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Evolution of a stream ecosystem in recently deglaciated terrain

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Abstract. Climate change and associated glacial recession create new stream habitat that leads to the assembly of new riverine communities through primary succession. However, there are still very few studies of the patterns and processes of community assembly during primary succession for stream ecosystems. We illustrate the rapidity with which biotic communities can colonize and establish in recently formed streams by examining Stonefly Creek in Glacier Bay, Alaska (USA), which began to emerge from a remnant glacial ice mass between 1976 and 1979. By 2002, 57 macroinvertebrate and 27 microcrustacea species had become established. Within 10 years of the stream's formation, pink salmon and Dolly Varden charr colonized, followed by other fish species, including juvenile red and silver salmon, Coast Range sculpin, and sticklebacks. Stable-isotope analyses indicate that marine-derived nitrogen from the decay of salmon carcasses was substantially assimilated within the aquatic food web by 2004. The findings from Stonefly Creek are compared with those from a long-term study of a similarly formed but older stream (12 km to the northeast) to examine possible similarities in macroinvertebrate community and biological trait composition between streams at similar stages of development. Macroinvertebrate community assembly appears to have been initially strongly deterministic owing to low water temperature associated with remnant ice masses. In contrast, microcrustacean community assembly appears to have been more stochastic. However, as stream age and water temperature increased, macroinvertebrate colonization was also more stochastic, and taxonomic similarity between Stonefly Creek and a stream at the same stage of development was <50%. However the most abundant taxa were similar, and functional diversity of the two communities was almost identical. Tolerance is suggested as the major mechanism of community assembly. The rapidity with which salmonids and invertebrate communities have become established across an entire watershed has implications for the conservation of biodiversity in freshwater habitats.

Key words: colonization; community assembly; stochastic vs. deterministic; deterministic; functional diversity; glacial streams; Glacier Bay, Alaska, USA; stochastic; succession; traits.

INTRODUCTION

Within stream ecosystems, community assembly is typically considered to be stochastic (e.g., Fisher 1983, Townsend 1989). However, Milner et al. (2001) suggested that low water temperature and channel stability in glacier-fed rivers close to the source creates a habitat template that selects for certain species traits (e.g., cold stenotherms, clinging habit), thereby invoking deterministic processes. More-recent research suggests it is possible that the process of community assembly is a blend of these two models. For example, Chase (2007) hypothesized that stochastic processes prevail in benign habitats whereas deterministic processes dominate where environmental conditions are harsh; Lepori and

Malmqvist (2009) provide evidence from Scandinavian streams along a disturbance gradient that partially supports this theory. Macroinvertebrate communities in particular are considered to be shaped both by deterministic processes, which allow widespread colonization by specialists from the regional species pool depending on niche differences and disturbance conditions, and by stochastic processes, which distribute the more generalist species randomly among individual reaches and patches. Thus, both processes can interact hierarchically (Lepori and Malmqvist 2009). However, of the studies that have examined the process of community assembly in rivers, none we are aware of have been undertaken in young river ecosystems in recently deglaciated terrain.

Rapid glacial recession over the last 200 years has been extensive in coastal Alaska, creating many new stream ecosystems (Arendt et al. 2002). However, colonization of postglacial stream habitats, and subse-

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quent community assembly at the scale of entire watersheds, is not well studied (Fisher 1983). Glacier Bay in southeast Alaska represents a unique and outstanding natural laboratory in which to study the evolution of stream ecosystems at this scale due to this rapid glacial recession (Kling 2000). We present in this paper the first study of a river ecosystem, Stonefly Creek in Wachusett Inlet, recently formed (<10 years) after ice recession, to examine colonization and development of riverine communities. The longest continuous record of colonization and community development for postglacial streams in Glacier Bay is for Wolf Point Creek (1977 to 2010). However, the stream emerged from the ice in the early 1940s and was not studied until 1977, at least 30 years after formation. Milner et al. (2008) suggested that the successional model most applicable to the colonization sequence in Wolf Point Creek was the tolerance model of Connell and Slatyer (1977) as, apart from the early pioneers, most taxa that have colonized still remain within the community. In contrast, the meiofaunal-sized copepod assemblage in Wolf Point Creek has undergone substantial extinctions. As the colonization record for Copepoda in this stream is relatively limited (from 1994), it is difficult to determine the most appropriate model of community assembly for this group (Milner et al. 2008). In Wolf Point Creek we attributed the poor persistence of copepods to a lack of suitable refuge habitat (Milner et al. 2008, Robertson 2000).

As primary succession proceeds following deglaciation, the instream habitat template (Southwood 1988, Poff 1997) shifts from one of cold, disturbed conditions dominated by autochthonous food production due to a lack of terrestrial vegetation to a warmer, stable, allochthonous-based system as alder and willow establish and develop close to the stream. Where glacierization is high, macroinvertebrates are typically cold stenotherms, with small-sized, streamlined/flattened bodies and possessing clinging habits (Snook and Milner 2002, Ilg and Castella 2006, Füreder 2007). Assessments of multiple biological traits allow characterization of community functional diversity (Poff 1997, Usseglio-Polatera et al. 2000, Statzner and Bêche 2010) rather than simply its structure. Thus, while community similarity between Stonefly Creek and adjacent watersheds may be low if colonizing species' identities diverge after stochastic processes take hold, the functional diversity of the macroinvertebrate within the two communities could theoretically be similar if environmental "filters" follow similar successional trajectories. However, testing of such hypotheses has to date been hindered by a lack of data sets from comparable basins undergoing primary succession.

The importance of Pacific salmon carcasses for increasing productivity in small streams of coastal southeast Alaska, through the provision of marine-derived nitrogen (MDN) into food webs, has been documented by Wipfli et al. (1998) and Naiman et al.

(2002). Previous studies in Glacier Bay indicated no evidence of marine-derived nutrients in food webs in young streams (Milner et al. 2000), reflecting the lack of salmon-carcass retention due to high flow variability and low geomorphological complexity (e.g., pools, woody debris accumulations; see Milner and Gloyne-Phillips 2005, Klaar et al. 2009). Similarly, Wilzbach et al. (2005) found no measurable effect of MDN in streams with alder-dominated riparian cover.

This study documented the distribution and abundance of biotic communities in a recently formed stream system. Four hypotheses were tested: (H_1) community assembly in streams following glacial recession follows deterministic pathways and the tolerance model; (H_2) non-insects will be poorly represented in the stream community; (H_3) biological traits of the community will be different than other streams if trajectories of development are not similar; and (H_4) MDN will not be assimilated into the food webs because the geomorphological "simplicity" associated with young streams in Glacier Bay should prevent significant salmon-carcass retention (Milner and Gloyne-Phillips 2005, Klaar et al. 2009). The findings from the development of Stonefly Creek are considered in the context of more general primary-succession theory.

