The Influence of Salmon Presence On Benthic Communities in Three Puyallup-White River Tributaries

by

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ABSTRACT

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Karen Seymour

Anadromous salmon (*Oncorhynchus spp*) act as nutrient vectors across the boundaries of salt and fresh water. After amassing nutrients during the ocean-going phases of their life cycles, they transport and deposit these abundant nutrients in spawning streams in the form of carcasses, eggs, and developing young fish. This influx of nutrients into relatively nutrient-poor lotic systems has effects that resonate throughout the ecosystem. One group of organisms that is a very integral component to freshwater ecosystems and is impacted by salmon presence is benthic macroinvertebrates. While invertebrate numbers may become drastically reduced by the spawning activity of salmon, these losses may be offset by the immense nutrient and temporary habitat value the salmon carcasses represent. This study examines the impact of salmon presence on macroinvertebrate assemblages on three streams in the Puyallup-White River watershed by analyzing samples from benthic communities above and below anadromous barriers. Each upper site yielded a lager sample of invertebrates than its corresponding downstream site, indicating greater densities of invertebrates above the barriers. For most metrics, which include total taxa and 3 functional feeding groups—collectors, predators, and scrapers—populations are more evenly distributed on lower sites, and diversity is similar or significantly greater on lower sites for most metrics. A partial Benthic Index of Biotic Integrity gives a higher score to each lower site than its corresponding upstream site. For total taxa, the communities above and below the barrier are the most similar on Boise Creek, followed closely by Fennel Creek, with Clark's Creek by far showing the least amount of similarity between sites. Interestingly, the density of fish that congregate on Clark's Creek vastly exceeds that of other two sites, raising the question of whether differences in benthic communities are related to carcass loading. After all data were analyzed, no definitive pattern emerged that clearly demonstrated whether or not salmon play a keystone role for benthic macroinvertebrates for any of the three streams. However, they do suggest interesting relationships and ways to further examine the interactions between these two groups of organisms with immense ecological value. Such knowledge is invaluable if we are to more fully understand the complexities of ecological relationships and apply our understanding to the preservation of salmon and the ecosystems that they are closely tied to.

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INTRODUCTION

Iconic of the Pacific Northwest, salmon represent a tremendous source of ecological, cultural, recreational, and commercial wealth for the region. Because of the multiple dimensions of these fishes' importance, their biology and ecology has been made the subject of extensive and meticulous scientific study. An important element of salmon ecology concerns their relationship to stream benthic macroinvertebrates. This is because salmon and many benthic macroinvertebrates are both highly dependent on and critical to the maintenance of vigorous stream health.

Although only a relatively brief portion of their life cycle is carried out in fresh water, Pacific salmon—pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), sockeye (*O. nerka*), coho (*O. kisutch*), and chinook (*O. tshawytscha*)—are crucial ecological components of the streams in which they emerge and to which they return to spawn. Conversely, various physical and ecological aspects of the freshwater system can have profound effects on salmon. For example, density, growth, and distribution of stream rearing juvenile salmon may be directly influenced by the availability of benthic macroinvertebrates, which serve as an important food source for the young fish (Hershey and Lamberti, 1998). The degree to which invertebrates exert a bottom-up influence on the populations of juvenile salmon and resident salmonids, however, is difficult to quantify, and remains an intriguing piece of the complex puzzle of salmon ecology that warrants further study. Indirect impacts that macroinvertebrates can exert on salmon come in the form of the vast and diverse scale of work that they perform throughout the watershed, making them key regulatory components in the dynamic stream processes on which flourishing salmon populations depend (Wallace and Webster, 1996).

While the bottom-up influence of stream invertebrates on salmon is one aspect of the direct relationship between these organisms, there is also a top-down effect exerted by juvenile salmon, resident salmonids, and other stream dwelling fishes upon invertebrate compositions through predation that is potentially a key sculptor of stream communities (Power, 1990; Thorp, 1986). Some studies that have endeavored to address these questions have revealed an intricate interplay among the organisms comprised of feedback loops and unexpected reverberations throughout trophic levels (Power and Marks, 1992; Power et al, 1985; Power, 1990; Power, 1992).

In addition to direct predation, salmon can influence benthic invertebrate assemblages in other ways. Some of the most profound effects salmon have on invertebrates come as a result of their semelparity. After amassing vast quantities of nutrients during the ocean-going phase of their life histories, salmon return to their natal streams to spawn and die, vastly enriching the stream with all of their marine-derived nutrients (Quinn, 2005). Invertebrates are among the many beneficiaries of this nutrient surge, which may help to enhance their growth and numbers (Honea, 2002). In turn, this enhanced population of invertebrates provides food for stream-dwelling salmonids, including juvenile salmon, and other fishes. In this way, invertebrates act as a bridge between valuable marine-derived nutrients delivered to streams by salmon and the next generation of the fish, as well as other stream dwellers.

The Ecology of Benthic Macroinvertebrates

Invertebrates as process regulators

Although not readily apparent upon casual observation of a stream or river, benthic macroinvertebrates are vital, prolific, and fundamental agents of maintenance and modification of a lotic ecosystem (Webster and Wallace, 1996). Many trophic levels and mechanisms of food acquisition are represented in an aquatic macroinvertebrate assemblage. Based on these mechanisms, which will be considered in greater depth later on, macroinvertebrates can be classified into the following categories: scrapers and grazers, usually of algae and periphyton; collector-gatherers, often of detritus or seston carried by the water's current; shredders, particularly of leafy material; and predators.

Not only does the work performed by these tiny stream dwellers take place on a surprisingly vast scale, but its ecological scope is also wide-ranging. By grazing on algae, bacteria, and fungi, breaking down course particulate organic matter (CPOM) into smaller fragments, and acting as a primary source of food for many fish species throughout the year, benthic macroinvertebrates play key roles in the cycling of nutrients within a river system (Webster and Wallace, 1996; Hershey and Lamberti, 1998).

Upstream macroinvertebrate assemblages can have significant roles in structuring downstream communities. For example, as described by the River Continuum Concept, streams high in the watershed generally support a relatively substantial shredder component (Vannote et al, 1980). Shredders are so intrinsic to nutrient cycling by processing vast amounts of allocthonous material that their removal from stream can have a more profound effect on biological stream processes than a weather event as extreme as a 50-200 year drought (Cuffney et al, 1990). By processing CPOM into smaller fine particulate organic matter (FPOM), which is more readily translocated to various reaches of the watershed than its larger, unprocessed predecessor, shredders create a very valuable food source for downstream benthic communities. These communities tend toward higher proportions of filter-feeding invertebrates and collector-gatherers that exploit the FPOM created upstream (Webster and Wallace, 1996; Cuffney et al, 1990; Vannote et al, 1980).

Adaptations and Life Histories

The multitudinous invertebrates of the lotic benthos constitute a highly diverse community which responds variously to the numerous challenges posed by a fluvial system (Covich et at, 1999). Existence in flowing water has created a host of adaptive body forms among benthic invertebrates that allow organisms to exploit substrate surfaces as well as interstitial spaces (Merrit and Cummins, 1996). Morphology and behavior allow for an array of food acquisition tactics, from active foraging to passive filtering (Wallace and Merritt, 1980). The downstream transport capacity of streams and rivers, which is used by some invertebrates to facilitate predator avoidance, foraging activities, and relocation to more hospitable microhabitats, renders benthic communities extremely open to immigration and emigration and is a factor in creating the heterogeneous patterns of invertebrate distribution found throughout the watershed

(Walton, 1980; Winterbottom et al, 1997). The continual restructuring of assemblages by immigration and emigration is essential in complex river systems, which typically foster patchy habitat. The tendency of many benthic invertebrate species to relocate via downstream drift allows for rapid recolonization of recently disturbed and denuded areas (Winterbottom et al, 1997).

Although both numbers and biomass of invertebrates remain fairly constant throughout the year, the temporally variable mosaic of species that comprise benthic assemblages is an adaptive response to the natural flow regime as well as environmental extremes that characterize many stream and rivers (Cummins and Klug, 1979). Frequency of life cycle completion, or voltinism, ranges widely between species, from as brief as 2 weeks or less to upwards of 5 years in length (Hershey and Lamberti, 1998). Within species, synchronized development of cohorts is common. The simultaneous emergence of the aerial adult phase, adopted by most insect taxa, contributes to a higher probability of mating success, and allows for migration between streams and even watersheds, as well as upstream dispersal, which helps to offset the downstream drift of larvae. (Hershey and Lamberti, 1998; Light and Adler, 1983).

Habitats

Patchily distributed microhabitats where benthic invertebrates concentrate are areas whose boundaries are indiscreet, but display locally variable gradients of chemicals and dissolved oxygen, changes in directions and rates of water flow, differential fine grain sediment deposition, and variable substrate size (Covich et al, 1999). Structurally, they are most frequently impacted by burrowing and fecal production of invertebrates, and the growth, death, and decomposition of roots (Wallace and Webster, 1996; Covich et al, 1999).

Aside from such factors as relief, lithology, and runoff, the presence of large woody debris (LWD) is integral in physically structuring the shape and habitat of a stream because of its ability to create various channel forms and hydrologic conditions. Such variations in stream morphology and hydrology increase the diversity of microhabitats available to stream organisms, and consequently allow for enhanced diversity within the biotic community (Collier and Halliday, 2000; Diez et al, 2000).

In addition to creating the hydrologic conditions necessary for a heterogeneous array of microhabitats, LWD itself is disproportionately important as a microhabitat for invertebrate communities compared to stream substrate. In the face of disturbance, not only are macroinvertebrate populations reduced significantly more on streambed substrata than on LWD, but recovery from disturbance proceeds much more quickly on LWD (Hax and Galloday, 1998). In the event of disturbance, many invertebrates seek out LWD, if available, as well as the bottoms of rocks and the hyporheic zone as refugia (Roeding and Smock, 1989; Merrit and Cummins, 1996). In addition to its function as refugia, LWD is also vital in the retention and distribution of organic matter, such as salmon carcasses and leaf packs (Diez et al, 2000). Similar to LWD, leaf packs function as microhabitats and refugia from both fish and invertebrate predators and support a disproportionately abundant community (Richardson 1992).

The Functional Feeding Groups

Basic to any discussion concerning aquatic macroinvertebrates is the classification system based on functional feeding groups, which have already been mentioned. This system distinguishes groups of invertebrates based on their mechanisms of food acquisition, rather than the food type exploited because of the prevalence of omnivory in most aquatic insect taxa (Merrit and Cummins, 1996). For example, while many filterers feed on FPOM, some are carnivorous, feeding on other invertebrates. Because of these variables, the functional feeding group classification system, while providing an excellent general framework by which to understand ecological roles of benthic invertebrates and their relationships, is not entirely precise (Cummins and Klug, 1979). However, in general, the functional feeding groups generally fall under the following categories:

Scrapers and grazers: The major food source for lotic representatives of this group is algae and periphyton, and microbial film on surfaces such as substrate, wood, plant matter, and salmon carcasses (Covich et al, 1999; Cederholm et al, 2000; Cummins and Klug, 1979). Grazer abundance is partially controlled by food limitation, and conversely, primary production can be differentially impacted by various levels of grazing pressure (Wallace and Webster, 1996).

The impacts that grazers have on primary producers are not limited to reduction by direct consumption. Grazing caddis flies can increase diatom production by grazing down filamentous blue-green algae, while case-building chironomids create additional surface area on which diatoms may colonize, with the additional possible benefit of protecting them from grazing mayflies (Power, 1992; Wallace and Webster, 1996). The reduction in periphyton biomass caused by grazers can influence local hydraulic conditions, create zones of stationary water, affect nutrient cycling by increasing the downstream export of fine particulate organic matter (FPOM), and enhance algal resistance to flooding (Wallace and Webster, 1996).

