Longitudinal Distributions of Macroinvertebrates In The Copper River, Alaska

Joel Passovoy

INTRODUCTION

While glacial rivers and their physical processes have been studied extensively by geologists and geomorphologists, the ecology of these systems remains relatively unstudied. Macroinvertebrate distributions and succession have been the focus of much of the work done in regard to the ecology of glacial river habitats. Glacial rivers are characterized by unique physical factors that have a strong influence on the biological communities that inhabit them. Cold temperatures, extremely variable flows and high sediment loads result in a limited number of taxa and usually low community diversity. Large rivers can be divided into two categories of habitats, those associated with the main channel of the river and others that are not. The intensity and frequency of the physical processes happening in the various habitats plays an additional role in complicating the patterns of macroinvertebate distribution associated with large glacial rivers. Milner and Petts (1994) examined existing data on macroinvertebrates in glacial streams and developed a qualitative model to describe the longitudinal changes in distribution observed for these habitats. Most of the data used in creating the model was taken from studies of relatively small glacial streams. As a result, the model must be modified in order to apply it to larger glacial rivers like the Copper River of southeastern Alaska. A possible modification for the model is proposed here.

PHYSICAL FACTORS INFLUENCING MACROINVERTEBRATE DISTRIBUTIONS

Glacial rivers are designated as such by a suite of conditions that in turn present serious challenges to any organisms attempting to occupy them. By definition they are cold, turbid, and subject to extreme variation in flow. The latter, combined with large sediment loads, creates a high level of channel instability and fluctuating habitats [refer to Wooster 2002, in this volume for more detail]. The criteria for designating a stream as glacial involve factors of climate, flow regime and geomorphology, and are discussed elsewhere in this volume (Bowersox 2002). (Milner and Petts 1994)

Temperature

Water temperature is the most important factor in macroinvertebrate distribution and can be as low as 0-2 ^{o}C at the glacier toe, but is defined as being below 10 ^{o}C (Milner and Petts 1994). Low levels of precipitation, annual mean temperatures below freezing and snow are the main climactic factors in classifying glacial streams. In most glacial systems, annual rain or snowfall is between 0 – 114 cm, and annual mean (air) temperature is between –6.5 ^{o}C and –18 ^{o}C. (Milner and Petts 1994) Snow cover generally lasts for at least one month and temperatures can range from 0 ^{o}C – 10 ^{o}C (Milner and Petts 1994).

Turbidity

Turbidity is high, in excess of 30 NTU (nephelometric turbidity units). This results from high sediment loads which contribute silt and clay particles into the water column [refer to (Wooster 2002) in this volume for more detrail]. The specific conductance can be an important tool in determining the major supply of water to the river (Gislason et al. 2001) and glacial rivers are often characterized by a maximum value of 10 $\mu S\ cm^{-1}$ (Milner and Petts 1994) [refer to (Ahearn 2002) in this volume for more detail].

Discharge and Geomorphology

Seasonal and long-term flow patterns also play an important role in the composition of macroinvertebrate communities. Glacial rivers typically show large variation in both annual and decadal (or longer) periods. On the seasonal scale, the Copper River has a mean discharge of 1,625 $m^3\ s^{-1}$, but most of this happens in the warm summer months. Large flood events happen on the lower Copper River as a result of glacial dam outbreaks on a period of about six years (Brabets 1997). These are sources of tremendous disturbance, which create and destroy invertebrate habitats. The ability to quickly colonize new areas is a common character of invertebrates in glacial rivers. The effects of ice-dam outbreaks or erosion and deposition are more completely reviewed elsewhere in this volume (Bowersox 2002, DePaoli 2002).

Shifting of substrates and available interstitial space has a strong influence over macroinvertebrate distributions. No single classification for the geomorphology of glacial rivers exists, but some loose generalizations can be made. Below the confluence with the Chitina, the narrow valley of the Copper River Gorge restricts braiding, and the river is channelized, reducing the amount of low disturbance habitat available for invertebrates. The lower Copper River is a sandur plain, see Figure 1, characterized by braided channels and a wide valley floor. These braided patterns form small pockets of slower water that may be important habitat areas. Water velocities are generally high in the main channel (Mount personal communication May 2002) and bed mobility is also likely high in the main channel. The high sediment supplies and large entrained particle size of glacial rivers plays an important role in determining the diversity of substrate size and amount of interstitial space available for invertebrate. Life in glacial rivers can therefore be considered challenging.