STUDY AREA AND STREAM FORMATION

During the Little Ice Age a glacial advance reached the present mouth of Glacier Bay in 1760 (Fastie 1995). This has since been followed by an extensive retreat of tidewater glaciers, uncovering a major fjord >100 km long with two principal arms, Muir Inlet and the northwest arm. This rapid retreat cut off remnant ice masses, whose meltwaters fed new streams flowing through deglaciated valleys. One such ice mass was the Plateau Remnant, separated from the receding Plateau Glacier on the north side of Wachusett Inlet ~20 km from its entrance (Fig. 1a). The lower reaches of the new stream (unofficial name Stonefly Creek) were uncovered by ice in approximately the late 1970s at the same time that the upper lake began to emerge (Fig. 1b). A turbid lake southeast of the ice remnant originally fed a stream flowing east to the inlet (Fig. 1b). By 1990 this proglacial lake and the two original channels were dry, although a wetland was evident in the vicinity of the channel flowing to the present stream mouth. By 1990 a spatially heterogeneous riverscape had been created with a large upper clear-water lake (area, 1.8 km²; maximum depth, >30 m) feeding the stream that flows for 0.9 km before reaching a lower lake that remains turbid due to runoff from the vestiges of the remnant Plateau Glacier. A series of steep falls ~0.4 km below the upper lake potentially constitutes a barrier to fish migration. A large kettle pond feeds a shallow stream that flows into the lower lake. The outlet from the turbid lower lake flows 0.8 km to the stream mouth (Fig. 1c). A wetland (>20 cm in depth) formed adjacent to the entrance of the clear-water stream to the lower turbid lake is fed by

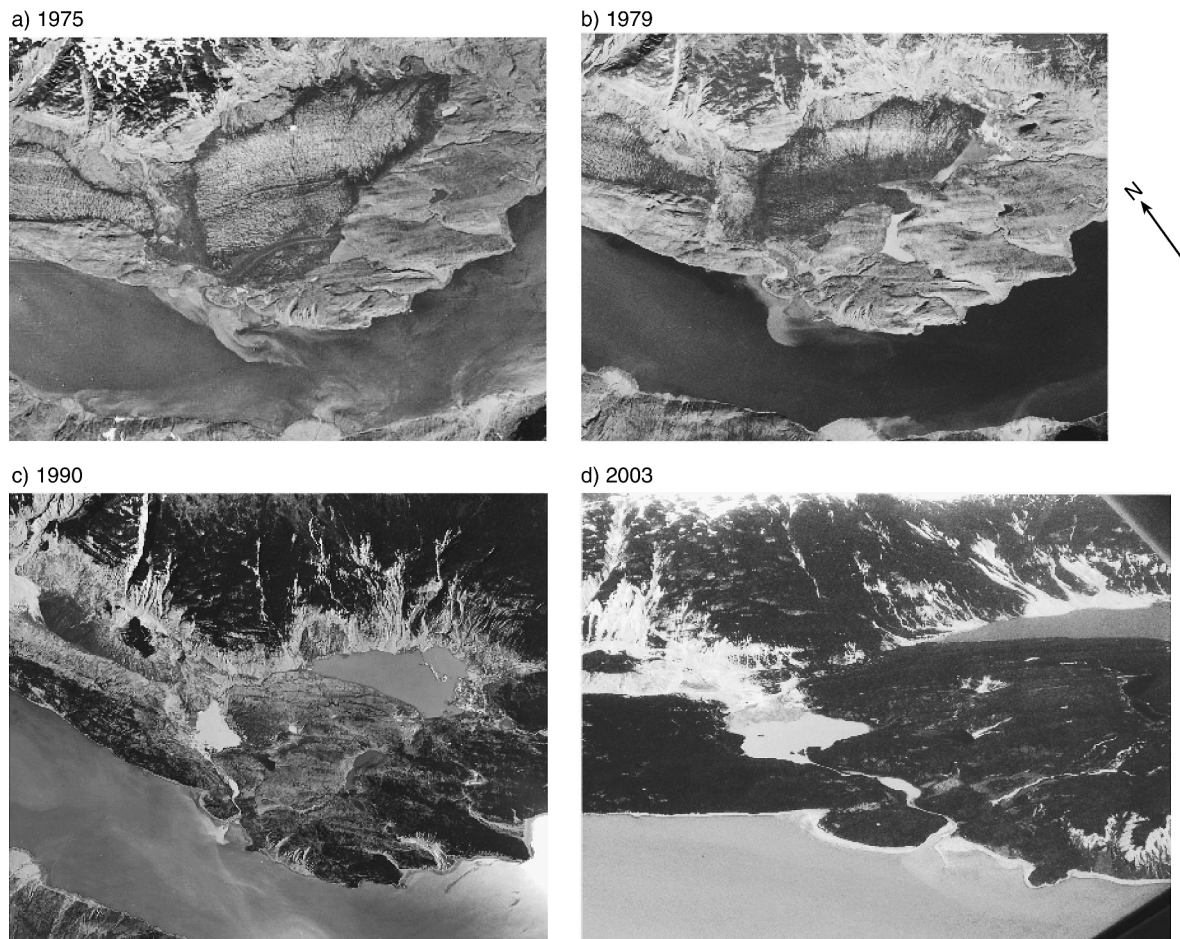


FIG. 1. Aerial photographs of the Stonefly Creek watershed (Glacier Bay, Alaska, USA) in four different years. The scale in photographs (a)–(c) is 1:20 000; in (d) it is 1:10 000.

groundwater and tributaries and a second wetland fed by subsurface flow from kettle lakes is evident near the main stream mouth (Fig. 2). In 1990 the lower floodplain was essentially barren, with mats of mountain aven (*Dryas* spp.; Fig. 1c), and isolated clumps (typically prostrate) of alder (*Alnus crispa*) and willow (*Salix* spp.). By 2003 the watershed was dominated by extensive growth of alder and willow (Fig. 1d), with the exception of the small area of the Plateau remnant that still remained (Fig. 2).