Shredders: This functional feeding group exploits a variety of food sources including allochthonous leaf litter from adjacent riparian trees, autochthonous CPOM, and woody debris. Shredders share their work with bacteria, which help break down litter. By softening the leaf tissue, decreasing its lignan content, immobilizing and enhancing its nitrogen content by digesting large molecules with exoenzymes, microbes condition it for macroinvertebrate consumption (Irons et al, 1994). The combination of microbial assistance, sufficiently high water temperature, pH-neutral conditions, and the dominance of certain shredder species, all contribute to maximizing shredder contribution to leaf decomposition (Melilo et al, 1984; Griffith et al, 1993).

Due to the fibrous, low-nutrient nature of the material upon which shredders feed, their assimilation efficiency is low. This translates into a vast amount—between 32 and 80%--of allochthonous input of being processed and transformed into FPOM and dissolved organic matter (DOM). The absence of shredders in a stream reach can result in a 50-

74% reduction in leaf processing rates, with a corresponding reduction in FPOM concentration (Cuffney et al, 1990).

Reflecting their tremendous importance to the decomposition process, shredders are capable of greatly influencing rates and pathways of nutrient cycling in woodland streams (Cuffney et al, 1990). The FPOM produced by shredders high in the watershed represents an important trophic link in fluvial systems, directly providing food for the many collectors that feed on FPOM. One indicator of this relationship is the elevated growth rates experienced by collectors in the presence of shredders (Cuffney and Wallace, 1989; Wallace et al, 1991).

Collector/gatherers: Collectors feed primarily on small particles of organic matter with diameters of less than 1 mm (Wallace and Merritt, 1980). As elaborated above, this functional feeding group is a direct beneficiary of the work of shredders in upstream reaches. In addition to the nutrients made available by shredders, this group is also heavily dependent on allocthonous inputs of dissolved organic matter and bacteria, as well as bacteria obtained via coprophagy (Wallace and Webster, 1996).

Using silk-like webs, filtering collector-gatherers remove FPOM from suspension, thereby shortening the nutrient spiral and curbing downstream transport of organic particulates. The density of filterers is generally higher than that of the other functional feeding groups, likely because they allow the kinetic energy of the stream current to deliver their food to them, rather than expending their own energy on foraging (Cummins and Klug, 1979).

Just as shredders convert organic material into a form more readily accessible as a food source to this feeding group, some collector-gatherers likewise process organic material into a form that feeds other invertebrates. Some filtering insects in the orders Ephemeroptera, Trichoptera, and Diptera, for example, ingest fine particles, but egest large fecal pellets that are then consumed by deposit-feeding detritovores (Wallace and Merritt, 1980; Cummins and Klug, 1979). Some of these detritivores, in turn, are important in altering the flow of nutrients. Burrowing sericostomids feed on processed leaf material and act as a conduit of transfer of organic material into the subsurface sediment, enriching its organic content by as much as 185% (Wallace and Webster, 1996).

Not all members of the collector feeding group rely on particulate matter as a food source. Certain filter feeding collectors, such as hydropsychids, are voracious, albeit species- and size-selective predators that prey upon drifting insects (Cummins and Klug, 1979; Peckarsky, 1982). These predatory filterers occur most abundantly in streams with low amounts of stable substrate that have sufficient current to carry a substantial amount of seston (Cummins and Klug, 1979). They greatly influence the amount and type of particulate organic matter (POM) in suspension, and may alter the drifting behavior of certain potential prey species (Wallace and Webster, 1996). In addition to exerting some top-down control over densities of their preferred prey, these insects are often preyed upon by fish (Harvey and Hill, 1991).

Predators: Whether active hunters or sit-and-wait ambushers, engulfing their prey or liquefying certain body parts, predatory insects are more likely than other functional feeding groups to exert top-down influence on the structure of benthic communities by directly consuming other invertebrates, although the extent to which they act as architects of the community is somewhat ambiguous. The high rates of immigration and emigration to which benthic communities are subject likely serve to obscure many of the effects that predators might otherwise exert (Hershey and Lamberti, 1998). Therefore, while predatory insects may, in some cases, depress the density and alter the behavior of some other invertebrates, their overall role in community structure is more regulatory than dominant (Thorp, 1986). Some aspects of such a function include inhibiting the process of competitive exclusion between ecologically similar species, reducing shredder density and therefore leaf processing rates during the autumn, decreasing drift rates in some species but increasing it in others, as well as the historical role they likely played in shaping past invertebrate communities to yield present-day species composition (Thorp, 1986; Walton, 1980; Oberndorfer et al, 1984).

Fish and Invertebrate Interactions

Just as the nature and extent of influence exerted by invertebrate predators on macroinvertebrate communities evades precise definition, so also the seasonally variable and spatially complex effects of fish predation on benthic community composition and dynamics remain somewhat nebulous (Gilinsky, 1984). Although invertebrate predators appear to exert a greater influence on both prey densities and behavior than their piscine counterparts, fish predation also can influence invertebrates. One such influence is on invertebrate behavior. For example, reduced time spent on substrate surfaces, and increased time spent in food patches and in nocturnal downstream drift are all behaviors that are adopted in response to predatory pressure from fish (Kohler and McPeek, 1989; Kohler, 1989).

In addition to modifying the behavior of certain invertebrates, fish predation can sometimes reduce total biomass of invertebrate communities while not decreasing the overall number of individuals, possibly indicating selective removal of larger individuals within species or a preference for certain species (Harvey and Hill, 1991; Carlisle and Hawkins, 1998). These selective pressures favor faster growth rates, earlier reproduction, and higher reproductive rates, and may lead to reduced density in certain species, especially in the case of species selection (Newman and Waters, 1984; Williams et al, 2003).

Not all studies yield statistically significant results when fish predation is examined in relation to macroinvertebrate populations. Juvenile coho salmon were shown to have no impact on the drift, biomass, or size distribution on macroinvertebrates except for 2 species that swim along the surface of the substrate (Culp, 1986). While immigration and emigration may erase some evidence of pelagic fish predation, interstitial predators such as cottids have been shown to reduce prey densities (Culp, 1986).

Ecology of Salmon Carcasses

The impacts that fish presence can have on benthic communities are not restricted simply to fishes' predatory capacity. One of the most dramatic examples of this is semelparous Pacific salmon, which acquire roughly 99% of their body mass while feeding on the bounty of nutrient-rich ocean and estuarine ecosystems (Quinn, 2005). When they return en masse to their natal streams to spawn and complete their life cycle, they act as vectors across the boundaries of marine and fresh water, bringing large amounts of marine-derived nutrients (MDNs) into relatively nutrient-poor freshwater systems.

Spawning salmon impact invertebrate communities by initially creating an abrupt disturbance as they carve out their redds in the gravel that may reduce invertebrate diversity, and reduce population density by as much as by as much as 83% (Field-Dodgson, 1987). However, after salmon spawning and death, stream invertebrates capitalize on the surge of nutrient availability provided by the salmon carcasses, eggs, and embryos, and may respond by an increase in density by up to 8-25 times, a two-fold or more increase in biomass, an increase in diversity in immediate proximity to the carcasses, and colonization of the carcasses themselves (Cederholm et al, 1999; Honea, 2002; Minakawa et al, 2002; Wipfli et al, 1998).

The presence of salmon carcasses impacts the various functional feeding groups differently, reflecting variable feeding ecology. Isotopic analysis has shown all groups except shredders utilize the marine-derived nitrogen delivered to streams by salmon (Cederholm et al, 1999; Kline, 1990). Increased growth rates and standing stock numbers are documented for some shredders and collectors, the latter group being particularly vital in transferring salmon-derived nutrients to the rest of the food web (Chaloner and Wipfli, 2002). Shredders, which do not show evidence of salmon-sourced nitrogen uptake, but whose density has been shown to increase with the presence of salmon carcasses, are believed to benefit from the increase in microbial biofilm that is made available by the carcasses. The amount of biofilm can be up to 15 times higher in carcass-enriched sites, and it supplies 20-40% of carbon within the benthic food web (Wipfli et al, 1998; Hall et al, 1998; Cederholm et al, 2000). The bottom-up effects of nutrient addition appear to be uniquely delivered by salmon carcasses and are related to levels of carcass loading. Studies of stream nutrient enhancement using sucrose, cereal grain, or detritus did not invoke the same positive responses from shredder and collector populations (Chaloner and Wipfli, 2002; Wipfli et al, 1999)

Although many invertebrates feed directly on salmon carcasses, the mechanism by which most of the nutrients enter many lotic food webs is remineralization—a process in which fungal and bacterial activity releases nutrients that are taken up by primary producers and then proceed to spiral throughout the trophic levels (Cederholm et al, 1999; Bilby et al, 1995). Of particular importance are those nutrients that are limiting in many stream systems, typically nitrogen and phosphorous. Limitation of these nutrients can affect detrital processing, primary producer biomass, invertebrate growth rates, the benthic community structure, and growth rates in fish (Peterson et al, 1993; Elwood et al, 1981). To nutrient-limited streams, salmonid carcasses can make huge additions to the nutrient budget (Willson et al, 1998). A single run of sockeye salmon, for example, has been estimated to deliver 169.3 metric tons of phosphorus to a river system (Quinn, 2005).

The nutrients delivered to a stream by salmon carcasses can have substantial impacts on lotic ecosystems by providing nutrients to the benthic food web and increasing local biomass and growth rates. Such benefits are not restricted to the benthos. In the circular manner typical of so many ecological processes, resident fishes and the next generation of stream-rearing salmon profit from the nutrients delivered to the stream by their forebears not only by direct consumption of carcasses, but also through the intricate web of resources that works its way through and is partially retained by the invertebrate community based on their consumption of salmon carcasses and eggs (Minikawa et al, 2002; Chaloner and Wipfli, 2002). Up to 30% of the nitrogen delivered to a stream by adult salmon has been estimated to be utilized by juvenile coho salmon (Bilby et al, 1996). Young coho occupying spawning streams consume not only salmon flesh and eggs directly, but also as many as five times more invertebrates than coho rearing in streams without the advantage of adult carcasses (Bilby et al, 1996). Even following the decomposition of the carcasses, more food remains available to the fish in spawning reaches due to elevated invertebrate populations.

While invertebrates are vital to the retention and redistribution of MDNs, other aspects, both physical and biological, of the river-riparian ecological complex also influence nutrient retention and dissemination. Physical factors include LWD, which helps prevent the downstream flushing of carcasses (Diez et al, 2000). Biological factors include stream-related fauna that utilize the wealth of nutrients delivered by salmon. For example, bear activity may facilitate aquatic insect growth by improving accessibility of consumable tissue for macroinvertebrates (Winder, 2005). Terrestrial scavengers may remove carcasses from streams, making them available as a food source for other organisms and aiding the transfer of nutrients into the riparian zone. This enhanced nutrient availability increased riparian productivity and benefits numerous species, including many that do not consume carcasses directly (Meehan et al, 2005; Gende and Willson, 2001). Also, many instream species, including young salmon, benefit from a vigorous surrounding riparian zone.

All of these interactions add another fold of complexity to the ecological significance of salmon, which act as vectors of nutrients across not only salt and freshwater boundaries, but also across aquatic and terrestrial boundaries. Functioning in such a capacity, returning spawners promote the vitality of the entire ecosystem that will support their next generation.