Figure 1: The braded sandur plain of the Copper River, shifting channels and high sediment loads make these habitats challenging for aquatic invertebrates (Wheaton 2002).

INVERTEBRATE ORDERS IN GLACIAL RIVERS

Diptera (true flies), Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddis flies) are the representative orders in glacial rivers. Diptera are by far the most dominant order with Chironomidae being the family with the most representatives (Miller and Stout 1989). Ephemeroptera are mostly represented by the Baetidae and Heptageniidae families. The Nemouridae, Capniidae, and Chloroperlildae families usually represent Plecoptera and Limnephilidae are the main family of Trichoptera. (Milner 1994, Chaloner et al. 2002) EPT (Ephemeroptera, Plecoptera, Trichoptera) are most likely to be found in habitats with limited glacial influence on the Copper River. In order to understand the distribution of these macroinvertebrates, a brief examination of each order is required.

Diptera

Diptera are one of the most dominant orders of insects in the world and are probably the dominant group at high latitudes. Members of this group have established themselves in almost all of the world's climates and habitats. (Daly, et al. 1978) Due to extreme diversity, generalizations about morphology or ecology are difficult to make. With exceptions aside, most adults have one pair of wings and one pair of halteres (vestigial wings). The head is mobile with compound eyes and a proboscis for feeding. (Daly et al. 1978) Larvae are maggot-like or vermiform and lacking true legs. The head of the larvae can be sclerotized or undifferentiated. (Merritt and Cummins 1996) The Alaskan representatives are mostly filtering-collectors, which sit in the current and filter out nutrients, or gatherer-collectors that roam around in search of deposits of detrital material and fine particulate organic matter (FPOM) (Merritt and Cummins 1996).

Chironomidae

The most common taxa in glacial streams is the Dipteran family, Chironomidae, or midges (Figure 2). The midges owe much of their success in adverse environments to a short lifecycle, which is very important in climates with high variability. Chironomidae have the largest range of suitable conditions of any family of insects, a fact that enables them to be the first colonists of many new habitats (Daly et al. 1978). The larvae have a hard, sclerotized head with lateral ocelli or eyes. They usually have one or two anterior prolegs that are used for clinging and mobility. As primary consumers Chironomids play an important role as food for juvenile fish and other predacious invertebrates. The four most common sub-families in nearctic (those surrounding the arctic) climates are Diamesinae, Orthocladinae, Chironominae, and Tanypodinae.

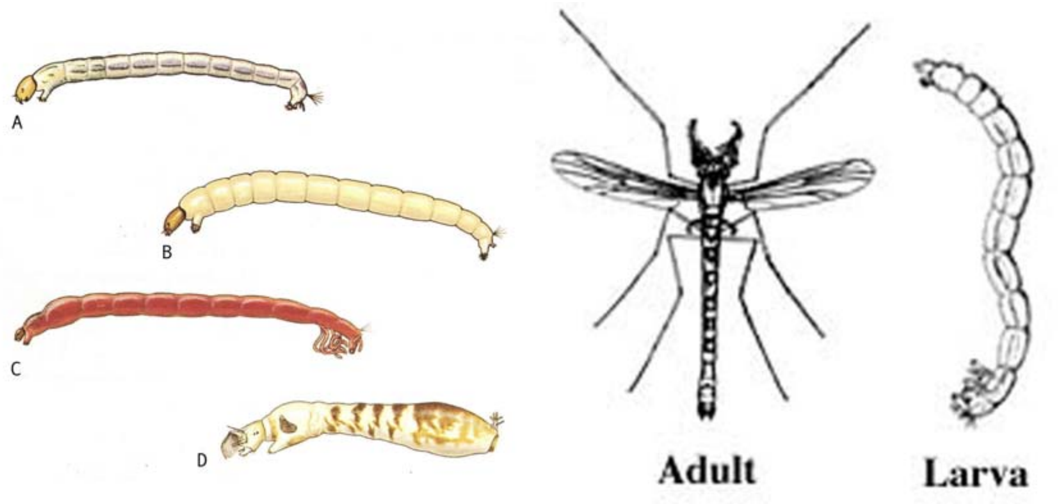

Figure 2. A-C: several Chironomidae larvae. D: Simuliidae larvae. Adult and larval Chironomidae on the right. (Lyon 2000, Mcafferty 1998)

In the kyral zone, where temperatures do not exceed 2 ^{o}C, the Chironomid genus Diamesa is the dominant group of macroinvertebrates (Milner and Petts 1994). Diamesinae (the family) will dominate in areas of low temperature and high disturbance such as the toe of the glacier (Milner and Petts 1994, Gislason et al. 2001). Diamesinae most likely dominates the main channel of the Copper River. As conditions become less extreme, Orthocladinae will add to the community composition and eventually competitively exclude Diamesa if not limited by temperature or disturbance (Flory and Milner 1999, Gislason et al. 2001,).