Two sites were used for sampling invertebrates: site 1 below the lower lake and the ponded area, and site 2 above the lower lake but below the falls (Fig. 2). The dominant substrate at site 1 was cobble with a diameter between 5 to 12 cm with some larger substrate; the site itself had a width of <5 m and depth typically <40 cm. The channel was relatively stable as evidenced by a close border of overhanging vegetation dominated by alder, and instream habitat was dominated by riffles and runs with little pool habitat. Turbidity at this site was between 60 and 80 nephelometric turbidity units (NTU). Physicochemical variables at site 2 were similar

except the predominant substrate size was larger, with more pool habitat behind boulders. Turbidity was lower, at between 10 and 20 NTU.

METHODS

During the summers of 2000 and 2001, invertebrates were collected in the Stonefly Creek watershed (Glacier Bay, Alaska) using a Surber sampler (Research Nets, Bothell, Washington, USA) with a 330- μ m mesh net (10 replicates) for macroinvertebrates and a 63- μ m mesh (5 replicates) for microcrustacea. Samples were also collected by this approach in the summer months of 1997 and 1999, while qualitative macroinvertebrate samples were collected at site 1 in 1992 using a 330- μ m mesh kick net. This mesh size matched that used in the long-term studies of Wolf Point Creek (Glacier Bay, Alaska).

Invertebrates were sorted from detritus and inorganic matter and identified and enumerated in the laboratory using the keys of Merritt and Cummins (1996), Stewart and Oswood (2006), Smith (2001), and Thorp and Covich, (1991). Head capsules of chironomid larvae

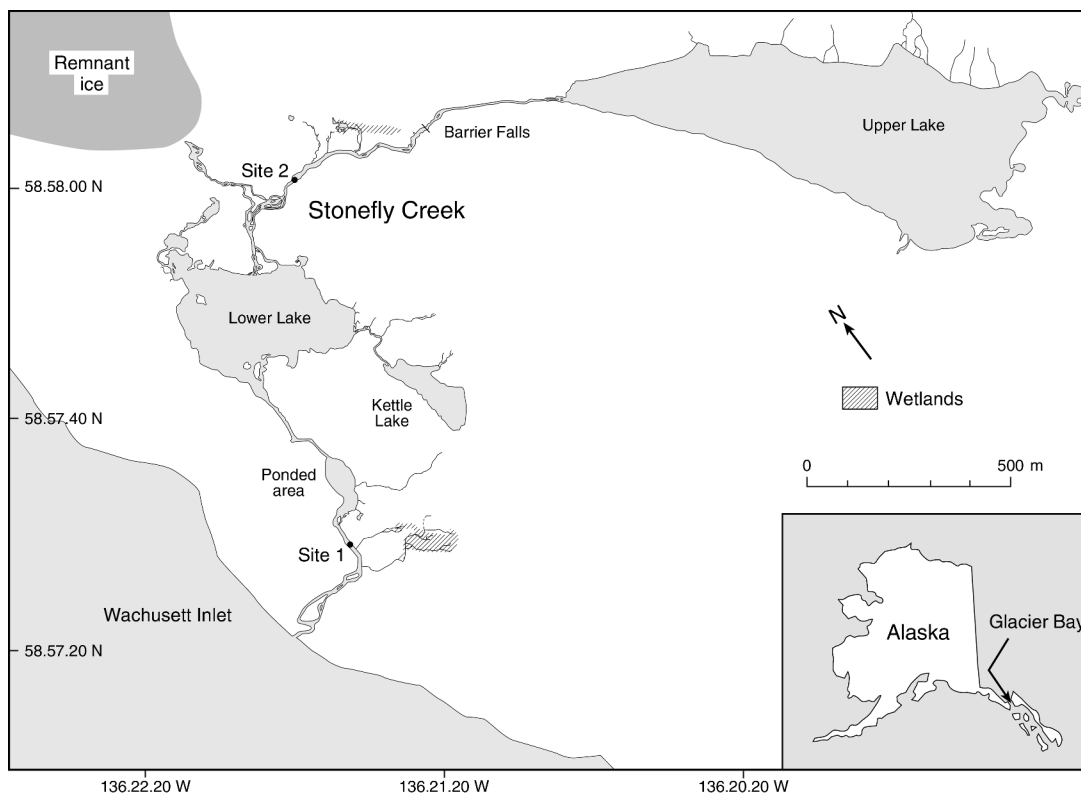


FIG. 2. Map of the Stonefly Creek watershed in 2004. Most of the identified features can be recognized in Fig. 1c and d.

were typically micro-dissected and cleared in 10% KOH prior to mounting ventrally, in either polyvinyl lactophenol or more latterly in Euparal, and identified under a dissecting microscope.

Adult salmon spawners were estimated by observation counts on foot along the length of the stream system (including above the falls) during the years of the study. This procedure involved two personnel walking the length of the stream and making estimates of the number of each species and then averaging. Juvenile salmonids were captured using minnow traps (minimum 10) baited with salmon eggs and fished for 1.5–2 h at selected reaches throughout the watershed in the summer of 2004 including above the barrier falls (Fig. 2). Data were expressed as catch per unit effort (CPUE) equating to the total catch divided by the number of minnow traps used. In the kettle lakes, juvenile salmon were captured using dip nets.

Stable isotopes were used to establish the potential incorporation of marine-derived nitrogen (MDN) in the food webs of Stonefly Creek. In 2004, vegetation, macroinvertebrates, and juvenile fish were collected for stable-isotope analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. New foliage was removed from riparian willows with forceps and stored in sample bags. Macroinvertebrates were collected from stones (two representative genera [typically collectors and grazers] were used for comparison).

Minnow traps and dip nets were used to capture juvenile coho (*Onchorhynchus keta*), and sockeye (*Onchorhynchus nerka*) salmon and juvenile Dolly Varden (*Salvelinus malma*). These were anaesthetized, sacrificed, and had dorsal muscle tissue between the head and the adipose fin removed for analysis. The amount collected generated ~ 0.20 and 0.40 mg dry mass of material that was analyzed by laboratory methods outlined in Milner et al. (2000).

Data analysis

A comparison of temporal changes in both macroinvertebrate and meiofaunal benthic communities in Wolf Point Creek (for study site description see Milner et al. [2008]) and Stonefly Creek was undertaken through the application of nonmetric multidimensional scaling (NMDS) using a Bray-Curtis dissimilarity matrix in PRIMER-E version 6 (Clarke and Chorley 2006) following \log_{10} transformation of abundance data. Jaccard's similarity coefficients were calculated to compare the compositional stability of the macroinvertebrate and meiofaunal community in Stonefly Creek in 1997 and 2001 with the Wolf Point Creek community from 1977 through to 2002. In both analyses only data from site 1 in Stonefly Creek were used as this site is the most comparable to the sampling site in Wolf Point Creek.

