblages**—The TWIN-SPAN classification showed a distinct division of meiofaunal assemblages between older ( $>140$  yr) and younger ( $<140$  yr) streams. Four harpacticoid species (*Bryocamptus hiemalis*, *B. zschokkei*, *Atheyella illinoisensis*, and *A. idahoensis*) were characteristic of the older streams, and the distribution of these species was explained by models variously incorporating stream nutrient levels, stream age, and indicators of habitat complexity. These species have relatively large body sizes (0.6–1 mm) and may inhabit the

epibenthos, where they may be particularly vulnerable to high flow disturbances (Robertson and Milner 1999). Nevertheless, they persist in streams perhaps because they use a refuge-as-habitat approach (Robertson et al. 1995; Lancaster and Belyea 1997). Here the actual habitat is a series of suitable habitat patches (in-stream refugia). Individuals may be present outside these patches when conditions are benign, but these are quickly lost during disturbance events. However, survival is high among individuals in the suitable habitat patches, and when recruitment occurs, the population may, temporarily, become more widespread again. Field studies by Robertson et al. (1995) and Golladay and Hax (1995) provide supporting evidence for this approach. We speculate that the survival of these harpacticoid copepods in streams may be dependent on the presence of in-stream refugia and that they are unable to establish populations in recently deglaciated streams until such habitat (e.g., CWD and pools) has developed. Thus, they occur in the older streams of Glacier Bay, where riparian zone development and increased retention and stability allows greater habitat complexity and the development of suitable habitat patches. CPOM may also function as a suitable habitat patch in Glacier Bay streams (Robertson and Milner 2001).

In contrast, harpacticoid species found in the younger streams (*Maraenobiotus*, *Epactophanes*, *Moraria*) are smaller (0.3–0.6 mm), vermiform, and frequently described as inhabiting the interstitial (e.g., Dole-Olivier et al. 2000). In this habitat, they may be less vulnerable to high surface flows (although see Palmer et al. 1992) and so less dependent on surface in-stream refugia. Thus, they can establish populations in the younger, recently deglaciated streams, where habitat complexity is minimal. Copepod species in the 15 Glacier Bay streams have a wide range of habitat affinities but have similar dispersal abilities (see previous); we argue that the observed copepod assemblage in a Glacier Bay stream is determined by habitat availability rather than dispersal constraints.

**Physicochemical variables and meiofaunal assemblages**—A major predictor of harpacticoid diversity and abundance in our study was the degree of sediment sorting (the sorting coefficient). Very few studies on epibenthic stream meiofauna have incorporated this variable (however, see Shiozawa 1986), but it is a principal factor determining meiofaunal distribution in marine communities (Jansson 1967; Hulings and Gray 1976). Here, as sediments become more poorly sorted (i.e., have a greater diversity of particle size), abundance and species diversity increase (Coleman et al. 1997), perhaps because well-sorted sediments offer a narrower range of habitats compared with poorly sorted sediments (Gray 1974; Marcotte 1986; Etter and Grassle 1992). The substrata of all 15 Glacier Bay streams fall into either the poorly sorted or very poorly sorted category, but within these limits, harpacticoid abundance and diversity were higher in streams that had better sorted substrates, the opposite of results from the marine environment. Freshwater and marine harpacticoid copepods may differ in their environmental requirements with freshwater meiofauna responding favorably to the more open interstitial spaces

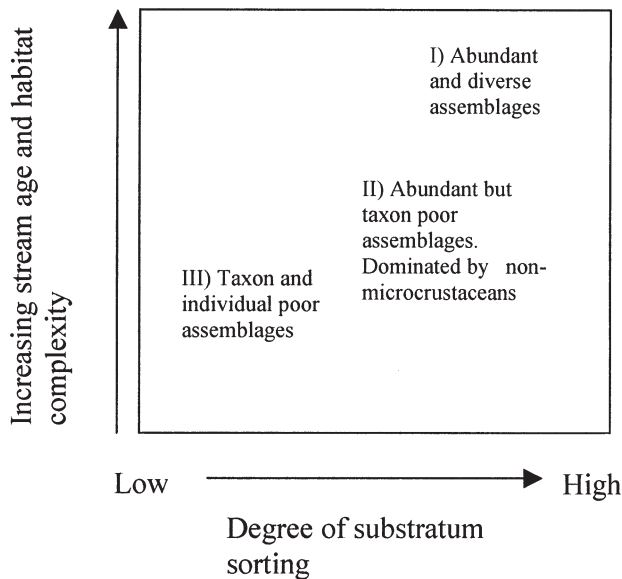


Fig. 6. Variation in the abundance and taxon richness of meiofaunal assemblages along the axes of a two-dimensional habitat templet. Numbers identify the position of the three stream groups along the axes of the templet (see Fig. 3, Table 5, and text for the definition of the three groups).