Orthocladinae

Orthocladinae are similar to Diamesinae, but need warmer temperatures and more stable habitats. They are both primarily collector-gatherers and cling or sprawl on benthic substrates (Merritt and Cummins 1996). Eukiefferiella and Orthocladius are typical genera found in northern rivers, and are often codominant with Diamesa (Milner and Petts 1994).

Simuliidae is another common Dipteran family in nearctic habitats. These are the black flies known for their biting swarms in the arctic tundra. The larvae are filterer-gatherers that cling to substrates in swift current. Their soft body has a very unique club shape, which makes them easy to identify. Simuliid larvae have anterior prolegs and a ring of anal hooks, which are important for attachment to rocks for foraging. Food is gathered in their labral fans, which project from the head and filter food particles from passing water. (Merritt and Cummins 1996) Living in swift habitats helps to protect them from predators that cannot move into the fast water (Allan 1995). Simuliidae are usually found in areas with relatively warmer waters and stable substrates, see Figure 2 D (Merritt and Cummins 1996).

Ephemeroptera

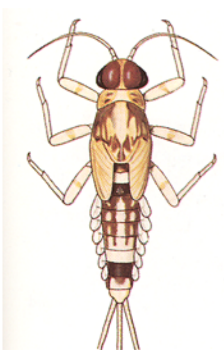

Figure 3. An Ephemeroptera larvae of the Beatidae family (Mcafferty 1998)

Commonly known as the mayflies, the Ephemeroptera are one of the oldest orders of insects. Indicative of this are the primitive wings of the adult, which do not fold flat against the body. The name Ephemeroptera refers to the brevity of the adult lifespan that can last from ninety minutes to a couple of weeks. The adults therefore, have no need for feeding and have reduced the mouthparts to vestigial structures. An identifying characteristic for this group, are the sexually dimorphic forelegs and eyes of the adults. The males have long forelegs that arch upwards in front of them for grasping females during copulation. The eyes are usually large in males and often touch on the medial plain. (Merritt and Cummins 1996)

Larvae are hemimetabolous, having part of the complete adult characteristics. Two to three tails or cerci on the abdomen are the most common identifying characteristic for the larvae. Abdominal gills are also a very prominent character for identifying the larvae of Ephemeroptera. They are usually streamlined and are adapted to both lentic and lotic habitats (still and moving water). These streamlined forms are then adapted to swimming, burrowing, or crawling on the bottom of the river. (Merritt and Cummins 1996) Beatidae, see Figure 3, are a group of swimmer and clingers that are most common in glacial rivers (Milner and Petts 1994, Miller and Stout 1989).

Baetidae are mostly gatherer-collectors adapted to living in the depositional areas of lotic environments. They have a vertically oriented head with antennae that are more than twice the head width (McCafferty 1998). Baetis and Callibaetis are two very common genera and are typically found in highly turbulent rivers and mountain streams where they exhibit positive rheotaxis or faceing into the current (McCafferty 1998).

Plecoptera

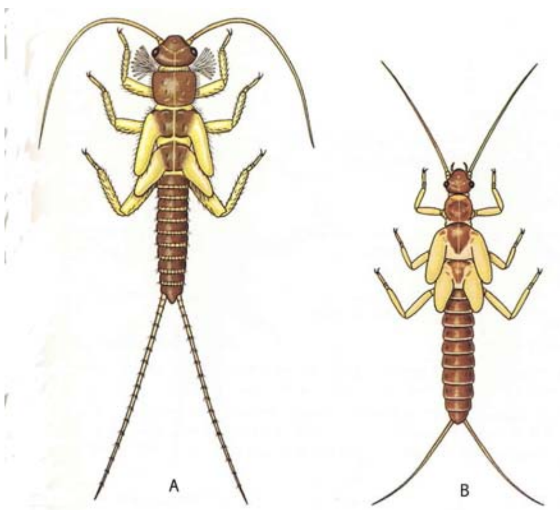

Figure 4: Plecoptera larvae, Nemouridae (A) and Capniidae (B), Nemouridae has tracheal gills and Capniidae lacks gills (Mcafferty 1998).

