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MACROINVERTEBRATE COMMUNITY RESPONSE TO RIPARIAN RED ALDER WITHIN HEADWATER STREAMS OF SECOND-GROWTH FORESTS IN SOUTHEAST ALASKA

presented by

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MACROINVERTEBRATE COMMUNITY RESPONSE TO RIPARIAN RED ALDER WITHIN HEADWATER STREAMS OF SECOND-GROWTH FORESTS IN SOUTHEAST ALASKA

by

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ABSTRACT

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by

Ryan K. Kimbirauskas

Recent declines in Pacific Northwest salmon returns and the subsequent loss of in-stream nutrients have increased consideration for watershed restoration practices to include Red alder (*Alnus rubra* Bong.). Red alder is an aggressive pioneer species that colonizes disturbed soils, particularly within riparian corridors of young-growth forests following clearcut timber harvesting. Although riparian red alder appears to add nutrients to aquatic ecosystems, the thinning and removal of alder within regenerating forests is still practiced. In an effort to improve scientific knowledge about the ecological role of red alder on aquatic ecosystems, we compared benthic macroinvertebrate colonization of wood substrates among 13 headwater streams with a range riparian alder (0-53%). Research was conducted within the Maybeso Creek and Harris drainages on eastern Prince Of Wales Island, southeast Alaska. Alder wood, especially pieces in more advanced decay, generally supported greater density and diversity of macroinvertebrates than did conifer wood. Collectors and shredders responded to the presence of riparian alder, and streams with more alder in riparian habitats produced greater mean macroinvertebrate density and biomass. Results from this study suggested that the presence of alder along headwater corridors enhances macroinvertebrate productivity and may subsidize lost nutrients within Pacific Northwest watersheds, thus managing forested uplands to include red alder should be considered as a management tool to improve salmonid production.

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CHAPTER 1

BACKGROUND OF PREVIOUS RESEARCH EXAMINING THE EFFECTS OF CLEAR-CUT LOGGING ON HEADWATER HABITATS AND ASSOCIATED AQUATIC ECOSYSTEMS IN THE PACIFIC NORTHWEST

INTRODUCTION

Forest management practices have improved dramatically since large-scale commercial forestry began in the 1950's. Among these improvements are shifts from strict timber management to practices that preserve biodiversity and maintain long-term sustainability of all forest resources. In the Pacific Northwest, considerable attention has been aimed towards the effects of clearcutting on large streams that contain fish, particularly Pacific salmon. In recent years, there has been a growing concern with the management of small, headwater streams and their associated riparian habitats. Currently, the small, often fishless, streams that drain forested watersheds receive little or no protection during logging operations and management is based on limited scientific knowledge. Here I present a brief synopsis of recent studies that address these issues. I will comment on the direct and indirect effects of clearcutting on 1) in-stream temperature and thermal recovery, 2) macroinvertebrate community structure and production, and 3) wood recruitment into headwater streams. These findings are primarily from sites in the Pacific Northwest and central British Columbia and mostly published within the last decade.

TEMPERATURE & THERMAL RECOVERY

Among the many physical responses of headwater streams to clearcutting, stream temperature dynamics are the most extensively studied. This is primarily due to the negative impacts that even slight increases in stream temperatures can generate on aquatic organisms, particularly cool-water fish species. Macdonald et al. (2003a) studied the effects of various riparian harvesting practices on the temperature of first-order streams in northern British Columbia, Canada. The harvesting practices represented a range of possible forest management options for headwater streams as outlined by the Forest Practices Code of British Columbia. Results from this study showed that the daily maximum temperature increased 4-6 °C following harvest—even when partial riparian vegetation was intact. They also found that these temperatures remained elevated for 5 yrs following harvest. In the western Cascades of Oregon, the thermal recovery period following canopy removal was reported to be as long as 15 yrs within small streams (Johnson and Jones 2000). Story et al. (2003) compared stream temperature in cleared and shaded reaches of small streams in central British Columbia and found that stream temperatures generally cooled downstream, where the canopy was complete, and the magnitude of cooling depended to a large extent on fluctuations in streamflow from upstream reaches. Moore et al. (2003) found similar trends in stream cooling in two small tributaries downstream of clearings associated with logging. In southeast Alaska, Hernandez et al. (2004) compared the temperatures of headwater streams that flowed through old-growth, second-growth, and recently clearcut forests. Results showed that daily maximums were higher in the old-growth condition, however the greatest differences in maximum and minimum temperatures were found in the clearcut condition.

Future research with regard to thermal recovery and riparian disturbance will investigate the role of stream substrates and hyporheic flow on temperature fluxes in headwater streams (Macdonald et al. 2003b, Moore et al. 2003, Story et al. 2003).

NUTRIENTS & MACROINVERTEBRATE RESPONSE

Headwater streams deliver nutrients to downstream reaches and regulate energy flow in aquatic systems. In the Pacific Northwest, many of these small streams drain into larger systems that support Pacific salmon. Several studies in this region have examined the effects of timber harvest on the accumulation, storage, and transport of organic matter in forested watersheds (Bilby and Bisson 1992, Culp and Davies 1985, Hall et al. 1987). Recent interest has been directed towards the effects of logging on macroinvertebrate communities in headwater streams and the drift of this food source to juvenile salmon. Anderson (1992) provided a detailed account of macroinvertebrate response to disturbance in small, upland streams of the Pacific Northwest and found that logging activities alter the food source for macroinvertebrates and therefore, change the functional feeding group composition of invertebrate communities. Greater solar inputs and increased periphyton growth is common within recently cleared streams and may lead to initial increases in macroinvertebrate production (Cole et al. 2003, Fuchs 1999, Hernandez et al. 2004). Fuchs et al. (2003) found similar results in small streams of the central interior of British Columbia and suggested that, with the onset of canopy closure, macroinvertebrate production may return to prelogging conditions as early as 10 years following timber harvest. Wipfli (1997) identified terrestrial macroinvertebrates originating from riparian vegetation in second-growth forests as a major food source for downstream juvenile salmon and later found that drifting invertebrates provide enough biomass annually to support up to 2000 juvenile salmonids per kilometer of river (Wipfli and Gregovich 2002). In regenerating forests of southeast Alaska, the presence of riparian alder along headwater streams appears to enhance macroinvertebrate production (Lesage et al. 2003, Piccolo and Wipfli 2002, Wipfli and Musslewhite 2004). Price et al. (2003) compared invertebrate communities in headwater streams of old-growth and recently clearcut forests of British Columbia and found that stream size, persistence of flow, and canopy cover were good predictors of invertebrate abundance. They also suggested that forest management practices should offer protection during logging operations for intermittent, as well as, perennial streams.

RECRUITMENT & DISTRIBUTION OF WOOD DEBRIS

Wood produced from riparian vegetation is critical to the physical and biological attributes of forested streams and in some small streams appears to play a more prominent role than previously understood. In the Oregon Coast Range, May (2002) found that large wood entering headwaters during landslides could be delivered downstream to fish-bearing reaches. In southest Alaska, Martin and Benda (2001) quantified wood recruitment and redistribution mechanisms at the watershed scale and provided information on how and where to protect sources of wood debris that enter headwater streams. May and Gresswell (2003) investigated the recruitment and redistribution of large wood in headwater streams of the southern Coast Range of Oregon, and concluded that stream size and slope stability strongly influence the processes that recruit and redistribute wood in low-order channel networks. They suggested that the recruitment of large wood to high gradient streams may not be possible in intensely harvested basins that lack streamside buffers. A substantial proportion of the volume and number of pieces of large wood in Cummins Creek Watershed in western Oregon is up-slope derived wood (Reeves et al. 2003). These results were similar to those found in Redwood National Park, California (Benda 2002) and Olympic National Park, Washington (Benda et al. 2003). In western Washington, Ralph et al. (1994) and McHenry et al. (1998) reported less large wood in streams that flowed through second-growth forests compared to pre-harvest records. Both concluded that the removal of streamside vegetation was the reason for the reduction in recruitment of wood into streams. For 15 steep, headwater streams in southeast Alaska and demonstrated that timber harvesting within riparian habitats influences the recruitment, distribution, and accumulation of woody debris in forested watersheds (Gomi et al. 2001). Hernandez et al. (2004) reported similar results and also found differences in the recruitment of large wood into streams of alder and conifer dominated second-growth forests.

SUMMARY & MANAGEMENT IMPLICATIONS

Although small streams account for nearly 90% of the total channel networks in forested watersheds of the Pacific Northwest (Gomi et al. 2002), only recent efforts have been directed towards understanding their ecological role in aquatic ecosystems. Current management of headwater habitats, particularly in the context of timber harvesting, is therefore based on limited scientific knowledge and has lead to inconsistent practices and generated debate over the degree at which these areas should be managed. Recent interest has been given to the potential of managing forests to include red alder (*Alnus rubra* Bong.)as a way of improving timber, wildlife and aquatic resources. The focus of my research was to examine the role of riparian red alder on macroinvertebrate communities within headwater streams that flow through second-growth forests of southeast Alaska. The development of new policy regarding the management of headwater habitats depends on increased knowledge of upland habitats and a compromise between ecological and economic interests.