Salmon as Keystone Species

With some biologists describing salmon as a keystone species, it is widely acknowledged that their ecological function is one of great influence (Stone 1995). The term "keystone" denotes species whose presence is essential to the integrity of their communities, and whose impact on their communities is greater than would be predicted from their abundance (Mills et al, 1993; Power et al, 1996). Whether salmon do, in fact, meet the criteria of keystone, however, is not a simple determination to make. As Power et al (1996) note, "[i]deally, experimental demonstration of keystone effects would come from manipulation of single species," a method which is often difficult to implement.

This study examines the question of whether salmon perform a keystone function in relation to benthic macroinvertebrates by comparing benthic assemblages above and below anadromous barriers on three salmon-bearing streams in the Puyallup-White River watershed. This approach allows for observation of the effects of single-species exclusion while avoiding some of the complications that come with exclosures, which do not always allow a clear conclusion to be drawn as to the cause of effects found in unmanipulated areas (Power et al, 1996). Various indices are applied to the invertebrate samples to assess their richness, evenness, and diversity, as well as the similarity between communities above and below the barriers. By comparing stream reaches that are used by salmon with those that are not, some insight may be gained into how and to what degree salmon influence the structure of invertebrate assemblages. Evidence that would lead to the rejection of the null hypothesis that salmon do not serve a keystone function in relation to the invertebrate communities would include significantly greater diversity and abundance of invertebrates collected from the salmon-bearing sites, and low community similarity between sites with and without salmon (Honea, 2002; Cederholm et al, 1999). Additionally, the relative composition of functional feeding groups is expected to diverge between sites with and without salmon, with the communities below the barriers containing relatively more shredders and collectors—two groups that have been shown to increase in number when salmon are present (Chaloner and Wipfli, 2002).

The ecological significance of salmon is substantial; in close concert with it is the vital role played by the invertebrates upon which stream-dwelling juvenile salmonids depend not only directly, via consumption, but indirectly, through the whole host of ecological processes that support a healthy and dynamic, lotic ecosystem that are carried out by the tiny inhabitants of the stream benthos. The relationship between these vital groups of organisms, therefore, merits scrutiny from as many angles and in as many lights as possible to understand their interactions.

Materials and Methods

Study Area

The Puyallup-White River Watershed

From their nascence amid the craggy, glacier-capped peaks of Mt Rainier, the Puyallup, White, and Carbon rivers flow down into the Puget lowland, where the Puyallup and Carbon merge at RKM 28.65. After being joined by the White River at RKM 16.58, the Puyallup flows westward to Commencement Bay. In total, this watershed provides drainage for an area over 2092 km (Marks et al, 2005).

Glacially fed, these rivers are turbid with glacial till throughout the summer and autumn months. The native salmonids hosted by this catchment are spring and fall chinook, coho, chum, and pink salmon, steelhead (*O. mykiss*) and cutthroat (*O. clarkii*) trout, and char (*Salvelinus confluentus* and *S. malma*).

Boise Creek

A tributary which joins the White River below the Highway 410 bridge at RKM 37.82, Boise Creek offers spawning habitat to one of the White River's most abundant runs of chinook, coho, and pink salmon, along with steelhead trout throughout the 7.24 km reach below the bedrock falls that cut off upstream migratory access (Marks et al, 2005). Below the falls, the stream wanders with step-pool morphology through a brief stretch of second growth forest, through a golf course, and finally through agricultural land from RKM 5.95 to 0.48, with minimal riparian zone. The riffle selected for sampling above the barrier is approximately .32 km above the falls, 7.32 m long and 7.41 m wide at bankfull width. Surrounded by alder, salmonberry, Indian plum, cedar, Himalayan blackberry, Japanese knotweed, and ferns, this riffle is shaded by overhanging vegetation and contains some instream LWD. The downstream study riffle, which measures 13.41 m long, 5.79 m at bankfull width, is roughly 1.29 km below the falls and immediately below a bridge. This reach is bordered by a concrete wall and private lawn on both sides.

Clark's Creek

A small, spring-fed stream, Clark's Creek converges with the Puyallup River at RKM 9.33. Most spawning activity, mainly by chinook and chum salmon, with a small number of coho, occurs between RKM 5.47 and 5.95, where gravel was introduced in 1997 and again in 1999 (Marks et al, 2005). With a riparian zone of maple, cottonwood, alder, salmonberry, Indian plum, elderberry, and sword fern, the 14.63 m long, 6.28 m wide riffle contains LWD and, at the time of sampling, numerous salmon bones. Above the dam at RKM 5.95, the creek is small and narrow, cutting through an extensive riparian zone of cedar, fir, elderberry, salmonberry, Indian plum and skunk cabbage along the creek. The upper riffle is 4.27 m long and 2.13 m wide.

Fennel Creek

Above its confluence with the main stem of the Puyallup River at RKM 24.94, Fennel Creek provides spawning habitat for chinook, coho, chum and steelhead before Victor falls, an anadromous block at RKM 3.06 (Marks et al, 2005). Below the falls, this stream has been subjected to relatively little development, is surrounded by a mature hardwood riparian zone, and contains an abundant supply of LWD. The lower sample riffle is 15.24 m long and 7.01 m wide. Surrounding vegetation includes alder, hemlock, cedar, sword fern, and Indian plum, as well as private lawn. Salmon bones and a partially decomposed chum salmon carcass littered the tiny tributary just upstream of the sampled riffle. The upper riffle is directly above the falls. One side is bordered by a riparian zone thick with Indian plum and salmonberry, interspersed with cottonwoods and cedar trees. The other side is a steep clay bank supporting mainly sword fern and blackberry. This riffle is 7.92 m long and 6.1 m wide.

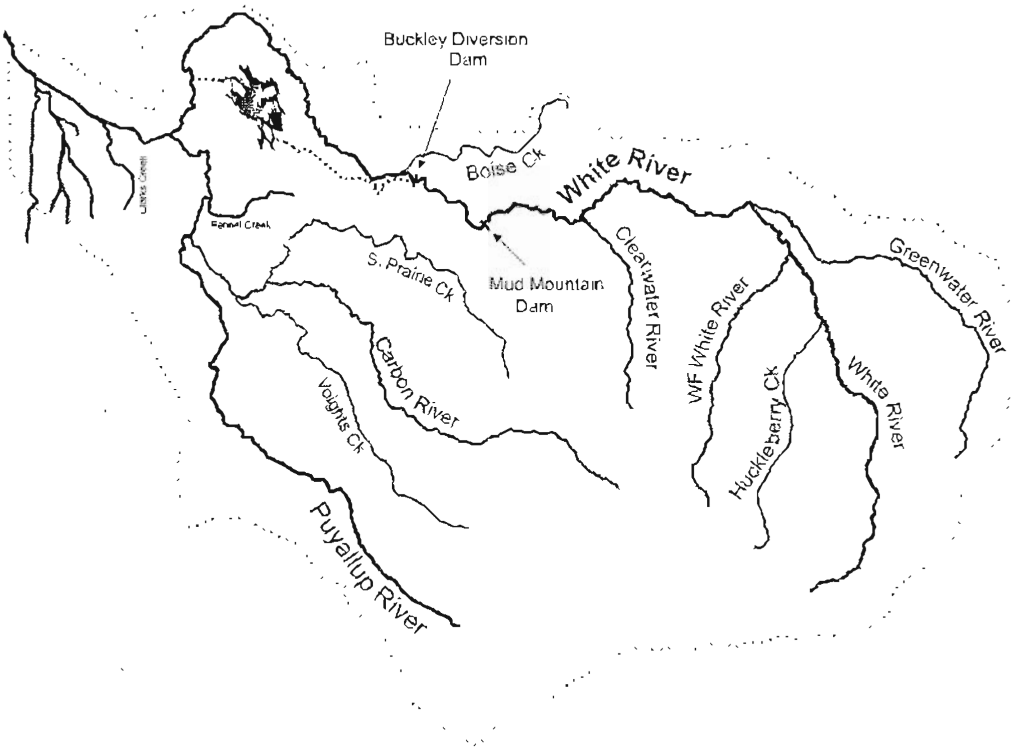


Figure 1. The Puyallup-White River watershed. Providing drainage to an area over 2092 km from the glaciers of Mt. Rainer to the mouth of the Puyallup River at Commencement Bay, this watershed hosts runs of spring and fall chinook salmon, coho salmon, pink salmon, and chum salmon, as well as anadromous and resident cutthroat trout, rainbow trout/steelhead, and char. The three streams that are the focus of this study are Boise, Clark's, and Fennel Creeks.

Wolman Pebble Count

Substrate was characterized using the Wolman pebble count method (Wolman, 1954; Kondolf, 1997). After the length and bankfull width of each riffle was measured, substrate was sampled along transects that stretched perpendicularly across the riffle, extending to bankfull width on each side of the stream. The number of transects per site varied with the width of the stream, but enough were used at each site to obtain 100 samples. Because a sample was taken at 0.3 m intervals along each transect (0.15 m intervals on the upper Clark's Creek site), bankfull width was divided by 0.3 (or 0.15 for upper Clark's), and that number was divided into 100 to yield the correct number of transects, which were spaced evenly throughout the riffle. At each interval along the transects, the first piece of substrate contacted by the sampler's finger was measured along its intermediate axis using Mitutoyo Digimatic calipers and recorded according to size class. Size classes were, in mm: 0-2; >2-4; >4-8; >8-16; >16-32; >32-64; >64-128; >128-256; >256-512; and >512-1024.

Results were recorded and graphically analyzed to obtain values for graphic mean, graphic standard deviation, inclusive standard deviation (sorting values), and skewness according to methods detailed by Folk (1974). To obtain these values, data were plotted on a phi scale, in which the negative logarithm to the base 2 of the substrate measurement is substituted for the actual measurement. The graphic mean, once obtained in phi units, was converted back into millimeters, and provides the mean substrate size for each site. Inclusive standard deviation is a sorting value, or a measure of how evenly substrate is distributed throughout the class sizes. Categories range from very well sorted to extremely poorly sorted. Skewness is a measure of whether the substrate sample contains a predominance of fine substrate, coarse substrate, or whether its distribution is log-normal, with neither fine nor coarse substrate predominating. Excessively coarse samples are positively skewed, while extremely fine samples are negatively skewed.

Determining Flow

Stream velocity was measured for the upper Boise Creek site on 3/5/06; upper and lower Clark's Creek on 3/10/06; upper and lower Fennel Creek sites on 3/18/06; and lower Boise of 4/1/06. Velocity and depth were measured at 0.3 m intervals along a perpendicular cross-section of each riffle using a 2100 Swoffer current meter. Discharge was calculated using the equation: Velocity x Depth x Distance.

Collecting and Identifying Invertebrates

Invertebrate samples were collected according to the protocol described in the Oregon Plan for Salmon and Watersheds (1998). Samples were collected at the bottom, halfway point, and head of each riffle using a Surber sampler, and then combined into a single sample for later analysis. Rocks inside the sample area were scrubbed to remove invertebrates and set aside for further inspection, and then the substrate was vigorously agitated for 1 minute to a depth of 10 cm. All invertebrates and substrate inside the collecting tube were gathered and placed in glass jars. Rocks were reexamined, and any remaining invertebrates were manually removed and placed into the jars. Samples were preserved in 70% ethyl alcohol. Invertebrates were manually separated from substrate in the lab under an American Optical Stereo Star stereoscope (0.7-4.2x magnification). In the lab, insects were identified to genus, and all other invertebrates to order, using several field guides (Merrit and Cummins, 1996; Pennak, 1978; Peckarsky et al, 1990; McCafferty, 1981; and Thorp and Covich, 2001).

