Determining the effects of sediment deposition on the growth, survival, and foraging efficiency of the endangered Nooksack dace (*Rhinichthys cataractae* sp. *cataractae*), and on the abundance, distribution, and community structure of their invertebrate prey.

by

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## Abstract

Alterations to riverine habitats from the excessive deposition of sediments present a challenge for the effective management and conservation of aquatic resources and endangered species. The Nooksack dace (*Rhinichthys cataractae* sp. *cataractae*) is an endangered, benthic riffle-dwelling specialist, which is threatened by sediment-induced habitat changes. The purpose of my thesis was twofold. First, using semi-natural streamside channels I experimentally tested how different levels of embeddedness and percentages of fine sediments <2 mm in diameter affected the biomass of benthic invertebrates and the growth of Nooksack dace. Second, using artificial foraging arenas I manipulated substrate characteristics (i.e., embeddedness) and water velocity to examine how they jointly affected the foraging efficiency of Nooksack dace. Goals were to use these complementary approaches to distinguish between reduced invertebrate prey abundance *vs*. physical impacts on foraging efficiency as mechanisms mediating sediment effects on Nooksack dace growth.

My results showed that invertebrate biomass generally decreased as embeddedness increased and that mortality through predation on Nooksack dace was highest over partially and fully embedded substrates. My findings also suggest that the loss of interstitial space had a more significant effect on invertebrate biomass and Nooksack dace survival than the percentage of fine sediments. However, the presence of fine sediments exacerbated the negative effects of embeddedness, especially for burrowing invertebrates.

I also found that Nooksack dace foraging efficiency decreased over all substrate types as water velocity increased. This suggests that although Nooksack dace are associated with unembedded gravels in high velocity riffle habitats, they are likely adapted to foraging in lowvelocity micro-habitats within the boundary layer. Sediment-induced habitat changes resulting in

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high near-bed water velocities likely have a negative impact on Nooksack dace foraging efficiency, which in turn could negatively affect their growth and survival.

# Preface

All the research presented in this thesis was designed, carried out, and analyzed by myself, the author, John Michael Champion. I received valuable feedback and guidance on my experiments from my supervisor Jordan Rosenfeld and my committee members Robert Shadwick and Rick Taylor. This project was funded by Fisheries and Oceans Canada, Ministry of Environment-Province of British Columbia, and NSERC discovery grants awarded to Jordan Rosenfeld.

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# **Chapter 1: General introduction**

#### 1.1 Background

Freshwater ecosystems cover less than 1% of the Earth's surface (Dudgeon *et al.* 2006), but contain approximately 9.5% of the 125,000 described animal species (Balian *et al.* 2008; Strayer & Dudgeon 2012), and an estimated 43-45% (12,000-13,000) of the 28,900 known fish species (Jelks *et al.* 2008; Lévêque *et al.* 2008). However, these ecosystems are also some of the most endangered (Sala *et al.* 2000; Dudgeon *et al.* 2006). In North America alone, 39% of freshwater fishes are considered vulnerable, threatened, or endangered (Jelks *et al.* 2008), and at least 57 species and subspecies have gone extinct since 1900 (Burkhead 2012). Habitat degradation is one of five groups of interacting threats that contribute to the imperilment of freshwater species, along with: water pollution, overexploitation, flow modification, and invasive species introductions (Allan and Flecker 1993; Richter *et al.* 1997; Dudgeon *et al.* 2006; Geist 2011).

The deposition of sediment was identified as the top factor contributing to degradation of riverine habitats by the US Environmental Protection Agency (Clean Water Act Section 303(d); USEPA 2000), and it is estimated that 46% of rivers in the United States suffer from sediment-induced habitat alterations (Berkman and Rabeni 1987; Richther *et al.* 1997). Anthropogenic land use such as forestry, road building, mineral extraction, and agriculture, accelerate the rate of fine sediment erosion, annually increasing both the quantity and frequency of sediment inputs to rivers and streams (Allan 2004). With land conversion expected to increase, it is imperative to understand how increased sediment loads will affect freshwater ecosystems, and to develop effective sediment management plans that can aid in the protection of freshwater resources (Wood and Armitage 1997; Benoy *et al.* 2012).

## **1.2** The role of sediment in streams

The transport of sediments by rivers is a natural part of the global denudation process, through which sediments are eroded from the surrounding watershed and carried downstream, where they are deposited in lakes, lowland sections of rivers, and eventually the ocean (Kemp *et al.* 2011). The quantity of sediment that enters a river depends on the geography, topology, and climate of each watershed (Nebonne and Vondracek 2001). As sediments are transported, deposited, scoured and re-deposited, they alter the physical structure of rivers, creating complex habitats for stream dwelling taxa (Kemp *et al.* 2011; Jones *et al.* 2012a). Riverine taxa are adapted to natural levels of sediment within a particular watershed, but are able to withstand temporary increases in sediment loads (e.g., the freshet and high flow events; Henley 2000; Kemp *et al.* 2011). However, increases in the amount and frequency of sediment inputs from anthropogenic land use, and their subsequent deposition, can alter benthic habitats resulting in the displacement, altered behaviour, or extirpation of stream biota (Henley 2000; Sutherland *et al.* 2002).

Sediments in river systems are broadly divided into two categories, the bed load and suspended load. The bed load is comprised of large sediments, > 6.35 mm in diameter, that are transported downstream by rolling or saltation when flows are sufficiently high (e.g., the freshet or heavy rain events), while the suspended load is comprised of smaller particles, <6.35 mm in diameter, that are maintained in suspension by turbulence under the same high flow conditions (Turowski *et al.* 2010). The suspended load can be further divided into suspended sediments and settleable solids. Suspended sediments are comprised of very fine sands, silts, and clays (<65  $\mu$ m) that remain suspended even at low velocities, while settleable solids are larger particles (6.35 mm - 65  $\mu$ m) that can be quickly deposited when flows decrease (Anderson *et al.* 1996). Within the suspended load, inorganic particles <2 mm in diameter are referred to as fine

sediments; their transport and subsequent deposition are generally considered to have the most detrimental effect on aquatic biota (Wood and Armitage 1999; Suttle *et al.* 2004; Owens *et al.* 2005; Kemp *et al.* 2011; Jones *et al.* 2012a).

The effects of sediments in stream ecosystems depend partly on stream flow, channel gradient, and the size of inorganic sediments introduced. When flows are sufficiently high, sediments are transported in suspension or by saltation, resulting in the potential displacement, altered behaviour, impaired respiration, and physical harm to stream organisms (Waters 1995; Wood & Armitage 1997). For example, sediment addition experiments have shown that high concentrations of suspended sediment can increase invertebrate drift by more than 50% above pre-sediment conditions (Culp *et al.* 1986). Similar studies on salmonid fishes have documented changes in territorial defense behaviours, reduced foraging activity, and in extreme cases, physical harm caused by abrasion (Caux *et al.* 1997; Finstad *et al.* 2007). However, events with high levels of suspended sediment usually occur as short pulses only, and the more prolonged negative impacts on aquatic communities tend to occur when flows decrease, as this causes suspended sediments to be deposited on benthic substrates (Berkman & Rabeni 1987; Iwata *et al.* 2003).

#### **1.3** Effects of sediment deposition

Structurally complex riverine habitats are closely associated with high species richness and abundance of fishes and benthic invertebrates (Schneider and Winemiller 2008). Benthic substrates that are composed of gravel and cobbles, with interstices relatively free of fine sediments, are positively correlated with high abundances of benthic invertebrates, which in turn

support higher densities of fishes (Waters 1995; Berkman and Rabeni 1987). This is because these substrates provide abundant interstitial habitat for foraging, as well as refugia from predation and high water velocities (Waters 1995). Therefore, alterations to the composition of riverbed gravels by excessive quantities of sediment are likely to have negative effects on stream biota.

One of the most significant physical habitat alterations associated with sedimentation is the loss of interstitial space. Deposited sediments increase substrate embeddedness by filling spaces between coarse particles, which reduces the availability of interstitial habitat for fish and benthic invertebrates (Frostick et al. 1984; Sylte and Fischenich 2002; Richardson and Jowett 2002), potentially increasing their exposure to predation or scour from high water velocities. Substrate embeddedness can also reduce the roughness of streambed gravels, which results in lower water depths, increased near-bed velocities, and a reduction in the thickness of the low velocity boundary layer above streambed gravels (Richardson and Jowett 2002; Smith et al. 2005; Evans and Wilcox 2013). Higher water velocities can negatively affect the foraging efficiency of fish by decreasing capture success, prey detection distances, and altering their search efficiency (Grant and Noakes 1987; Hughes et al. 2003). These reductions in efficiency can increase the active foraging costs and energy expenditures of fish, leading to lower growth rates (Hill and Grossman 1993; Piccolo et al. 2008). Infilling of interstitial spaces may also reduce the ability of substrates to capture and store organic matter that supports benthic invertebrate production, resulting in lower prey availability for fish (Angradi 1999; Rosenfeld 2000; Negishi and Richardson 2003). In extreme cases, deposited sediments such as sand and silt can become the dominant particle type (by covering coarse particles), and may not provide suitable habitat for many benthic invertebrates because they are less stable and easily moved at

low velocities (Wood and Armitage 1997; Jowett 2003). The frequent movement of these sediments can increase drift rates; abrade soft tissues causing physical harm; prevent the establishment of epilithic periphyton that constitutes food for grazing invertebrates; and interfere with the establishment of sessile filter feeding invertebrates, such as Simuliidae and Hydropsychidae caddisflies (Henley 2000; Izagirre *et al.* 2009; Berkman and Rabeni 1987; Rabeni *et al.* 2005).

The severity of the effects of embeddedness is influenced partly by the size of sediment particles that infiltrate gravel interstices (Waters 1995). In particular, the fraction of sediments that are <2 mm in diameter can have disproportionately negative effects on fish and benthic invertebrate communities (Caux et al. 1997; Owens et al. 2005; Benoy et al. 2012). Very fine particles (e.g., clays) are primarily transported in suspension, but their small size and high surface area make them adhesive, allowing them to easily flocculate to larger particles in suspension, or attach to the surface of epilithic periphyton and coarse benthic substrates (Waters 1995; Izagirre et al. 2009). Reductions in water levels from water withdrawals or drought can significantly reduce river flow, allowing fine sediment to be deposited (Wood and Armitage 1999). Once deposited, these sediments can clog micro-interstitial spaces, which decreases the porosity and permeability of streambed gravels, and restricts the inter-gravel flow of oxygen-rich water (Lisle and Lewis 1992). Fine sediments may also compact deposited sediment, which may increase substrate stability and the shear stress required to effectively scour and transport sediments stored within interstitial spaces. Threshold effects of fine sediments vary depending on the species and life stage of interest. For example, the survival of incubating bull trout (Salvelinus confluentus; Caux et al. 1997) eggs and the abundance of benthic invertebrates (Ryan

1991) can be adversely affected when the volume of embedding particles that are fine sediments (< 2 mm in diameter), make up as little as 4 to 12% of the volume, respectively.

Habitat alterations from sedimentation can have direct effects on fish growth and survival. The loss of interstitial refugia can directly increase the risk of stream fishes to predation (Allouche 2002). For example, experimental studies have shown that predation rates of rainbow trout (*Oncorhynchus mykiss*; Harvey *et al.* 2009) and prickly sculpin (*Cottus asper*; White and Harvey 2001) increased over substrates lacking cover. Reduced cover may also induce sublethal effects by elevating stress, which may manifest as increased activity levels, predator vigilance, conspecific aggression and metabolic rates, at the expense of foraging activity (Fisher 2000; Finstad *et al.* 2007). For example, growth rates of juvenile steelhead trout (*Oncorhynchus mykiss;* Suttle *et al.* 2004), juvenile Atlantic salmon parr (*Salmo salar;* Finstad *et al.* 2007), and spinous loach (*Cobitis shikokuensis;* Kawanishi *et al.* 2014) have been shown to decrease as embeddedness increases.

Indirect effects on fish occur when sediment deposition decreases the abundance or availability of their invertebrate prey. Most research on the effects of fine sediment deposition on benthic invertebrates has focused on Ephemeroptera, Plecoptera, and Tricoiptera (EPT) because of their high productivity and availability as food for stream fishes (Waters 1995). The loss of interstitial volume has been shown to directly affect the abundance of EPT taxa, which in turn reduces the availability of food for insectivorous fishes. For instance, Burdon *et al.* (2013) found that the abundance of EPT significantly decreased when 20% of streambed gravels were covered by fine sediments, and their abundance decreased non-linearly with increased sediment cover. Similarly, significant declines in EPT abundance have been observed as embeddedness increased from 0 to 30% (Angradi 1999). However, studies that examined the effects of embeddedness on

taxa other than EPT, or on total invertebrate abundance, have identified higher embeddedness thresholds before significant declines were detected (40% for scrapers (Mebane 2001), 60% for surface dwelling invertebrates (Suttle *et al.* 2004), and 70% for total invertebrate abundance (Bo *et al.* 2007)). Although previous research has shown that surface dwelling invertebrates (e.g., EPT and scrapers) are sensitive to deposited sediments, the range of observed embeddedness thresholds indicate that the effects of sedimentation are species- and functional feeding groupspecific. Moreover, total invertebrate abundance may not be the most informative metric when determining the effect of sediment deposition on the availability of invertebrate prey for fish, as sediment-induced habitat alterations may result in changes to the taxonomic assemblage of invertebrates (Rabeni *et al.* 2005). For example, as sedimentation increases, communities dominated by surface dwelling taxa, such as ETP, may be replaced with more sediment-tolerant burrowing taxa, such as oligochaetes and chironomids, which may be less available or lower quality prey items for fish (Zweig and Rabeni 2001; Matthaei *et al.* 2006; Jones *et al.* 2012b).

