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BENTHIC INVERTEBRATE COMMUNITY STRUCTURE AS AFFECTED BY FOREST SUCCESSION AFTER CLEAR-CUT LOGGING ON PRINCE OF WALES ISLAND, SOUTHEAST ALASKA

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By

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ABSTRACT

BENTHIC INVERTEBRATE COMMUNITY STRUCTURE AS AFFECTED BY FOREST SUCCESSION AFTER CLEAR-CUT LOGGING ON PRINCE OF WALES ISLAND, SOUTHEAST ALASKA

By

Osvaldo Hernandez

The primary industries of Prince of Wales Island are toursim, timber harvesting and sport and commercial fisheries. Because timber harvesting is a disturbance that affects both physical and biological characteristics of adjacent streams and rivers, the effects of clear-cutting on spawning and rearing habitats of commercial and sport fish species have been investigated. However, many small fishless headwater streams in upland forests, with potential sources of benthic invertebrates as major food items for economically important fish species have received little attention. In an effort to assess the effects of timber harvest practices in upland forests, benthic invertebrate community structure was contrasted among four dominant forest management conditions and instream habitats. Timer harvest caused increases in invertebrate richness, densities and biomass relative to old growth conditions, particularly in second growth managements with an alder-dominated riparian vegetation. Large woody debris and gravel habitats supported high densities and biomass of invertebrates. In addition, large woody debris also supported a richer and more diverse fauna than either cobble or gravel substrates. Alternatives to clear-cut harvesting should be employed for the maintenance of wood recruitment into streams and growth of red alder along riparian margins.

Este trabajo es para mi familia que se encuentra muy lejos de mí y que quiero mucho. También para mis gran amigos Robert y Hook que me dieron mis primer experiencias en las ciencias.

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CHAPTER 1

SUMMARY OF SELECTED STUDIES EXAMINING FOREST HARVEST EFFECTS ON STREAM ATTRIBUTES IN NORTH AMERICA

INTRODUCTION

The effects of forest clear-cutting upon physical and biological characteristics of streams have been well studied from eastern to western United States and British Columbia. These studies have been conducted with a number of designs, from before and after studies to comparative and long-term studies. Often, experimental forests have been established for this purpose. The following consists of a brief introduction into several studies at different localities examining forest harvest effects on stream attributes, and are summarized in Table 1.

Eastern North America

Rishel et al. (1982) conducted a study at the Leading Ridge Watershed Research Unit in Pennsylvania to investigate changes in stream temperatures. They compared temperatures of headwater streams whose riparian vegetation was clear-cut and herbicide treated to streams with a buffer strip and streams with undisturbed riparian vegetation and found significant increases in daily maximum and significant decreases in daily minimum temperatures relative to the reference streams. Diurnal fluctuations increased four times from the control, and the highest temperature recorded was 32°C.

Silsbee and Larson (1983) investigated numerous physical parameters (Table1) and responses of benthic macroinvertebrates in second order streams to clear-cut logging in the Great Smokey Mountains National Park in Tennessee and North Carolina. Their treatment streams had been clear-cut in the early 1900s (1905 to 1926) and their control streams had previously been uncut. They found that unlogged streams had less numbers of invertebrates than clear-cut streams, and that scraper and shredder functional groups were dominant in these systems. They attributed these results to differences in the riparian vegetation community.

Martin et al. (1985) and Noel et al. (1986) conducted studies of the biogeochemistry of streamwater in New England after a clear-cut. Their approach involved comparing streams whose riparian vegetation was clear-cut (2 years previous) to reference streams (uncut for 35 years) within areas of different vegetation communities (coniferous, Northern Hardwoods and Central Hardwoods). Streams with clear-cut riparian vegetation within the Northern Hardwood forests showed greatest differences in stream chemistry after a clear-cut. They found greater numbers of macroinvertebrates (Ephemeroptera and Diptera) in the clear-cut streams and attributed this to increases in temperature and light, leading to increases in food supply for invertebrates by accelerating the mineralization of organic matter as well as by increasing algal growth.