found in better sorted substrata. In the very poorly sorted sediments of Glacier Bay streams, reduced porosity may result in lowered oxygen levels, to which harpacticoid copepods are very sensitive (Strayer et al. 1997; Malard and Hervant 1999). Additionally, the sorting coefficients of Glacier Bay streams (1.71–2.74) are considerably higher than those of Coleman et al. (1997) (0.2–0.7). Previous studies on hyporheic communities have identified grain size as an important predictor of assemblage diversity and abundance; streams with larger grain sizes possessed more abundant assemblages (Strayer et al. 1997; Hunt and Stanley 2003). However, only *Atheyella idahoensis* followed this pattern in our study.

Another important environmental predictor for the distribution of total meiofaunal abundance was the bottom component of the Pfankuch index, a measure of the stability of the stream substratum. Streams with lakes had relatively stable substrates compared with streams without lakes. Tardigrada and *Chaetogaster* sp. were particularly responsive to high levels of substratum stability and may use the fungal–algal–mineral mats that develop in these streams as a habitat and/or food source (see also Milner et al. 2000), although the coarse level of taxonomic resolution may obscure species-specific responses.

*Comparison of meiofaunal and macroinvertebrate responses to stream age and physicochemical variables*—One of our objectives was to determine how the responses of the meiofaunal and macroinvertebrate assemblages to stream age and physicochemical variables differed. Here, we consider mostly the Copepoda subset of the meiofaunal assemblage because the species-level identification allows comparison with the macroinvertebrates. Milner et al. (2000) determined that macroinvertebrate species richness

rose with increasing stream age, substrate stability, and indicators of habitat complexity; and this was confirmed by further analysis in this study. In contrast, copepod species richness was significantly related to the sorting coefficient. Total macroinvertebrate abundance responded to stream gradient and temperature (Milner et al. 2000), and this study suggested that macroinvertebrate abundance also increased with increasing substratum stability and in well-sorted streams. Total meiofaunal abundance rose with increasing stream-bed stability and entrenchment. In many respects, therefore, macroinvertebrate and meiofaunal assemblages differ in their response to environmental variables in developing streams. It may be that meiofauna perceive their environment with a different grain than macroinvertebrates (Stead et al. 2003).

*The meiofaunal habitat templet for Glacier Bay streams*—The habitat templet, developed to synthesize our understanding of meiofaunal assemblage development in recently deglaciated Glacier Bay streams, indicates that there are three groups of streams that differ in their physical characteristics and possess distinctive meiofaunal assemblages (Fig. 6). Group I streams have the greatest stream age and habitat complexity, with relatively well-sorted substrata; their meiofaunal assemblages are abundant and diverse, being characterized by two genera of harpacticoid copepods only found in older Glacier Bay streams. Group II streams are the youngest, with relatively stable substrata, resulting from the presence of lakes in three out of four stream systems. They have abundant meiofaunal assemblages that are taxon poor relative to group I. The assemblage is dominated by a noncrustacean meiofaunal component (e.g., Tardigrada, *Chaetogaster*) that shows a strong positive relationship between abundance and bed stability (Table 4). Group III streams are intermediate in age, with relatively poorly sorted, unstable substrata and minimal habitat complexity. They have impoverished meiofaunal assemblages both in terms of taxon richness and abundance.

Newly deglaciated areas of Glacier Bay, i.e., group II streams, often have abundant lakes and/or wetlands in their systems and these features may have the effect of temporarily ameliorating hostile conditions for meiofauna by stabilizing flow and improving habitat heterogeneity (Milner 1997; Milner et al. 2000). Frequently, such features are nonpermanent and are subsequently lost to stream systems as they age. Meiofaunal assemblages then become less diverse and abundant (i.e., more similar to group III streams) until streams develop habitat heterogeneity through age with the development of riparian vegetation and the recruitment of coarse, woody debris dams, i.e., group I streams (Milner and Gloyne-Phillips 2005).

This study is the first to look in detail at meiofaunal community development across 15 streams, using the spatial gradient of glacial recession in Glacier Bay National Park, to make reach scale comparisons across a temporal gradient of 200 yr. It is also the first study in lotic freshwaters to show that sediment sorting is as crucial to meiofaunal communities here as it is in the marine environment. The response of meiofauna to sediment

sorting, however, differs between the two environments, and more research is needed to elucidate whether this difference is widespread in lotic environments and to determine the underlying reasons for this response. We have developed a habitat templet to synthesize our understanding of meiofaunal assemblage development in Glacier Bay streams; the next stage is to test whether this templet can be used to explain meiofaunal assemblage development in recently deglaciated streams from other areas or indeed assemblage development in new streams that are not the result of deglaciation, such as flood alleviation channels.

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