The negative effects of increased sediment deposition from anthropogenic land use on the structure of physical habitat, benthic invertebrates, and drift feeding salmonids are well documented (e.g., Zweig and Rabeni 2001; Waters 1995; Owens *et al.* 2005; Kemp *et al.* 2011). However, few studies have directly examined the effects of sedimentation on riffle-dwelling benthic fishes (see Brusven and Rose 1981; Haro and Brusven 1994; Mebane 2001; White and Harvey 2001; Kawanishi *et al.* 2010; 2014). This group may be particularly sensitive to fine sediment embeddedness due to their close association with coarse unembedded substrates (Grossman 2013; Kawanishi *et al.* 2014), and a previous study has shown that their abundance decreases as embeddedness increases (Berkman and Rabeni 1987). A benthic species that may be significantly impacted by increased embeddedness is the Nooksack dace (*Rhinichthys cataractae*)

sp. *cataractae*), a cyprinid fish endemic to northwestern Washington State, USA, and southwestern British Columbia, Canada, which is listed as Endangered under Canada's *Species at Risk Act* (see COSEWIC 2007). Nooksack dace are found in seven watercourses in British Columbia (Brunette, Alouette, and Coquitlam Rivers, and Kanaka, Bertrand, Pepin, and Fishtrap Creeks; Taylor *et al.* 2015). Many of these watercourses have been impacted by flow modification and increased sediment inputs as they flow through landscapes that have been heavily modified by urbanization, mining, forestry, and agriculture. The Nooksack dace recovery team has identified deposition of fine sediments as one of the top risks facing this species, along with physical destruction of habitat and seasonal lack of water (COSEWIC 2007; Pearson *et al.* 2008). However, the absolute and relative effects of sediment-induced habitat changes to the distribution and abundance of dace populations are unknown, in part due to our lack of knowledge about dace habitat requirements, ecological behavior, and adaptability to habitat change.

This thesis is organized into four chapters. Following this introduction (Chapter 1), Chapter 2 describes a field experiment designed to test the effects of varying degrees of embeddedness on the growth rates of Nooksack dace and their invertebrate prey. Specifically, this experiment manipulated the volume of interstitial spaces filled with sediments, and the proportion of those sediments that were <2 mm in diameter. My predictions were that: i) the loss of interstitial spaces from embeddedness would result in a decrease in invertebrate abundance and biomass; ii) invertebrate communities in the embedded treatments would be dominated by more sediment-tolerant, burrowing invertebrates; and iii) Nooksack dace growth would be negatively impacted by sediment-induced changes in biomass and community structure of their invertebrate prey. Chapter 3 describes an experiment designed to examine how substrate

characteristics (i.e., embeddedness) and variation in water velocity interact to affect the foraging efficiency of Nooksack dace. My predictions were that: i) foraging efficiency would decline at higher velocities because of reduced boundary layer thickness; and ii) foraging efficiency would decrease with sediment inputs that reduce surface roughness, and therefore be highest over unembedded substrates with the thickest boundary layer. Chapter 4 provides a summary of the two experiments described above, with emphasis on how these results can help to better predict the effects of increased fine sediment deposition on both the production of benthic invertebrates, and the growth and survival of riffle-dwelling benthic fishes. The findings of this research may also provide a technical basis for the identification and protection of habitats critical for the survival and recovery of the endangered Nooksack dace.

Chapter 2: The effects of embeddedness on the benthic invertebrate abundance and community structure and the survival of Nooksack dace (*Rhinichthys cataractae* sp. *cataractae*)

### 2.1 Introduction

The transport and deposition of fine sediments (<2 mm diameter) has been shown to negatively affect freshwater ecosystems, presenting a challenge for the effective management and protection of aquatic resources and endangered species (Wood and Armitage 1997; Pearson *et al.* 2008; Kawanishi *et al.* 2014; Benoy *et al.* 2012). Under natural conditions, sediment transport and deposition are important processes that shape channel morphology and create structurally diverse habitats for aquatic organisms (Kemp *et al.* 2011; Jones *et al.* 2012a). Anthropogenic land use, however, has increased both the frequency and quantity of sediment inputs entering watercourses worldwide (Ryan 1991; Owens *et al.* 2005; Jones *et al.* 2012b), resulting in higher loads of both suspended and deposited sediments that can degrade freshwater habitats and negatively impact aquatic biota (Berkman and Rabeni 1987; Kaufmann *et al.* 2009; Sutherland *et al.* 2010).

One of the most significant effects of fine sediment deposition is high substrate embeddedness, which reduces the availability of interstitial habitat and refugia for benthic invertebrates and fish, potentially increasing their exposure to predation or scour from high water velocities (Frostick *et al.* 1984; Waters 1995; Sylte and Fischenich 2002; Jowett 2003). Negative effects on biological communities have been observed when the volume of fine sediments comprises as little as 15% of benthic substrates (Henley *et al.* 2000; Owens *et al.* 2005; Benoy *et* 

*al.* 2012). Filling of interstices can reduce the porosity and permeability of benthic substrates, restricting sub-gravel flow (Lisle and Lewis 1992; Anderson *et al.* 1996), and reduce the storage of interstitial organic matter that supports invertebrate production (Angradi 1999). Sedimentation can also reduce streambed roughness, which increases water velocities and reduces the thickness of the low velocity boundary layer immediately above the streambed surface (Smith *et al.* 2005; Kaufmann *et al.* 2009; Evans and Wilcox 2013). Although loss of interstitial space has been implicated as the main structural change associated with sedimentation, the size composition of added sediment – in particular the fraction less than 2 mm in diameter – has been shown to strongly influence the negative impacts on biota (Caux *et al.* 1997; Owens *et al.* 2005). Disproportionately large impacts of sediment have been reported when embedding particles less than 2 mm in diameter exceed a threshold of 12-17% (Ryan 1991).

Sediment inputs can have both direct and indirect effects on fish growth and survival. Loss of interstitial refuges can directly increase predation (White and Harvey 2001) or induce sublethal effects by increasing stress, which may manifest as a higher resting metabolic rate when refuges are reduced (Finstad *et al.* 2007; Fisher 2000). Indirect effects on fish occur when sediment reduces the abundance of their invertebrate prey. Habitat alterations induced by embeddedness (in particular the loss of interstitial spaces) can change the taxonomic assemblage of invertebrates, which in turn can reduce prey availability for fish. For example, as sedimentation increases, invertebrate communities dominated by mobile taxa (e.g., Baetidae and Perlodidae) that forage on unembedded coarse substrate surfaces may be replaced by more sediment-tolerant burrowing taxa (e.g., Oligochaeta and Tubificidae) that tend to be less available as prey for benthic fishes (Zweig and Rabeni 2001; Jones *et al.* 2012b). Changes in the abundance and distribution of invertebrates associated with embeddedness (Wood and Armitage

1997) can also increase active foraging costs, leading to sublethal effects on fish growth (i.e., weight loss) and survival (Suttle *et al.* 2004; Finstad *et al.* 2007). Most studies on the negative effects of fine sediment deposition have focused on habitat structure, benthic invertebrates, and economically important fisheries (e.g., salmonids; Suttle *et al.* 2004; Harvey *et al.* 2009); few studies, however, have focused on impacts to less economically important species, particularly benthic fishes (but see Mebane 2001; Kawanishi *et al.* 2010, 2014).

The Nooksack dace (*Rhinichthys cataractae* sp. *cataractae*) is a small, benthic, riffledwelling cyprinid, endemic to southwestern British Columbia and northwestern Washington, USA. It is listed as Endangered under the *Species at Risk Act* in its Canadian range, and the Nooksack dace recovery team identified fine sediment deposition as one of the top three threats to its survival and recovery (COSEWIC 2007; Pearson *et al.* 2008). Like many riffle-dwelling benthic fish species, such as longnose dace (*Rhinichthys cataractae*; Mullen and Brown 1998), sculpins (Cottidae; Haro and Brusven 1994), and loaches (Cobitidae; Kawanishi *et al.* 2014), Nooksack dace are associated with unembedded coarse substrates. Although the specific mechanisms underlying this habitat preference remain unclear, several studies have proposed that higher availability of interstices in unembedded substrates provide more habitat and refugia for both benthic fishes and their invertebrate prey, compared to embedded substrates (Petty and Grossman 2010).

In this study, I used semi-natural stream-side channels to independently manipulate both the proportion of filled interstitial spaces (either 0, 50, or 100% filled) and the percentage of fine sediments (<2 mm in diameter) used to fill these interstices. My goal was to assess how variation in embeddedness and the size composition of embedding fines would affect the abundance, biomass, and community structure of benthic invertebrates, and what effect these changes would

have on growth rate as a correlate of fitness of Nooksack dace. Specifically, I expected i) a decrease in invertebrate abundance and biomass resulting from the loss of interstitial spaces, ii) that invertebrate communities in the embedded treatments would be dominated by more sediment-tolerant, burrowing invertebrates, and iii) that Nooksack dace growth would be negatively impacted by sediment-induced changes in biomass and community structure of their invertebrate prey.

### 2.2 Methods

## 2.2.1 Study site and Nooksack dace collection

Field work took place in Pepin Creek, a lowland stream in southwestern British Columbia that flows south into the Nooksack River in Washington State, USA. Experiments were conducted from June to August during 2012 and 2013, when water temperature was consistently above 11°C, as Nooksack dace activity and growth are reduced below this temperature (COSEWIC 2007; Pearson *et al.* 2008). Nooksack dace were captured in nearby Bertrand Creek using a kick seine and immediately transferred 6 km to the secure experimental site at nearby Pepin Creek. Each Nooksack dace was weighed to the nearest 0.1 g, measured (fork length) to the nearest mm, tagged with visible implant elastomer (Northwest Marine Technology), and stocked in the stream-side channels. Recovered Nooksack dace were returned to their site of capture after the experiment concluded.

## 2.2.2 Experimental streamside channel design

I manipulated the degree to which gravel interstices were embedded with fine sediments in experimental streamside channels, first in a pilot experiment in 2012, and then in a final 2013 experiment where the design was modified based on results from the 2012 pilot. Fine sediments refer to particles that are <2 mm in diameter, which have been shown to negatively impact some fishes (Owens *et al.* 2005) and benthic invertebrates (Benoy *et al.* 2012). Four stream-side channels (1.2 m x 4.9 m) were constructed adjacent to Pepin Creek, and divided longitudinally into four parallel 20 cm wide raceways, each of which was further transversely divided into two sequential 2.4 m long experimental units in 2012, and four sequential 1.2 m long experimental units in 2013 (for a total of thirty-two 0.44 m<sup>2</sup> experimental units in the 2012 pilot, and sixty-four 0.22 m<sup>2</sup> experimental units in the final 2013 experiment; Figure 2.1). Experimental units were separated by a 6.4 mm flow-through exclusion mesh. Discharge in each raceway was adjusted to achieve average velocity and depths of  $21 \pm 1.3$  cm-s<sup>-1</sup> and  $5.6 \pm 0.5$  cm, respectively, which are within the suitable range of conditions for riffle habitat used by Nooksack dace (Inglis 1997; Avery-Gomm *et al.* 2014).

Four substrate treatments were established in the 2012 pilot experiment that differed in both embeddedness (the proportion of filled interstitial spaces; either 0, 50, or 100%) and the proportion of fines less than 2 mm in diameter (0, 9, and 16% by volume; Table 2.1; Figure 2.2). Treatments were 0% embedded (henceforth unembedded), 50% embedded with fine sand, 100% embedded with fine sand, and 100% embedded with coarse sand (Table 2.1). Each sediment treatment was randomly assigned to one entire raceway in each of the four streamside channels (i.e., each treatment was applied to four raceways in total). To prevent the downstream transport

of fines that could contaminate unembedded treatments below highly embedded ones, all experimental units within a raceway received the same substrate treatment. To determine the quantities of sediment needed to fully embed the coarse and fine sediment treatments, the volume of water needed to fully cover 1 l of 5-cm deep river-washed gravel was measured and multiplied by the total volume of river-washed gravel placed in each raceway (48 l).

In the 2012 pilot experiment sediment (Table 2.1) was added to each raceway under dry conditions and gently shaken to ensure that all interstitial spaces were filled. The 50% embedded fine sand and the 100% embedded fine sand treatments contained 9% and 16% fine sediments <2 mm in diameter, respectively, which is the approximate threshold at which the negative effects of fine sediments have been observed (Owens *et al.* 2005; Bryce *et al.* 2008; Bryce *et al.* 2010; Benoy *et al.* 2012). Percent fine sediment was calculated as the proportion (by volume) of all substrate added to each raceway that was <2 mm in diameter. Three cobbles (10-15 cm diameter) were placed transversely across each 1.2 m long experimental unit to create small weirs at equal intervals to provide cover for Nooksack dace, and to generate resistance to flow which ensured that water depths were a minimum of 5 cm throughout each raceway. A single Nooksack dace was stocked in each experimental unit in 2012 at densities equivalent to 2 fish·m<sup>-2</sup>.