Macroinvertebrate traits were compared between Stonefly Creek in 2001 and Wolf Point Creek in 1997 when annual degree-days were approximately similar (1500 centigrade temperature units; CTU), to ascertain possible similarity in taxonomic and functional attributes between the two streams at similar stages of development. Functional traits were characterized for 20 taxa using the database of Poff et al. (2006) for insects, and the meta-database of traits for North American invertebrates developed by Vieira et al. (2006) for non-insects. Taxa were classified according to 20 individual traits coded in 63 modalities that can be broadly categorized as life-history, mobility, morphological, and ecological traits (Poff et al. 2006). The chosen categories encompassed a wide range of biological and functional traits, and from this trait analysis a subset that have been demonstrated to respond strongly to ecosystem changes associated with decreasing glacier influence (Snook and Milner 2002, Ilg and Castella 2006) was selected for more detailed analysis. Each taxon was assigned to one trait state (i.e., a binary approach) because trait information used to underpin “fuzzy coding” approaches in Europe is not as readily available for North America (Finn and Poff 2006, Poff et al. 2006). Traits were assigned at the genus level for most taxa. For taxa identified only to family level, we used the “majority rule” approach of Poff et al. (2006) to assign the most common genus-level trait state to this family. Due to the diversity of this group in glacial rivers, traits were assigned for individual species of Chironomidae wherever possible based on expert opinion or additional information drawn from the literature. Functional diversity was calculated simply as the number of traits present in the community. We used *t* tests to identify any significant differences in arcsine-transformed trait relative-abundance data using replicate Surber sample data collected in Stonefly Creek and Wolf Point Creek in years with similar CTU (i.e., 2001 and 1997, respectively).

To assess the relative contribution of MDN we converted average $\delta^{15}\text{N}$ values for each stream to percentage MDN following conventions in Kline et al. (1990). We assumed that $\delta^{15}\text{N}$ reference points described for the mixing model were applicable; i.e., that 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 ± 1.0 (Mathisen et al. 1988). Percentage 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 (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 percentage total nitrogen.

RESULTS

Macroinvertebrate colonization

The five initial colonizers collected at site 1 in 1992 below the lower lake were chironomids (nonbiting midges) belonging principally to the genus *Diamesa*, although a number of Orthoclaadiinae were found including *Paratrachocladus* (Appendix). Simuliidae (blackflies) and the mayfly *Baetis* (Baetidae) were also collected. By 1997 the macroinvertebrate richness had increased to 15 taxa, with an increase in Chironomidae diversity, and the collection of the stonefly family Capniidae. Chironomidae were dominated by *Diamesa*, *Cricotopus tremulus*, and *Eukiefferiella rectangularis*. *Paratrachocladus* was also found in large numbers. Total mean macroinvertebrate abundance exceeded 4000 individuals/m². By 2001 the taxonomic richness at site 1 had increased to 31 taxa of which only three were non-insects (Oligochaeta, Hydracarina, and Gammaridae). Total mean abundance had increased to 4600 individuals/m². *C. tremulus* was still the dominant chironomid but *Eukiefferiella claripennis* increased to over 1000 individuals/m² to become codominant. *Pagastia partica*, which first colonized in 1999, increased rapidly to similar abundance. *Orthocladus manitobensis* and *Orthocladus mallochi* were also notable colonizers in 2000 but *E. rectangularis* decreased in abundance and *Paratrachocladus* was not found in 1999 (Appendix). *Diamesa* was absent or in extremely low densities following colonization by *P. partica*. The stonefly *Suwallia forcipata* (Chloroperlidae) was also collected in 2000 and 2001 but in low numbers. By 2001 a total of 57 macroinvertebrate taxa were collected from both sites of the new stream system including site 2 above the lower lake, of which 47 taxa were chironomids (Appendix) including the predator *Krenopelopia*.

The NMDS (nonmetric multidimensional scaling) plot indicates temporal shifts in Wolf Point Creek and Stonefly Creek macroinvertebrate communities over time, with the Stonefly Creek community separate from Wolf Point Creek but showing the most similarity with the 1996 to 2002 cluster of years (Fig. 3a). Jaccard similarity coefficients over time supported this finding, indicating the macroinvertebrate community in Stonefly Creek in 1997 and 2001 increased in similarity to these years in Wolf Point Creek (Fig. 4a). Nevertheless Jaccard similarity values were always <0.50 although all the abundant macroinvertebrate taxa at site 1 in Stonefly Creek had colonized Wolf Point Creek at an earlier date, including all non-chironomid taxa (Appendix). A number of major groups were not collected in Stonefly Creek by 2001 compared to Wolf Point Creek at a similar temperature and number of degree days (1997). These groups were the dipterans Tipulidae, Muscidae, and Ceratopogoniidae, but Planorbidae, Gammaridae, and Hydracarina, which colonized Wolf Point Creek two to three years later at a warmer temperature, were found in Stonefly Creek at site 2

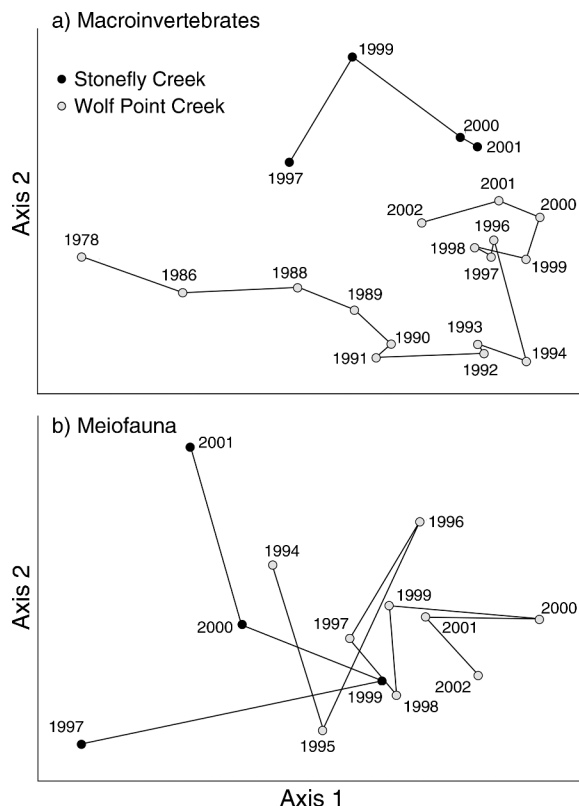


FIG. 3. NMDS (nonmetric multidimensional scaling) plots of invertebrate communities [(a) macroinvertebrates and (b) meiofauna] in Stonefly Creek (site 1; 1997–2001) and Wolf Point Creek (1978–2002) using \log_{10} -transformed abundance data and the Bray-Curtis resemblance matrix. Rare taxa were not downweighted.

above the lower lake (Fig. 5). All the common chironomid taxa that had colonized Wolf Point Creek by 1997 were found in Stonefly Creek, and two genera, *Corynoneura* and *Paracladopelma*, which colonized Wolf Point Creek later in its development were also found. However 18 species of chironomid collected at site 1 in Stonefly Creek by 2001 were never found in Wolf Point Creek, although these taxa were typically low in abundance except for *Diplocladius* spp. and *Sergentia* spp. (Appendix).