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CHAPTER 2

MACROINVERTEBRATE COMMUNITY RESPONSE TO RIPARIAN RED ALDER WITHIN HEADWATER STREAMS OF SECOND-GROWTH FORESTS IN SOUTHEAST ALASKA

INTRODUCTION

Riparian zones are the interfaces between terrestrial and aquatic environments and represent one of the most dynamic habitats of forested watersheds. The water, sediment, and wood that enter small streams from riparian habitats are critical to the structure and functional stability of headwaters and their downstream reaches (Carline and Spotts 1998, Haigh et al. 1998, Naiman et al. 1992, Wipfli and Gregovich 2002). Wood produced from riparian vegetation controls embankment erosion, stabilizes channel flow, provides habitat for invertebrates and fish, and regulates nutrient and energy flow (Bilby and Likens 1980, Cummins et al. 1989, May 2002, Reeves et al. 2003, Wallace et al. 1997, Webster et al. 1992). Disturbing riparian habitats alters the physical characteristics of adjacent streams and disrupts the energy flow in aquatic ecosystems (Bisson et al. 1987, Bryant 1985, Dudley and Anderson 1982, Philips and Kilambi 1994). In the Pacific Northwest, the freshwater ecosystems that support juvenile salmon appear to be nutrient limited (Ashley and Slaney 1997); disturbing headwater habitats may reduce nutrients downstream and limit the production of salmon (Hayes et al. 2000, Resh et al. 1988, Wipfli and Gregovich 2002).

Timber harvesting has been identified as a both a short and long-term disturbance that alters the energy base upon which forested headwaters and downstream food webs are dependent (Alaback 1982, Duncan and Brusven 1985, Stone and Wallace 1998, Wipfli 1997). Clearcutting, a method of harvesting and regenerating timber in which all trees are cleared from a site, can immediately reduce total benthic macroinvertebrate densities up to 50% (Hartman et al. 1996). Removing riparian vegetation also directly eliminates input of wood debris into adjacent streams and reduces input of large wood for many years (Bragg 1997, Bryant and Sedell 1995, May and Gresswell 2003, McHenry et al. 1998). Maintaining in-stream wood habitat is advantageous for large numbers of benthic invertebrates that could potentially benefit the diet of fish downstream (Hernandez et al. 2004, Wipfli 1997). Small streams are more easily disrupted than larger rivers and clearcutting and the process of forest regeneration in headwaters may alter downstream production (Plotnikoff 1994). Because red alder is a common riparian hardwood of regenerating forests in the Pacific Northwest, recent interest has been generated with respect to its effect on macroinvertebrate communities and associated food webs (Haggerty et al. 2004, Richardson and Shaughnessy *in press*, Wipfli and Gregovich 2002).

Red alder is an aggressive pioneer species with a range extending from southern California to southeast Alaska (Harrington 1990). The process of clearcutting creates a disturbance where mineral soils are exposed (Newton and Cole 1994) and the shade intolerant alder quickly colonize riparian habitats along cleared stream banks, abandoned logging roads and log transfer sites (Harrington 1990, Hulten 1968, Newton et al. 1968)(Figure 1). Red alder may remain at these locations up to 80 years before being outgrown by conifers (Hibbs et al. 1994). Historically, forest managers regarded red alder as an undesirable species and attempted to remove it from riparian and upland forest stands; however, its ability to supply the soil with fixed nitrogen (Briggs et al. 1978, Gordon et al. 1979, Trappe et al. 1968) encouraged its use as a management tool to enhance productivity of young-growth conifer forests in the Pacific Northwest (Binkley 1981, DeBell et al. 1978). The presence of red alder in riparian habitats also appears to benefit associated aquatic ecosystems (Allan et al. 2003, Irons et al. 1988, Wipfli 1997, Wipfli et al. 2002) and may increase benthic macroinvertebrate abundance (Hernandez et al. 2004, Wipfli et al. 2003). Therefore, managing upland young-growth forests to include red alder may have substantial effects on salmon production in southeast Alaska.

Large-scale commercial logging and clearcutting in southeast Alaska began in the 1950s (Swanston 1967). During this period, management of riparian debris was inconsistent (Bragg and Kershner 1999) and harvesting timber and developing logging roads took priority over all other uses and resources of the forest (USDA 1997). Clearcutting is still the most common practice of removing trees in southeast Alaska; however, current policies include protection for streams and rivers that support salmon (USDA 1999). For example, riparian buffer strips are required on fish-bearing streams during logging operations to prevent loss of allochthanous inputs to aquatic ecosystems; however, many of the small fishless streams within forested areas receive little or no protection during a clearcut (USDA 1997). Headwater streams account for 70% - 90% of watershed channel systems in southeast Alaska (Gomi et al. 2002, Swanston 1967), and food generated from these headwaters plays a major role in regulating salmonid production (Hayes et al. 2000). Wipfli (1997, et al. 2002) found that over half of the prey biomass ingested by juvenile salmonids in southeast Alaska is terrestrial invertebrate prey that originates from upstream riparian vegetation. Because headwater streams drain into larger systems containing salmon, the immediate and long-term effects of clearcutting along headwaters need to be addressed.

Wood is critical to the formation of debris dams and retention of organic materials in streams (Bilby and Likens 1980, Cummins and Klug 1979), therefore it is important to understand the strength properties and decay patterns of wood in streams. Wood in terrestrial environments is broken down by saprophytic fungi and wood-boring invertebrates causing weight and strength loss (Lesage 2003, Worrall 1999). Aerobic fungal hyphae do not penetrate saturated wood surfaces and most aquatic invertebrates that contribute to the degradation of wood do not bore or penetrate deeply (Anderson et al. 1978, Chergui and Pattee 1991). Therefore, logs similar in size and species decay slower in streams than in terrestrial environments (Bilby et al. 1999). Studies comparing the breakdown of red alder and conifer wood in streams of the Pacific Northwest showed that alder decays more rapidly than conifer, and after three years begins to lose structural integrity from advanced decay and breakage (Cederholm et al. 1997, Keim et al. 2000). In Alaska, all types of wood in streams are expected to decay slower than more southern states due to cooler average air and water temperatures (Wipfli et al. 2002). Interest in wood decomposition in aquatic environments has primarily involved the importance of wood strength and decay on the stream structure and fish habitat. Less is known about the role of decaying wood as a source for macroinvertebrate community recruitment and colonization.

My overall objective was to assess the ecological role of red alder in benthic macroinvertebrate community structure in headwater streams of regenerating forests in southeast Alaska. I compared and contrasted macroinvertebrate density, biomass, and diversity associated with red alder and conifer wood in headwater streams with a range of riparian red alder. The hypotheses I tested were: 1) all macroinvertebrate community attributes would be greater on red alder than on conifer wood; and 2) these same attributes would increase as the presence of riparian red alder increased. In addition to the role of alder in and along streams, I was interested in potential effects that the stages of wood decay might have on benthic macroinvertebrate communities. I tested the null hypothesis that there is no difference in macroinvertebrate density, biomass and diversity on pieces of wood in early stages of decay versus wood in more advanced decay.

METHODS/MATERIALS

I. Stand Selection & Study Sites

Research was conducted on Prince of Wales Island, southeast Alaska (132°67'W, 55°49'N)(Figure 2). This region contains more extensive tracts of virgin, old growth forest than anywhere else in the United States (USDA 1997) and offers exceptional opportunities to study ecological interactions between red alder, site conditions and stream communities in an evolutionary context. Study sites were in the Maybeso Creek and Harris watersheds (46 km^2 and 108 km^2, respectively) on the eastern end of Prince of Wales Island (Figure 3). This area was heavily logged in the 1950s, and in the 1960s local and federal governments established the Maybeso Experimental Forest to study the impacts of commercial logging on wood production, wildlife, and fisheries (Wipfli et al. 2002). The varying amounts of riparian alder and standing old growth within the Maybeso Experimental Forest made this an ideal site to complete our research objectives. Sampling sites for this project were limited to fishless headwater streams within forested stands of 5-10 ha with elevations less than 150 m. The primary sample site selection criterion was riparian tree species composition to provide a range of 0-53% red alder.