Data Analysis

To compare the communities, Margalef's index of richness, evenness of distribution, and Simpson and Shannon indices of diversity were calculated (Table 8; Brower et al, 1998). Simpson and Shannon indices from the upper and lower sample of each creek were compared statistically. Both indices of diversity were used because they utilize different criteria in assessing diversity and so highlight different aspects of the assemblages. Each index except evenness was applied not only to the overall sample, but also to the compositions of the collector, predator, and scraper functional feeding groups.

Community similarity between upper and lower creek sites was assessed using the Jaccard coefficient, an index which compares communities based on the taxa they share in common. (Brower et al, 1990). Morisita's index of community similarity, based on the Simpson's index, was also used. This index measures the probability that randomly selected individuals from each community will belong to the same taxon, relative to the probability that two randomly selected individuals from the same community will belong to the same taxon (Brower et al, 1990). Both indices were calculated for total taxa, and for each of the functional feeding groups. A Multi-Response Permutation Procedure was performed for overall data using the PC-ORD™ computer software program.

In addition to total taxa and the functional feeding groups, some of the metrics of the Pacific Northwest Benthic Index of Biotic Integrity (B-IBI) were utilized as categories for comparison between samples for some of the comparisons, including Ephemeroptera, Plecoptera, and Trichoptera taxa, clinger taxa, predator percentage, and percent dominance for 1 and 3 taxa (Karr, 1998; http://www.cbr.washington.edu/ salmonweb/). Some of these metrics were used in an overall comparison of the samples, and in calculating percent compositions for each sample. Percent composition also compares the percentage of each sample belonging to the order Diptera.

A partial Index of Biotic Integrity score was also tabulated as a means of comparison for each site (Thorne and Williams, 1997; Karr, 1991; http://www.cbr.washington.edu/salmonweb/). Developed as a means by which to evaluate the health of a stream and detect human-induced alterations, the Index of Biotic Integrity (IBI) is one of a few methods that utilizes benthic macroinvertebrates as indicators of stream health. The method utilizes a range of biological indicators evaluated for their appropriateness in a given ecoregion to assess a habitat's biotic integrity, which is defined as its "capacity to support and maintain a balanced, integrated and adaptive biological system having full range of elements and processes expected in a region's natural habitat" (Karr, 1998).

The metrics determined for a Benthic Index of Biotic Integrity (B-IBI) —which, for the Pacific Northwest ecoregion are numbers of total, Ephemeroptera, Plecoptera, Trichoptera, long-lived, intolerant, and clinger taxa, percentage of individuals belonging to tolerant taxa, predator percentage, and percent dominance for three taxa—are indicative of disturbance and therefore overall ecological health of a stream (Karr, 1998). Therefore, while this study does not make use of a full IBI, which is calibrated for sampling in September in the Pacific Northwest, a partial one is calculated for comparison purposes (Karr, 1998, James Karr, personal communication).

Salmon abundance and biomass

Based on spawning survey estimates conducted by the Puyallup Tribal Fisheries, salmon populations and densities were estimated for each creek (Marks et al, 2005). Total biomass was estimated using live counts/escapement estimates for each site and the following general estimates of salmon mass for the four species found on the creeks: pink, 2.5kg; chum, 4.4 kg; coho, 3.25 kg; chinook, 5 kg (Groot and Margolis, 1991; Quinn, 2005).

RESULTS

Wolman Pebble Count and Flow

Graphical analysis of Wolman pebble count data show that the substrate of all sites is fine-skewed, except upper and lower Clark's Creek sites, which are both strongly fine-skewed (Table 1). Sediment for all sites is poorly sorted, except for lower Boise, which is very poorly sorted. Graphic mean values show the smallest average sediment on the lower Clark's Creek site, followed by upper Clark's, lower Boise, lower Fennel, upper Boise, and finally upper Fennel with the largest average substrate.

Discharge, measured in cubic meters per second, was slightly higher on lower sites than upper sites due to additional water from tributaries feeding into lower sites (Table 2). Boise Creek is an exception, with the upper site having greater discharge than the lower site. This is because, unlike the other sites, flows on the upper and lower portions of Boise Creek were measured a month apart.

Taxa Richness and Diversity

Samples from each upper site contain more individuals than each corresponding lower site. The number of genera is similar on upper and lower sites for each creek, except for Clark's, whose sample for the lower site contained far more genera than the upper site (Table 3). Similarly, the greatest difference in community evenness occurs between the upper and lower sites of Clark's Creek. The contribution of predators to the total invertebrate fauna deviates from this pattern, because lower Fennel Creek as well as lower Clark's Creek samples both contain substantially higher percentages of predators than the corresponding upper sites.

According to the Margalef index, upper and lower sites for Boise and Fennel Creeks are similarly taxa-rich for most metrics (Table 4). The exception here is the relatively large difference between predator taxa on the upper (D=2.78) versus lower (D= 4.751) Fennel Creek sites. Little similarity in taxa richness exists between upper and lower Clark's Creek sites. For most of the metrics considered, the lower site is far more diverse, except for the only slight difference between predator richness scores (D=1.913 and 2.174 for upper and lower respectively).

Table 1. Results of graphical analysis of Wolman pebble count.

	Upper Boise	Lower Boise	Upper Clark's	Lower Clark's	Upper Fennel	Lower Fennel
Graphic mean (mm)	34.78	25.99	14.62	8.34	47.18	32.67
Graphic standard deviation	1.33	1.7	1.75	2.1	1.48	1.51
Inclusive graphic standard deviation	1.44	2.19	1.38	1.88	1.38	1.76
Skewness	-0.18	-0.16	-0.31	-1.4	-0.29	-0.26

Table 2. Discharge (cms) of the six sites.

	Boise Creek	Clark's Creek	Fennel Creek
Upper	0.82	0.013	0.276
Lower	0.341	0.048	0.5

Table 3. Results of invertebrate identification.

	Upper Boise	Lower Boise	Upper Clark's	Lower Clark's	Upper Fennel	Lower Fennel	All Upper Sites	All Lower Sites
Total invertebrates	977	544	751	341	672	507	2369	1425
Total taxa	35	31	17	26	28	26	47	45
Evenness	0.539	0.647	0.327	0.753	0.656	0.678	0.574	0.605
% Predators	3.07	3.49	4.2	7.04	1.79	6.5	3.25	4.49
% Dominant (1 taxa)	38.18	42.46	79.36	28.74	24.4	34.12	26	32
% Dominant (3 taxon)	77.27	50.73	90.68	59.82	58.48	64.89	70	61

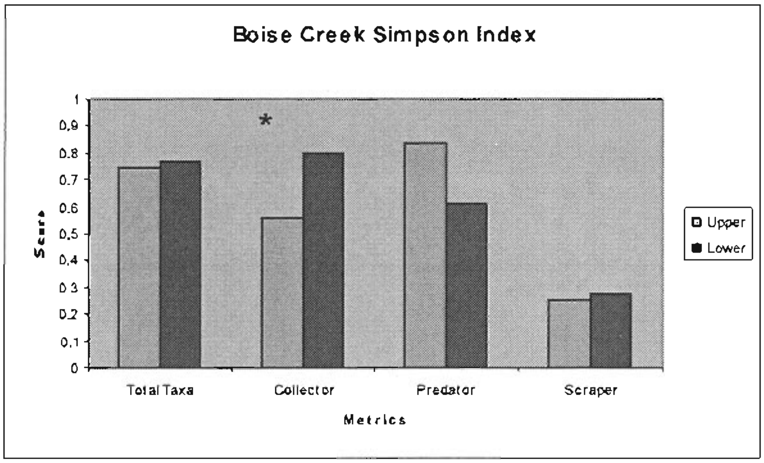
Table 4. Margalef index of community richness.

	Upper Boise	Lower Boise	Upper Clark's	Lower Clark's	Upper Fennel	Lower Fennel	All Upper Sites	Al Lowe Sites
Total Taxa	11.372	10.967	5.564	9.871	9.550	9.242	13.631	13.951
Collector	5.963	5.801	2.148	3.066	4.598	4.561	6.915	6.665
Predator	3.353	3.591	1.913	2.174	2.780	4.571	4.204	4.321
Scraper	1.516	1.642	0.518	2.073	1.285	1.750	1.737	2.189

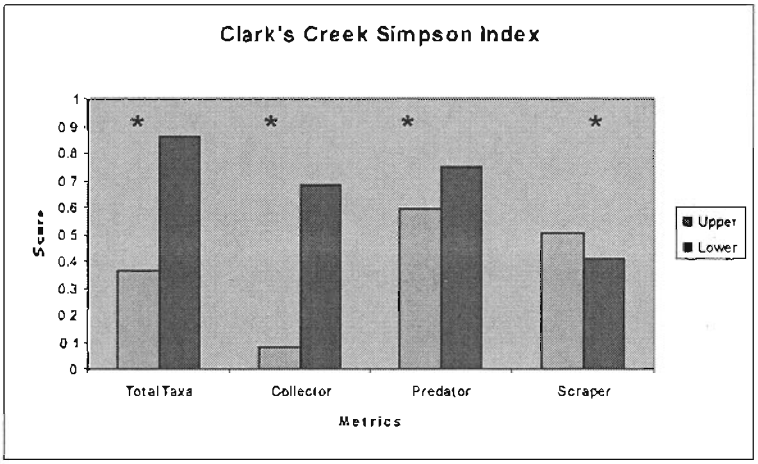
According to Simpson's index of diversity, the diversity of the total taxa and the three functional feeding groups is greater on lower Boise Creek for each metric except for predator taxa, which is greater on the upper site (Figure 3). Statistical comparison ($\alpha=0.05$, DF=∞, student t=1.96 for all Simpson index comparisons) shows that the greater diversity in predator taxa for the upper site is significant on this creek (t=-7.878), as is the greater diversity among collector taxa on the lower site (t=8.839). The diversity of the lower Clark's Creek site is significantly greater than that of the upper site for all metrics except for scraper taxa, which is significantly more diverse on the upper site (total taxa t=-19.639; collector taxa t=-17.108; predator taxa t=-7.5; and scraper taxa t = 3.105). The diversity of Fennel Creek is greater on the upper site for total taxa and scraper taxa, while the lower site scores higher for diversity of collector taxa and predator taxa. Significant differences occur between predator taxa diversity (t=-7.201) and scraper taxa (t=4.592). For combined data, there is greater diversity overall on lower sites for all metrics except scraper taxa; this is significantly greater for upper sites (t=-3.551). Lower sites are significantly more diverse in predator (t=-2.624) and collector taxa (t=2.468).