Griffith and Perry (1991) compared leaf pack processing rates in second order streams flowing through 20 year and 80-year-old forests with differing vegetation types. The 80-year-old forests were dominated by Red Oak (*Quercus rubra*), Sugar Maple (*Acer saccharum*) and American Beech (*Fagus grandifolia*) while the 20-year-old forest was dominated by black cherry (*Prunus serotina*) and black birch (*Betula lenta*). Sugar Maple leave leaf packs were used and they found leaf pack processing rates were faster in the 20-year-old forests, which they attributed to significantly greater densities of total macroinvertebrates, shredders and collector gatherers than in the 80-year-old forests.

In Maine, a 1.2 km section of the east branch of the Piscataquis River was studied before and after a clear-cut in 1982 for timber harvesting effects on fish diet and production (Garman and Moring 1993). As part of the fish diet studies, the investigators found significant changes in the macroinvertebrate community. Mean densities were higher in the spring and lower in the fall than they were the previous year (before harvesting). After the harvest, Ephemeroptera, Plecoptera and Odonata were significantly less abundant while Chironomidae abundance increased threefold.

The responses of macroinvertebrates to different degrees of timber harvesting also have been investigated in pools of small headwater intermittent streams of the Quachita National Forest in Arkansas (Brown et al. 1997). The authors found significantly higher total densities and significantly lower diversity in harvested streams, as well as an increase in the ratio of shredders to collectors possibly due to increases in CPOM from harvesting techniques.

Coweeta Hydrologic Laboratory

The effects of clear-cutting on second order streams have been studied extensively at the Coweeta Hydrologic Laboratory in Franklin, North Carolina. The two primary streams under study were the Big Hurricane Branch whose watershed was clear-cut in 1977, and Hugh White Creek whose watershed has been undisturbed since 1924. Many faunal changes occurred in the benthic macroinvertebrate community that was sampled on a monthly basis (Webster et al. 1983). Greater abundances of collector-gatherer mayflies (*Baetis spp.* and *Ephemerella spp.*) were found in the logged stream. The dominant shredder, *Peltoperla maria*, declined in numbers and was virtually nonexistent within three years of the harvest. The changes in the macroinvertebrate community were attributed to changes corresponding to their food availability.

Other studies conducted at Coweeta include Gurtz and Wallace's (1984) investigation of substrate-mediated responses of macroinvertebrates to logging disturbance. Of the four substrates (rock face, cobble, pebble and sand) investigated, rock face was the preferred substrate in the clear-cut stream and cobble was the preferred substrate in the reference stream. They concluded that larger substrates, requiring more energy to move, had increased numbers of macroinvertebrates colonizing them. Wallace and Gurtz (1986) concluded that *Baetis spp.* mayflies respond quickly to take advantage of increases in autochthonous production, therefore, being important to energy processing in the disturbed stream.

Stone and Wallace (1998) investigated the effects of sixteen years of forest succession on benthic macroinvertebrate community structure, as well as the efficacy of five indices in determining recovery. Macroinvertebrate abundance, biomass and secondary production were greater in the disturbed stream than in the reference stream. The authors found that the percentage of scrapers initially present increased after logging, following the increase in algae production, and then declined with the decline in primary production. The trend in shredders present was an initial decline following the decrease in allochthonous inputs and successive increase in percentage following the return of allochthonous inputs. Once again, changes in macroinvertebrate community structure were directly corresponding to changes in the type and quantity of food available to them. Of the indices examined, percent *Baetis*, shredder to scraper ratios, and the North Carolina Biotic Index showed the greatest ability to detect differences between the logged and the reference stream. They all showed recovery or no difference between clear-cut and reference streams after sixteen years of forest succession.

<u>Western North America</u>

Newbold et al. (1980) investigated the effects of logging, with and without buffer strips, on numerous streams across northern California. Their first objective was to establish macroinvertebrate community differences between logged and reference sites. Of three indices of dissimilarity, only Euclidean distance showed a significant logging effect. Diversity of macroinvertebrates was lower and total density was higher in the logged streams, which the authors attributed to high densities of *Baetis*, *Nemoura spp.* and *Chironomidae*. Their second objective was to determine what effects buffer strips of differing widths had on logging effects. They found significant logging effects with narrow (<30m) buffer strips and no significant logging effects with wide (>30m) buffer strips.