Aerial photographs, U.S. Forest Service district files and field visits were used to select 13 headwater streams for this study. To reduce variability, all streams were 3rd order or less, had channel slopes between 10-28 degrees, and bankfull widths between 0.7-3.4 m (Wipfli et al. 2002). Stream flow in 2002 ranged from 1-116 $L \cdot s^{-1}$ (Table 1). Sampling was restricted to 250-300 m reaches within each stream. Riparian understory vegetation and tree species composition was measured within the designated sampling area at each stream as described by Wipfli *et. al.* (2002). Salmonberry (*Rubus spectabilis* Pursh.), Devils Club (*Oplopanax horridum* Miquel.), Skunkcabbage (*Lysichitum americanum* Hutten and S. J.), ferns, and mosses dominated the riparian understory. Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Alaska yellow cedar (C*hamaecyparis nootkatensis* (D. Don) Spach.), and Sitka spruce (*Picea sitchensis* (Bong.) Carriere.) were common coniferous species, and the dominant hardwood was red alder. Streams were from stands with mixed alder-conifer vegetation that represented a range of riparian red alder from 0-53 % (Table 1).

II. Wood Collection & Experimental Design

In order to survey the macroinvertebrates associated with wood, pieces of naturally occurring alder and conifer (approx. 5 x 20 cm) representing early and late decay classes were randomly collected from all 13 streams (except one site that had no alder) during May and July of 2001 and 2002. A piece of wood was considered late decay if a thumbnail could easily penetrate the surface—all others were considered early decay. In addition to collecting macroinvertebrates from naturally occurring wood, we also collected macroinvertebrates from wood that had been secured to substrate holders and was experimentally added to streams as describes below.

Wood to be secured to substrate holders was collected from standing snags within the Maybeso Experimental Forest. Boles from alder and conifer were initially divided into early and late decay classes based on color, weight, and presence or absence of bark and branches. Boles had uniform diameters ranging from 3 - 5 cm and lengths of 1 - 6 m. The longer pieces were later cut into 20 cm sections. The middle section and end pieces from each bole were dried, weighed, and water displacement was used to test for consistency across the density gradient and to confirm the stage of decay. Boles that showed irregularities in density and sections containing knots were excluded from the study. Wood pieces representing four treatments: early decay alder, late decay alder, early decay conifer, and late decay conifer were then randomly arranged and secured to plastic substrate holders (Figure 4). A total of nine substrate holders were placed in each of six streams in a randomized complete block design. The sub-plot factor was wood type and consisted of the treatments: EA, LA, EC, and LC. The whole-plot factor was riparian alder-conifer species composition and represented a range of riparian red alder from 1.5 - 47%. Substrate holders were placed in a variety of habitats, however placement was often restricted to shallow pools due to low water levels. All holders were set July 7-14, 2000 and remained in the streams for either 1 or 2 yrs. Three substrate holders from each site were randomly selected and collections took place in early July of 2001 and 2002.

III. Macroinvertebrate Sampling and Analysis

Macroinvertebrates were sampled from both added wood substrates and naturally occurring woody debris. Individual pieces were pulled from the stream and transferred to a 19 L bucket for processing. Each piece of wood was rinsed with a hand-pumped portable pressurized sprayer and the contents of the bucket were strained through a 250-micron sieve. Invertebrates were washed into 250-ml Whirlpaks® with 80-percent ethanol and returned to the lab for sorting under a dissecting microscope. Macroinvertebrates were picked from each sample and identified to the lowest taxonomic unit possible using Merritt and Cummins (1996a). Measurements of the total length were made for each identified specimen and length-weight regressions were used to estimate individual biomass (Benke et al. 1999, Hodar 1996, Smock 1980). Wood surface area was estimated from length and diameter using the equation for the surface area of a cylinder, and macroinvertebrate biomass m^2 and number m^{-2} were calculated for each piece of wood. Diversity was measured using the Shannon-Weiner diversity index

(Hauer and Resh 1996). Functional feeding group ratios were calculated to help assess stream ecosystem parameters (Merritt and Cummins 1996b).

Results from the dependant variables of invertebrate density, biomass m^2, and diversity were tested for normality, log (x + 1) transformed when necessary, and analyzed for significance using SAS (SAS Institute 1996). Multiple T-tests and ANOVA were generated contrasting the dependant variables with percent riparian alder, wood type (conifer or red alder), and decay class (early or late decay). Percent riparian alder was grouped into three bins of low (0-9%, n=4), medium (10-35%, n=5) and high alder (36-53%, n=4) and Bonferroni adjustments were made for the analysis. Pairwise comparisons were generated for all dependant variable results with a significant ANOVA ($p < 0.05$)(Sokal and Rolf 1969) using Tukey's Studentized Range (HSD) post-hoc test. All graphs and tables are presented using nontransformed data.

RESULTS

I. Macroinvertebrates Community Composition & Functional Feeding Groups

Over 10, 000 macroinvertebrates from 14 different orders were recorded from wood samples. At least 54 insect taxa were identified, but of those taxa a relatively small number comprised most of the total count and biomass densities (Table 2). Total chironomid taxa comprised 56% of the total relative abundance, and chironomids in the subfamily Orthocladiinae accounted for 70% of all chironomids (Figure 5). Nearly half of the total count biomass was from only two genera—a heptageniid mayfly, C*inygma* and a rhyacophilid caddisfly, *Rhyacophila*. Functionally, collector-gatherers (Chironomidae, Baetidae, Leptophlebiidae) were the most abundant group collected (71%), followed by predators (Rhyacophilidae, Chloroperlidae, Empididae)(11%), shredders (Nemouridae, Leuctridae)(10%), scrapers (Heptageniidae)(8%), and collector-filterers (Simuliidae)(1%)(Figure 6).

Overall, functional feeding group colonization of alder and conifer wood was not different. A slight increase in scrapers on alder wood (79%) compared to conifer wood (59%) was observed in May 2001, however, by July 2001 the relative abundance of scrapers was similar (58%). During the same period in 2001, the relative abundance of predators on alder increased from 6% in May to 36% in July. This was primarily due to an increase in numbers of *Rhyacophila* on pieces of alder wood. The relative abundance of predators and the caddisfly *Rhyacophila* were consistant on conifer wood throughout 2001 and 2002 (34%). The amount of riparian alder did appear to influence the distribution of some feeding groups and individual taxa. Over the entire sampling period, collector-gatherer relative biomass increased from 9% to 20% as the percentage of riparian alder increased from low (0-9%) to high (36-53%). The realtive biomass of collector-filterers, exclusively *prosimulium*, also increased with gretaer amounts of riparian alder. The relative biomass of scrapers, on the other hand, decreased from 71% to 56% as the percentage of riparian alder increased, and shredder biomass also decreased as the amount of riparian alder increased. Total predator distributions did not appear to be influenced by the presence of riparian alder in this study (Figure 7); however, the caddisfly *Rhyacophila* was positively correlated with an increasing presence of riparian alder.

II. Macroinvertebrate Density, Biomass & Diversity

Overall, streams with more riparian alder generally supported greater density and biomass of macroinvertebrates than did streams with low riparian alder. The densities of macroinvertebrates associated with natural wood were significantly greater ($p > 0.05$) in streams with high percentages of riparian alder (>36%) than in streams with low riparian alder (<10%)(Figure 8A). Densities of macroinvertebrates collected from added wood were also greater in streams with more riparian alder, however these differences were not significant ($p < 0.05$). Likewise, the mean biomass of macroinvertebrates collected from added wood was greater in streams with more alder, but were not significantly different. The presence of riparian alder did have an effect on the biomass of macroinvertebrates collected from naturally occurring wood ($p < 0.05$; Figure 8B), but variability among groups led to difficulty in clearly establishing differences among individual levels of alder. The diversity of macroinvertebrates collected from added wood was slightly greater in streams with more riparian alder, however, these differences were not significant and the diversity of macroinvertebrates collected from natural wood showed no differences with lower or higher amounts of riparian alder.

Wood type and decay class had some effect on benthic macroinvertebrate density, biomass, and diversity. Both density (Figure 9A) and diversity (Figure 10A) of macroinvertebrates collected from natural and added wood substrates were greater on alder than on conifer, but statistically these differences were not significant. However, when converted to biomass, naturally occuring pieces of conifer wood supported a significantly greater mass of benthic macroinvertebrates than naturally occuring alder wood (Figure 9B; $p < 0.01$). Mean biomass of macroinvertebrates collected from added wood substrates was not significantly different and was greater on alder. Overall, pieces of wood in later stages of decay generally supported greater density, biomass (Figure 11), and diversity than did pieces of wood in more recent stages of decay, however, only diversity of macroinvertebrates (associated with natural wood in later stages of decay was significantly different $p < 0.05$)(Figure 10B).