The Shannon index of diversity yields some results that corroborate those of the Simpson index, and others that contradict it. According to this index, lower Boise and Clark's Creek sites are significantly more diverse for both total taxa (Boise t=-3.985; Clark's t=-13.064) and collector taxa (Boise t=-4.824; Clark's t=-11.509) than the upper sites on these creeks, and the combined data shows significantly greater diversity on lower sites than upper for collector taxa (t=-4.479) (Figure 4). Lower Fennel Creek, according to this index, contains significantly more diverse assemblages of predator taxa than the upper site (t=-2.261), and the upper site hosts a more diverse assemblage of scraper taxa (t=2.267).

a)


Boise Creek Simpson Index
Score
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
*
Total Taxa
Collector
Predator
Scraper
Metrics
Upper
Lower

b)


Clark's Creek Simpson Index
Score
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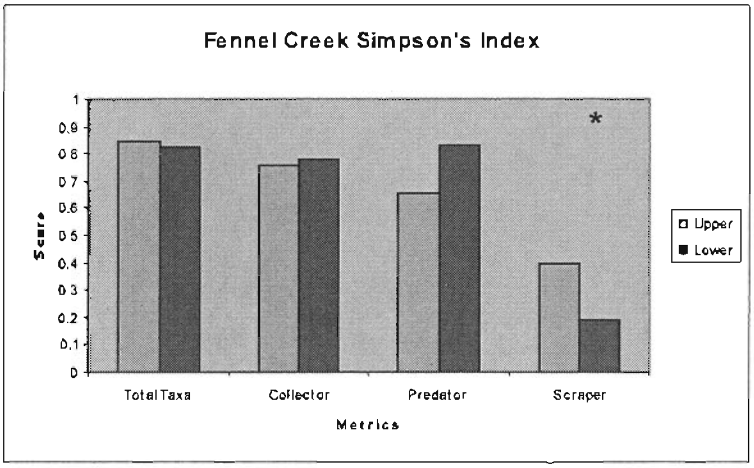
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
*
*
*
*
Total Taxa
Collector
Predator
Scraper
Metrics
Upper
Lower

c)


Fennel Creek Simpson's Index
Score
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0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
*
Total Taxa
Collector
Predator
Scraper
Metrics
Upper
Lower

d)

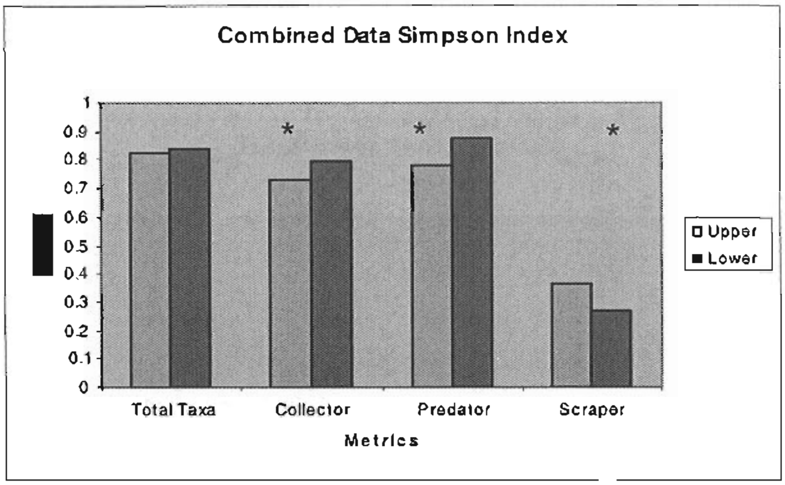
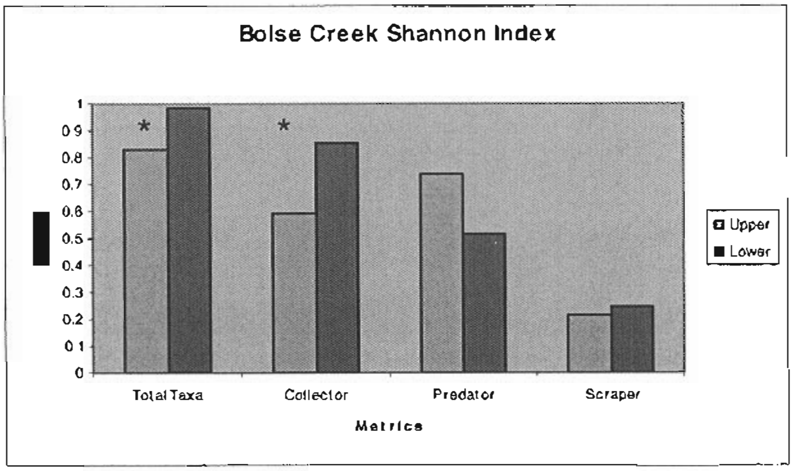
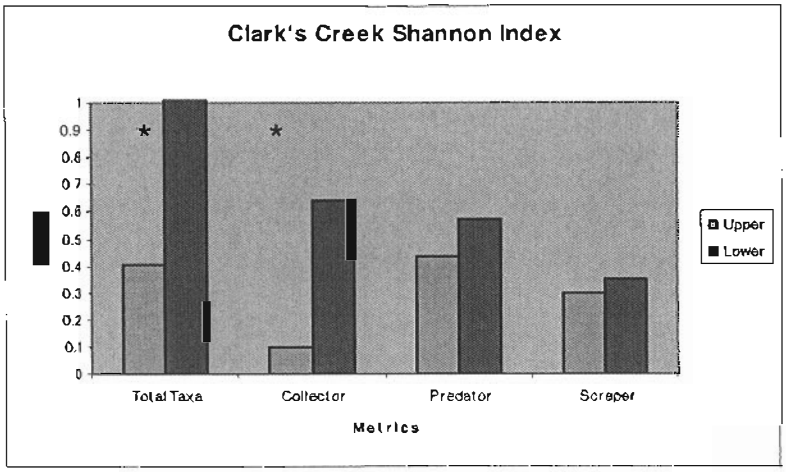


Figure 2. Simpson's index for a) Boise Creek; b) Clark's Creek; c)Fennel Creek; and d) all upper and lower sites combined. Asterisks indicate significant differences.

a)


Boise Creek Shannon Index
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
*
*
Total Taxa
Collector
Predator
Scraper
Metrics
Upper
Lower

b)


Clark's Creek Shannon Index
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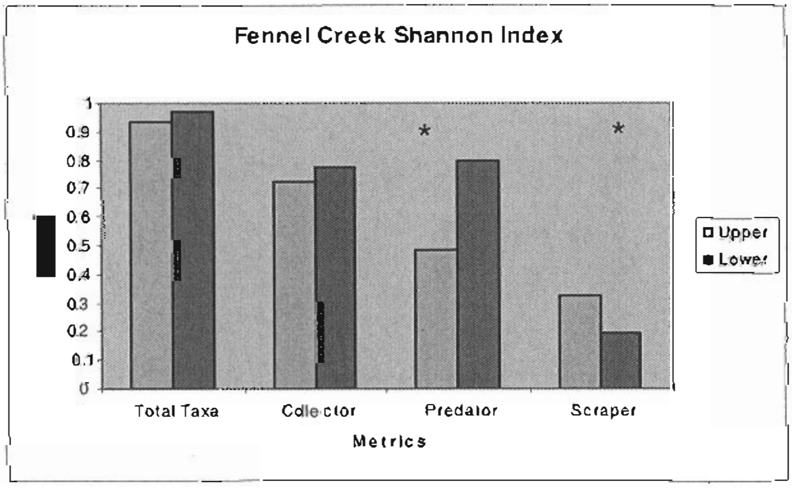
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
*
*
Total Taxa
Collector
Predator
Scraper
Metrics
Upper
Lower

c)


Fennel Creek Shannon Index
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
*
*
Total Taxa
Collector
Predator
Scraper
Metrics
Upper
Lower

d)

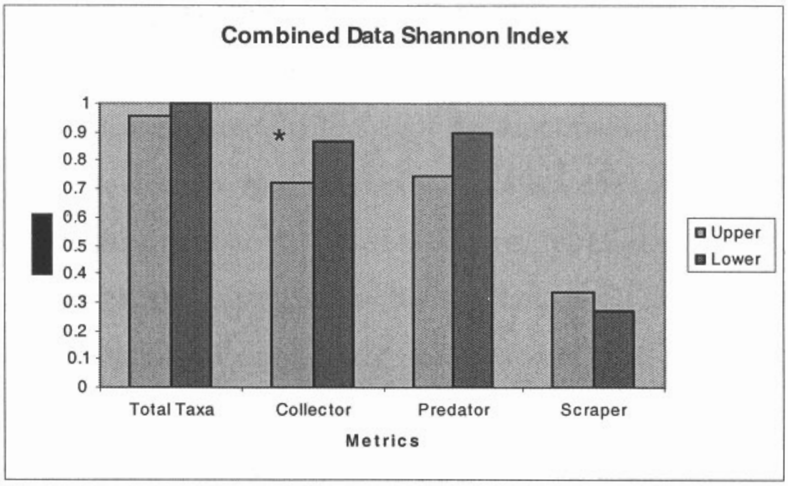


Figure 3. Shannon index for a) Boise Creek; b) Clark's Creek; c)Fennel Creek; and d) all upper and lower sites combined. Asterisks indicate significant differences.

Community Similarity

The Jaccard coefficient of community similarity shows that the total taxa composition hovers around 50% similarity for both Boise and Fennel creeks, but drops to about 30% similarity for the Clark's Creek sites (Table 5). Of the functional feeding groups, each creek showed the most similarity in collector taxa composition, and the least among predators. When the scores for all metrics are summed for each creek, the totals (Boise, 1.496; Clark's, 1.273; and Fennel, 1.689) indicate that the Fennel Creek sites have the most taxa in common, while the Clark's Creek sites have the fewest.

Similar to the trend uncovered by the Jaccard coefficient, the Morisita index, which is based on the Simpson index, shows strong overall similarity between upper and lower sites for Boise and Fennel Creeks, with relatively low similarity between upper and lower Clark's Creek sites (Table 6). This index shows the most similarity between the scraper components of all communities, and the least similarity among predators.

Percent composition shows relatively similar compositions for most metrics on both Boise and Fennel Creeks, with the greatest disparities between upper and lower Clark's Creek for most metrics. Overall, percent composition is fairly similar between upper and lower sites for combined data, with the greatest difference between upper and lower sites occurring for clinger taxa (Figure 4). There are consistently slightly more scrapers, clingers, and predators on lower sites than upper, and upper sites tend to have larger collector components, particularly upper Clark's Creek, with its large proportion of collector chironomids.

Although a complete IBI is not applicable to this study because the objective of this study is not to measure water quality, because samples were not taken in September, and because not all metrics were applied to the data, scores are a useful means of comparison for the three creeks. The partial IBI calculated here gives each lower site an overall higher score than its upstream counterpart (Table 6). Total, Ephemeroptera, Plecoptera, and Trichoptera taxa all receive the highest scores on both sites of Boise Creek, whose upper site also receives the highest score for number of clinger taxa, and whose lower site attains the highest score for having the lowest percent dominance for 3 taxa. Lower Clark's Creek receives a higher score on all metrics than upper except for total, Ephemeroptera, and Trichoptera taxa, which are identical for the two sites. The only differences that occur between upper and lower Fennel Creek are for number of clinger taxa and predator percentage, both of which have higher scores on the lower site. Each lower site receives a higher score than its upstream counterpart, and overall, Boise is the highest-scoring creek, followed by Fennel and then Clark's.

Analysis of community similarity using Multi-Response Permutation Procedure did not uncover any significant differences between upper and lower sites (p=0.53). However, the visual representation of the analysis shows the lower sites forming a distinctive cluster, indicating strong similarity between these communities (Figure 5). In contrast, the upper sites are widely dispersed relative not only to each other, but also to the lower sites. This indicates that the variation among upper sites is similar to that found between upper and lower sites.