There was no significant effect of substrate on Nooksack dace growth in the 2012 pilot experiment (see results), which was unexpected given previous reports of negative impacts of sediment on benthic (Kawanishi *et al.* 2014) and drift-feeding fishes (Suttle *et al.* 2004; Finstad *et al.* 2007). I identified potential design artefacts that may have obscured the effects of sediment on Nooksack dace and modified the 2013 experiment accordingly. First, Pepin Creek has relatively high benthic invertebrate biomass, which could potentially mask any indirect effects of sediment on fish if experimental Nooksack dace densities (and associated consumptive demands)

are low relative to benthic prey abundance. Scour associated with cobble weirs may also have created sufficient unembedded habitat for invertebrates to support low densities of Nooksack dace with no impacts to growth (see results and discussion for more detail). The percentage of fine sediments which were set at the presumed 15% harm threshold (see above; Owens et al. 2005), combined with low replication (i.e., n = 8) may have also lowered statistical power to detect any negative effects of sediment addition. To address these issues, weirs were removed and replaced with a single 6.4 mm transverse mesh divider that reduced the length and area of experimental units by 50%, thereby effectively doubling Nooksack dace density, as well as, the total number of experimental units (i.e., 32 to 64). The proportion of fine sediments <2 mm in diameter was also increased from 16% to 31% in the 100% embedded fine sand treatment (Table 2.1). All sediment was added to the channels following the same methods used in 2012, except that flow in the channels was turned off multiple times during sediment placement to allow fine sediments to settle into interstitial spaces as the water drained out of the channels, which better simulates the process of fine sediment infiltration into interstices in natural streambeds (Brett Eaton pers. comm.). One substrate-filled permeable tray (40.6 cm<sup>2</sup>) made of 6.4 mm wire mesh was embedded in each experimental unit to standardize benthic invertebrate collection at the end of the experiment. Additionally, in the absence of cobble weirs a single cobble was placed at the downstream end of each experimental unit to provide cover for Nooksack dace.

In both 2012 and 2013 water was piped from Pepin Creek into a central header box, where a splitter distributed water to the four channels. Total discharge in each channel was stabilized at 5.8 l-s<sup>-1</sup>, with an average velocity of  $21 \pm 1.3$  cm-s<sup>-1</sup>, and an average depth of 5 cm based on previous research on Nooksack dace flow requirements (Avery-Gomm 2013; Avery-Gomm *et al.* 2014). Invertebrates were allowed to naturally colonize the channels for four weeks prior to fish introduction, when a single Nooksack dace was randomly stocked into each experimental unit (n = 32 in 2012, n = 64 in 2013) from July 27 - August 31 in 2012, and from July 30 - August 29 in 2013. Two-cm mesh bird netting was placed over the channels to protect Nooksack dace from terrestrial predators, and all screens separating experimental units were cleaned twice daily.

Five weeks after stocking fish, invertebrates were sampled from each experimental unit by gently lifting wire mesh trays into a 250 µm mesh Surber sampler located immediately downstream. Trays and sediment collected in the Surber sampler were backwashed into a 5 1 bucket filled with 1 litre of filtered stream water. Sediment within the bucket was agitated to suspend invertebrates and organic matter, and repeatedly decanted into another bucket to separate invertebrates and organic matter from sediment. This process was repeated at least three times until invertebrates and organic matter were removed from the sediment. All decanted water was filtered through a 250 µm mesh and invertebrates and organic matter were transferred to glass jars and preserved in a 5% formalin solution. Nooksack dace were removed from experimental units following invertebrate collection, measured (fork length), weighed to 0.01 g, and released at their site of capture in Bertrand Creek.

Invertebrates were identified to family using Merritt and Cummins (1996), with the exception of chironomids and mayflies, which were identified to subfamily and genus, respectively. A digitizing pad (Roff and Hopcroft 1986) and dissecting microscope outfitted with a drawing tube were used to measure the length of 17,617 invertebrates to the nearest 0.1 mm. Invertebrate biomass was estimated using digitized lengths and length-weight coefficients from Smock (1980), Meyer (1989), Sample *et al.* (1993) and Benke *et al.* (1999). Organic matter from

each sample was dried at 75° C to a consistent weight, and then ashed at 550° C for four hours to determine ash-free dry weight.

Particle size and embeddedness affects bed roughness and near-bed velocity (Carlson and Lauder 2011), which may affect the foraging environment of benthic fishes (Haro and Brusven 1994). To characterize differences in the near-bed velocity profiles above the different substrate treatments, a modified nozzle velocity meter (Wilkinson 1968) was used to measure velocity profiles at 5 mm vertical increments at two replicate locations over each substrate treatment type.

#### 2.2.3 Data analysis

#### 2.2.3.1 Treatment effects on invertebrate biomass and community structure

The effects of embeddedness and fines on the biomass of individual taxa were analyzed in mixed effects models using SAS version 9.4. Substrate treatment (four levels - unembedded, 50% embedded fine sand, 100% embedded fine sand, and 100% embedded coarse sand) was considered a fixed effect. Because there may have been gradients associated with proximity to the header box, I also included experimental unit position (four classes – top, upper middle, lower middle, and bottom) as a fixed effect. Channels (1-4) and raceways within channels (1-4) were considered random effects, and experimental units were treated as nested within raceways (four units per raceway). Organic matter was also included in the model as a covariate, however, it was only significant for copepod biomass, and was therefore dropped from all other models. A Tukey test was used for assessing differences in treatment means when there was a significant treatment effect. To simplify data analysis, I excluded rare taxa, i.e., those that were present in

 $\leq$ 0.2% of samples or were not consistently found in the stomach contents of Nooksack dace or the closely related longnose dace found in other areas (Gerald 1966; McPhail 1997); a total of 21 taxa were included in the final analysis (n = 21; Table 2.2).

In addition to potential effects of downstream position on invertebrate abundance in experimental units, units located in the same raceway may not be independent from one another because water, organic matter, and invertebrates flow from one to the other. To account for any potential lack of independence in the analysis, abundance of each taxon was modelled under two covariance structures, simple (which assumes independent observations with homogenous variance) and autoregressive (which assumes that covariance of observations is greatest in adjacent units, thereby accounting for any effects of spatial autocorrelation). To determine which covariance structure best fit each model, I used the Akaike Information Criterion (AIC). The covariance structure from the model with the lowest AIC values was determined to have the best fit (Johnson and Omland 2004). The Box-Cox power transformation was used to normalize the biomass of most taxa (Box and Cox 1964; Sakia 1992; see Table 2.2 for lambda and constant values). However, I was unable to transform the biomass of Simuliidae, Glossosomatidae, Nematoda, Acrina, and Heptageniidae sufficiently to normalize residuals using the Box-Cox or any other power transformation. Residuals from data analyses were tested for normality using the Shapiro-Wilks W statistic. To reduce Type I error, the sequential Bonferroni correction for multiple comparisons was used when testing substrate effects on the 21 analyzed taxa.

I tested for substrate and organic matter effects on total community biomass (all invertebrate taxa combined) using a two-way analysis of covariance (ANCOVA). Organic matter was removed from the model as it was not a significant predictor of total biomass, and a one-way ANOVA was then used to test for substrate effects on total invertebrate biomass. Residuals from

data analyses were tested for normality and homogeneity using the Shapiro-Wilks W statistic and Bartlett's K-squared statistic. All ANOVA and ANCOVA analyses were conducted in R version 3.2.0 (R Core Team 2015).

Differences in invertebrate community structure among the four substrate treatments was assessed using a one-way Analysis of Similarities (ANOSIM) and Principal Components Analysis (PCA), using data from each experimental unit in each of the four substrate treatments (n = 64). Relative abundance of invertebrates within each experimental unit was calculated by dividing each taxon by the maximum observed density (scaling all data from 0-1). Only the most abundant 21 taxa were included to minimize the influence of extremely rare taxa on the ordination, and to emphasize the effects of the most abundant taxa likely to constitute prey for Nooksack dace. The PCA analyses were computed using the FactomineR package with the covariance matrix (Lê and Husson 2008) and the ANOSIM analyses were computed using the vegan package (Oksanen *et al.* 2015), in R 3.2.0.

#### 2.2.3.2 Treatment effects on fish growth

Treatment effects on Nooksack dace growth from the 2012 pilot were analyzed using a mixed effect model with the same treatments and structure used to analyze biomass of invertebrate taxa. Unfortunately, only 4 of 64 Nooksack dace were recovered at the end of the experiment in 2013, precluding a mixed effect model analysis on growth. Installation of a wildlife camera immediately after recovery of fish revealed that mink (*Neovison vison*) were nocturnally foraging in the channels by crawling under the bird mesh. Of the Nooksack dace that survived, all four

were present in the unembedded treatment. A Kruskal-Wallis test was preformed to determine whether there were substrate effects on Nooksack dace survival in 2013.

2.3 Results

#### 2.3.1 Substrate effects on invertebrate biomass

Mixed effects models showed a significant substrate effect on the biomass of 10 of 21 invertebrate taxa (Table 2.2). Substrate affected the abundance of most taxa that made a significant contribution to total biomass, with over 80% of total invertebrate biomass in each treatment accounted for by the 10 taxa for which substrate effects were significant. Biomass of most taxa decreased as embeddedness increased, with highest biomass in the unembedded treatment followed by 50% embedded fine sand, 100% embedded coarse sand, and biomass was lowest in the 100% embedded fine sand treatment (Figure 2.3). Only Oligochaeta and copepod biomass showed a contrasting response, as their biomass was highest in the 100% embedded coarse sand treatment and lowest in the unembedded treatment (Table 2.2). There was a significant effect of position on Orthocladiinae chironomids, copepods, Glossosomatidae, and Tipulidae biomass. There was a significant downstream effect on Glossosomatidae biomass (i.e., biomass was highest in the upstream experimental units compared to downstream units), but there was no consistent upstream or downstream effect on biomass of the other three taxa. Organic matter only had a significant (positive) effect on copepod biomass.

There was a significant substrate effect on total invertebrate community biomass ( $F_{[3,60]}$  = 4.3, *P* = 0.008; Figure 2.3). A Tukey test showed that the 100% embedded fine sand treatment

was significantly lower than the three other treatments (unembedded, 50% embedded fine sand, and 100% embedded coarse sand), with approximately 50% less biomass. However, Oligochaeta comprised 63% of the total biomass in the 100% embedded coarse sand treatment, compared to 6% in the unembedded, 7.6% in the 50% embedded fine sand, and 19.1% in the 100% embedded fine sand treatment. If Oligochaeta are excluded from the analysis, substrate effects remained significant ( $F_{[3,60]}$  = 30.7, *P* <0.001; Figure 3), but total community biomass in the 100% embedded coarse sand treatment becomes statistically indistinguishable from the 100% embedded fine sand treatment. Organic matter was not significantly related with total invertebrate community biomass ( $r^2$  = 0.002, *P* = 0.69; Figure 2.4) or significantly different among substrate treatments ( $F_{[3,60]}$  = 0.3, *P* = 0.83; Figure 2.5), suggesting that invertebrate biomass was limited by interstitial space independent of the total availability of interstitial detritus in this experiment.

#### 2.3.2 Analysis of similarities and principal components analysis

Analysis of Similarities showed that invertebrate communities were significantly different among the four substrate treatments (R = 0.5, P < 0.001), and pairwise comparisons showed invertebrate communities were significantly different between all substrate treatments (Table 2.3). The ordination of invertebrate samples from different substrate types (n=4 substrate types, n = 21 invertebrate taxa) showed that community structure is well defined and partially differentiated among the four substrate treatments (Figure 2.6A). The first principal component (Dim 1) explained 24% of the variation in community structure and principal component two (Dim 2) explained an additional 15.3% of variation. Invertebrates that were positively correlated with Dim 1 tend to be detritivores (e.g., Amphipoda spp.) and grazers (e.g., Orthocladiinae spp.; Figure 2.6B). Dim 2 was positively correlated with grazing mayfly abundance (Baetidae spp.) and negatively correlated with chironomid, oligochaetes, and copepod abundance. Dim 1 and Dim 2 appear to separate unembedded treatments with high availability of interstitial spaces (unembedded and 50% embedded fine sand) from the highly embedded treatments (100% embedded fine and coarse sand). The unembedded treatment was positively correlated with Dim 1, and the 50% embedded fine sand treatment was positively correlated with Dim 2, while both the 100% embedded coarse and fine sand treatments were negatively correlated with Dim 1 and 2, indicating that collectors, detritivores, and grazers are proportionally more abundant in habitats with more interstitial space.