DISCUSSION

Results from naturally collected wood showed that the presence of riparian alder in second-growth forests appeared to influence the density of benthic macroinvertebrates associated with wood surfaces in southeast Alaskan headwater streams. Anderson et al.'s (1978) findings in two Oregon watersheds were similar and he suggested that the higher in-stream macroinvertebrate densities were due increased organic inputs from alder vegetation. Culp and Davies (1985) also found higher macroinvertebrate abundance associated with alder litter. On Prince of Wales Island, Hernandez et al. (2004) found that streams with alder-dominated young-growth riparian vegetation supported higher densities of benthic macroinvertebrates on gravel, cobble, and wood substrates. Wipfli and Musselwhite (2004) found that the density of macroinvertebrates collected in 24-hour drift samples increased with the presence of riparian alder, and Wipfli and Gregovich (2002) indicated that the abundance of terrestrial insects collected from stream drift significantly increased as the percent basal area of alder increased along riparian zones. In a study concurrent with this one, Lesage et al. (2003) compared macroinvertebrates colonizing terrestrial litter and wood along the same streams. Results from their study showed that invertebrate density, taxa richness, and biomass increased when the percentage of riparian alder increased.

Naturally collected wood debris from streams also showed an increase in macroinvertebrate biomass associated with an increasing presence of alder in riparian forests. This increase in biomass may be the result of greater nutrient availability. Alder is a better food source for herbivorous invertebrates and aquatic shredders than is conifer litter (Irons et al. 1988, Webster and Benfield 1986) and alder leaves are processed more quickly than conifer needles (Cummins et al. 1989, Lesage et al. 2003, Sedell et al. 1975). Streams with alder in riparian forests deliver more alder litter to macroinvertebrate communities than streams with more conifer and this may lead to increased production of benthic macroinvertebrates (Stone and Wallace 1998). Piccolo and Wipfli (2002) identified alder in forested riparian zones as critical habitat for terrestrial invertebrates that fall prey to fish, and Wipfli (1997, et al. 2002) found that over half of the prey biomass ingested by juvenile salmonids in southeast Alaska was drifting terrestrial invertebrates that originated from upstream riparian vegetation. In an ensuing study, Wipfli and Gregovich (2002) found that the biomass of drifting macroinvertebrates in headwater streams increased as the presence of alder increased in riparian forests. In southeast Alaska, where freshwater ecosystems appear to be nutrient limited (Ashley and Slaney 1997, Wipfli and Gregovich 2002), prey biomass generated from riparian alder vegetation and its associated litter may improve stream productivity. Past management practices in southeast Alaska include removing alder from regenerating forests, however results from recent studies in the Pacific Northwest and southeast Alaska show that including an alder component to young-growth upland forests generates more prey biomass to downstream salmon and may increase salmonid production (Hernandez et al. 2004, LeSage 2003, Wipfli and Gregovich 2002, Wipfli and Musselwhite 2004).

This research did not show a relationship between macroinvertebrate diversity and an increasing presence of alder in riparian habitats on either added wood substrates or naturally collected wood in headwater streams. Previous studies in the Pacific Northwest have shown that benthic macroinvertebrate diversity was greater in old-growth than in either recently clearcut or second-growth forest riparian habitats (Anderson 1992, Newbold et al. 1980). However, on Prince of Wales Island, Hernandez et al. (2004) found that the diversity of stream macroinvertebrates was significantly greater in alder dominated second-growth than in old-growth watersheds and suggested that the greater diversity was due to changes in food resources and the availability of more labile allochthonous inputs generated from deciduous alder vegetation. Lesage (2003) found that terrestrial invertebrate richness and diversity was significantly greater in riparian habitats where alder was present and concluded that increasing the presence of alder may contribute to increased production of higher tropic levels. We did not find a difference in macroinvertebrate diversity, however the mean biomass of the trichopteran *Rhyacophila* (Rhyacophilidae)—the most common predator collected—did increase with the presence of riparian alder. This suggests that the presence of alder in riparian corridors may contribute to an increased production of specific higher trophic levels in aquatic organisms.

Macroinvertebrate colonization of wood surfaces showed that mean biomass was significantly greater on conifer compared to alder wood debris. The greater biomass on conifer wood was primarily due to an increase in the presence of two taxa: the heptageniid mayfly *Cinygma* and the rhyacophilid caddisfly *Rhyacophila.* Mayflies in this genus are largely restricted to wood substrates (Anderson et al. 1978), and were observed in this study scraping wood surfaces—presumably feeding on periphyton and detritus. The caddisfly *Rhyacophila,* one of the larger invertebrates collected, was often found associated with protective niches on wood surfaces and may have been more common on conifer due to its cracking nature during decomposition (Wipfli et al. 2003). Both mean density and diversity of macroinvertebrates were greater on alder, however differences were not statistically significant due to large variation between samples. Contributing to the variation in mean densities between conifer and alder were higher counts of midge taxa on some individual pieces of alder. Because chironomids tend to be ubiquitous, it is difficult to identify the specific role alder plays in their colonization, but the presence of xylophagous midges in the subfamily Orthocladiinae and large numbers of pupae and tubes of midges in the subfamily Tanytarsani, suggests that the wood surfaces are being used as both food source and refuge. Results from this study did indicate that macroinvertebrate colonization of wood surfaces appears to be more closely associated with stage of decay than wood type.

Overall, macroinvertebrate density, biomass and diversity was greater on wood in advanced stages of decay. Dudley and Anderson (1982) suggested that wood as a food resource becomes available to more taxa as surface decay progresses, and Golladay and Webster (1988) found that functional feeding groups using wood were directly associated with the decay of wood surfaces. There was evidence of feeding on wood in our study, however most of the macroinvertebrates colonizing wood were probably using this habitat for resting, refuge, and oviposition. Wood in later stages of decay provided more area of this habitat. Evidence that the decay of wood surfaces may be a greater contributor to macroinvertebrate colonization than wood type was found in the results of our experiments with added wood substrates. Although two decay classes of conifer and alder were used as added wood, the surfaces of all wood pieces used were smooth and very similar structurally. The similarities in wood surfaces may explain why there were no differences in colonization between wood types. The *rhyacophilid* caddisflies commonly collected within cracks and crevices of natural wood was further evidence that decay influenced colonization patterns. Anderson et al. (1978) described several taxa from streams in the Pacific Northwest that used the protective niches on wood surfaces for oviposition, as a nursery for early instars, molting, pupation, emergence, and as a source of prey. McLachlan (1970) found that mayflies more readily colonized submerged wood with bark previously damaged compared to newer pieces with solid bark. High densities of *baetid* mayflies were collected from wood surfaces in our study, and both conifer and alder wood classified as late decay supported greater mean densities. Whether the decaying process conditions wood surfaces for feeding or creates more interstitial spaces for refuge, it appears as though wood with greater surface decay and more available interstitial spaces are more attractive to benthic macroinvertebrates. Managing young-growth forests to include Red alder may improve benthic macroinvertebrate habitat, because alder generally dies standing (Wipfli et al. 2002) and produces more litter in advancing stages of decay than do conifers (Zavitkovski and Newton 1971).

Changes in macroinvertebrate functional feeding groups shifted in relation to riparian alder vegetation. Collector-gatherer communities, dominated by midge taxa and the baetid mayfly (*Baetis sp.*), gradually increased as the percentage of riparian alder increased. Increases in collector-gatherer groups have been associated with increased loads of fine particulate organic matter (Cuffney and Wallace 1989, Cummins 1973, Richardson and Neill 1991), and inputs from riparian alder may contribute to this nutrient load. Scraper populations, on the other hand, decreased with more riparian alder. In the light-limited small streams of the Pacific Northwest, clearcutting can result in increased solar radiation (Bisson and Bilby 1998), which also increases primary production and the abundance of scrapers (Hernandez et al. 2004, Murphy et al. 1981, Wallace et al. 1988). The lower percentage of scrapers found in headwaters on Prince of Wales Island was comparable to results found in other headwater streams in regenerating forests of the

Pacific Northwest, most likely due to canopy closure (Cole et al. 2003, Haggerty et al. 2004). Although it was difficult to determine the specific role of alder on macroinvertebrate functional group relationships from this study, changes in feeding group compositions are typically the result of changes in food type and its availability (Merritt and Cummins 1996b, Vannote et al. 1980). It does appear that increased organic material from riparian alder vegetation provides more food resources for some macroinvertebrate taxa in headwater streams on Prince of Wales Island.

CONCLUSION

Managing upland forests to include a red alder component may provide more suitable conditions for macroinvertebrate communities and therefore, improve the potential of nutrients to reach downstream ecosystems. In southeast Alaska, fresh water ecosystems are generally nutrient limited (Ashley and Slaney 1997, Wipfli 1997) and the presence of red alder in riparian habitats could protect or even improve the productivity of aquatic organisms—including downstream salmonids. Current forest management plans for southeast Alaska include clearcutting and alder-thining within headwater habitats (USDA 1999), which may greatly effect macroinvertebrate communities and food resources for juvenile Pacific salmon (Hayes et al. 2000, Hernandez et al. 2004, Resh et al. 1988, Wipfli and Gregovich 2002). Recent declines in Pacific salmon returns have increased consideration for the development of new policies which protect salmon and all forest resources. Results from this study, and recent findings in the Pacific Northwest, suggest that provisioning for red alder in forested uplands should be considered as a management tool to improve downstream salmonid production in southeast Alaska, and elsewhere.