In the comparison of macroinvertebrate functional traits between Stonefly Creek and Wolf Point Creek, a significant difference ($P < 0.01$) was found for the mean number of traits, with a higher number identified in Wolf Point Creek (47.3) than Stonefly Creek (41.6) (Table 1). However the total number of traits was similar with 47 traits at Wolf Point Creek and 45 traits at Stonefly Creek. The principal traits that created significant differences between the two streams in their relative abundance were body size (with Stonefly Creek being completely dominated by taxa < 9 mm; $P < 0.05$) and feeding group (Stonefly Creek supporting fewer grazers, collector-filterers and predators, all $P < 0.05$) (Table 1). Other traits (voltinism, dispersal distance,

adult flying strength, thermal preference) were not significantly different.

Microcrustacea colonization

We collected 27 species of microcrustacea (animals passing through a 1mm sieve but retained on a 63- μ m sieve) in the epibenthic running-water habitats of the Stonefly Creek watershed, including seven cyclopoid copepods, eight harpacticoid copepods, six ostracods, and six cladocerans (Appendix). Additionally, Nematoda, Hydracarina, and three genera of tardigrades (*Pseudobiotus*, *Dactylobiotus*, and *Hypsibius*) were collected. *Dactylobiotus* and *Hypsibius* have not previously been reported in Alaska. The microcrustacean assemblage increased in diversity over the course of the study from five taxa in 1997 to 1915 taxa in 2001. Mean abundance also increased from 38 individuals/m² in 1997 to 936 individuals/m² in 2001 (Appendix). The Wolf Point Creek and Stonefly Creek microcrustacean assemblages underwent temporal shifts (Fig. 3b) but unlike the macroinvertebrate community, the microcrustacean assemblage in Stonefly Creek did not become more similar to that in Wolf Point Creek over time. Jaccard similarity coefficients (Fig. 4b) suggested microcrustacean assemblages in the two streams had low/no similarity throughout the study period.

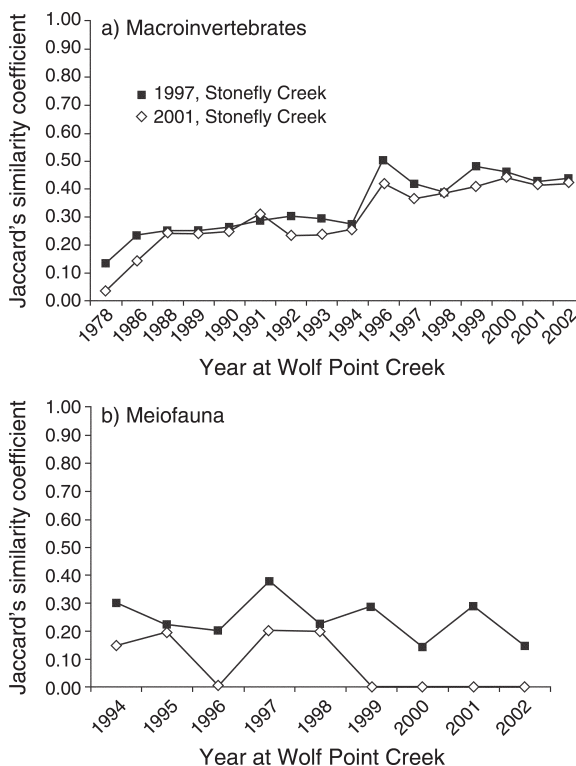


FIG. 4. Jaccard's similarity coefficients between (a) macroinvertebrates and (b) meiofauna in 1997 and 2001 at site 1 in Stonefly Creek and at different years of the communities in Wolf Point Creek.

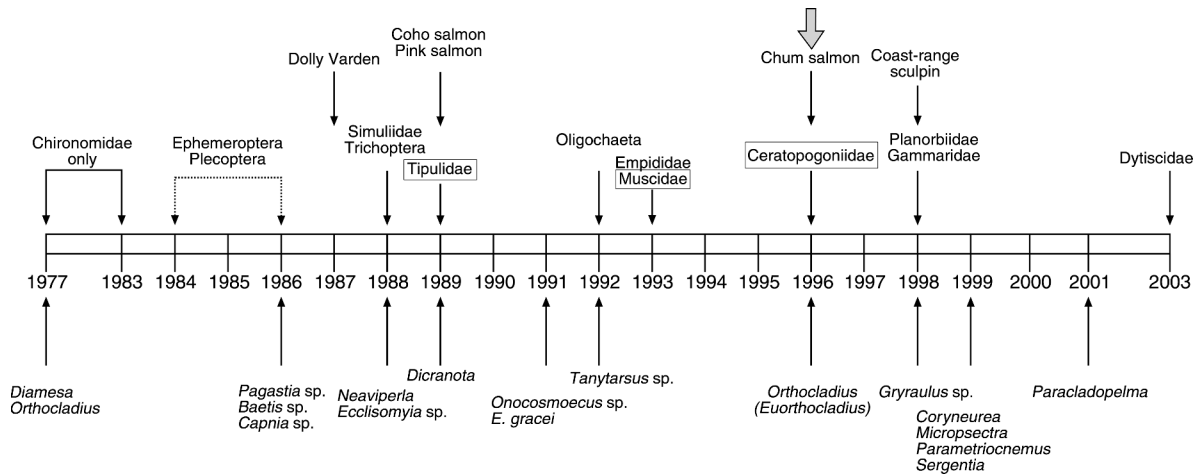


FIG. 5. Chronosequence of colonization of Wolf Point Creek by the most common macroinvertebrate taxa and fish. Groups in boxes have not been collected in Stonefly Creek; a large gray arrow shows the point along the chronosequence in Wolf Point Creek at which site 1 in Stonefly Creek was at the same maximum temperature and similar number of degree days. (The dotted arrow indicates uncertainty as to exact year of colonization.)