The Plecoptera are commonly known for the exuviates (left over exoskeleton), which are left clinging to rocks after the last molt from larvae to adult. This gives them their common name of stonefly and is a telltale sign of their presence in a river (McCafferty 1998). The adults are identified using the wings and genetalia (Merritt and Cummins 1996). Wings that fold back against the body make them easy to distinguish from the mayflies (Merritt and Cummins 1996). In cold climates some species are brachypterous, having a wingless adult form (Daly et al. 1978).

The larvae of Plecoptera have two tails and can be confused with Ephemeroptera larvae. However, Plecoptera have two claws on each foot, while Ephemeroptera only have one. Other characters are tracheal gills behind the head or around the anus, sclerites on each thoracic segment and two long, multisegmented tails. (Daly et al. 1978) The body is flattened dorsoventrally for clinging to benthic structures in swift current. The larvae are detritivores or predators, the former being shredders specializing on course particulate organic matter (CPOM) (Merritt and Cummins 1996). Nemouridae, see Figure 4, and Chloroperlidae are two families most often found in glacial rivers, being shredders and predators respectively (Milner and Petts 1989). Nemouridae larvae are important members of low order streams or areas with large amounts of CPOM because they are one of the few aquatic insects capable of digesting cellulose. This creates a supply of FPOM that can be used by filterers and gatherers in the rest of the system. (Allan 1995)

Trichoptera

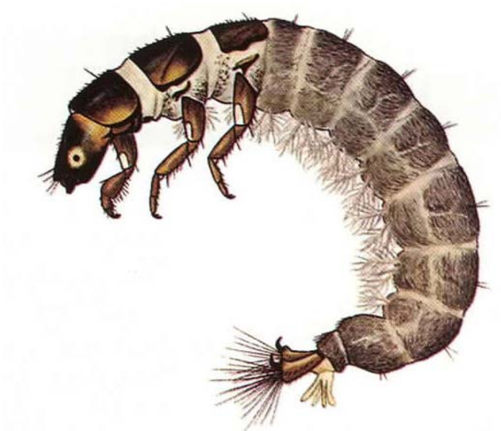

Figure 5: Hydropsychidae is one of the few free living members of the order Trichoptera (Mcafferty 1998).

Better known as the caddis flies or "tube worms", the Trichoptera are an order dominated by case builders. They are small winged individuals, which are closely related to the Lepidoptera (moths). Trichos (hair) and pteron (wing) come from Greek and refer to the hairs that cover the wings and most of the body of the adult, similar to scales in moths. (McCafferty 1998) The adults have 2-3 ocelli, filliform antennae, a labium with a large mentum and the first segment of the thorax is usually reduced compared to the following two segments (Daly et al. 1978). Larvae are soft bodied with the exception of one free-living family, the Hydropsychidae see Figure 5. The thorax has three pairs of well-developed legs and variably sized sclerites (hard plates). The head is divided into a distinct Y pattern by ecdysial lines (sutures), and may have lateral ocelli and short antennae. (Merritt and Cummins 1996) As previously mentioned, some Trichoptera are free living, but the trademark of this order is the cases built by the larvae. Cases provide protection and anchoring to the substrate, and a place to retreat to after collecting food from webs spun in the current (Allan 1995). Foraging methods mainly include gatherer-collectors and filterer-collectors (Merritt and Cummins 1996). Like Plecoptera and Ephemeroptera, Trichoptera prefer relatively warmer water and more stable substrates in which to live (Milner and Petts 1994). In the Copper River, Trichoptera are most likely found in the tributaries and off of the main channel.

HABITATS

Large glacial rivers can have a very wide array of habitat types. Murphy et al. (1989) divided the Taku river, into two main habitat categories, active river channel and off channel habitats. Active river habitats include main channels, channel edges, backwaters, sloughs and braids, (Figure 6). These are in the part of the channel that is most actively changing and subject to the greatest levels of disturbance. With high water velocities and erosion, the main channels and channel edges have the highest level of disturbance and present the most challenging environments for invertebrates, resulting in low species diversity. The sloughs and backwaters will have lower velocities and possibly lower turbidity. Off channel habitats include beaver ponds, terrace tributaries, tributary mouths, and upland sloughs on the valley floor. These off channel habitats are subject to lower levels of disturbance and probably have water temperatures that are warmer than the main channel to varying degrees. Detailed descriptions of each habitat type are reviewed elsewhere in this volume (Wheaton 2002).