Table 1. Physical and biological characteristics of headwater streams and adjacent riparian forest on Prince of Wales Island, Alaska, 2000.

Stream	Channel Slope[1] (deg.)	Bankfull Width[2] (m)	Stream Flow[3] ($L \cdot s^{-1}$)[3]	Basal Area[4] (% red alder)
Lost Bob	19.5	0.7	7.4	0.0
Upper Good Example	13.6	0.9	3.0	1.5
Cedar 2	18.8	1.7	4.5	3.8
Upper Morning	14.5	1.1	4.7	3.9
Creature Creek	15.2	1.1	36.0	10.0
Gomi	26.1	1.0	5.5	25.0
Mile 22	18.3	1.2	1.5	29.2
Big Spruce	26.3	0.9	0.9	31.5
Cedar 1	19.3	1.6	16.0	35.6
Broken Bridge West	22.5	1.5	3.9	38.7
Cotton	27.2*	3.4	116.2	43.2
Broken Bridge East	10.7*	2.2	24	47.3
Brushy	15.5	0.9	1.4	53.3

[1] Channel slope gradient of entire stream; * measured on 25% of stream length only.

[2] Bankfull width – the dominant channel forming flow (Dunne and Leopold 1978).

[3] Mean stream flow at transition zone.

[4] Percent red alder as a proportion of total stand basal area.

Table 2. Checklist of taxa collected and the percent relative density and biomass for each taxon collected. Totals are combined over the entire study period.

Taxon	**% Relative Abundance** **Numbers**	**Biomass**
Collembola		
Entomobryiidae	0.7	0.1
Hypogastruridae	<0.1	<0.1
Sminthuridae	0.1	<0.1
Coleoptera		
Dytiscidae, *Liodessus*	<0.1	<0.1
Elmidae, *Narpus*	<0.1	<0.1
Hydrophilidae, *Ametor*	0.1	0.5
Ptilodactylidae, *Araeopidius*	<0.1	0.1
Diptera		
Ceratopogonidae, *Ceratopogon*	<0.1	<0.1
Ceratopogonidae, *Probezzia*	0.2	<0.1
Chaoboridae, *Eucorethra*	<0.1	<0.1
Chironomidae	1.2	0.2
Chironomidae, *Chironominae*	4.2	1.1
Chironomidae, *Diamesinae*	0.1	<0.1
Chironomidae, *Orthocladiinae*	39.5	1.3

Table 2. (cont.)

Chironomidae, *Tanypodinae*	2.2	0.6
Chironomidae, *Tanytarsani*	10.8	2.2
Dixidae, *Dixa*	0.7	<0.1
Empididae, *Chelifera*	3.5	0.4
Empididae, *Clinocera*	<0.1	<0.1
Empididae, *Oregeton*	<0.1	<0.1
Psychodidae, *Pericoma*	<0.1	<0.1
Pyralidae	<0.1	<0.1
Sciaridae	<0.1	<0.1
Simuliidae, *Prosimulium*	0.9	3.0
Tipulidae, *Dicranota*	0.3	0.1
Tipulidae, *Hexatoma*	0.1	<0.1
Tipulidae, *Limonia*	<0.1	<0.1
Tipulidae, *Molophilus*	<0.1	<0.1
Ephemeroptera		
Ameletidae, *Ameletus*	<0.1	<0.1
Baetidae, *Baetis*	6.7	7.3
Ephemerellidae, *Drunella*	0.8	1.6
Heptageniidae, *Cinygma*	4.1	37.6
Heptageniidae, *Cinygmula*	0.3	19.3

Table 2. (cont.)

Heptageniidae, *Epeorus*	1.8	0.4
Heptageniidae, *Ironodes*	<0.1	1.0
Heptageniidae, *Rhithrogena*	<0.1	<0.1
Leptophlebiidae, *Paraleptophlebia*	6.4	2.6
Plecoptera		
Chloroperlidae, *Suwalia*	0.1	0.1
Chloroperlidae, *Sweltsa*	0.9	1.0
Leuctridae, *Despaxia*	1.3	0.9
Nemouridae, *Zapada*	7.0	1.7
Trichoptera		
Brachycentridae, *Micrasema*	1.3	0.2
Goeridae, *Goeracea*	0.2	0.2
Hydropsychidae, *Arctopsyche*	0.1	0.7
Limnephilidae, *Allomyia*	<0.1	<0.1
Limnephilidae, *Chyranda*	<0.1	0.5
Limnephilidae, *Cryptochia*	0.2	0.1
Limnephilidae, *Ecclisiomya*	<0.1	<0.1
Limnephilidae, *Moselyana*	<0.1	<0.1
Limnephilidae, *Psychaglypha*	0.2	1.5

Table 2. (cont.)

Philopotamidae, *Dolophiloides*	0.2	0.1
Philopotamidae, *Wormalidia*	<0.1	<0.1
Ryacophilidae, *Rhyacophila*	3.4	13.6
Uenoidae, *Neophylax*	0.2	0.3
54 total taxa	100	100

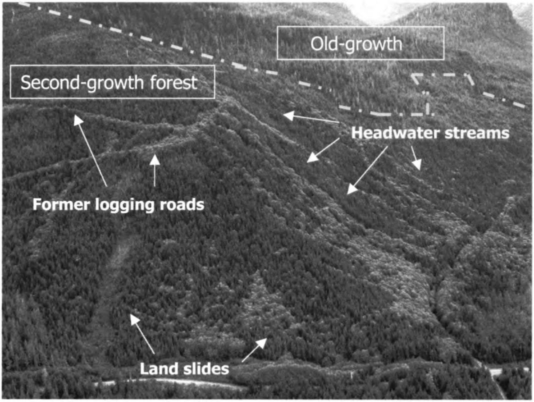


Figure 1. Red alder colonization following soil disturbance along cleared stream banks, abandoned logging roads and landslides within the Maybeso Experimental Forest on Prince of Wales Island, southeast Alaska.