#### **2.3.3** Substrate effects on Nooksack dace growth and survival

Nooksack dace length ( $F_{[3,11]} = 1.8$ , P=0.20; Figure 2.7) and weight ( $F_{[3,11]} = 2.9$ , P = 0.09; Figure 2.8) were not significantly different among the four substrate treatments in the 2012 pilot experiment. Position of experimental units was not significant for either change in weight or length, and therefore a simple covariance structure was used to analyze fish growth. In 2013, I only recovered 4 of the 64 stocked Nooksack dace due to predation by mink, and was unable to calculate treatment effects on Nooksack dace growth. However, all recaptured Nooksack dace were in the unembedded treatment, providing strong evidence that unembedded gravel provided better refuge from predation ( $X_{[3, N = 64]} = 12.6$ , P = 0.006), and that embedded substrate increases the vulnerability of Nooksack dace to predation.
### 2.3.4 Micro-velocity measurements

Velocities at the substrate-water interface were approximately 2-4 cm-s<sup>-1</sup> in the unembedded and 50% embedded fine sand treatments compared to approximately 12 cm-s<sup>-1</sup> in the 100% embedded coarse and fine sand treatments (Figure 2.2), which also had somewhat steeper vertical velocity gradients close to the bed (i.e., a more rapid increase in velocity with height above the bed, based on visual inspection of slopes in Fig. 2.2). Differences in near-bed velocities between treatments is consistent with greater frictional drag associated with the rougher substrate in less embedded treatments, which creates a thicker boundary layer (i.e., velocities below a height of 5 cm above the bed where Nooksack dace are likely to forage) relative to the smooth surfaces in the highly embedded treatments (Figure 2.2). Velocities in the unembedded and 50% embedded fine sand treatments also increase more steeply with water depth (i.e., steeper slopes in Figure. 2.2), indicating that the smooth surfaces of the 100% embedded coarse and fine sand treatments create a more homogenous vertical velocity profile compared to the less embedded treatments.

#### 2.4 Discussion

#### 2.4.1 Substrate effects on Nooksack dace growth

Risk of predation from terrestrial and aquatic predators is a major source of mortality in fishes (Harvey *et al.* 2009; Heggenes *et al.* 1988; White and Harvey 2001). Terrestrial predators are a particular threat for fishes that inhabit relatively shallow habitats, where wading and diving birds

and mammalian predators can forage most effectively (Lonzarich and Quinn 1995; Harvey and Stewart 1991; Power 1984). The unforeseen predator impacts by mink in my experiment resulted in a significant substrate effect on Nooksack dace survival, clearly demonstrating the importance of refuges associated with unembedded substrate. White and Harvey (2001) used tethering experiments to demonstrate the importance of cover to survival of benthic sculpins in the presence of predators. The strong positive correlation between benthic fish abundance and unembedded substrate for sculpin (White and Harvey 1999) and other species (e.g., Atlantic salmon parr; Valdimarsson and Metcalfe 1998) provides additional circumstantial evidence for the role of substrate interstices in reducing predation risk. Structurally diverse habitats increase the availability of refuges for prey species (Warfe and Barmuta 2004) while decreasing the capture efficiency of predators (Gotceitas and Colgan 1989). Although the unplanned predator intervention in my experiment was from a terrestrial source, it would seem likely that interstitial spaces associated with unembedded substrate would also reduce Nooksack dace mortality from aquatic predators, although the effectiveness of interstitial refuges is likely dependent on the foraging mode of the predator (e.g., Huey and Pianka 1981).

In addition to the direct positive effects of interstitial space in reducing predation risk, lack of interstitial cover can also induce sublethal effects on fitness correlates. For example, Fisher (2000) showed that loss of substrate interstices increased metabolic rates and lowered growth of burbot (*Lota lota*), even in the absence of a predator. Similarly, Finstad *et al.* (2007) demonstrated that lack of interstitial cover reduced growth of juvenile Atlantic salmon parr, and attributed this to elevated stress from lack of cover. That fish experience elevated stress in the absence of interstitial refuges indicates selection to avoid simplified habitats, which in itself suggests elevated mortality risk in the absence of refuges over the course of evolution. Therefore,

it would appear that refuges associated with unembedded substrate may reduce both the sublethal effects of vulnerability to predation as well as the direct effects of predation itself, as observed here.

The greater roughness of unembedded substrate also resulted in a thicker boundary layer (Figure 2.2; Carlson and Lauder 2011) that likely provided Nooksack dace with low velocity habitats within the high velocity riffle habitats. Some benthic fishes are able to hold against benthic substrates with negligible energetic costs, even at high velocities, by placing their large pectoral fins laterally in high currents to generate downward pressure as water flows over them (Facey and Grossman 1990,1992; Grossman 2013). Despite this, it remains likely that Nooksack dace benefit from the thicker boundary layer associated with low embeddedness because it provides a velocity refuge for both foraging and resting, as seen in the closely related longnose dace (Mullen & Brown 1995; 1998). Substrate interstices associated with larger bed particles may also be particularly important as hydraulic refuges during very high flows when smaller bed particles can mobilize (Erman *et al.* 1988).

## 2.4.2 Substrate effects on benthic invertebrates

The biomass of most invertebrate taxa was highest in the unembedded and 50% embedded fine sand treatments, and decreased as embeddedness filled all of the available interstitial spaces. Most invertebrate taxa did not decrease in the 50% embedded fine sand treatment which was unexpected, as other studies have identified impact thresholds much lower than 50% embeddedness (e.g., Angradi 1999; Zweig and Rabeni 2001; Burdon *et al.* 2013). For example, Burdon *et al.* (2013) documented significant declines in the abundance of Ephemeroptera,

Plecoptera, and Trichoptera (EPT) at 20% fine sediment cover. However, the presence of sediment favored some taxa, particularly oligochaetes, which increased in abundance in the 100% embedded coarse sand treatment despite the general decrease in biomass of most other taxa, thereby stabilizing changes in total invertebrate community biomass (Figure 2.9). The increase in oligochaete biomass in the 100% embedded coarse sand treatment suggests that small interstices in coarse sands (2-6 mm particle diameter) provided both increased habitat for oligochaetes and a refuge from potential invertebrate or fish predators. This inference is reinforced by the depression of oligochaete abundance in the 100% embedded fine sand treatment, when the micro-interstices in coarse sands were filled with fines. Indicating that the effects of sediment addition on fish and invertebrates can be understood in terms of the hierarchical loss of interstitial spaces at different substrate sizes. Just as infilling of primary interstitial spaces within the gravel framework reduced the amount of interstitial habitat for fish and larger invertebrates, infilling of smaller interstitial spaces in coarse sand by fines <2 mm diameter drastically reduced the abundance of habitat for burrowing oligochaetes.

As interstitial spaces are filled with sediment, both the epibenthic surface area and interstitial habitat is reduced (Lenat *et al.* 1979; Henley 2000), resulting in the loss or reduction of sediment intolerant benthic taxa. The Amphipod and Isopod detritivore functional groups appeared to be the most sensitive to the effects of sediment, as their biomass decreased by more than half in the 50% embedded fine sand treatment relative to the unembedded treatment. Loss of interstitial spaces can decrease the quantity of organic matter deposited in benthic substrates (Angradi 1999), reducing the availability of food for detritivorous invertebrates. Despite previous studies that have shown strong relationships between benthic organic matter abundance and invertebrate biomass (e.g. Culp *et al.* 1983; Rosenfeld 2000; Negishi and Richardson 2003),

organic matter was not significantly different between substrate treatments in my study, suggesting that differences in invertebrate biomass were not driven by the quantity of organic matter trapped in interstices, but rather by the availability of interstitial habitat itself. However, my analysis of organic matter did not distinguish between fine and coarse particulate organic matter. Larger particles of coarse organic matter typically represent lower quality food for most invertebrates, and their random presence in some of my benthic samples may have obscured any relationship between organic matter and invertebrate biomass.

Strong declines in the abundance of the grazing baetid mayflies at high embeddedness suggests a reduction in the availability of suitable grazing surfaces. The effect of embeddedness on the biomass of chironomids is less clear than for larger bodied detritivores (e.g., amphipods) and may be attributable to an interaction between habitat loss and competition, rather than sediment effects alone. The biomass of two chironomid subfamilies, Tanypodinae and Orthocladiinae, decreased by more than half in the 50% embedded fine sand treatment, but increased in the 100% embedded coarse sand treatment. In contrast, the biomass of grazing mayfly larvae (Baetidae) was lowest in the 100% embedded coarse sand treatment. Chironomid abundance may be reduced in the presence of large bodied grazing invertebrates like mayfly larvae, through competition for periphyton and direct predation on small instar chironomids (Harvey and Hill 1991; Bechara *et al.* 1992; Rosenfeld 2000). Inverse trends in Baetid and chironomid biomass among treatments suggest that competitive interactions may modulate overall trends in community structure imposed by sediment inputs.

Suttle *et al.* (2004), using a more continuous gradient of sediment embeddedness treatments, found linear declines in juvenile trout growth with increasing embeddedness, although the drop in abundance of surface-dwelling invertebrates they observed was steepest in

the range of 60% embeddedness. However, lower thresholds of negative effects on benthic invertebrates have been observed. For example, Mebane (2001) found significant decreases in scraper abundances when fine sediment embeddedness exceeded 40%, while others have shown significant declines in the abundance of EPT taxa at embeddedness levels between 12 and 30% (Ryan 1991; Burdon et al. 2013). Although taxa like amphipods showed a linear decline in abundance with embeddedness in my experiment, the most abundant grazing taxa (baetid mayflies) displayed more of a threshold function with no apparent reduction at 50% embeddedness (Figure 2.9). Consequently, large impacts of sediment on total invertebrate community biomass were only manifest at embeddedness levels in excess of 50% in this study. Although the small number of treatment levels (0, 50, and 100% embedded) limits conclusions with respect to thresholds of impact, a conservative conclusion from this and other studies (see Angradi 1999; Mebane 2001; Burdon et al. 2013) is that embeddedness levels in excess of 50% are more likely to shift substrate embeddedness into a range where negative effects on benthic invertebrates are likely to manifest. Consequently, streams with natural or ambient embeddedness levels near a 50% threshold are especially vulnerable to increased sediment loads. Streams predisposed to naturally high levels of embeddedness include those in low-relief landscapes where low channel gradient limits the power of the stream to transport fines, or small streams where peak flows are insufficient to export sediment and rework the streambed. Small, low gradient valley bottom streams like those inhabited by Nooksack dace are thus naturally predisposed to being sensitive to sediment inputs; the co-incidence of these low-relief valley bottom streams with agriculture further heightens their vulnerability to both fine and coarse sediment inputs.

This experiment and earlier studies (Iwata *et al.* 2003; Suttle *et al.* 2004; Bo *et al.* 2007) suggest that responses to sediment addition characteristically differ among invertebrate functional groups. Decreases in the abundance of grazers at high embeddedness may be associated with a reduction in the surface area of available grazing habitat, rather than a decrease in total interstitial volume. Loss of interstitial space would reduce available grazing habitat rather than completely eliminating it at high embeddedness, provided that the embedded substrate is sufficiently stable to support biofilm production; this appears to be the case for baetid mayflies in my study. In contrast, loss of larger interstitial spaces for detritivores like amphipods, which require low velocity depositional micro-habitats, may lead to their virtual elimination in fully embedded substrate (Table 2.2, Figure 2.9). Lastly, loss of very small interstitial spaces by compaction from very fine sediment (<2 mm) may lead to the loss of smaller burrowing taxa (e.g., oligochaetes).

Earlier research has highlighted the negative impacts associated with the very fine sediment size fraction (<2 mm diameter; Ryan 1991; Angradi 1999; Mebane 2001; Owens *et al.* 2005; Bryce *et al.* 2008; Kaufmann *et al.* 2009; Burdon *et al.* 2013), and identified thresholds for detectable impacts on benthic community structure in the range of 12-30% fines <2 mm (by volume). However, my results indicate that the overall loss of interstitial space through embeddedness has a larger impact on total benthic invertebrate community biomass than the fraction of fines <2 mm diameter; even a 20% proportion of fine sediment by volume did not significantly reduce total invertebrate community biomass in this study when overall embeddedness was less than 50%. Concomitantly, significant decreases in abundance of surface dwelling taxa were observed at 100% embeddedness even in the absence of very fine sediments. However, very fine sediment exacerbated the negative effects of embeddedness, particularly for

oligochaetes. This was likely due to very fine sediments infiltrating and clogging microinterstitial spaces used by oligochaetes. The small size and high relative surface area of very fine particles also causes them to be adhesive, resulting in compaction of benthic substrates (Waters 1995; Iwata *et al.* 2003) and potential negative impacts that are difficult to detect over short time scales in experimental channels. For instance, enhanced compaction may increase substrate stability and the threshold shear stress required for bed scour to effectively clean gravel and transport fines, as well as limiting substrate permeability to interstitial flow and colonization by burrowing invertebrates (Lisle and Lewis 1992; Iwata *et al.* 2003).

Although substrates may be fully unembedded in natural streams, this typically occurs only in very well sorted substrate patches, and fines are usually present to varying degrees depending on natural sources of sediment and channel transport capacity (Rosenfeld *et al.* 2011). Consequently, the unembedded treatment in my experiment, although useful to anchor an experimental gradient, may be less representative of average substrates available in an unimpacted stream than the 50% embedded treatment (e.g., Harvey *et al.* 2009). While the unembedded treatment may not be truly representative of natural substrate conditions, the survival of all remaining Nooksack dace and the high invertebrate biomass associated with this substrate treatment provides strong evidence that interstitial habitat represents high quality foraging and refuging habitat for benthic fishes and their invertebrate prey.