Fish colonization

Within 10 years of the lower reaches of the stream emerging from under the ice, pink salmon (*Oncorhynchus gorbuscha*) and Dolly Varden (*Oncorhynchus malma*) had colonized. By 2004 a wide diversity of habitat was being exploited by different species. Sockeye salmon (*O. nerka*) were spawning in the shallow outlet stream from the kettle lake and in the margins of the lower turbid lake where this stream entered (see watershed map, Fig. 2). Overall numbers of sockeye spawners were <200 individuals. The principal rearing habitat for juvenile sockeye was the kettle lake, although small numbers were present in the margins of the lower turbid lake and the kettle lake outlet stream. Juvenile coho salmon (*Oncorhynchus kisutch*) were widespread throughout the drainage and were found in the kettle lake (catch per unit effort [CPUE] = 3.3), the outlet stream from the kettle lake (CPUE = 3.8) and above the

lower turbid lake (site 2 CPUE = 2.9). Dolly Varden were also common in the wetland areas and a number of tributaries flowing into the stream above the lower turbid lake. Dolly Varden dominated the main river, most notably in the reaches above a potential barrier falls between the upper and lower lakes. No adult spawning salmon have been documented in this section of the stream during seven years of observations. At least four age classes of Dolly Varden were evident. Coast-range sculpin (*Cottus aleuticus*) and the nine-spined stickleback (*Pungitius pungitius*) were also found, with sticklebacks being particularly common in the kettle lake.

The number of pink salmon spawners in Stonefly Creek in 2001 ranged from 2500 to 3000 individuals above the lower lake to the falls and from 2000 to 2500 individuals below the lower lake totaling 4500 to 5500

TABLE 1. Number of traits and relative abundance of selected traits (mean \pm SD) for the macroinvertebrate replicate samples, together with significance values of *t* tests.

Trait	Stonefly Creek	Wolf Point Creek	P
Total number of traits	41.6 \pm 3.4	47.3 \pm 2.3	0.006
Relative abundance of traits			
Univoltine	0.95 \pm 0.03	0.89 \pm 0.10	0.083
Adult dispersal >1km	0.96 \pm 0.03	0.85 \pm 0.10	0.181
Weak adult flying ability	0.97 \pm 0.03	0.89 \pm 0.10	0.102
Maximal body size <9 mm	1.00 \pm 0.00	0.95 \pm 0.04	0.04
Maximal body size 9–16 mm	0.00 \pm 0.00	0.04 \pm 0.03	<0.001
Maximal body size >16 mm	0.00 \pm 0.00	0.01 \pm 0.01	<0.001
Cold stenotherm	0.94 \pm 0.04	0.85 \pm 0.09	0.428
Collector–gatherer	0.75 \pm 0.05	0.53 \pm 0.12	0.099
Collector–filterer	0.03 \pm 0.03	0.10 \pm 0.10	0.006
Grazer	0.21 \pm 0.05	0.32 \pm 0.18	0.014
Predator	0.01 \pm 0.01	0.05 \pm 0.03	0.001
Shredder	0.00 \pm 0.00	0.00 \pm 0.00	0.035
Burrowing habit	0.85 \pm 0.05	0.73 \pm 0.07	0.474

spawners. Numbers were lower in 1999 and 2003 when estimates varied between 2000 and 3000 spawners.

Mean $\delta^{15}\text{N}$ values for juvenile coho salmon were 8.78‰ ($n = 11$) (Fig. 6) with older 1+ fish having a mean value of 9.8‰ ($n = 4$) for the kettle lake and its outflow stream. Values for sticklebacks from the same habitats averaged 8.52‰ ($n = 4$). Juvenile Dolly Varden from the main river, wetland or tributary habitats showed a mean $\delta^{15}\text{N}$ value of 5.31‰ ($n = 12$) although one fish above the barrier falls had a value of 2.54‰ and were also low in higher tributary streams. Caddisfly larvae (*Ecclisomyia*) and willow leaves showed mean $\delta^{15}\text{N}$ values of 0.57‰ and -3.78 ‰, respectively. Mean $\delta^{13}\text{C}$ values were between -25 ‰ and -30 ‰ for willow leaves and between -20 ‰ and -25 ‰ for juvenile coho, Dolly Varden, and sticklebacks.

DISCUSSION

This study has shown for the first time the rapidity with which invertebrates and fish can colonize new stream ecosystems following ice recession and how quickly marine derived nutrients can be incorporated into stream food webs following colonization by anadromous salmon. Streams emerging from melting remnant ice in Glacier Bay (Alaska) typically possess proglacial lakes at the ice margin, which play an important role in buffering flow variations and preventing coarser sediment from impacting downstream reaches (Sidle and Milner 1989). The stabilization of the Stonefly Creek channels by this process has enabled vegetation to develop on the lower floodplains, which, through intercepting precipitation and subsurface runoff, further stabilizes flow variations and contributed to the rapidity of stream ecosystem development.

Invertebrates

Similar to the early stages of Wolf Point Creek, Stonefly Creek was initially colonized by Chironomidae, which continued to dominate in 2001. Despite being weak fliers, adult chironomids are relatively light and may be carried long distances by wind thereby making this group the typical first colonizers of new stream habitat (Brodersen and Bennike 2003). *Diamesa* has previously been shown to be the first genus that colonized these cold streams in Glacier Bay (Milner 1994) but in Stonefly Creek abundance decreased rapidly following colonization by *Pagastia partica*. A similar pattern was documented in Wolf Point Creek and experimental evidence by Flory and Milner (1999) suggested competitive dominance by *Pagastia* to be a likely cause. Interestingly, the most persistent chironomid taxa in Wolf Point Creek, *Paratrichocladius*, collected every year from 1997 to 2005 (Milner et al. 2008) was abundant in Stonefly Creek in 1997 so its absence or extremely low abundance in subsequent years was surprising. The additional 18 chironomid taxa collected at site 1 in Stonefly Creek but absent from Wolf Point Creek were responsible for Jaccard coeffi-