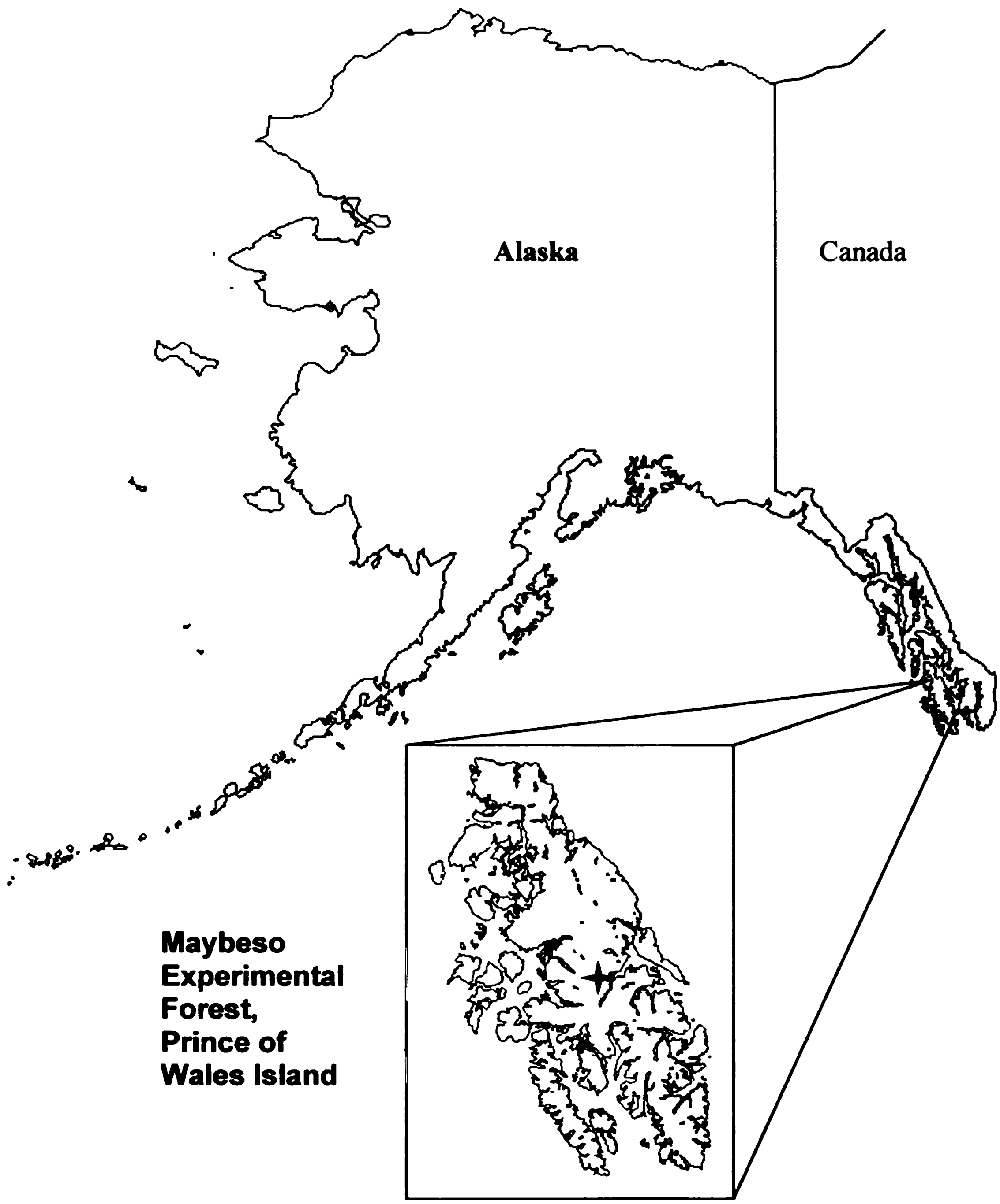


Figure 2. Research was conducted within the Maybeso Experimental Forest on eastern Prince of Wales Island, southeast Alaska (132°67'W, 55°49'N).

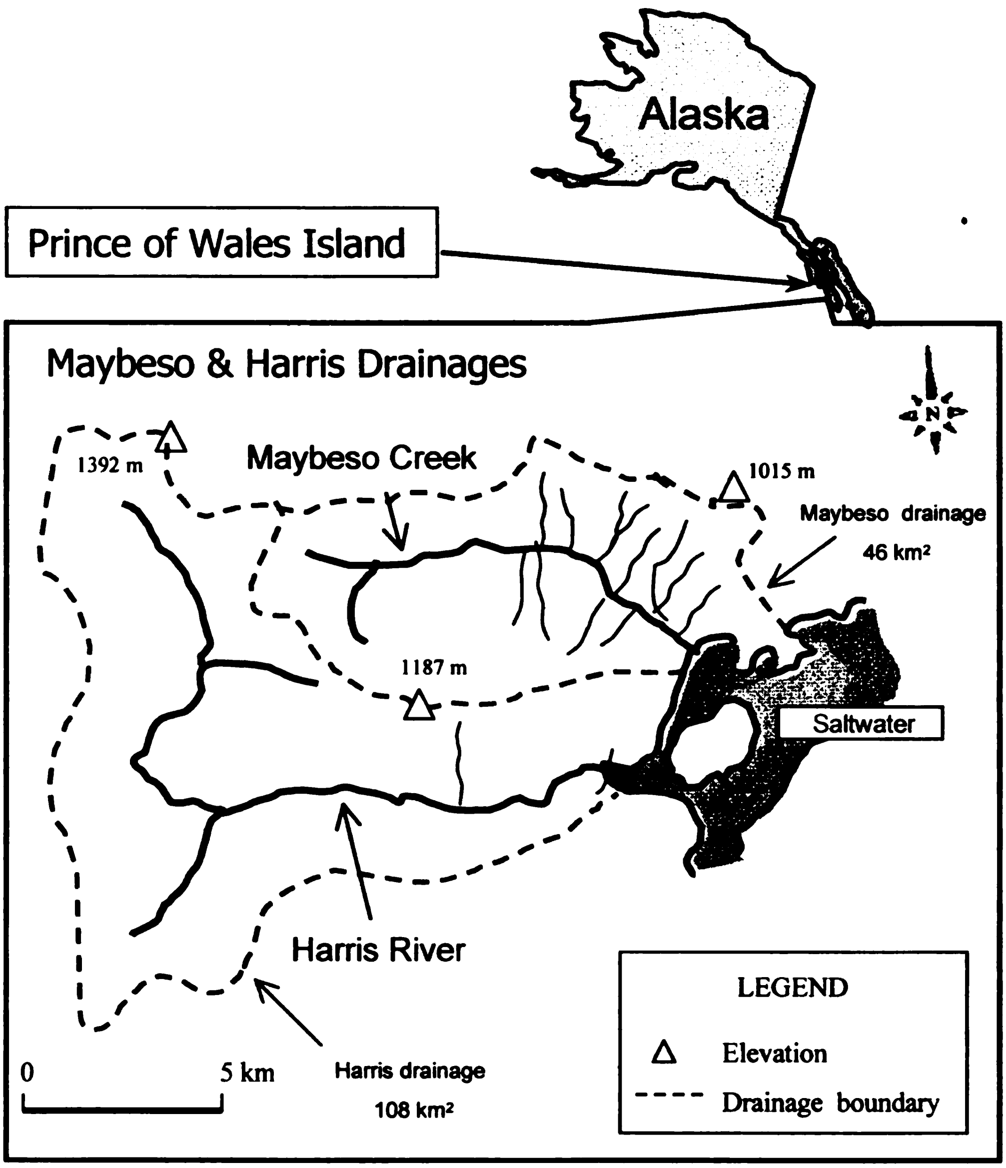


Figure 3. Study sites within Maybeso Creek and Harris River drainages on Prince of Wales Island, SE Alaska (132°67'W, 55°49'N).

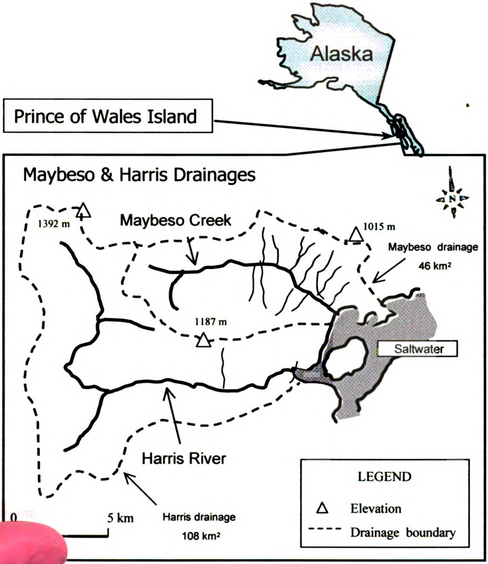


Figure 3. Study sites within Maybeso Creek and Harris River drainages on Prince of Wales Island, SE Alaska (132°67'W, 55°49'N).

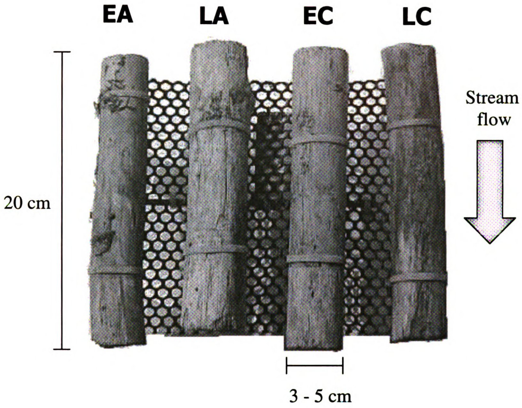


Figure 4. Macroinvertebrates were collected from the surfaces of wood pieces representing four treatments: early decay alder (EA), late decay alder (LA), early decay conifer (EC) and late decay conifer (LC). Pieces were randomly arranged and secured to plastic substrate holders.

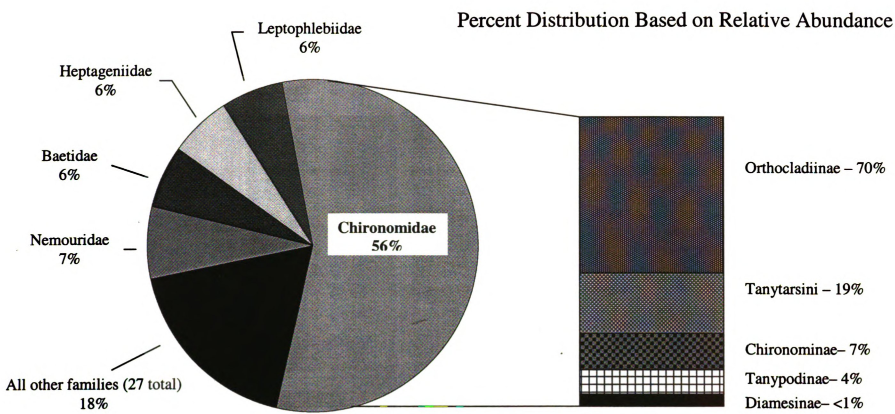
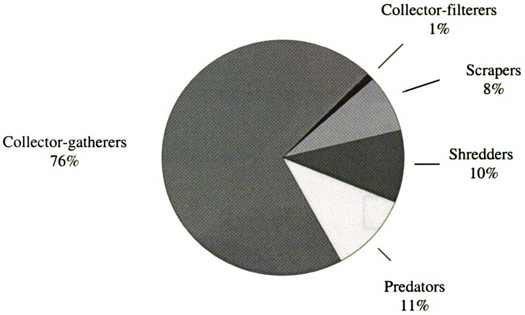


Figure 5. Relative abundace of the top five families collected and represented midge subfamilies. Values are combined for all three sampling dates between 2001 and 2002.