The preference of Nooksack dace for fast flowing riffle habitats dominated by coarse unembedded substrates (Inglis 1997; Pearson *et al.* 2008) appears to be influenced by both the availability of interstitial spaces that provide refuge from predation, and a high abundance of invertebrate prey. If Nooksack dace growth and biomass is limited by the abundance of benthic prey, my results suggest that fish production should be sensitive to the indirect effects of

sediment on benthic invertebrate abundance, as observed for drift-feeding fishes (e.g., Suttle et al. 2004; Harvey et al. 2009). Growth of Nooksack dace is likely prey limited during at least some times of the year, since I have observed Nooksack dace drift-feeding in mixed assemblages of salmonids in residual pools during extreme summer low-flow events when habitat area is severely restricted and fish density is high (Avery-Gomm et al. 2014; Rosenfeld pers. obs.). Drift-foraging during the day is strongly suggestive of prey limitation for a nocturnally foraging benthic fish. However, lack of an effect of sediment on Nooksack dace growth in my 2012 pilot experiment suggests that Nooksack dace can grow under high embeddedness, at least at low fish densities. Nooksack dace have been shown to forage efficiently over a range of substrates types (see Chapter 3), and longnose dace can use rooting behaviour to feed on invertebrates in interstitial spaces or below the substrate surface (Beers and Culp 1990), which could partially mitigate a shift in community structure to burrowing invertebrates. However, the depth to which Nooksack dace and other small insectivorous fish can root into substrate to capture subsurface prey is unclear. Eutrophication that increases overall benthic abundance in Pepin Creek could also partially mask any negative effects of sediment infilling on Nooksack dace growth. While enhanced prey production through nutrient runoff could provide some mitigating effect to sediment impacts, eutrophication carries attendant water quality concerns (e.g., hypoxia), especially under projected climate warming scenarios (Pörtner and Kunst 2007).

Small riffle-dwelling fishes like Nooksack dace appear to have adopted a life-history strategy that minimizes predation risk when foraging in prey-rich riffle habitats with relatively low energy expenditures. Their small body size facilitates foraging within the boundary layer of high velocity meso-habitats (Carlson and Lauder 2011; Meyers and Belk 2014) thereby minimizing energy expenditures while exploiting benthic invertebrates that are unavailable to

larger fish (Grossman and Freeman 1987). At the same time, coarse substrates and high water velocities provide both a refuge from predation and an energetic barrier to many larger predatory fish that are too large to fit within the boundary layer (a predator stress environment; Menge and Sutherland 1987). This experiment and associated literature review highlights the importance of unembedded substrates for adopting this lifestyle. Consequently, the protection of stream reaches with coarse unembedded substrates should be viewed as a conservation priority for Nooksack dace and similar obligate riffle insectivores. This work also highlights the importance of reducing both the frequency and quantity of fine sediment inputs as a management priority for Nooksack dace. This goal can be achieved through re-establishing riparian forest where it has been removed, and by working with land owners to implement best management practices that minimize soil erosion and other sources of fine sediment, particularly in smaller streams that lack the transport capacity to export large quantities of sediment.

**Table 2.1** Quantities of sediment added to each raceway in the 2012 pilot and 2013 final experiments. Quantities of sediment are expressed in weight (kg) and volume (litres). Total mass and volume of drain rock differ between the pilot and final design because mixed pebbles were added to more closely simulate substrate gradations found in natural streambed gravels.

Treatment	Drain Rock (20-50 mm)		Mixed Pebble (7-19 mm)		Fine Gravel and Coarse Sand (2-6 mm)		Fine Sand (2-0.5 mm)		Silt and Clay (<0.5 mm)		Total Fines (<2 mm)		Available Interstitial	Total % Fines <2 mm	
	Mass (kg)	Volume (l)	Mass (kg)	Volume (l)	Mass (kg)	Volume (l)	Mass (kg)	Volume (l)	Mass (kg)	Volume (l)	Mass (kg)	Volume (l)	Volume (l)	Mass (kg)	Volume (l)
2012 Pilot Design															
Unembedded	74.2	48	-	-	-	-	-	-	-	-	-	-	24	0%	0%
50% Fine Sand	74.2	48	-	-	12.6	6.4	6.6	4.4	1.36	1.2	7.96	5.6	12	8%	9%
100% Coarse Sand	74.2	48	-	-	47	24		-	-	-	-	-	7	0%	0%
100% Fine Sand	74.2	48	-	-	25.2	12.8	13.2	8.8	2.74	2.4	15.9	11.2	3.4	14%	16%
2013 Final Design															
Unembedded	62	40	13.2	8	3.6	1.8	-	-	-	-	-	-	24	0%	0%
50% Fine Sand	62	40	13.2	8	3.6	1.8	13.2	8.8	2.74	2.4	15.9	13.6	12	17%	22%
100% Coarse Sand	62	40	13.2	8	47	24	-	-	-	-	-	-	7	0%	0%
100% Fine Sand	62	40	13.2	8	3.6	1.8	26.2	17.72	5	4.8	31.2	22.5	0.02	28%	31%



**Figure 2.1** Four semi-natural experimental stream-side channels (1.2m x 4.9m) were longitudinally divided into 4 raceways and further divided transversely into 32 experiment units in 2012 and 64 experimental units in 2013. One substrate treatment was assigned all experimental units in each raceway.



**Figure 2.2** Vertical-velocity profiles over the four substrate treatments. Squares and diamonds represent two replicate velocity profiles over each substrate type; the y-axis is height above the streambed, and arrows indicate contrasting water velocities at the substrate surface (2-4 cm s<sup>-1</sup> in the 0 and 50% embedded treatments (a,b), and 10-12 cm s<sup>-1</sup> in the 100% embedded treatments (c,d)).



**Figure 2.3** Total invertebrate community biomass (g-m<sup>-2</sup>; n =16 per substrate treatment), including Oligochaeta biomass (solid squares), and total invertebrate community biomass excluding Oligochaeta biomass (open circles) in each substrate treatment.

**Table 2.2** Summary of mixed effect model analysis results for effects of embeddedness and fines on invertebrate biomass. All taxonomic groups with non-normal distributions were transformed using the Box Cox power transformation. Untransformed means  $(g-m^{-2})$  are reported in the table above. Degrees of freedom (df), F statistic (F), *P* value, and differences between treatments are reported for transformed data. To account for Type I error the sequential Bonferroni correction for multiple comparisons was used when testing substrate effects on the 21 analyzed taxa, there was a significant sediment effect on the taxa above the solid line.

		Least Squa	ares Means										
Таха	Covariance	Unomboddod	50% Fines	100% Coarse	100% Fine	SE	Position	Organic	df	F	Pr>F	Lambda (λ)	λ=(Y+C)
	structure	Ullembedded	Sand	Sand	Sand		effect	effect					
Amphipoda	simple	2.39 (A)	1.02 (B)	0.45 (C )	0.09 (D)	0.015	N	Ν	45	76.72	< 0.0001	0.3030	0.01
Baetidae	simple	5.01 (A)	6.52 (A,B)	1.51 (C )	2.51 (C )	0.062	N	Ν	45	13.84	< 0.0001	-	-
Chironomid Pupae	simple	0.04 (A)	0.01 (B)	0.02 (A,B,C)	0.01 (B)	0.001	N	Ν	45	9.63	< 0.0001	-0.0202	0.01
Isopoda	simple	0.32 (A)	0.07 (B)	0.01 (B,C)	0.003 (C )	0.017	N	Ν	45	29.13	<0.0001	-0.1414	0.01
Oligochaeta	simple	0.62 (A)	0.79 (A,B)	6.2 (C )	0.89 (A,B)	0.008	N	Ν	45	12.97	<0.0001	0.1010	-
Tanypodinae	simple	0.16 (A)	0.03 (B)	0.09 (A,C)	0.01(B)	0.005	N	Ν	45	28.74	<0.0001	0.1010	0.01
Tanytarsini	simple	0.3 (A)	0.14 (B)	0.07 (C )	0.06 (C )	0.01	N	Ν	45	38.33	< 0.0001	0.3030	0.01
Plecoptera	simple	0.03 (A)	0.07 (A,B)	0.001 (C)	0.01 (C )	0.157	N	Ν	45	11.79	<0.0001	-0.4646	0.01
Orthocladiinae	simple	0.35 (A)	0.19 (B)	0.24 (A,B,C)	0.08 (D )	0.016	Y	Ν	45	11.65	< 0.0001	0.3030	0.01
Copepod	simple	0.1 (A)	0.09 (A,B)	0.17 (C )	0.09 (A,B)	0.014	Y	Y	45	6.47	0.001	-	-
Chironomini	simple	0.08 (A)	0.05 (A,B)	0.32 (A,C)	0.07 (A,B)	0.007	N	Ν	45	4.78	0.0056	0.1010	-
Simuliidae	simple	0.08 (A)	0.26 (B)	0.08 (A,C)	0.2 (A,B,C)	0.014	N	Ν	45	4.45	0.008	0.1414	0.01
Glossosomatidae	AR	0.13 (A)	0.11 (A,B)	0.0004 (B,C)	0.001 (B,C)	4.669	Y	Ν	15.6	5.45	0.0093	-1.1515	0.01
Hydropsychidae	simple	0.02 (A)	0.07 (A,B)	0.01 (A,C)	0.01 (A,B,C)	0.240	N	Ν	45	4.05	0.0124	-0.5051	0.01
Diptera Pupae	simple	0.06 (A)	0.07 (A,B)	0.01 (A,B,C)	0.01 (B,C)	0.354	N	Ν	45	3.67	0.0189	-0.5859	0.01
Chironomidae	simple	0.06 (A)	0.02 (B)	0.03 (A,B,C)	0.02 (B,C)	0.01	N	Ν	45	3.5	0.0229	0.2222	0.01
Nematoda	Simple	0.01	0.03	0.01	0.03	0.033	N	Ν	45	2.6	0.0635	-0.4646	0.01
Ephemeroptera	simple	0.21	0.20	0.06	0.14	0.014	N	Ν	45	1.63	0.196	0.1414	0.01
Acarina	simple	0.01	0.01	0.06	0.01	0.005	Y	Ν	45	0.62	0.6086	0.2222	0.01
Tipulidae	simple	0.29	0.47	0.37	0.39	0.029	Ν	Ν	45	0.58	0.6321	0.2222	0.01
Heptageniidae	simple	0.16	0.07	0.11	0.03	0.008	Ν	Ν	45	0.31	0.8147	0.0606	0.01



**Figure 2.4** Linear regression of total invertebrate biomass as a function of organic matter in each substrate replicate (n = 64;  $r^2 = 0.002$ , P = 0.69).



Figure 2.5 Mean ash free dry weight of organic matter (g-m-2) in each substrate treatment with 95% confidence intervals (n =16 replicates per substrate treatment).

**Table 2.3** Analysis of Similarities pairwise comparisons of similarities in benthic invertebrate community structure between each substrate treatment (n = 64). R statistic and *P* value were obtained after 10,000 permutations.

Pairwise Comparison	R Statistic	P value
Unembedded - 50% Embedded Fine Sand	0.38	0.001
Unembedded - 100% Embedded Coarse Sand	0.76	0.001
Unembedded - 100% Embedded Fine Sand	0.78	0.001
50% Embedded Fine Sand - 100% Embedded Coarse Sand	0.60	0.001
50% Embedded Fine Sand - 100% Embedded Fine Sand	0.33	0.001
100% Embedded Coarse Sand - 100% Embedded Fine Sand	0.33	0.001



**Figure 2.6** A) Principal component ordination plotting the experimental unit scores (n = 64) for all substrates. Ellipses are 95% confidence intervals for differences between substrate treatments. B) Principal component vectors of invertebrate taxa (n = 21). In both panels, Dim 1 is positively correlated with unembedded substrates and negatively correlated with 100% embedded coarse and fine sand treatments. Detritivores (e.g., amphipods, highlighted blue) tend to be positively correlated with Dim 1 (unembedded treatments). Dim 2 is positively correlated with 50% embedded fine sand substrates and negatively correlated with the 100% embedded fine sand substrates and negatively correlated with the 100% embedded fine sand substrates and negatively correlated with the 100% embedded fine sand substrates and negatively correlated with the 100% embedded fine sand substrates and negatively correlated with the 100% embedded fine sand substrates and negatively correlated with the 100% embedded fine sand substrates and negatively correlated with the 100% embedded fine sand substrates and negatively correlated with the 100% embedded fine sand substrates and negatively correlated with the 100% embedded fine sand substrates and negatively correlated with the 100% embedded fine sand substrates and negatively correlated with high fines along Dim 2.



Figure 2.7 Mean change in Nooksack dace fork length (mm) over the five-week experiment by substrate treatment, with 95% confidence intervals (n = 8 replicates per substrate treatment).



**Figure 2.8** Mean change in Nooksack dace weight (g) over the five-week experiment by substrate treatment, with 95% confidence intervals (n = 8 replicates per substrate treatment).



**Figure 2.9** Biomass (g·m-<sup>2</sup>) of Amphipoda, Baetidae, and Oligochaeta in each substrate treatment along a gradient of increasing embeddedness from left to right. Error bars represent 95% confidence intervals.