Figure 6: Braided main channels and a backwater (center) (Wheaton 2002).

Habitat Utilization

Temperature and channel stability play a major role in the distribution of macroinvertebrates in glacial rivers. Milner and Petts (1994) developed a qualitative model for predicting this longitudinal distribution (Figure 7). As the most critical factors, temperature and stability were assumed to increase in a downstream direction. The general model related "zoobenthic gradients to temperature and geomorphologic instability (in terms of channel migration and avulsion, and bed sediment movement) as a function of distance from the glacier and time since deglaciation."(Milner and Petts 1994) In other words, the further one travels downstream, the warmer and more stable the channel becomes on an annual scale. With this, the distribution of invertebrates changes and becomes increasingly diverse downstream. Of course there are modifiers to this, and the distribution will show temporal and spatial patchiness as a result of fluctuating channel stability.

Driving forces behind the longitudinal distribution of macroinvertebrates are hydrological, sedimentalogical and biogeographical. Hydrological controls include changes in flow variability, sedimentalogical relate to sediment size and load, and biogeographical controls include streamside vegetation. (Milner and Petts 1994) Miles Lake, on the Copper River reduces the sediment load and therefore has sedimentological influences on the channel just below the lake (Brabets 1997). Biogeographical drivers can affect bank stability and contribute allochthonous inputs (energy inputs from outside the river system), which affect the species diversity capable of surviving in the area. All of these drivers exhibit high levels of variability. (Milner and Petts 1994)

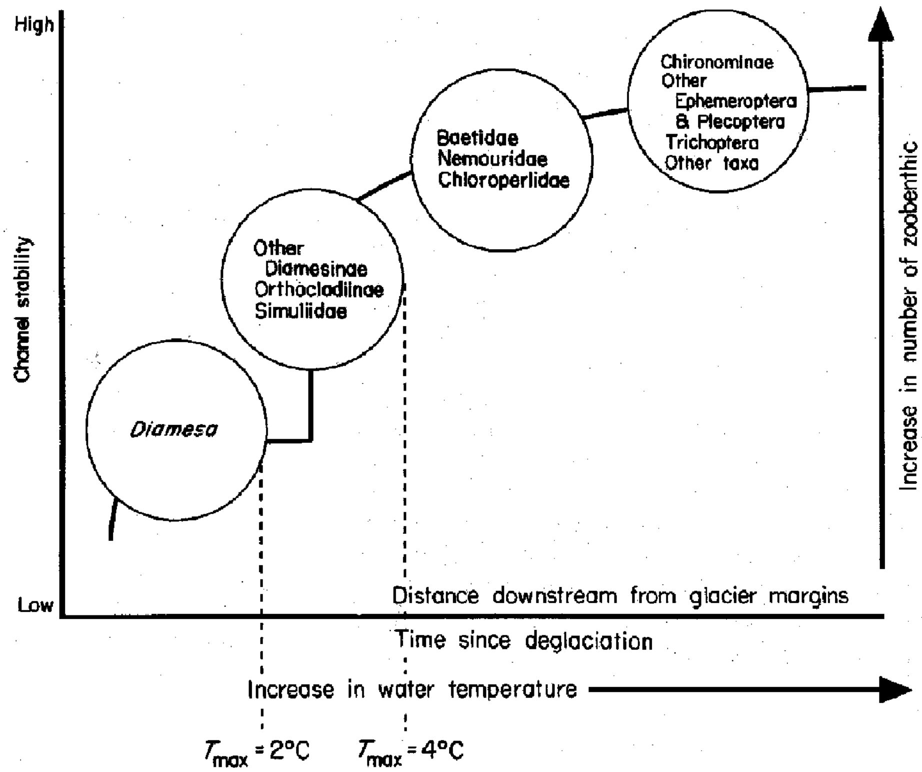

Figure 7: Qualitative model of longitudinal distribution of macroinvertebrates in a glacial river. Distribution related to temperature, disturbance and time since deglaciation (Milner and Petts 1994)

Exceptions and modifiers to the model are numerous. Tributaries, if large enough, can have multiple effects on the downstream distribution. Additions of sediment can have sedimentological impacts, or temperature can be altered to the extent that the distribution is reset if the tributary is colder than the main river. If the tributary is warmer, the opposite can occur and the distribution may be accelerated. (Milner and Petts 1994) This is unlikely in a river as large as the Copper but similar changes might be observed in a lateral direction. The transition from the active channel to the off channel habitats might show a similar distribution. This idea will be examined in closer detail later.