Functional Feeding Group Relative Abundance



Dominant Families Within Feeding Groups:

Collector-gatherers	Predators	Shredders	Scrappers	Collector-filterers
Chironomidae	Rhyacophilidae	Nemouridae	Heptageniidae	Simuliidae
Baetidae	Chloroperlidae	Leuctridae		
Leptophlebiidae	Empididae			

Figure 6. Relative abundance of functional feeding groups and the dominant families within each of the five feeding groups represented.

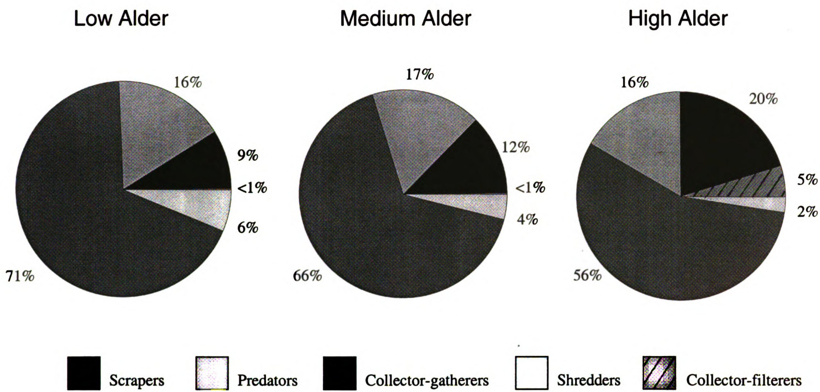


Figure 7. Functional feeding group relative biomass in streams with low (0-9%, n=4), medium (10-35%, n=4), and high (36-53%, n=5) percentages of riparian red alder. Relative biomass is combined total over the two year sampling period.

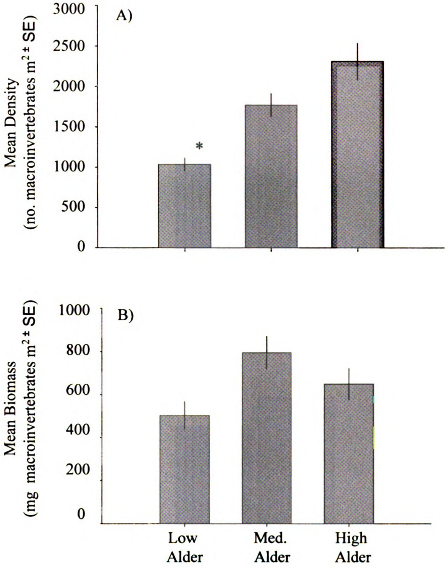


Figure 8. Mean macroinvertebrate density (A) and biomass (B) on naturally occurring wood in streams with low (0-9%, n=4), medium (10-35%, n=4), and high (36-53%, n=5) percentages of riparian red alder. Means with * are significantly different ($p < 0.05$). Percent riparian alder did significantly influence biomass ($p = .047$), but the individual levels of alder could not be identified.

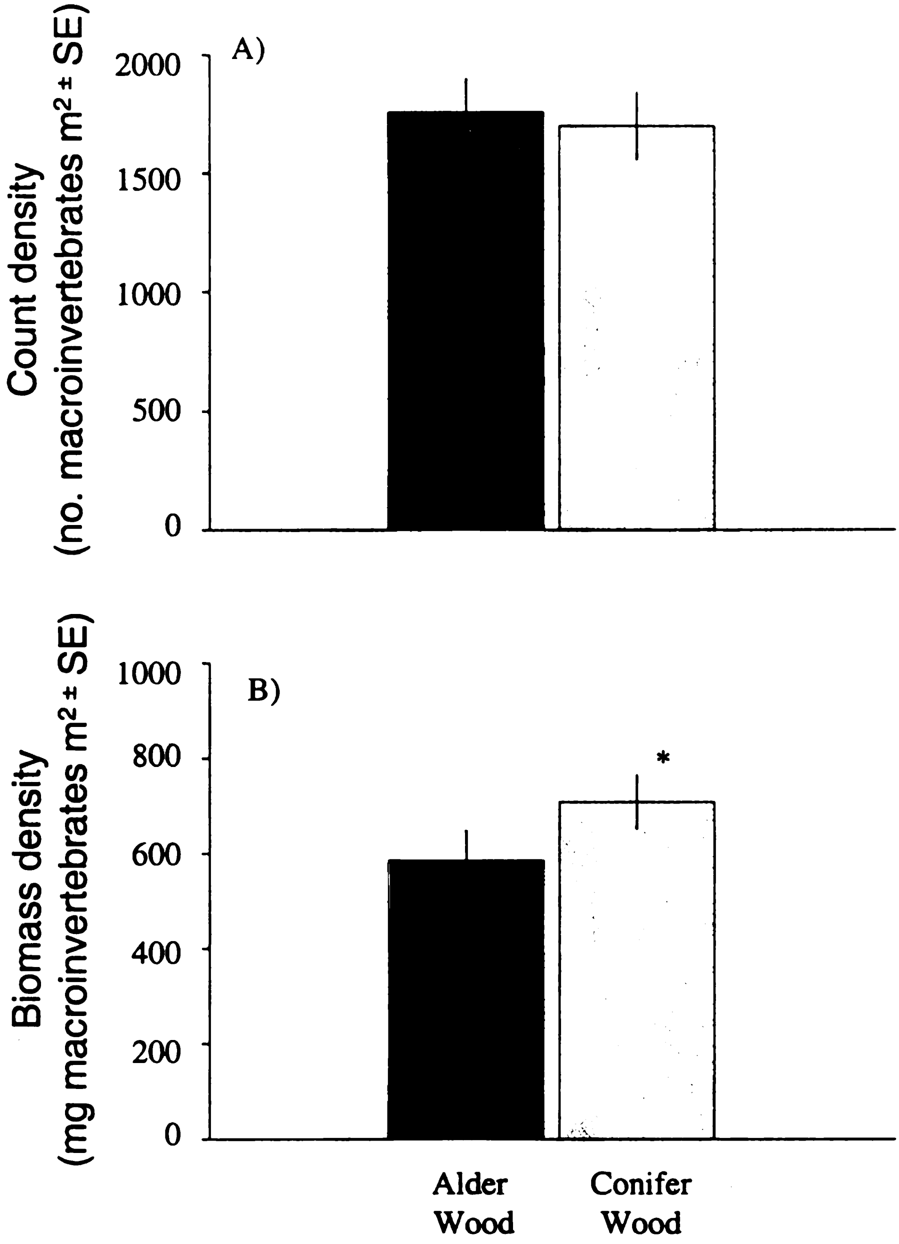


Figure 9. Mean macroinvertebrate (A) count and (B) biomass collected from the surfaces of naturally collected alder and conifer wood between 2001 and 2002. Means with * are significantly different (p=0.05).