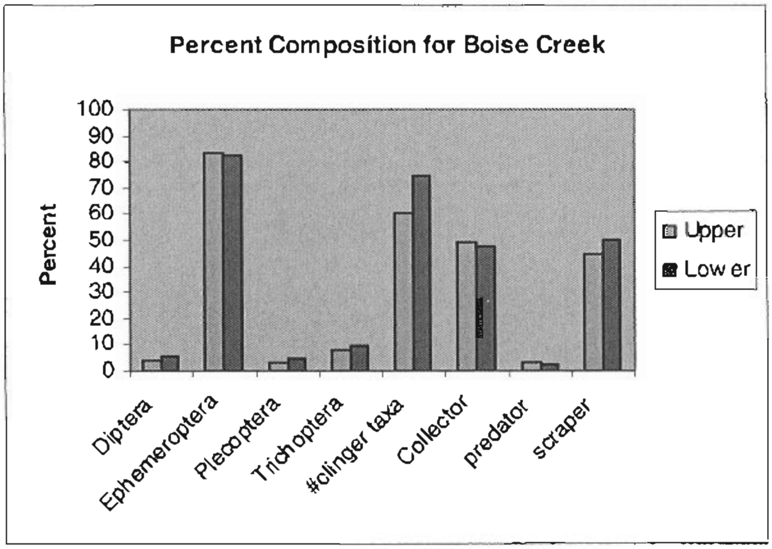
Table 5. Jaccard coefficient of community similarity.

	Boise	Clark's	Fennel	Combined
Total Taxa	0.467	0.297	0.536	0.508
Collector	0.6	0.5	0.667	0.654
Predator	0	0.143	0.2	0.5
Scraper	0.429	0.333	0.286	0.625
Sum	1.496	1.273	1.689	2.287

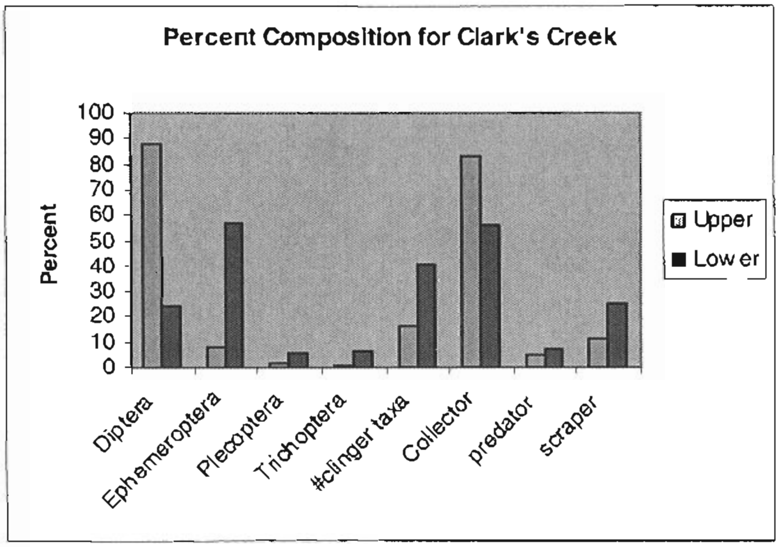
Table 6. Morisita index of community similarity.

	Boise	Clark's	Fennel	Combined
Total Taxa	0.955	0.290	0.840	0.768
Collector	0.876	0.511	0.741	0.764
Predator	0.092	0.103	0.095	0.693
Scraper	1.000	0.832	0.975	0.970

a)


Percent Composition for Boise Creek
Percent
100
90
80
70
60
50
40
30
20
10
0
Diptera
Ephemeroptera
Plecoptera
Trichoptera
#clinger taxa
Collector
predator
scraper
Upper
Lower

b)


Percent Composition for Clark's Creek
Percent
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80
70
60
50
40
30
20
10
0
Diptera
Ephemeroptera
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Trichoptera
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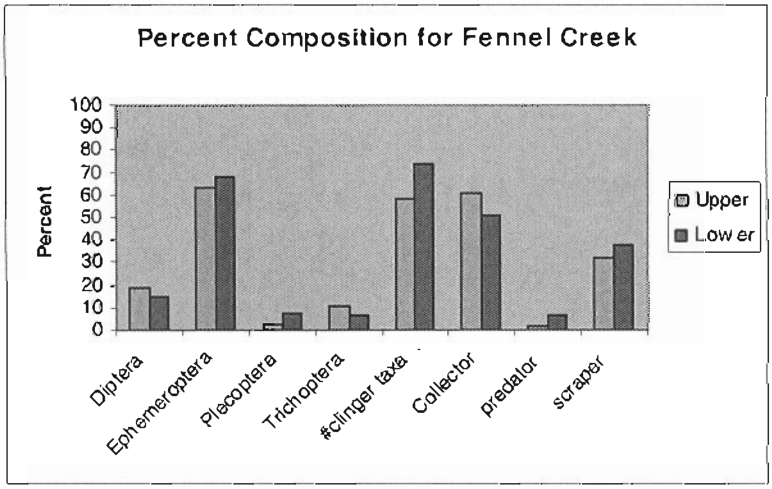
Collector
predator
scraper
Upper
Lower

c)


Percent Composition for Fennel Creek
Percent
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80
70
60
50
40
30
20
10
0
Diptera
Ephemeroptera
Plecoptera
Trichoptera
#clinger taxa
Collector
predator
scraper
Upper
Lower

d)

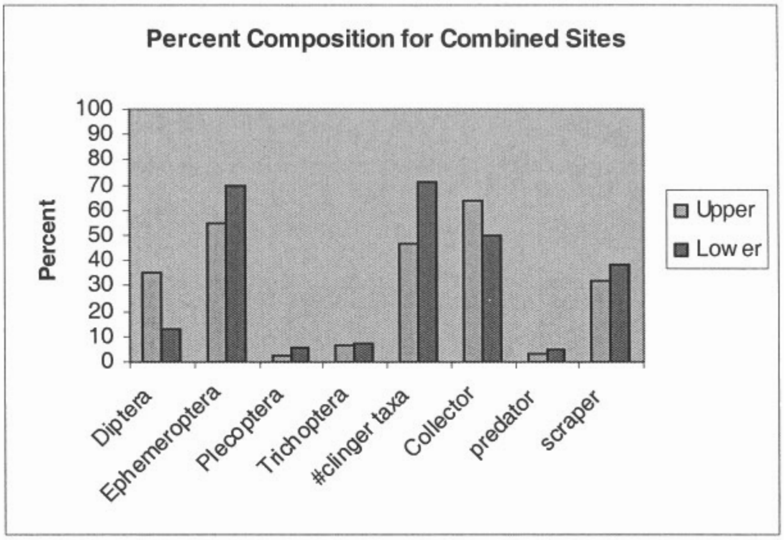
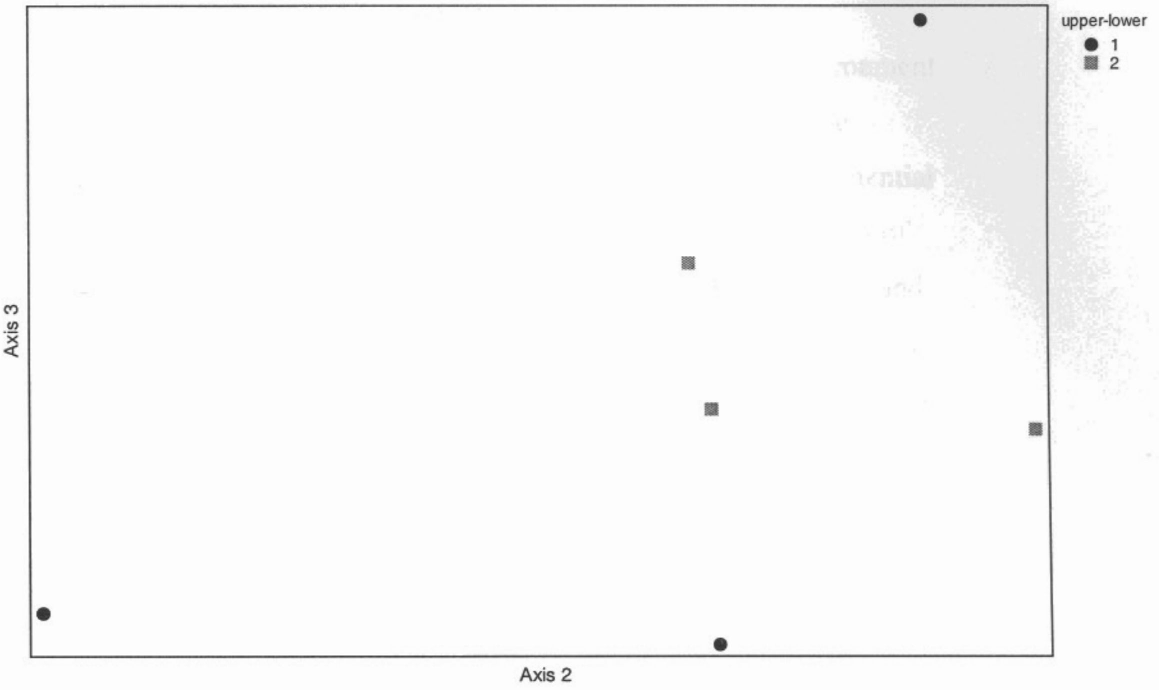


Figure 4. Percent compositions of various metrics on upper and lower sites for a) Boise Creek; b)Clark's Creek; c) Fennel Creek; and d) upper and lower sites combined.

Table 7. Benthic Index of Biotic Integrity scores.

	Upper Boise	Lower Boise	Upper Clark's	Lower Clark's	Upper Fennel	Lower Fennel
Total taxa	5	5	3	3	3	3
Ephemeroptera	5	5	3	3	3	3
Plecoptera	5	5	1	3	3	3
Trichoptera	5	5	1	1	5	5
Clinger taxa	5	3	1	3	3	5
% predators	1	1	1	3	1	3
% dominant (3 spp)	1	5	1	3	3	3
sum	27	29	11	19	21	25

Figure 5. Relative community similarity based on Multi-Response Permutation Procedure (MRPP).



Discussion

Discharge and Substrate Characterization

At a local level, one of the two factors of the physical environment that can have the most substantial impact on the composition of the benthic community is discharge (Hershey and Lamberti, 1998). Potential effects of elevated discharge may include increased downstream drift of invertebrates, especially in reaches whose substrate is dominated by sand and small pebbles. Of the three creeks in this study, the lowest discharge levels were calculated for both Clark's Creek sites. The highest discharge was recorded on the upper Boise Creek site. The velocity of the stream at this site, used to calculate discharge, was measured a month prior to the same measurement was taken on the lower site. The difference in discharge recorded between the two sites, therefore, is not an accurate reflection of the potential differences between these two sections. The discharges on upper and lower sites are more likely to be identical if measured on the same day because no tributaries feed into Boise Creek between the upper and lower sample sites, and no water is diverted or removed at any point. Discharge rates for lower Boise Creek and both Fennel Creek sites are in close range to each other, so any differences seen between the communities on these two sites are likely not attributable to discharge. However, discharge may be a small factor in some of the differences found between Clark's Creek and the other two creeks.

In addition to discharge, another stream feature of particular importance in affecting the microdistribution of benthic invertebrates is substrate size. Since they provide greater surface area, interstitial space, and possibly trap detritus and thereby enhance food availability, larger gravel and cobbles—in the size range of approximately 24-41 mm and even larger—constitute the preferred habitat of many invertebrate taxa, and have been shown to be related to increased community density and diversity (Flecker and Allan, 1984; Williams and Mundie, 1978; Orth and Maughan, 1983).