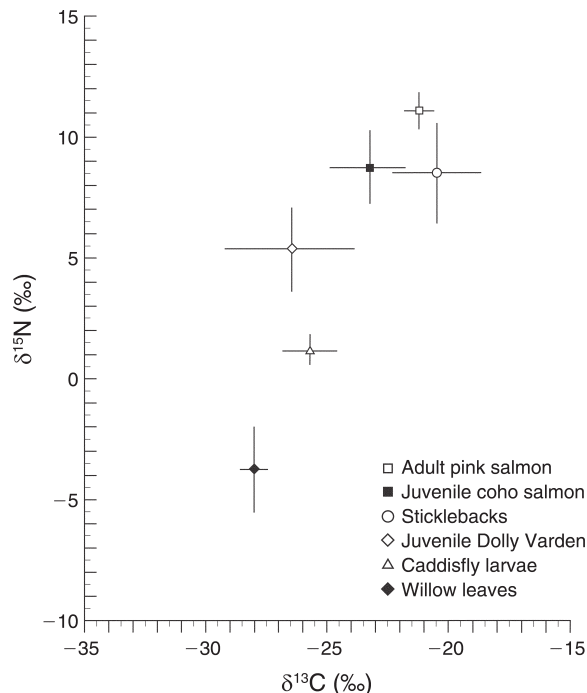


FIG. 6. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for willow (*Salix* spp., $n = 10$ individuals), Trichoptera larvae ($n = 6$), Dolly Varden ($n = 12$), sticklebacks ($n = 4$), and juvenile coho salmon ($n = 11$). Data are means, and lines represent $\pm\text{SD}$. Data for adult pink salmon were taken from Johnson and Schlinder (2009).

cient values being <0.5 between the two streams. *Simuliidae* and *Baetis* were the earliest non-chironomid colonizers, as occurred in Wolf Point Creek and as seen in other colonization studies in non-glacial stream habitat (Mackay 1992). Oligochaeta, Gammaridae, and Hydracarina were the only non-insect taxa collected at site 1 while Planorbidae was collected at site 2, indicating likely dispersal constraints from source populations across mountain and water barriers to this emergent stream system. Most macroinvertebrate taxa that have colonized Stonefly Creek have persisted in the community with stream development, apart from a few chironomids, including the cold stenotherm *Diamesa* which also declines in abundance in alpine glacier-fed rivers as meltwater input decreases (Brown et al. 2007). Thus tolerance is likely the dominant mechanism of succession in these streams as suggested for Wolf Point Creek (Milner et al. 2008), thereby supporting H_1 (see Introduction for full statement).

From our comparison of Stonefly Creek and Wolf Point Creek what general conclusions can we draw regarding the colonization of recently deglaciated streams? Initial community development at cold water temperature was similar to Wolf Point Creek, thereby indicating deterministic processes influenced community assembly. Indeed, the Jaccard similarity coefficient in 1997 of <0.5 masks that all the macroinvertebrate taxa found in Stonefly Creek in 1997 had previously been

found in Wolf Point Creek (Appendix). This provides partial support for H_1 that colonization follows deterministic pathways. However, at warmer water temperature colonization trajectories may follow different paths and become more stochastic in nature, as supported by the additional taxa found in Stonefly Creek at the equivalent water temperature and number of annual degree days as Wolf Point Creek. However since the most abundant taxa were the same in both streams, some of the stochastic nature of the community can be attributed to the rarer chironomid taxa found in Stonefly Creek as conditions became less harsh and water temperature increased. These data support the conclusions by Chase (2007) that deterministic pathways dominate when conditions are harsh (i.e., low water temperature) and by Lepori and Malmqvist (2009) that as conditions become less harsh (increased water temperature) a mixture of stochastic and deterministic processes come into play.

Microcrustacean assemblages in Stonefly Creek exhibited little similarity to those in nearby Wolf Point Creek but species richness in Stonefly Creek (21 species of Copepoda and Chydoridae during 1997–2001) was higher than that in the older Wolf Point Creek (10 species of Copepoda and Chydoridae during 1994–2002) suggesting microcrustacean colonization is unlikely to be restricted by dispersal constraints. Most taxa that have colonized Stonefly Creek have persisted in the microcrustacean assemblage (with the exception of *Maraenobiotus insignipes*, a specialist of glacial margins; Husmann 1975). Thus, in contrast to Wolf Point Creek, it is possible that tolerance is an important mechanism of microcrustacean succession in this stream. The Copepoda in Stonefly Creek and Wolf Point Creek are widely distributed (although see Reid 1998) and, in contrast to the early macroinvertebrate colonizers, are largely eurytopic with the exception of *M. insignipes*. Additionally, a previous study (McDermott et al. 2010) suggested that the hyporheos of Stonefly Creek comprises a subset of the epibenthic assemblage with an absence of obligate groundwater forms. Unlike winged aquatic insects, microcrustacea have no obvious method of colonization, but numerous dispersal routes exist. Several of the copepod species found (e.g., *Acanthocyclops vernalis* and *Moraria affinis*) undergo diapause, thereby facilitating dispersal by water, wind, and wildfowl (Careres and Soluk 2002, Figuerola et al. 2005). Other meiofauna have different dispersal strategies, for example, some water mites (Hydracarina) use phoresis, hitching a ride on emerging aquatic insects that disperse to different habitats (Bilton et al. 2001). Additionally, feces of Canada Geese collected in the wetlands of Stonefly Creek, and subsequently wetted and incubated, have yielded viable early instar water mites indicating waterfowl as a key dispersal agent. Canada Geese in Glacier Bay select roosting sites in remote areas close to ice masses, such as those occurring in the Stonefly Creek watershed, to avoid predation by

wolves or coyotes (Stephenson and Van Ballenberghe 1995). In contrast to the macroinvertebrates, microcrustacean assemblage development in Stonefly Creek differed from that of Wolf Point Creek throughout the colonization trajectory, suggesting that the processes influencing microcrustacean community assembly may be stochastic in nature. Hypothesis H_2 , that non-insect taxa would be poorly represented in the benthic community, was true for the macroinvertebrates but not for the meiofaunal community, with 27 taxa having colonized the stream.

We suggest that the higher overall invertebrate diversity in Stonefly Creek, in comparison to Wolf Point Creek, results in part from the elevated habitat complexity (see Fig. 2) and channel stability. For example, microcrustacean persistence in streams results from a combined strategy of high resilience (due to rapid recruitment), and the adoption of “refuge as habitat” and is dependent on habitat diversity (Robertson et al. 1995, Robertson 2000, Robertson and Milner 2006). The additional chironomid taxa found at site 1 compared to Wolf Point Creek may result from their wide dispersal capacity; Stonefly Creek is closer than Wolf Point Creek to possible colonizer sources in older streams of the northwest arm, and adult insects could disperse up glacial valleys rather than over high mountain ridges.