Chapter 3: The joint effect of water velocity and substrate composition on the foraging efficiency of an endangered benthic cyprinid, Nooksack dace *(Rhinichthys cataractae sp. cataractae)* 

# 3.1 Introduction

The ability of a fish to effectively forage depends on the overall abundance and distribution (i.e., patchiness) of prey, and the vulnerability of prey to capture (Gerald 1966; Charnov 1974; Beers and Culp 1990; Thompson et al. 2001; Nachman 2006; Grossman 2013). Prey abundance tends to be higher in habitats with high structural complexity (Diehl 1992; Hurlbert 2004) as complexity may provide more refugia for prey (Warfe and Barmuta 2004; Schneider and Winemiller 2008) and the resources they consume (Culp and Davies 1983; Negishi and Richardson 2003). However, predator foraging efficiency decreases in complex habitat due to reduced prey vulnerability and encounter rates (Gotceitas and Colgan 1989). Aspects of the physical environment other than complexity - such as water velocity or wind speed - may also affect the capture success rate of predators. For instance, Gilchrist and Gaston (1997) showed enhanced seagull predation on thick-billed murre (Uria lomvia) eggs at moderate wind speeds that optimized maneuverability near cliff ledges. Similarly, several studies have shown that velocity decreases capture success per strike as well as the distance at which salmonid fishes detect drifting invertebrates in streams, resulting in lower capture success per prey encounter (Hill and Grossman 1993; Piccolo et al. 2008).

Alterations to habitat structure through anthropogenic impacts are now pervasive, and can directly impact the mechanics of prey capture success, alter search efficiency, or reduce predator encounter rates with prey by directly reducing prey abundance (Kemp et al. 2011; Jones et al. 2012b). In freshwater habitats, excessive sediment inputs that alter aquatic environments by embedding substrates are an increasingly common habitat alteration that can decrease the availability of prey for fish, adversely affecting growth or survival (Suttle et al. 2004). Although the negative effects of sediment are well documented (Frostick et al. 1984; Berkman and Rabeni 1987; Ryan 1991; Anderson et al. 1996; Owens et al. 2005; Finstad et al. 2007; Kemp et al. 2011), the underlying mechanisms whereby sediment reduces the energy intake of benthic fishes remain somewhat ambiguous, in particular the potential role of changes in velocity and substrate characteristics (e.g., embeddedness) on foraging efficiency. Previous studies have demonstrated that velocity (Grant and Noakes 1987; Jean-Guy et al. 1989; Tyler 1993; Piccolo et al. 2008) and sediment (Caux et al. 1997; Nerbonne and Vondracek 2001; Suttle et al. 2004; Finstad et al. 2007) have strong effects on the foraging efficiency of drift feeding fishes, but similar studies on benthic stream fishes are largely absent.

Fine sediment has direct effects on invertebrate abundance and community structure, as well as the physical environment that constitutes the foraging arena for benthic fishes. Increased sediment loads in streams can alter prey abundance and distribution by smothering periphyton and filling interstitial spaces in benthic substrates that trap organic matter and provide habitat for both benthic invertebrates and fishes (Negishi and Richardson 2003; Kaufmann *et al.* 2009; Sutherland *et al.* 2010; Kemp *et al.* 2011; Jones *et al.* 2012b), thereby reducing the abundance of benthic prey for stream fishes (Thompson *et al.* 2001; Suttle *et al.* 2004). Abiotic changes associated with embeddedness include decreased streambed roughness resulting in increased

near-bed water velocities (Chapter 2), decreases in the porosity and permeability of stream gravels, and a reduction in the thickness of the low velocity boundary layer above the streambed (Smith et al. 2005; Kaufmann et al. 2009; Evans and Wilcox 2013). Riffle dwelling benthic fishes are generally found in high velocity habitats over unembedded coarse substrate (Gibbons and Gee 1972; Facey and Grossman 1990; Mullen and Burton 1995; 1998; Pearson et al. 2008), where the ability to use their pectoral fins as hydrofoils allows them to hold against the substrate at high velocities with minimal energy expenditure (Facey and Grossman 1990; Grossman 2013). Although it is unknown how velocity affects the costs of active foraging by benthic fishes, it is thought that a thicker boundary layer associated with a rough bottom substrate plays a critical role in facilitating the use of fast water habitat by small benthic fishes (Carlson and Lauder 2011). While studies have considered the role of prey abundance and water velocity in habitat selection by benthic fishes (Hansen et al. 1986; Thompson et al. 2001; Petty and Grossman 2010; Grossman 2013), I am not aware of any studies that have simultaneously manipulated benthic substrates and velocity to determine how they jointly influence the foraging efficiency of benthic stream fishes.

The objective of this study was to identify how water velocity and substrate interact to affect the foraging efficiency of a riffle-dwelling, benthic insectivorous fish, with the goal of understanding the physical constraints on foraging effectiveness, and the underling mechanisms whereby sedimentation can affect foraging success. Using experimental foraging arenas, I manipulated gravel embeddedness and water velocities (0, 25, and 35 cm-s<sup>-1</sup>) to evaluate their interactive effects on the foraging efficiency of a typical benthic cyprinid, the Nooksack dace (*Rhinichthys cataractae* sp. *cataractae*), an endangered species in the Lower Mainland of southwestern British Columbia, Canada. My expectations were: i) that foraging efficiency would

decline at higher velocities because of reduced boundary layer thickness, and ii) foraging efficiency would decrease with sediment inputs that reduce surface roughness, and therefore be highest over unembedded substrates with the thickest boundary layer.

# 3.2 Methods

## 3.2.1 Study site

Experiments took place in southwestern British Columbia adjacent to Pepin Creek, a lowland stream that flows south into the Nooksack River in Washington State, USA. Experiments were conducted from June 2-16, 2014 when water temperatures were consistently above 11 °C, as Nooksack dace are less active below this temperature (COSEWIC 2007; Pearson *et al.* 2008). Nooksack dace were captured in nearby Bertrand Creek using minnow (Gee) traps and transferred to the secure experimental site at nearby Pepin Creek immediately after capture. To ensure that each Nooksack dace had similar motivation to feed during foraging trials, all fish were held in Pepin Creek in covered containers with flow-through mesh sides for a minimum of 36 hours prior to the foraging experiments. Nooksack dace were returned to their site of capture after the conclusion of each trial.

# 3.2.2 Foraging arena design

Experimental arenas were constructed using 5-liter plastic buckets, 19 cm high and 18.5 cm diameter, each fitted with a water intake hose attached to a 3,820 l per hour bilge pump. Intake

hoses were inserted 10 cm above the bottom of each bucket tangential to the outside curvature of the bucket wall to allow water to flow in a clockwise direction inside each arena, creating a circular current. To minimize the low velocity zone in the center of each arena, a 4 cm diameter stand pipe was installed in the center of each bucket. Four arenas and bilge pumps were placed in a 57 litre water bath on the bank of Pepin Creek, which was supplied with fresh water from the creek via a bilge pump (Figure 3.1). All water entering the tank was filtered through two 250 µm mesh bags to prevent suspended stream invertebrates from entering the arenas. Five water outflow windows were cut out of the upper 4 cm of each bucket wall and covered with 250 µm mesh, allowing water to flow out of the top of the arenas during the experiment. Lids constructed from 250 µm mesh were secured to each bucket to prevent invertebrates or Nooksack dace from escaping from the arenas during experiments.

#### 3.2.3 Experimental design

A single foraging efficiency trial was run daily, using a total of four foraging arenas each day (the maximum capacity of the stream-side experimental set up; Figure 3.1). I randomly assigned one of three sediment treatments that represented observed natural conditions in Nooksack dace streams (smooth surface, unembedded gravel, and embedded gravel; personal observation) to each of the four arenas. Smooth surface treatments did not include any substrate additions and the bottom of the arena was left as the bare plastic surface, which is similar to bed rock or hard clay substrates that provide no interstitial refuges for Nooksack dace or their invertebrate prey; unembedded gravel treatments contained 1 l of river-washed gravel (drain rock 2-5 cm diameter), 0.2 l of mixed pebbles (8-19 mm diameter), and 0.5 l of coarse sand (2-7 mm

diameter); embedded gravel treatments contained an additional 0.36 l of coarse sand to completely fill all interstitial spaces. The volume of coarse sand needed to fill interstitial spaces was estimated as the volume of water needed to cover one liter of drain rock. One of three velocity treatments meant to mimic low to zero velocity pool habitat (0 cm-s<sup>-1</sup>), moderate velocity riffle habitats ( $25 \text{ cm-s}^{-1}$ ), and high velocity riffle habitats ( $35 \text{ cm-s}^{-1}$ ) was randomly assigned to each sediment treatment, and each substrate x velocity combination (n=9) was replicated five times (total n = 45). The three velocities used in this experiment were based on both previous research on Nooksack dace flow requirements (Avery-Gomm 2013; Avery-Gomm *et al.* 2014), and on field observations (unpublished data). Velocities in each arena were adjusted by using a relief ball valve installed between the bilge pump and intake hose.

Three different taxa of invertebrates were stocked in each arena (mayfly larvae (Ephemeroptera, Baetidae), black fly larvae (Simuliidae), and chironomid larvae (Chironomidae, primarily Orthocladiinae). These invertebrates were selected based on their common occurrence in the diet of Nooksack dace (McPhail 1996; Avery-Gomm *et al.* 2014; personal observation) and other closely related dace species (Gee and Northcote 1963; Culp 1989), and their widespread availability as prey within Pepin Creek. Invertebrates used for stocking foraging arenas were collected using a Surber sampler from experimental stream-side channels built at Pepin Creek. Each arena was stocked with seven large- (4.5 - 6.5 mm) and eight medium-sized (2.5 - 4.5 mm) mayflies, six medium-sized (3 - 6 mm) chironomids, and seven large (4 - 8 mm) and medium-sized (2 - 4 mm) black fly larvae. After allowing the invertebrates to acclimate in the arenas for one hour, a Nooksack dace ( $85.5 \pm 9.2 \text{ mm}$  and  $3.7 \pm 0.7 \text{ g}$ ) was stocked in each arena. Invertebrates and Nooksack dace were stocked in arenas in the late afternoon, and foraging trials were conducted from dusk until dawn as Nooksack dace are generally nocturnal

feeders (Culp 1989; McPhail 1997; COSEWIC 2007). Nooksack dace were removed the following morning and water and sediment were decanted from each arena and rinsed to remove unconsumed invertebrates, which were counted to estimate percent capture efficiency. In order to estimate the recovery efficiency of invertebrates independent of fish consumption, I included two control replicates (no Nooksack dace present) for each substrate x velocity combination.

Nooksack dace forage primarily at night (McPhail 1997), which precluded easily observing fish foraging behaviour or invertebrate predator avoidance behaviour in experimental arenas. However, to obtain some understanding of how invertebrates respond to changes in velocity in foraging arenas in the absence of predation risk, I made simple quantitative observations of *Baetis* responses to increased velocity over unembedded gravel substrate. Twelve mayflies were stocked in two replicate foraging arenas with GoPro<sup>®</sup> cameras installed at the water surface, and the number of mayflies present on upper substrate (gravel surfaces) was recorded five times at 10 minute intervals in still water (0 cm-s<sup>-1</sup>). After one hour with no flow, bilge pumps were turned on to increase velocity to 15 cm-s<sup>-1</sup>, and the number of mayflies visible on substrate surfaces was again recoded five times at 10 minute intervals.

#### **3.2.4** Measurement of velocity and turbulence

Velocities were systematically measured before each experiment at 12 points (Figure 3.2) in each arena using a Marsh-McBirney model 2000 flowmeter. Because velocity increased with distance from the center of each arena, velocity was measured at three points along four radii in each quadrant of the arena floor to more precisely estimate mean velocity. To estimate temporal variation in velocity (i.e., turbulence), I used a GoPro<sup>®</sup> camera to record flowmeter readings of

the variability in water velocity for one minute at each of the 12 measurement locations for each of the substrate x velocity combinations. Average velocity and its standard deviation (as an estimate of turbulence) were calculated for the three regions in the arenas: the outside (along the outer edge of the arena), the middle, and the inside (next to the central standpipe of the arena; Figure 3.2).

#### 3.2.5 Statistical analysis

Foraging efficiency was calculated as the total number of individuals consumed by Nooksack dace divided by the total number of prey stocked in each arena for each taxon separately and for all taxonomic groups in each foraging arena. To correct for invertebrates, I was unable to recover from control replicates (no Nooksack dace present), a conservative estimate of foraging efficiency was generated by calculating prey consumed as the total number of invertebrates stocked less the number of invertebrates recovered and the average number of individuals I was unable to recover from control trials (i.e., the average number of unrecovered individuals from controls were not treated as consumed prey). For each taxon and all taxa combined, I tested for effects of substrate, velocity, and fish length on capture efficiency using a two-way analysis of covariance (ANCOVA) with fish length as a covariate, including an interaction between velocity and substrate. Fish length was not significant (i.e., P > 0.05) and was removed from all models. To test for differences in capture efficiency among taxa, I also used an ANCOVA to test for effects of taxa, substrate, and velocity on capture efficiency with all two and three way interactions included between the aforementioned variables. An ANCOVA was used to assess velocity effects on capture efficiency treating velocity as a continuous (rather than class) variable

to determine the incremental decrease in capture efficiency with increasing velocity for individual taxa and all taxa combined. To identify the significance of interaction terms and the minimum adequate model, I used the Akaike Information Criterion corrected for small sample size (AIC<sub>e</sub>). The best model was identified as having the highest AIC<sub>e</sub> weight and the lowest ΔAIC<sub>c</sub> (Burnham and Anderson 2004). All model selection was performed using the AICcmodavg package in R (Mazerolle 2015). Residuals were tested for normality and homogeneity using (Shapiro-Wilks W and Bartlett's K-squared statistics). All dependent variables met assumptions of normality and homogeneity of variance, except for percent capture efficiency of mayfly and blackfly larvae, which were arcsine transformed to normalize residuals. The effects of velocity (0, 25, or 35 cm-s<sup>-1</sup>), substrate (smooth surface, unembedded gravel, and embedded gravel), and location (outside perimeter, middle, and inside), on the standard deviation of velocity (i.e., turbulence) was assessed using a three-way ANCOVA, with an interaction between location and velocity. All statistical analyses were conducted in R version 3.2.0 (R Development Core Team 2015).