Analysis of Wolman pebble counts reveals few differences between sorting values and skewness of most sites. The substrate of most sites is poorly sorted and fine-skewed, except for lower Boise Creek, which is very poorly sorted, and the Clark's Creek sites, which are very fine-skewed. Graphic mean values show that the average substrate size is greatest on upper Fennel Creek, followed by upper Boise Creek, and smallest on the lower Clark's Creek site. Because the sites with larger substrate tended to yield larger sample sizes, relative availability of larger substrate may be a factor in the difference between numbers of individuals able to occupy these sites. The exception to this is upper Clark's Creek, with the second smallest average substrate size and the second largest sample size. However, an overwhelming component of the upper Clark's Creek sample consisted of chironomids, filter feeders that do not necessarily require a particular size of substrate.

Community Analysis

The primary aspects of the six communities that were compared are abundance, diversity, and evenness, and similarity between each upper and lower site. Factors including habitat and food availability, competition, and predation all interact to varying degrees, influencing these attributes of benthic communities and determining local distribution patterns (Merritt and Cummins, 1996).

Not only were overall assemblages examined at each location, but they were also analyzed according to the functional feeding groups. By examining the benthic community according to the functional feeding group classification, the degree to which the invertebrates of a given stream reach depend on particular food resource can be assessed (Merrit and Cummins, 1996; Hershey and Lamberti, 1998). The only group omitted from this analysis is shredders, which were found in extremely low abundance on all sites. This may be because shredders are typically more numerous in low-order, headwater streams rather than lowland streams such as the ones in this study (Vannote, 1980). Also, as Chaloner and Wipfli (2002) observe, shredders are highly abundant in autumn, whereas samples were gathered for this study in early spring.

After examining the diversity, richness, similarity, and other aspects of the communities sampled in this study, few clear trends emerge that point to a tangible link between community composition and salmon presence. There are, however, many interesting features of the data that merit closer examination.

Boise Creek

With its vigorous left bank riparian buffer, its comparatively large distance from any roads, and otherwise relatively low level of anthropogenic disturbance, upper Boise Creek could reasonably be expected to host a diverse and abundant benthic faunal community, as it in fact does. Nearly twice as many individuals were collected from the upper Boise Creek site as from the lower.

The lower Boise site provides a rather stark contrast to its upstream counterpart, with its razed riparian buffer replaced by concrete wall, rip rap bank support, and manicured lawn, and its probable input of toxic substances from the road immediately above it and the golf course just upstream of it. The lower site is part of an amazingly productive salmon stream, however, and so in spite of its degraded condition, high levels of abundance and diversity can reasonably be expected at this site.

Despite the greater abundance of invertebrates sampled at the upstream site, according to the Morisita index, the overall compositions of the two communities are very similar. This index shows the greatest similarity between the samples from upper and lower Boise compared to the other two creeks, although, according to the Jaccard coefficient, the two sites only share 46% of the total taxa comprising their samples. Other population parameters such as evenness, taxa richness, and diversity as measured by the Margalef and Simpson indices, along with B-IBI scores, likewise show strong similarity between the relative diversities of the two communities. The sole exception to the suggestion of overall community similarity is the Shannon index, which detects significantly greater diversity of overall taxa on the lower Boise Creek site.

While diversity is similar for the total taxa of the two Boise Creek sites according to most measures, differences in diversity are found upon comparison of the functional feeding groups. According to Simpson's index, significant differences exist between collector and predator diversities, with the lower site being richer in the former and the upper site the latter. Similarly, the Shannon index ascribes significantly greater diversity to the collector taxa on the lower site.

Both sites on Boise Creek meet the prediction stated above of high diversity. According to the partial B-IBI calculated here, Boise is the highest-scoring creek of the three stream systems. Considering the relative degradation of the lower site, it comes as somewhat of a surprise that it earns a higher B-IBI score than the upper site.

Clark's Creek

For Clark's Creek, which contains the two sandiest sites of any of the creeks—both very fine-skewed and with the smallest average substrate sizes of all the sites—low overall diversity is a reasonable prediction for both sites. Because of the relatively large sand component on both sites, an elevated abundance of chironomids would be expected to comprise a large proportion of each community, particularly the lower site, whose substrate composition is almost 25% sand, relative to the 12% found on the upper site. This is because, in contrast to many other taxa which prefer the interstitial space and surface area provided by gravel and cobbles, chironomids are capable of flourishing in sandy microhabitats in astounding concentrations (Hershey and Lamberti, 1998).

The above predictions are fulfilled by the upper site which, for total taxa, demonstrates the least evenness (0.327) and the highest percent dominance for both 1 (79%) and 3 (91%) taxa, indicating low diversity. Both the taxa richness—(D=5.63) according to the Margalef index—and diversity, according to both the Simpson (0.363) and the Shannon index (0.402), are the lowest of all sites. With an overwhelming 88% of the individuals collected on this site belonging to the order Diptera (90% of these are chironomids), the invertebrate community of upper Clark's Creek hosts the most concentrated chironomid component of any site.

In spite of the high proportion of fine substrate and the lack of large gravel on lower Clark's Creek, its invertebrate assemblage does not conform to the habitat-based predictions that hold true for the upper site. To the contrary, lower Clark's Creek, despite having the lowest number of individuals collected in any site, has the highest diversity for total taxa of any site according to both the Simpson index (0.858) and Shannon index (1), as well as the highest evenness of any site (0.74); and among the lowest percent dominance of all sites for both 1 (29%) and 3 taxa (60%). A comparison of the upper and lower portions of the creek shows that the fauna of the lower site is significantly more diverse than that of the upper creek. Further, lower Clark's Creek—whose high percentage of unfavorable sandy substrate and the small amount of diversity-fostering large gravel may be the cause of its relatively low component of clinger taxa—does not show similar composition to upper Clark's Creek according to the Jaccard (0.297), Morisita (0.29), and Horn (0.48) indices. Instead, lower Clark's Creek excels in diversity and evenness of overall taxa, as well as for most functional feeding groups, earning the highest rankings in these categories of any site according to both the Simpson and Shannon diversity indices.

Fennel Creek

Just as for the other two creeks, more individuals were collected on the upper portion of Fennel Creek than on the lower. Similar to Boise Creek, both upper and lower sites display highly similar diversity for overall taxa according to both Simpson (0.828 for upper and 0.824 for lower) and Shannon indices (0.935 for upper and 0.971 for lower), neither of which yield any basis for rejecting the null hypothesis of equally diverse communities when compared statistically. Both indices show that upper Fennel Creek is significantly more diverse in scraper taxa; however, the lower site is proportionally richer in scrapers. The Morisita index detected considerable similarity between all metrics except predator taxa, which are proportionally more abundant on the lower site relative to the upper, as well as significantly more diverse on the lower site according to both the Simpson and Shannon indices. The greater relative abundance of predators can be readily accounted for by the presence of *Eccoptura sp.* and *Beloneura sp.*, two predaceous genera of perlids that are more numerous on the lower Fennel Creek site than on any other site, and whose presence contributes to the higher B-IBI score received by the lower site for Plecoptera taxa compared to the upper site. The relative abundance of this family of large predators on lower Fennel Creek may indicate enhanced availability or nutritional quality of prey as a result of the nutrients delivered to the stream by salmon (Chaloner and Wipfli, 2002). Just as is the case for the other two creeks, lower Fennel receives a higher overall B-IBI score than the upper site.

Combined data

Analysis of combined data shows similar evenness and diversity between upper and lower sites for total taxa, while the Simpson index shows significantly greater diversity on lower sites for collector (t=-3.55) and predator taxa(t=-2.62), and significantly greater diversity for scraper taxa (t=2.49) on upper sites. The Shannon index attributes significantly greater diversity to collector taxa on lower sites (t=-4.48). From greatest to least, the similarity of the functional feeding groups between upper and lower sites according to the Morisita index are scraper (0.970), collector (0.764), and lastly, predator taxa (0.693). The value for predator taxa does not reflect trends on individual streams, for which predator taxa similarity was highest on Clark's Creek, attaining a Morisita score of merely 0.103. However, the scores for the other two feeding groups and total taxa are reflective of what was observed on individual streams.

The Multi-Response Permutation Procedure (MRPP) depicts the lower sites as forming a distinctive cluster, indicating relative homogeneity between these, and widely dispersion among upper sites, suggesting substantial differences between them. Variation among upper sites, therefore, is great enough to statistically offset the differences between upper and lower sites.

Do Salmon Play a Keystone Function in These Tributaries?

Salmon have been labeled keystone species, although some researchers note that they do not necessarily earn this distinction under all conditions (Stone, 1995; Willson and Halupka, 1995). In particularly nutrient-depleted streams, the nutrient influx of a prolific salmon run can have a very dramatic effect on the ecology of the stream. Therefore, the degree to which a system is relies on salmon for nutrient input is directly related to the degree to which nutrients are limited (Wipfli et al, 1999).

After analyzing the six communities in this study, no clear trend emerges that would support or refute the hypothesis that salmon play a keystone role in the three creeks. While they may actually play a crucial role in the ecology of the three creeks, the small sample size of the study limits the statistical power, making it very difficult to identify any factors within the benthic community that are clearly a function of salmon presence.

While no definitive patterns emerge from the data, some interesting relationships are suggested, as well as opportunities for further research. Among these relationships are two that do not coincide with expectations based on findings from other studies. The first of these, and perhaps the most consistent aspect of the samples, is the greater number of individuals collected from each upper site relative to each lower site. Such a pattern is somewhat surprising, because one frequently-cited effect of salmon presence is an increase in invertebrate density (Cederholm et al, 1999; Honea, 2002; Minakawa et al, 2002). A possible explanation might be that the substrate, as reflected in the graphic mean shown in Table 1, is generally smaller at lower sites. Additionally, much of the larger substrate found in lower Fennel and Boise Creeks is associated with the bank support rather than being interspersed throughout the riffle as on upper sites.

Another variable that leads to depressed invertebrate densities, at least temporarily, is the disturbance created by the redd-building activities of salmon (Field-Dodgson, 1987; Honea, 2002). However, there is evidence to suggest that redd-building is not likely to be responsible for the smaller sample sizes on lower stream sections. All three lower sections yielded smaller invertebrate samples relative to upper sites, but not all sites had been recently disturbed; Boise Creek does not support a run of chum salmon, which spawn from roughly late November to late January. Presumably, then, the invertebrate population of Boise Creek would have had sufficient time to rebound from disturbances created by pink, chinook, and coho salmon, which finish spawning by mid-November (Puyallup Tribal Fisheries, personal communication; Marks et al, 2006). An interesting question raised here is whether the increase in invertebrate population density cited in the studies referenced above was limited to the proximity of carcasses, or if the overall population was enhanced. This further leads to the question of whether the effects of salmon presence are dependent on the densities at which they spawn. Finally, the question is also raised about the temporal influence of salmon presence—do the effects of salmon on benthic invertebrates linger after the carcasses have decomposed?

Although redd excavation typically leads to an initial depletion in invertebrate densities, the disturbance created by this activity may actually contribute to the greater diversity found for many metrics on lower sites by inducing a state of non-equilibrium (Ward and Stanford, 1983). The depletion of density from redd building may be offset by the positive interaction that results from the delivery of salmon-based nutrients to the stream, thus enabling the survival of certain taxa that might not otherwise survive circumstances such as the gravel disturbance of redd building, degraded stream conditions, or poor substrate (Hacker and Gaines, 1997).