Macroinvertebrate biological traits showed little difference between Wolf Point Creek and Stonefly Creek except for body size and feeding group, yet mean values of these two attributes were relatively similar and were only significantly different due to the low standard deviation (Table 1). The maximal larger-body-size trait found in Wolf Point Creek was due to colonization by Tipulidae and Muscidae and the absence of Oligochaeta from Stonefly Creek in 2001. Overall though, both rivers were dominated by small body size, a common feature of glacial stream macroinvertebrates (Milner et al. 2009). The lower number of collector filterers may have been due to the higher turbidity in Stonefly Creek, because suspended sediments are predominantly inorganic in glacial rivers, and are unlikely to be coated in useable biofilm. Higher turbidity and associated suspended sediment particles may restrict biofilm and algal growth on the streambed, which thereby limits grazers. Despite the differences in individual-trait relative abundance, the results illustrate that community functional diversity (measured simply as the number of traits) remained quite similar between streams at the same stage of development, despite the Jaccard similarity in macroinvertebrate community structure between the two being less than 50%. This is potentially a result of the dominant environmental variables in these postglacial environments selecting for the same traits despite differences in constituent taxa. From this evidence, H_3 can be rejected and functional diversity appears to be largely independent of community structure. This finding may be due to similar trait-based

assembly rules operating in the two streams, despite differences in taxonomic composition that may reflect more random colonization and developmental processes (cf. Fukami et al. 2005). However, more detailed trait-based studies are necessary to better understand the operation of assembly processes in stream ecosystems undergoing primary succession.

Fish

The presence of juvenile Dolly Varden above the barrier falls in Stonefly Creek illustrates their ability to disperse by mechanisms other than anadromy, perhaps in a similar manner to Coast-range sculpin and the nine-spined stickleback, which are also found in the system. The Dolly Varden found above the falls probably constitute a land locked population. Both Coast Range sculpin and sticklebacks are euryhaline (Wrona et al. 2006) and can migrate through brackish water from proximal streams, but they could also have been dispersed by their eggs attaching to waterfowl (Green and Figuerola 2005). Rapid colonization of Stonefly Creek by a variety of salmonids and other fish species was facilitated by the creation of a wide variety of habitats, particularly the kettle lakes and ponds connected to the main stream system, which are used by juvenile sockeye and coho salmon and sticklebacks. Juvenile sockeye salmon typically favor lentic conditions or slow-flowing areas in streams.

In southeast Alaska, Pacific pink salmon have a fixed two-year life cycle, with separate stocks that do not intermix reproductively, and the number of pink spawning salmon in this area is an order of magnitude higher in odd years (2001) than even years (2000). Colonization by anadromous pink salmon occurred within 10 years of the lower reaches of Stonefly Creek being uncovered from glacial ice. In contrast pink salmon first spawned in 1989 in Wolf Point Creek (Milner et al. 2008), at least 50 years after the lower reaches of the stream were uncovered by the retreating ice. This difference in the pink salmon colonization may be due to the close proximity of source populations in the late 1970s when Stonefly Creek was uncovered, whereas in the case of Wolf Point Creek (uncovered in the 1940s) source populations were perhaps more distant. In a number of other systems formed by ice recession, sockeye salmon populations have later become extinct as lakes have become disconnected from the system with stream development (Milner et al. 2008). We consider this unlikely in the case of Stonefly Creek as the size of the lake means it should be a permanent feature of the system.

The $\delta^{13}\text{C}$ values higher than -30‰ indicate that the predominant source of carbon for caddisflies in the stream was of allochthonous origin as these values are typical of terrestrial vegetation. Values below -30‰ would normally indicate autochthonous sources of carbon (Milner et al. 2000). The $\delta^{13}\text{C}$ values for the juvenile fish would indicate a mix of carbon sources

from marine-derived sources from ingested salmon tissue and freshwater-derived food. Compared to the range of $\delta^{15}\text{N}$ values for juvenile salmon consumers from 6.5‰ (0% marine-derived nitrogen [MDN]) to 12.5‰ (100% MDN) in the mixing-model approach of Kline (1990) and to the mean of 11.3‰ for adult pink salmon (Johnson and Schindler 2009), the mean values of 8.78‰ obtained for juvenile coho salmon indicates significant contributions of MDN for these salmon consumers. There was a difference between age groups, with a mean of 8.2‰ obtained for 0+ juvenile coho salmon ($n = 7$) and 9.8 ‰ for 1+ coho salmon ($n = 4$). In contrast, the mean $\delta^{15}\text{N}$ value of 5.39 ‰ for juvenile Dolly Varden from the main river, wetland, and tributary habitats suggested MDN was contributing to their diet to a lesser degree, although some of these fish were away from the major spawning areas including above the falls that are a barrier to pink salmon migration to spawning grounds. Those Dolly Varden captured close to spawning areas had $\delta^{15}\text{N}$ values close to those for juvenile coho salmon. This clear indication of the early incorporation of MDN into the food webs involving juvenile coho and Dolly Varden of Stonefly Creek contrasts markedly with the older Wolf Point Creek, where no evidence of MDN in food webs has yet been found despite over 12,000 pink salmon spawning in this short stream (Milner et al. 2008). The absence of MDN in Wolf Point Creek food webs is attributed to the limited carcass retention due to the lack of heterogeneity of habitat and associated off-channel habitats and higher flood flows. These habitats are clearly evident within Stonefly Creek, which facilitates carcass retention at higher flows (see Fig. 2) and therefore H_4 was not supported.

Summary

Our study illustrates that colonization of new stream systems can be extremely rapid where a diversity of habitats is created following ice recession. The initial assembly of macroinvertebrate communities in these newly formed streams is deterministic due to the overriding influence of water temperature, but as water temperature increases stochastic elements come into play. However, this process appears to involve the less abundant taxa, and in particular several of the chironomids. The most abundant taxa are still similar between streams as development proceeds. In contrast, microcrustacean community assembly may be dominated by stochastic processes. Tolerance would seem to be the most appropriate mechanism of succession as proposed previously for Wolf Point Creek (Milner et al. 2008). Even though the overall taxonomic structure of the community may be different between streams undergoing development, the functional traits within the macroinvertebrate community can remain similar. Salmon colonization can rapidly provide important nutrient contributions to the stream food web where retentive properties for carcasses are high. These

findings have implications for the conservation of biodiversity in freshwater habitats with climate change, or the recovery of stream ecosystems following restoration efforts, which may be reliant on long distance and rapid dispersal of aquatic invertebrates (Trakhtenbrot et al. 2005, Woodward et al. 2010). Glacial recession is occurring worldwide (Brown et al. 2007, Milner et al. 2009), and the findings of this study provide unique insights into how associated stream ecosystems can be expected to respond.

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APPENDIX

A table showing mean invertebrate abundance in Stonefly Creek, together with the year the taxon was first collected in Wolf Point Creek (*Ecological Archives* E092-164-A1).