## 3.3 Results

### **3.3.1** Velocity and substrate effects on capture efficiency

Capture efficiency for all three taxa decreased significantly with increasing velocity across all substrate types (mayflies,  $F_{[2,36]}$ =36.6, *P*<0.001; Figure 3.3A; chironomids ,  $F_{[2,36]}$ =6.4, *P*=0.04; Figure 3.3B; black flies,  $F_{[2,36]}$ =25.2, *P*<0.001; Figure 3.3C; and for capture efficiency of all taxa combined,  $F_{[2,36]}$ =44.7, *P*<0.001; Figure 3.3D). Capture efficiency declined most sharply over

unembedded gravel between 0 to 25 cm-s<sup>-1</sup>, decreasing 64% for mayflies, 48% for chironomids, 46% for black flies, and 54% for all taxa combined. Treating velocity as a linear covariate, every 1 cm-s<sup>-1</sup> increase in velocity reduced Nooksack dace capture efficiency by 1.4% for mayflies ( $F_{[1,39]}=51.4$ , *P*<0.001); 0.1% for chironomids ( $F_{[1,39]}=12.0$ , *P*=0.001); 1.5% for black flies ( $F_{[1,39]}=49.8$ , *P*<0.001); and 0.8% for all taxa combined ( $F_{[1,39]}=70.0$ , *P*<0.001).

In general, there was a strong velocity by substrate interaction, with minimal substrate effects on capture efficiency at zero velocity, and substrate effects only becoming evident at higher velocities. However, substrate type significantly affected Nooksack dace capture efficiency for mayflies ( $F_{[2,36]}=22.9$ , P<0.001) and all taxa combined ( $F_{[2,36]}=11.8$ , P<0.001), but did not have a significant main effect on chironomids ( $F_{[2,36]}=1.9$ , P=0.16) or black flies ( $F_{[2,36]}=0.5$ , P=0.47). Nooksack dace foraging efficiency was lowest over the unembedded substrate for all taxonomic groups at velocities above 0 cm-s<sup>-1</sup>, which was contrary to my hypothesis that Nooksack dace would forage most effectively over unembedded substrates, regardless of velocity. However, there was also a significant substrate by velocity interaction for mayflies ( $F_{[4,36]}=5.0$ , P=0.003), chironomids ( $F_{[4,36]}=2.7$ , P=0.04), and all taxa combined ( $F_{[4,36]}=4.7$ , P=0.004), with the exception of black flies ( $F_{[4,36]}=0.7$ , P=0.58). This is evident in the generally non-linear decrease in foraging efficiency over unembedded gravel substrates, while capture efficiency decreased more linearly with velocity over embedded gravel and the smooth bottom surface (Figure 3.3).

Limited daytime observations of mayfly orientation in arenas over gravel substrate in the absence of Nooksack dace showed a shift from 44% of stocked mayflies visible on upper substrate surfaces at 0 cm-s<sup>-1</sup>, to 1% visible at 15 cm-s<sup>-1</sup>. (F<sub>[1,18]</sub>= 241.3, P < 0.001).

## 3.3.2 Taxon effects on capture efficiency

When taxon was included as a factor in ANCOVA, there was a significant effect of taxon on Nooksack dace foraging efficiency ( $F_{[2,108]}=22.5$ , P<0.001). Foraging efficiency was significantly lower for chironomids than for mayflies (Tukey HSD P<0.001) and black flies (Tukey HSD, P<0.001), with no differences among other taxa. There was a common decrease in foraging efficiency for all taxa as velocity increased ( $F_{[2,108]}=53.9$ , P<0.001), a common decrease in foraging efficiency over unembedded substrate across taxa ( $F_{[2,108]}=11.2$ , P<0.001), and a strong velocity by substrate interaction ( $F_{[4,108]}=6.9$ , P<0.001). There was also a significant taxon by velocity interaction ( $F_{[4,108]}=3.0$ , P=0.02), whereby increased velocity had a smaller effect on capture efficiency of chironomids than other taxa. However, there were no taxon by substrate ( $F_{[4,108]}=1.6$ , P=0.16), or taxon by velocity by substrate interactions ( $F_{[8,108]}=1.6$ , P=0.13), suggesting that substrate effects on capture efficiency were broadly similar across taxa.

#### **3.3.3** Turbulence effects on capture efficiency

Variation in velocity among the three substrate types were not significant ( $F_{[2,16]}=3.6$ , P=0.051; Figure 3.4), as was the interaction between velocity and location ( $F_{[4,16]}=2.9$ , P=0.054). In general, there was a trend for turbulence to be lower over the smooth substrate surface, particularly along the outside perimeter (high velocity) of the foraging arenas (see size of error bars in Figure 3.4). Turbulence (expressed as variation in velocity) significantly increased towards the outside perimeter of arenas (location effect,  $F_{[2,16]}=9.1$ , P=0.002) and at higher velocities (0, 25, or 35 cm-s<sup>-1</sup>;  $F_{[2,16]}=18.7$ , P<0.001; Figure 3.4). Turbulence along the outside perimeter of arenas was significantly higher than in the middle (Tukey HSD, P=0.02) and inside (Tukey HSD, P=0.002) of arenas and between zero and 25 cm-s<sup>-1</sup> (Tukey HSD, P<0.001) and 35 cm-s<sup>-1</sup> (Tukey HSD, P<0.001) velocity treatments.

### 3.4 Discussion

The decrease in Nooksack dace foraging efficiency over all substrates under the high velocity conditions (25 and 35 cm-s<sup>-1</sup>) is perhaps surprising given that these fish are characterized as being specialized to high velocity habitats (i.e., riffles; Pearson et al. 2008). Boundary layer thickness generally decreases with smaller substrate particle size, because a fine-particle stream bed decreases friction (i.e., surface roughness) with the overlying water surface and reduces turbulence and drag at the interface between the stream bed and the water column, resulting in higher water velocities closer to the substrate surface (Carlson and Lauder 2011). At extremely high bottom water velocities Nooksack dace may be unable to hold position or forage effectively. However, Facey and Grossman (1990) found that a close relative of Nooksack dace, the longnose dace (*Rhinichthys cataractae*), can hold position at velocities up to 55 cm-s<sup>-1</sup> without significant increases in oxygen consumption. I observed decreased foraging efficiency at velocities well below the holding thresholds observed for longnose dace, suggesting that decreased overall foraging efficiency in my experiment was not caused by velocities that exceeded the absolute velocity tolerances of dace. Rather, my data suggests significant impairment of foraging ability at velocities well below the threshold for maintaining position in a flume.

The higher velocities on the outer perimeter of the arenas may have exceeded Nooksack dace foraging tolerances, reducing the total area available for effective prey capture and therefore lowering overall foraging efficiency. This would cause Nooksack dace to encounter prey less frequently if they were unable to forage near the outside perimeter of the arenas due to high velocities, as black fly larvae, for example, select high velocity habitats as refuges from predation (Malmqvist and Sackmann 1996; Fonseca and Hart 2001). The outer perimeter of the arenas also had the greatest variation in velocity (i.e., turbulence), particularly in the embedded and unembedded substrate treatments, so that foraging efficiency may have been reduced near the outer perimeter of the arenas, even if Nooksack dace were not excluded completely. While greater turbulence and lower capture success over unembedded (rough) substrate are consistent with a hypothesis of lower capture success under high velocity variation, capture success on smooth and embedded (semi-rough) substrates were broadly similar, despite lower turbulence over the smooth substrates. Consistent declines in foraging efficiency with increased velocity across all substrate types suggests that overall, water velocity has a stronger influence on Nooksack dace foraging efficiency than substrate effects on turbulence, at least in my experimental system.

High water velocities have been observed to delay prey identification, decrease strike accuracy, and reduce capture success in salmonid fishes (Hill and Grossman 1993; Piccolo *et al.* 2008). Although I did not directly observe Nooksack dace foraging activity during these experiments, it is plausible that increased turbulence at higher velocities could also degrade strike accuracy (and therefore capture success) of Nooksack dace. Additionally, Beers and Culp (1990) showed that low light levels decreased the distance at which longnose dace could visually detect mayfly larvae, resulting in longnose dace adopting "rooting" behavior (i.e., using their

snouts to disturb the substrate), which may include the use of olfactory or mechanical sensory cues to detect prey in low light conditions (Nooksack dace are nocturnal foragers, like longnose dace; McPhail 1997). While I conducted all experimental trials at night in covered arenas that minimized variation in light intensity, it is possible that turbulence associated with higher velocities incrementally degrades either olfactory or mechanical cues that Nooksack dace use to detect prey, decreasing their reaction distance at higher velocities and thereby reducing capture efficiency. An alternative explanation could be that invertebrates spend less time on upper substrate surfaces, or exhibit greater refuging behaviour at higher water velocities. While this could explain decreased foraging success over unembedded substrate, it would not account for deceased foraging efficiency at high velocities (i.e., 25 and 35 cm-s<sup>-1</sup>) over the smooth substrate where interstitial refuges were absent.

Although decreased foraging efficiency over unembedded substrate was only statistically significant for mayflies and all taxa combined, the pattern of decreased capture success over unembedded substrate was broadly consistent across taxa (Figure 3.3). This suggests that both the physical attributes of unembedded substrate (i.e., greater availability of interstitial spaces) and potential velocity effects (i.e., reduction in foraging area, lower prey encounter rates, reduced accuracy per strike attempt, or decreased prey detection distance) jointly contributed to the reduction in Nooksack dace foraging efficiency, although a behavioural shift by invertebrates to interstitial habitat at higher velocities may also have played a role. Interstitial spaces were absent in the smooth surface treatment and reduced in the embedded treatment, suggesting that greater abundance of interstitial refuges in the unembedded substrate was the primary mechanism underlying reduced capture success, which is consistent with the observed refuging behaviour of mayflies in the presence of predators (Flecker and Allan 1984; Culp *et al.* 1991)

and high water velocities (personal observation). It is also consistent with generally reduced predator foraging success in high-complexity habitats that provide abundant refuges for prey (Gotceitas and Colgan 1989). Lower Nooksack dace foraging efficiency for all taxa over unembedded substrates was somewhat counterintuitive, as Nooksack dace are usually found in high velocity riffle habitats with coarse unembedded substrate (Inglis 1997; Pearson et. al. 2008), and I expected Nooksack dace to be efficient foragers under the least embedded substrate conditions. However, a generally positive association of Nooksack dace with unembedded substrate in nature (Pearson et al. 2008) may reflect i) higher biomass of benthic invertebrate prey over unembedded substrate (e.g., Iwata et al. 2003; Suttle et al. 2004; Bo et al. 2007) that supports higher overall prey intake, despite somewhat reduced capture efficiency; and/or ii) greater refuge from potential avian or aquatic predators of Nooksack dace in coarse, unembedded riffle habitat (Chapter 2). Higher benthic foraging efficiency over embedded substrate is also consistent with observations by Brusven and Rose (1981), who found extremely high consumption efficiencies (90-100%) by the torrent sculpin (Cottus rhotheus) on benthic invertebrates over heavily sand-embedded substrate, relative to consumption rates over unembedded gravel and cobble.

In general, with the exception of mayflies, the effects of velocity on Nooksack dace foraging success were greater than the effects of substrate. However, this observation needs to be tempered by the consideration that, in the zero velocity treatment, I introduced riffle-adapted taxa into effectively suboptimal habitats (i.e., foraging arenas with no velocity), which may have caused them to drift (Lancaster 1990; Fonseca and Hart 2001; Wilcox *et al.* 2008), potentially increasing their vulnerability to predation and artificially elevating observed Nooksack dace foraging efficiency. A recent study found reduced growth rates of Nooksack dace reared in low velocity

pool habitat compared to growth in higher velocity riffles over coarse substrate, and decreased prey availability was proposed as a possible mechanism for lower growth in pools (Avery-Gomm *et al.* 2014). Substrate in depositional pool environments are usually characterized by soft sediments and invertebrate communities with a proportionally higher abundance of burrowing taxa (Malmqvist 2002); although longnose dace are capable of rooting behaviour to feed on prey below the substrate surface (Beers and Culp 1990), my observation of higher Nooksack dace foraging efficiency at zero velocity may apply primarily to foraging on surface dwelling invertebrate taxa, rather than burrowing taxa that may be unavailable at depth.