In addition to the smaller sample sizes on lower sites, relative diversities and abundances within the functional feeding groups also proved unexpected. Wipfli et al. (1999) found that as salmon carcasses accrue in streams under natural conditions, chironomid density in particular increases with carcass load. An increased population of chironomids, which are collectors, corroborates the finding that collectors are one of the functional feeding groups that is most responsive to the addition of salmon to a system (Chaloner and Wipfli, 2002). The greatest benefit collectors derive from the presence of salmon is a rich food supply in the form of tissues and cells that are sloughed as carcasses decompose. Chironomids in particular gain the additional value of increased habitat as they burrow into the carcasses (Wipfli et al 1998).

In contrast to the expectation of greater collector and chironomid densities in salmon-bearing sites, however, neither chironomids specifically nor collectors as a whole show any notable elevation in population on the lower portions of any of the three creeks examined in this study. Instead, collectors are relatively more abundant on upper sites, particularly on upper Clark's Creek. Relative diversity is difficult to determine because the Simpson and Shannon indices, which use different criteria to measure diversity, yield conflicting results. Whereas Shannon's index attributes significantly greater diversity to the collector assemblages of lower Boise and lower Clark's Creeks, Simpson's index attributes significantly greater diversity to the collectors from the upper sections of these two creeks.

The unexpectedly low concentration of collectors on salmon-bearing sites, as compared to studies that discovered a positive collector response to salmon presence, may be attributed to the different times of the year the studies were conducted. Studies by Wipfli et al (1998 and 1999) and Chaloner and Wipfli (2002) were conducted during autumn months, while sampling for this study took place in early springtime. Densities of the various invertebrate taxa may fluctuate throughout the year due to varying patterns of development and emergence, possibly altering relative abundances of the functional feeding groups throughout the year.

Another major aspect of the seasonal differences between this study and those cited is that the others were conducted during the salmon runs themselves, and so invertebrates are responding to a fresh influx of nutrients. This study, however, considers invertebrate communities at a time of the year after the carcasses have been depleted through decomposition and downstream flushing. Without a fresh supply of nutrients or habitat in the form of fresh carcasses, invertebrate density may drop. A valuable way to investigate this question might be to sample the creeks at different times throughout the year in order to observe temporal variation within the benthic communities, particularly when salmon are present in the lower portions of the streams. Documenting the temporally variable composition of the invertebrate communities is very relevant to this study because it would help reveal relationships between the reproductive cycles of the various invertebrate taxa in relation to the different components of the freshwater portions of salmon life cycles. Since oviposition, incubation, hatching, and in some species, length of aquatic phase, are dependent on environmental cues that help to optimize the broods' chances of fully exploiting seasonal food resources and favorable environmental conditions, as well as minimizing unfavorable interactions such as competition and predation, more elaborate knowledge of these invertebrate life cycle elements on the streams in question would provide greater insights into how salmon influence benthic assemblages (Merrit and Cummins, 1996). In addition to addressing questions regarding the reaction of invertebrate communities as salmon enter the streams and then decompose, monitoring the communities throughout the year might be useful in elucidating any role invertebrates might play in the retention and spiraling of salmon-based nutrients.

While collector abundance and diversity were not elevated on salmon-bearing sites as predicted, proportionately more scrapers were found on each of the lower sites relative to the upper. For this functional feeding group, salmon carcasses provide the benefit of an enhanced supply of biofilm growing on the carcasses from which to graze. However, with the most recent spawners being reduced to bones, this benefit was no longer available to this feeding group at the time of sampling. One possibility is that nutrients from salmon carcasses were made available to primary producers via remineralization, thus bolstering the standing stock of primary producers and providing a source of food for the scrapers that outlasts the presence of the salmon themselves (Cederholm et al, 1999). Under this scenario, primary producers would play a vital part in retaining nutrients in the system. Scrapers, in turn, might provide the valuable function of spiraling the benefits of additional nutrients upward through trophic levels as prey for predatory invertebrates and fish, including juvenile salmon.

Interactions between invertebrates and salmon when salmon function as predators rather than as nutrient vectors in these streams is another important topic of further investigation that may help reveal how salmon predation affects invertebrate assemblages on these streams. Fish predators alter the flow of resources to different components of the food web, with effects that can resonate throughout multiple trophic levels (Carlisle and Hawkins, 1998). For example, species- or size-based selection of prey by young salmon may alter the invertebrate community composition to favor certain functional feeding groups, depending on such variables as substrate and availability of refugia such as LWD and leaf packs (Diehl, 1992; Power et al, 1985; Power, 1990; Power, 1992; Reice, 1991).

In addition to considering top-down impacts that salmon may have on invertebrate communities, it would also be beneficial to study the role invertebrates may play in structuring fish assemblages through the bottom-up effects of food limitation. The observation has been made that there appear to be more fish in streams than macroinvertebrate populations can support, and some have certainly speculated that food supply is a limiting factor for salmonid density (Richardson, 1993; Chapman, 1966). Evidence for salmonid growth and distribution being limited by the benthic community includes such relationships as the positive correlation between growth rates of stream-rearing salmonids with aspects of invertebrate prey populations, particularly the abundance of shredders, and the positive correlation of salmonid populations with benthic biomass (Richardson, 1993).

In addition to differences in sample sizes on upper versus lower sites and unexpected findings for some functional feeding groups, another interesting feature of the data is the overall relative similarity of invertebrate communities between the upper and lower sites for both Fennel and Boise Creeks for many metrics. In contrast, upper and lower Clark's samples show almost no agreement between most metrics. While the upper site ranks the lowest of any on most diversity measures and the B-IBI, lower Clark's is among the most highly diverse sites for many metrics, including overall taxa. As considered before, Clark's Creek is possibly the site with the greatest disadvantage from the perspective of physical attributes because of the predominance of small substrate and high percentage of sand. However, in terms of fish usage, this creek is set apart from the other two by the sheer volume of fish that amass on this tiny tributary (Table 9). While Boise Creek receives the largest number of salmon of all three creeks, the density of fish that swarm to the scant stretch of viable habitat on lower Clark's dwarfs that of the other two creeks: a stunning 9,037 fish/km (Clark's actually only received roughly a third of this number of fish on its 0.48 m of spawning habitat), compared to 5,527 fish/km in Boise and 1,835 fish/km in Fennel. Not only fish density, but overall fish biomass is estimated to be surpassing on Clark's Creek relative to the other two because most of the fish utilizing Clark's Creek belong to large species—chinook and chum salmon—compared to the smaller pink salmon that dominate the runs on Boise and Fennel Creeks (Table 10).

As noted earlier, however, the small sample size of this study does not allow for verification of whether a causal relationship exists between density of spawners and diversity of invertebrate communities. One way to examine the relationship between salmon density and invertebrate diversity would be to sample creeks in years with pink salmon runs versus years without these fish and therefore the substantial load of nutrients they deliver. Another way to probe the question of the relationship between spawner density and the response from the benthic community would simply be to sample a large number of creeks with varying densities of spawning salmon. It should be noted that if the effects that salmon have on a give system increase with their biomass, then the label of "keystone" becomes inaccurate. That distinction is made for species which have the greatest ecological impact relative to their biomass (Mills et al 1993). Instead, salmon would more appropriately be called dominant species, which "are crucial for the maintenance of their communities, because they typically provide the major energy flow" for their community (Power et al, 1996).

The interactions between salmon and benthic macroinvertebrates are a closely linked portion of a much larger dynamic ecosystem which encompasses, and in part, is driven by these two groups of creatures. Continuing inquiry into this relationship is important in order to understand the ecological workings of the freshwater systems that these organisms share and also to continue to expand our knowledge of regarding the ecological significance of salmon at various stages of their life histories. Defining the role that salmon play in lotic systems and identifying the ways and degrees to which they affect or benefit the ecosystems of which they are a part are crucial steps in developing optimal strategies for the management and protection of this unique resource, whose full ecological complexity and value is incompletely understood.

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Table 8. Equations used to analyze samples. The equations listed below were used to derive the tables found in Results section. The various equations listed below are useful for obtaining numerical values for taxa richness, diversity, evenness, and similarity between 2 sites. All equations were obtained from Brower et al., 1989 and Zar, 1984.

Index	Equation	Application	Notes
Margalef	$D_a = \frac{(s-1)}{\log N},$ [1]	Community Richness	Incorporates total number of taxa and total number of individuals
Simpson's	$D_s = 1 - l$ [2]	Community Diversity	In addition to above variables also factors in proportion of sample occurring in each tax Calculates probability of randomly selecting 2 individuals from same taxon; based on dominance.
Statistical comparison of Simpson's	$t = \frac{(D_s)_1) - (D_s)_2}{\sqrt{s_1^2 + s_2^2}}$ [3]	Comparison of relative diversity of 2 sites	Allows null hypothesis that two communities are similarl diverse to be tested.
Shannon's	$H' = -\Sigma p_i \log p_i$	Community Diversity	Based on uncertainty principle: diversity is considered higher when ther is less certainty of the taxon a randomly selected individual.
Statistical comparison of Shannon's	$t_i = \frac{H_1' - H_2'}{\sqrt{s_1^2 + s_2^2}}$ [4]	Comparison of relative diversity of 2 sites	Allows null hypothesis that two communities are similar diverse to be tested.
Degrees of Freedom	$DF = \frac{(s^2_{H1'} + s^2_{H2'})}{\frac{(s^2_{H1'})^2}{n_1} + \frac{(s^2_{H2'})^2}{n_2}}$	To determine degrees of freedom for which t-value in above equation will be compared to critical Student *t*	
Evenness	$J' = H'/H_{max'}$ [5]	Evenness	Considers how closely abundances in samples compare to a hypothetical sample with same *N* and *s*, b with maximal diversity.
Jaccard	$CCj = \frac{c}{s_1 + s_2 - c}$ [6]	Similarity of taxa compositions	Quantifies community similarity based on presence or absence of taxa.
Morisita	$IM = \frac{2\Sigma x_i y_i}{(l_1 + l_2) N_1 N_2}$ [7]	Community Similarity	Based on Simpson's index Morisita refers to probabilit of randomly selecting individuals from same taxon from 2 communities relative probability of randomly selecting 2 individuals from the same taxon from 1 community.

1. s = number of taxa and N= total number of individuals

2. $l = \frac{\Sigma n_i(n_i-1)}{N(N-1)}$, where n=number of individuals in taxon

3. $s^2 = 4[\Sigma p_i^3-(\Sigma p_i^2)^2)]/N$, and $p_i= n_i/N$

4. $s^2 = \frac{\Sigma fi \log^2 fi-(\Sigma fi \log fi)^2/n}{n^2}$, where f=n and n=N

5. $H_{max'}= \log s$

6. c = common species

7. The "l" values are as defined for the Simpson's index

Table 9. Total 2004/2005 live count/escapement estimate of salmon on Boise, Clark's and Fennel creeks.

Creek	KM Spawning Habitat	Estimated escapement: Chinook	Estimated escapement: Coho	Estimated escapement: Chum	Estimated escapement : Pink	Density: Fish/km
Boise	7.24	397	3,285	0	36,335	5,527
Clark's	0.48	22	3	2,686	0	9,037
Fennel	2.74	13	133	1,596	3,287	1,835

Table 10. Salmon biomass estimates for Boise, Clark's, and Fennel creeks.

Creek	Chinook (kg)	Coho (kg)	Chum (kg)	Pink (kg)	Total estimated biomass (kg)	Total estimated biomass: kg/km
Boise	1,985	10,676.26	0	93,834.35	107,495.5	14,847.42
Clark's	110	9.75	12,006	0	12,126.17	25,265.85
Fennel	65	432	7,134.12	859.07	8,490.44	3,098.70