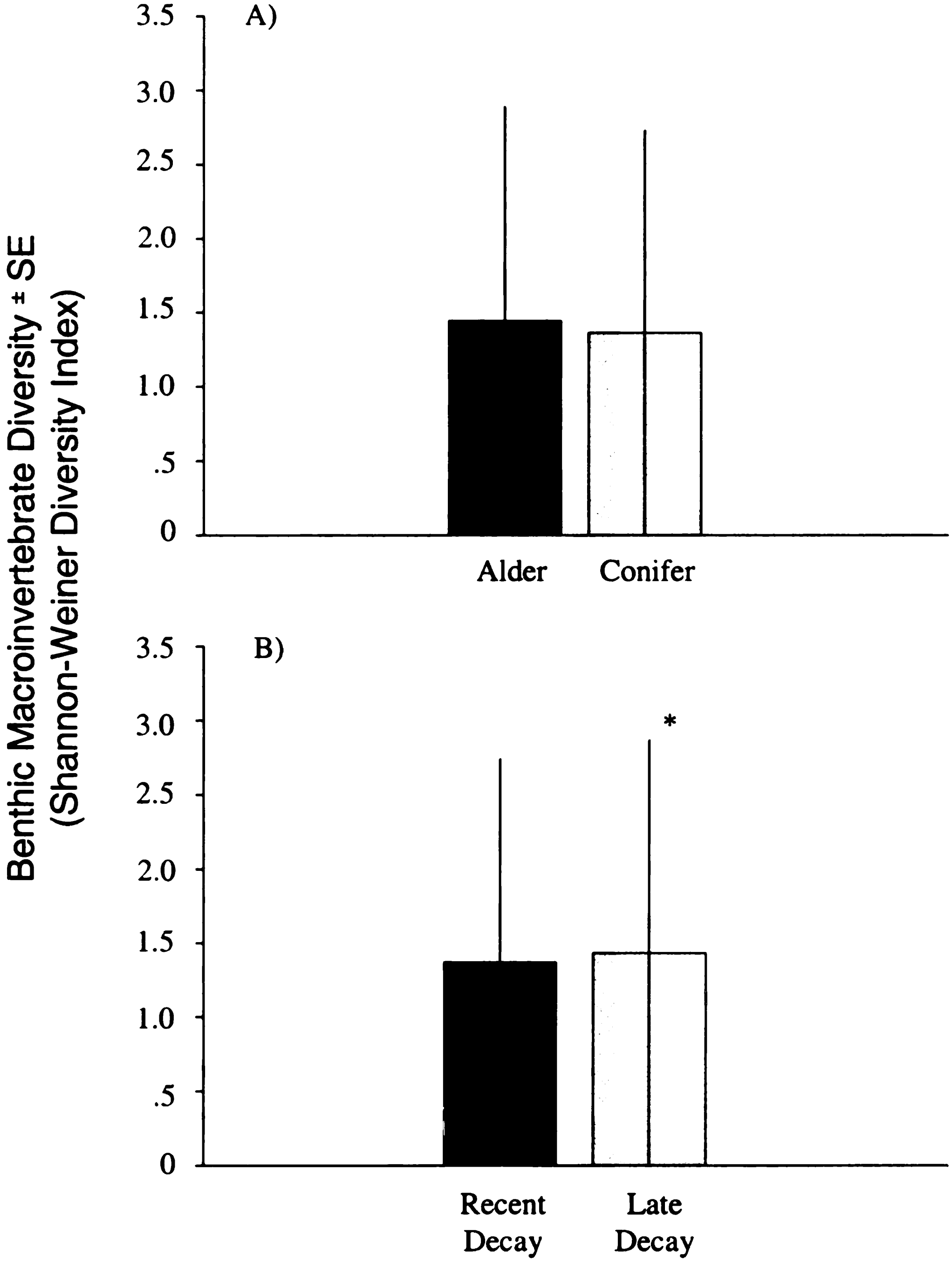


Figure 10. Shannon-Weiner diversity on (A) naturally occurring alder wood versus naturally occurring conifer wood and (B) recent versus late decay classes of naturally occurring wood pieces. Totals are from wood collected over the 2001 and 2002 sampling seasons. Means with * are significantly different (p=0.05).

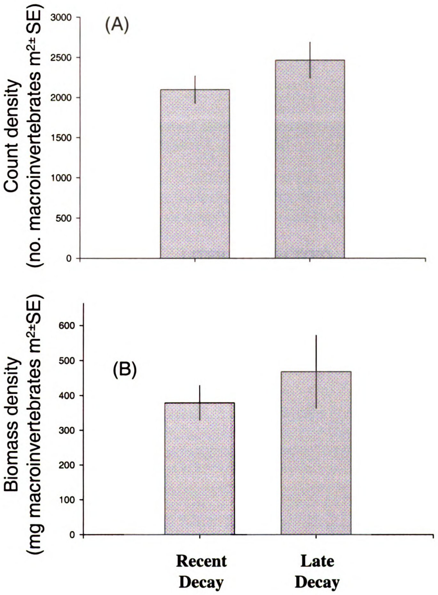


Figure 11. Mean macroinvertebrate (A) density and (B) biomass collected from naturally occurring alder and conifer wood in recent and late stages of decay. Results based on collections made between 2001 and 2002.

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Appendix 1

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 2004-05

Title of thesis or dissertation (or other research projects):

Macroinvertebrate Community Response to Riparian Red Alder within Headwater Streams of Second-Growth Forests in Southeast Alaska

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Investigator's Name(s) (typed)
Ryan K. Kimbirauskas

Date December 13, 2004

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24: 141-42.

Deposit as follows:

Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.

Copies: Include as Appendix 1 in copies of thesis or dissertation.
Museum(s) files.
Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

Appendix 1.1

Voucher Specimen Data

Species or other taxon	Label data for specimens collected or used and deposited		Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
	USA, AK, Prince of Wales Island									
COLEOPTERA										
Amphizoidae *Amphizoa*	Harris Drainage	July 2002					1			
Dytiscidae *Liodessus*	Maybeso Drainage	July 2001					1			
Hydrophilidae *Ametor*	Harris Drainage	July 2002					5			
Ptilodactylidae *Araepidius*	Maybeso Drainage	July 2002		1						
COLLEMBOLA										
Entomobryiidae	Maybeso Drainage	July 2002					1			
Sminthuridae	Maybeso Drainage	July 2001					1			
DIPTERA										
Chaoboridae *Eucorethra*	Maybeso Drainage	July 2001		1						
Chironomidae *Chironomini*										
Chironomidae *Diamesinae*	Maybeso Drainage	July 2001		2						
Chironomidae *Orthocladiinae*	Maybeso Drainage	July 2002		1						
Chironomidae *Tanypodinae*										
Chironomidae *Tanytarsini*										

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Ryan K. Kimbirauskas

Date December, 13 2004

Voucher No. 2004-05

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

[signature] 17 DEC 2004

Curator Date

Appendix 1.1

Voucher Specimen Data

Species or other taxon	Label data for specimens collected or used and deposited		Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
	USA, AK, Prince of Wales Island									
DIPTERA, Continued										
Ceratopogonidae *Ceratopogon*	Maybeso Drainage	July 2002		1						
Dixidae *Dixa*	Maybeso Drainage	July 2001		1						
Empididae *Chelifera*	Maybeso Drainage	July 2001		2						
Empididae *Clinocera*										
Empididae *Oregeton*	Maybeso Drainage	July 2001		4						
Simuliidae *Prosimulium*	Maybeso Drainage	July 2001		1						
Tipulidae *Dicranota*	Maybeso Drainage	July 2001		1						
Tipulidae *Hexatoma*	Maybeso Drainage	July 2001		1						
Tipulidae *Molophilus*	Harris Drainage	July 2002		1						
EPHEMEROPTERA										
Ameltidae *Ameltus*	Maybeso Drainage	July 2001		1						
Baetidae *Baetis*	Maybeso Drainage	July 2001		2						
Ephemerellidae *Drunella*	Maybeso Drainage	July 2001		2						
Heptageniidae *Cinygma*	Maybeso Drainage	July 2002		1						
Heptageniidae *Cinygmula*	Maybeso Drainage	July 2001		1						
Heptageniidae *Epeorus*	Maybeso Drainage	July 2001		2						

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

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Appendix 1.1

Voucher Specimen Data

Page 3 of 4 Pages

Species or other taxon	Label data for specimens collected or used and deposited		Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
	USA, AK, Prince of Wales Island									
EPHEMEROPTERA, Continued										
Heptageniidae *Ironodes*	Maybeso Drainage	July 2002		1						
Heptageniidae *Rithrogena*	Maybeso Drainage	July 2001		2						
Leptophlebeiidae *Paraleptophlebia*	Maybeso Drainage	July 2001		13						
PLECOPTERA										
Chloroperlidae *Suwalia*	Maybeso Drainage	July 2001		3						
Chloroperlidae *Sweltsa*	Maybeso Drainage	July 2001		5						
Leuctridae *Despaxia*	Maybeso Drainage	July 2001		1						
Leuctridae *Perlomyia*	Maybeso Drainage	July 2002		2						
Nemouridae *Ostracerca*	Maybeso Drainage	July 2002		1						
Nemouridae *Zapada*	Maybeso Drainage	July 2001		11						

(Use additional sheets if necessary)
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Appendix 1.1

Voucher Specimen Data

Page 4 of 4 Pages

Species or other taxon	Label data for specimens collected or used and deposited		Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
	USA, AK, Prince of Wales Island									
TRICHOPTERA										
Brachycentridae Micrasema	Maybeso Drainage	July 2001		1						
Goeridae Goeracea	Maybeso Drainage	July 2001		1						
Hydropsychidae Arctopsyche	Maybeso Drainage	July 2001		1						
Hydropsychidae Parapsyche	Maybeso Drainage	July 2001		1						
Limnephilidae Allomyia	Maybeso Drainage	July 2002		1						
Limnephilidae Chyranda	Maybeso Drainage	July 2002		1						
Limnephilidae Cryptochia	Maybeso Drainage	July 2001		1						
Limnephilidae Ecclisomyia	Maybeso Drainage	July 2001		3						
Limnephilidae Psychaglypha	Maybeso Drainage	July 2001		1						
Philopotamidae Wormaldia	Maybeso Drainage	July 2001		2						
Rhyacophilidae Rhyacophila	Maybeso Drainage	July 2001		3						

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