Ecological traits of different taxa should influence their vulnerability to predation. Nooksack dace foraging efficiency across all velocities and substrate types was lowest for orthoclad chironomids. Some of these chironomids attach themselves to benthic substrates using tubes made of fine sediment, which provides protection from predators and scouring flows (Hershey 1987), reducing their availability to Nooksack dace. Chironomid tubes in smooth surface arenas were also frequently observed in the corner angles of foraging arenas where the side and central standpipe met the arena bottom, which may have provided some protection from Nooksack dace predation. In the unembedded and embedded substrate arenas, chironomids were less visible but likely attached to the substrate within sheltered interstitial spaces, further reducing their availability to Nooksack dace. In contrast, the more active non-sessile prey like baetid mayflies were observed on the surfaces of rocks in the unembedded arenas at zero velocity, which likely increased their availability to Nooksack dace. However, at higher velocities fewer mayflies were visible on the substrate surface, suggesting their use of interstitial space as refuges from high water velocities, potentially reducing their vulnerability to predation. Refuging behaviour in response to higher water velocities likely explains the significantly greater
decrease in Nooksack dace foraging efficiency for mayflies over unembedded substrate at high water velocities (Figure 3.3A), although it cannot account for reduced capture efficiency over smooth substrate at higher velocities. Black fly larvae, while sessile like chironomid larvae, tend to attach to exposed surfaces rather than substrate interstices, which also likely elevated their vulnerability to Nooksack dace predation.

Substrate types and velocities within foraging arenas were broadly representative of foraging conditions within Bertrand and Pepin creeks, where Nooksack dace and invertebrate prey were collected. However, the limited size of foraging arenas did not allow the inclusion of larger substrate particles like cobble and boulder, which provide important refuges for Nooksack dace (Mullen and Burton 1995) and also alter hydraulics. Large substrate and associated heterogeneity also increases bed roughness, thereby increasing the depth of the boundary layer, which provides habitat for many benthic organisms (Davis 1986). Although Nooksack dace most likely live and forage in the low velocity micro-habitats present in the boundary layer and in the interstitial spaces of unembedded coarse substrate riffles, scale limitations in my experiment precluded testing the effect of larger substrates on Nooksack dace foraging efficiency.

Nooksack dace are riffle specialists (Pearson 2000) similar to the closely related longnose dace which have been shown to avoid areas of low velocity when high velocity riffle habitats are available (Mullen and Brown 1998). However, Nooksack dace may be forced into habitats with low to zero velocity (i.e., glides and pools) during periods of drought when riffle habitat area shrinks (Avery-Gomm *et al.* 2014; Hodges and Magoulick 2011) or when riffle habitat is severely degraded. Despite their preference for high velocity riffles, my foraging efficiency experiments indicate that Nooksack dace are not necessarily adapted to foraging effectively at high focal velocities; rather, they appear to be adapted to foraging in relatively low-velocity

micro-habitats (i.e., the boundary layer) nested within high-velocity meso-habitats (riffles). My observation of high foraging efficiency of Nooksack dace at low water velocities supports the inference that it is higher predation risk in the absence of benthic substrate complexity, in combination with lower available prey abundance (Avery-Gomm *et al.* 2014; Chapter 2), that reduces the suitability of pool habitats. Consequently, the general ecological picture that emerges is one of Nooksack dace functioning as generalized small benthic invertivores that can generally forage effectively across a broad range of substrate types and water velocities, including slower velocity meso-habitats where they are not commonly found. This suggests that a significant component of the overall ecological strategy of Nooksack dace and similar small-bodied benthic riffle specialists is to adopt a small body size that allows access to abundant invertebrate resources within the refuge of the boundary layer of high velocity riffles (Carlson and Lauder 2011). In this way, these fishes avoid the high energy costs of swimming in the water column (e.g., Facey and Grossman 1990; Grossman 2013), while simultaneously minimizing predation risk from larger-bodied-fishes that are constrained to operate outside of the boundary layer.



**Figure 3.1** View of foraging arena experimental set up. Inflow of water from Pepin Creek (A), inflow hose attached to a bilge pump, pumping water into a foraging arena (B), stand pipe in center of arena to minimize central low velocity dead zone (C), relief valve on arena inflow hose to control velocity (D), 250 µm mesh lids (E), and 3,820 l per hour bilge pump (F).



**Figure 3.2** Top view of a foraging arena. Tick marks indicate locations of velocity measurements; four in each of the outside perimeter, middle, and inside. Velocity was measured over each substrate type at 25 and 35 cm-s<sup>-1</sup>.



**Figure 3.3** Nooksack dace foraging efficiency for (A) Mayfly, (B) Chironomids, (C) Black fly, and (D) all taxa combined for all three substrate treatments (Smooth surface, Unembedded Gravel, and Embedded Gravel), for each experimental velocity (0, 25, or 35 cm-s<sup>-1</sup>). Foraging efficiency is defined as the proportion of prey stocked that were consumed over a 12-hour experimental period. n = 5 for each treatment group.



**Figure 3.4** Mean velocities for the three locations (outside perimeter, middle, and inside) of the foraging arenas for each of the substrate treatments (Smooth surface, Unembedded Gravel, and Embedded Gravel) at each experimental velocity. Error bars are the standard deviation of the variation in velocity at each location within the foraging arenas.

## **Chapter 4: General discussion**

The objective of this thesis was to examine how sediment-induced habitat changes affect benthic invertebrates and riffle-dwelling benthic fishes, in particular the Nooksack dace. Specifically, I examined the effects that the deposition of coarse (2-6 mm in diameter) and fine (<2 mm in diameter) sediments have on i) the abundance and community structure of benthic invertebrates, and how any shifts in these would, in turn, affect fitness correlates (e.g., growth, survival) of Nooksack dace; and ii) the physical and hydrological structure of benthic habitats (e.g., substrate characteristics and water velocity), and the joint effects of these habitat alterations on Nooksack dace foraging efficiency. Nooksack dace are listed as Endangered under Canada's Species at *Risk Act*, and sediment deposition poses a primary threat to individual survival and population recovery (COSEWIC 2007; Pearson et al. 2008). Clarifying how sedimentation alters physical habitat and the abundance of invertebrate prey is a conservation priority, because many of the streams that Nooksack dace inhabit flow through urban and agricultural landscapes where high sediment inputs are common. The findings of this study are intended to support the identification and protection of critical habitat essential for the conservation and recovery of this endangered fish.

The experiment described in Chapter 2 demonstrated that both the survival of Nooksack dace and the abundance of their invertebrate prey are influenced by the quantity of interstitial space within benthic substrates. Despite a lack of significant effect on Nooksack dace growth in the 2012 pilot experiment, the death from predation of all Nooksack dace from embedded treatments (e.g., 50 or 100% embedded) in 2013, shows that high sediment levels decrease the quality and/or quantity of predator refuges available for Nooksack dace. Previous research has

established the importance of cover for reducing the exposure of fishes to both aquatic and terrestrial predators (Harvey and Stewart 1991). Predation rates on benthic (e.g., sculpins (*Cottus* spp.); White and Harvey 2001) and drift feeding fish (e.g., juvenile rainbow trout (*Oncorhynchus mykiss*); Harvey *et al.* 2009) are highest in habitats lacking complex substrates and other forms of cover.

The loss of interstitial refuges was the primary driver of predation on Nooksack dace; however, two additional constraints may have also contributed to the high levels of predation observed. First, the small area (0.22 m<sup>2</sup>, 19 x 115 cm) in which Nooksack dace were confined may have reduced their ability to evade predators, while likely increasing the efficiency of their predators (e.g., mink). Secondly, the size limitation of the artificial channels did not permit the inclusion of large substrate (>25 cm). Large cobbles can increase streambed roughness, water depth, and the depth of the boundary layer—all of which may provide Nooksack dace with enhanced protection from predation (Davis 1986; Mullen and Burton 1995). Unfortunately, high predation rates did not allow me to resolve how changes in the abundance and availability of benthic invertebrates affected Nooksack dace growth. However, if Nooksack dace growth is limited by the abundance of benthic invertebrates, my results suggest that Nooksack dace growth and production would be sensitive to the effects of sediment inputs on benthic invertebrate abundance that were observed in this study.

Previous investigations have consistently found reduced invertebrate abundance in embedded *vs*. unembedded substrates (Culp *et al.* 1986; Rabeni *et al.* 2005; Jones *et al.* 2012b; Burdon *et al.* 2013), leading to reduced growth in both juvenile steelhead trout (*O. mykiss*; Suttle *et al.* 2004) and benthic-dwelling loaches (Cobitidae; Kawanishi *et al.* 2014). Most of these studies have focused on the fraction of fine sediments (<2 mm in diameter), because there is a

general acceptance among stream ecologists that this fraction of sediments are the most detrimental to aquatic biota. However, because both coarse and fine sediments are likely deposited together, it is difficult to disentangle the individual effects of each particle size class on the growth and survival of stream fish (Zweig and Rabeni 2001). To my knowledge, this study represents the first experimental manipulation that has directly examined the independent effects of both the volume of interstitial spaces filled with sediments (0, 50, and 100%) and the percentage of those sediments that are <2 mm in diameter on the growth of a benthic fish, the Nooksack dace, and the abundance of their invertebrate prey.

A major finding from my research is that the loss of interstitial space resulting from embeddedness appears to have a larger impact on the biomass and community structure of benthic invertebrates than does the fraction of fines <2 mm in diameter. Total invertebrate community biomass was not significantly affected by a 20% proportion of fine sediments by volume, when overall embeddedness was limited to a 50% loss of interstitial space. This result was unexpected because previous studies documented significant declines in invertebrate abundance at levels of embeddedness at or below 50% (e.g., Angradi 1999; Mebane 2001; Zweig and Rabeni 2001). However, the presence of coarse sediment favoured burrowing oligochaetes, which were the most abundant in the 100% coarse sand treatment despite the overall decrease in biomass of most other taxa, thereby stabilizing changes in total invertebrate community biomass (Figure 2.9). This suggests that micro-interstices in coarse sediments likely provide oligochaetes with greater foraging habitat and refuge from potential predators. However, a 50% overall decline in total invertebrate community biomass in the 100% fine sand treatment indicates that fine sediments exacerbate the negative effects of embeddedness, particularly for burrowing invertebrates. While total invertebrate community biomass remained unchanged in the 100%

coarse sand embedded treatment, the shift away from surficial invertebrates towards burrowing oligochaetes would likely have a negative impact on the net availability of prey and potentially growth rates of Nooksack dace. However, it remains unclear the extent to which burrowing invertebrates are either accessible to Nooksack dace or constitute high quality forage.

The loss of interstitial spaces also reduced the roughness of streambed gravels, and consequently, the depth of the low velocity boundary layer above benthic substrates, resulting in higher near-bed velocities (Carlson and Lauder 2011; Figure 2.2). While the closely related longnose dace is capable of holding in water velocities up to 55 cm-s<sup>-1</sup> (Facey and Grossman 1990), the maximum velocities at which a fish can hold likely differ from the optimum velocities to perform important activities, such as foraging and predator evasion. My initial hypothesis was that foraging efficiency of Nooksack dace would be negatively affected by high near-bed water velocities associated with embedded substrates. Contrary to my predications, Nooksack dace foraging efficiency was more sensitive to water velocity than to substrate composition, and was lowest over unembedded substrates in the presence of velocity. These results were unexpected as Nooksack dace are generally found over unembedded coarse gravels in high velocity habitats (i.e., riffles), and generally avoid embedded and low velocity habitats (Ingles 1994; Pearson et al. 2008; Avery-Gomm et al. 2014). Lower foraging efficiency over unembedded substrates may have been caused by invertebrates retreating into interstitial spaces to avoid high water velocities and/or predation from Nooksack dace, which is consistent with my field observations and the theory and empirical observations on other fishes that predators are generally less efficient at foraging in structurally complex habitats that provide abundant refuges for prey (Gotceitas and Colgan 1989). However, these results need to be tempered by the consideration that the invertebrates used in this study are typical riffle-dwelling taxa, which were shown to be more

abundant in unembedded substrates (Chapter 2); including them in the fully embedded and smooth bottom treatments may have increased their vulnerability to predation, artificially elevating Nooksack dace foraging efficiency over these substrate types. This experiment clearly demonstrated that Nooksack dace foraging efficiency is reduced at high water velocities, and that they are able to forage over a range of substrate types. However, it remains unclear how the reduced abundance and changes to the community structure of benthic invertebrates induced by sedimentation affect the foraging efficiency of Nooksack dace. My results demonstrating relatively high foraging efficiency over a range of substrate types indicate that Nooksack dace are more generalized benthic insectivores than previously understood and that they can likely forage effectively in lower velocity pool habitats as well as in riffles. Overall, my results suggest that, the strong association between Nooksack dace and unembedded substrates in nature is driven primarily by predation avoidance, and secondarily by prey availability.

In general, fish select habitats that optimize their foraging efficiency and limit predation risks (Vehanen and Hamari 2004; Petty and Grossman 2010). The results of the two experiments presented in this thesis suggest that unembedded riffle substrates provide Nooksack dace with both abundant invertebrate resources and refuge from predation. It appears that the thick low velocity boundary layer and interstitial spaces associated with coarse unembedded substrates, provide Nooksack dace and other small-bodied benthic riffle specialists with micro-habitats to forage and refuge from predators within the high velocity meso-habitat of stream riffles. The effects of sedimentation are therefore likely to have a negative effect on the growth and survival of this endangered species, making the identification, protection, and restoration of stream reaches characterized by unembedded riffle habitat a conservation priority. My results indicate that the identification and protection of unembedded coarse substrate as critical habitat is

important for the conservation of this species, and supports the application of land management practices that minimize soil erosion and prevent other sources of fine sediments from entering streams inhabited by Nooksack dace and other small benthic riffle-dwelling fishes.

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