Diptera

The first invertebrates to appear in the longitudinal distribution are the Diptera. The Chironomidae (Midges) appear first, and are followed by the Simuliidae (Blackflies) and then theTipulidae (Craneflies) as conditions become less variable and warmer. The chironomid genus *Diamesa* is by far the most prevalent and well adapted for the kryal, with very short lifecycles and ability to attach to very unstable substrates (Milner and Petts 1994). Either temperature or channel instability can exclude other groups and allow *Diamesa* to be dominant. Favorable conditions further downstream allow first Orthocladinae and other Diamesinae to become codominent with *Diamesa*, followed by Simuliidae and Tipulidae. (Milner and Petts 1994) In more mild conditions, Chironominae and Orthocladinae are likely to out-compete the *Diamesa* and become the dominant Chironomidae subfamilies in the system. Stability is the important factor. In the Kenai fiords, a warm (9 ^{O}C) stream with a high level of disturbance, *Diamesa alpinus* and *Diamesa lupus*(these species cannot be distinguished in the field) were the dominant species. Yet, in a very similar stream with a lower frequency of disturbance, *Pagastia partricia*, a Chironominae, dominated the community. (Flory and Milner 1999)

Ephemeroptera, Plecoptera and Trichoptera (EPT)

As channel stability and temperature increase, so does the diversity of EPT. Beatidae is often the first non-Chironomid family to appear. This is typically at 4 ^{o}C, but can happen at lower temperatures if stability is high. Nemouridae and Chloroperlidae are often seen in close proximity to Beatidae. Trichoptera, the most sensitive order, need the warmest and most stable conditions and is the last to add to the longitudinal gradient. (Milner and Petts 1994)

EPT are often used as indicators for bioassessment analysis of riverine habitats. Their relative levels of sensitivity are good indicators of water quality and stream health. The presence of these species is not only indicative of favorable physical factors, but is also indicative of an increasing resource base (Davis et al 2001). The exposed gills of Ephemeroptera make them susceptible to fine sediments and toxins. Ephemeroptera are also sensitive to drops in pH (Brittain 1982). The larvae of Plecoptera are good indicators of reduced dissolved oxygen levels due to their lack of gills. As a group these three orders are sensitive to thermal pollution, chemical pollution, and other changes in the watershed (Brittain 1982).

Combining Habitat Types and the Model

Applying the model of Milner and Petts (1994) to the habitat types of Murphy et al. (1989) will be necessary for examining macroinvertebrate distributions on a large river, since the Milner and Petts model was developed on small streams. The active river channel habitats will most likely conform to the model well. It is possible that the level of disturbance may be high enough that the kyral zone extends the full length of the main channel, with only the channel edges showing longitudinal changes. This means that Chironomidae, mainly *Diamesa* may occupy the main channel habitats. The sloughs and backwaters may have lower levels of short-term disturbance, and greater disturbance than off channel habitats. The temperature in the backwaters and sloughs may be similar to that of the main channel. Therefore, these habitats may have at least the same invertebrate species as the associated main channel with the possibility of Beatidae and Nemouridae or Chloroperlidae, due to lower current velocities and increased habitat stability.

In the off channel habitats there may be greater species diversity due to increases in channel stability. Terrace tributaries may be glacial, humic or clear, and just this diversity of water type will contribute to high species diversity (Murphy et al. 1989). Factoring in possible variations in substrate composition leads to the conclusion that just about any position on the model could exist within a given terrace tributary. Flory and Milner (1999) show that glacial and non-glacial does not mean high and low disturbance, respectively. Tributary mouths may tend to support taxa that do well in areas of low disturbance, but the composition of species may look more like the main channel as the drivers active in the main channel begin to be dominant over those of the tributary. These areas of slower water and deposition of FPOM are commonly inhabited by net-collectors (Trichoptera) and burrowing members of Ephemeroptera (Allan 1995). Beaver ponds and upland sloughs will have species that rely on high levels of habitat stability and higher temperatures, or the upper positions of the Milner and Petts model. Depending on the time since the last major disturbance, these habitats will be dominated by Chironominae and the main groups of EPT. Ponds and sloughs are the most likely place to find Trichoptera.

APPLYING THE QUALITATIVE MODEL TO THE COPPER RIVER

Due to a complete lack of research on invertebrates of the Copper River, a proxy study was selected in an attempt to draw conclusions about what the invertebrate species composition might look like on the Copper river. Gislason et al. (2001) applied the Milner and Petts (1994) model to the West Jokulsa River in Iceland and this will be used as a example for glacially influenced habitats.

The W. Jokulsa River is small in comparison to the Copper River. With a peak annual discharge of about 80 m^3 s^{-1}, it is less than one twentieth of the mean annual discharge of the Copper River. Although size and discharge differences between the rivers is great, the W. Jokulsa River is glacially influenced for its first 45 km and showed strong adherence to the model proposed by Milner and Petts (1994)(Gislason et al. 2001). Over the first 45 km, the W. Jokulsa showed a maximum temperature range from 0.2 ^{o}C at the glacier toe to 13 ^{o}C at the lower end of the study area. The river was dominated by suspended material from June to October and varied from 0-2.1 g L^{-1} across the three forks that form the W. Jokulsa. (Gislason et al. 2001) Conductivity was high at both the upstream and downstream sites, but was high enough at the downstream sites to indicate that only about 20% of the water was from glacial sources. Higher densities and diversities of invertebrates were observed in a downstream direction, and variation was also observed as the season progressed from the spring to the fall. *Diamesa* was the dominant genera in the higher reaches at all times during the study period, and Orthocladinae became the dominant group in the lower reaches by mid summer. Chironominae and EPT occurred at the sites furthest away from the glacier, where the extent of glacial influence was negligible, but never became abundant. (Gislason et al. 2001)

The data from the W. Jokulsa for July and August most applicable to the Copper River. Due to the difference in basin size and discharge, these data may represent in small scale the conditions that exist on the Copper River. Therefore the distribution observed on the W. Jokulsa may be observed on the Copper River. It is likely that, as one descends the Copper River, conditions in the main channels never become warm enough or stable enough for the more sensitive species in the Milner and Petts model. The extremely low level of diversity that is expected in the main channel will most likely be contrasted by the diversity of the off channel habitats and non-glacial side streams. A very steep species distribution (rapid change from the low to high levels of the model) may extend laterally from the center of the river with its glacial influence, to the valley edge where only the largest of flood events exerts influence on the habitats. Tributaries are not likely to have much influence on the main channel because of their small size, but they may introduce some variability of species in local areas. Finally, exceptions to the model are sure to present themselves; armoring of the channel below Miles Lake (Brabets 1997), for example, may introduce variations that are hard to fit into the model.

CONCLUSION

The Copper River is a large river with in which extreme conditions make life challenging. Physical factors inherent to glacial rivers include low temperatures, variable flows, high sediments loads, high flow velocities and mobile channel beds. Annual patterns of fluctuation in discharge are one of the components that contribute to channel instability. This is further amplified by periodic flood events such as glacial ice dam outbreaks every six years (Brabets 1997) that exert influence on the off channel habitats and keep them in successional stages.

A model has been presented by Milner and Petts (1994) that supports a longitudinal downstream distribution of macroinvertebrates, sorted by each group's ability to adapt to cold temperatures and channel instability (Milner and Petts 1994). Chironomidae show the greatest ability to cope with low temperatures and shifting substrates, therefore they are the dominant family throughout these systems. *Diamesa* is the first genus to be present downstream of glaciers according to the Milner and Petts

(1994) model and this was duplicated by Gislason et al. (2001). Orthocladinae, other Diamesinae and Tanypodinae are other Chironomid families that follow *Diamesa* in the downstream distribution. Baetidae (Ephemeroptera), Plecoptera, and Trichoptera all appear as temperature and channel stability increase, both in downstream and lateral directions. Finding good examples for comparison was difficult due to the unique nature of the Copper River, in terms of size and geomorphological activity. There are many factors influencing the distribution of invertebrates in this system, and the geological factors behind those drivers further complicate the picture.

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