<u>Alsea Watershed Study</u>

The Alsea Watershed Study as described by Hall et al. (1987) was a long-term study of the effects of timber harvesting, with and without buffer strips, on physical and biological characteristics of headwater streams along the Oregon coast. The sampling was conducted seven years prior and seven years after timber harvest on three watersheds. The first watershed was completely clear-cut, the second was cut with buffer strips and the third was left as a control. They found slight physical characteristic changes in the watershed with buffer strips, and large changes in the suspended sediments, dissolved oxygen, and temperature in the clear-cut watershed. However, these changes returned to prelogging levels as riparian vegetation returned. The biological aspect of their study included periphyton responses (Hansmann and Phinney 1973), however, focused on fish population responses to timber harvest (Connolly and Hall 1999).

H.J. Andrews Experimental Forest

Forest and stream interactions have been studied extensively at the H.J. Andrews Experimental Forest in Oregon. Rothacher (1970) and other follow-up studies (Harr et al. 1982 and Hicks et al 1991) compared changes between water yield in streams whose riparian vegetation was entirely clear-cut and another that was patch cut. Within a larger study looking at community structure of periphyton communities, Lyford and Gregory (1975) found standing crop and rates of colonization of periphyton to be greater in a clear-cut section of Mack Creek than in a forested area of the same stream. They believed light was the limiting factor determining growth rates of algae in those cascade mountain streams. Hawkins et al. (1982) addressed the relative importance of differences in riparian vegetation, instream substrates and gradient in benthic invertebrate communities of streams at the H.J. Andrews Experimental Forest. The canopy types in their study consisted of clear-cut, second growth deciduous, and old growth conifer. Substrate composition varied with gradient. High gradient streams (~ 10%) had primarily boulder and gravel substrates, while substrates in low gradient streams (~1%) consisted of cobble, gravel, and sand. They found canopy type to be more important in influencing invertebrate communities than substrate composition, with greater abundances of invertebrates in streams with clear-cut riparian vegetation. Anderson (1992) examined the influence of disturbance on invertebrate communities of Pacific North West streams where he compared aquatic insect adult emergence in a 3rd order stream flowing through: 1) 450 year old coniferous forest; 2) recent clear-cut; and 3) second growth deciduous riparian canopy 40 years after a clear-cut. He found that streams in old growth forests had the highest richness and greatest evenness among Ephemeroptera, Plecoptera and Trichoptera, and biomass of populations were similar across treatments. He also found strong grazer dominance in the clear-cut streams and a shift to detritivores using allochthonous materials in the second growth streams. Studies of peak flow responses to clear-cutting (Thomas and Megahan 1998) and stream temperature responses to forest harvest (Johnson and Jones 2000) also have been conducted at the Andrews Experimental Forest.

Washington State

The effects of forest harvest on stream characteristics also have been studied in Washington. Bilby and Bisson (1987) compared emigration and production of stocked coho salmon fry in streams flowing through old growth and recently clear-cut streams. Bilby and Ward (1991) contrasted the characteristics and function of large woody debris in streams draining old growth, clear-cut and second growth forests. They measured abundance, size and species of wood across the three riparian types. In addition, they documented the number and type of pools associated with large woody debris, the number of pieces of large woody debris that formed waterfalls and sediment storage created by large woody debris. The authors found their second growth stands, which were composed largely of red alder, do not supply enough large woody debris to streams, and that which is supplied is not as effective at influencing channel structure as coniferous large woody debris. Bilby and Bisson (1992) sought to determine whether autochthonous organic matter was more important to fish than allochthonous organic matter in streams draining old growth and clear-cut forests. They measured leaf litter inputs, periphyton, fluvial organic matter sources (dissolved organic matter, coarse particulate organic matter, fine particulate organic matter), discharge, water temperature, nutrients, fish production and diet, as well as invertebrate drift. Both fish diet and drift samples consisted predominantly of invertebrates belonging to scraper and collector-gatherer functional groups in both old growth and clear-cut streams. Invertebrates relied heavily on algae and algal-based detritus as a primary food source, lending to the overall hypothesis that autochthonous organic matter sources are more important to fish production in Washington streams (Bilby and Bisson 1992).

British Columbia

Carnation Creek is a small drainage on the west coast of Vancouver Island, British Columbia, where long-term (15 years) study of timber harvest effects on stream attributes was initiated in 1971. The study was divided into three phases. The first phase, from 1971 to 1975, was the prelogging monitoring phase. Phase two, from 1976 to 1981, involved studies during logging and road construction, and phase three consisted of postlogging monitoring. Three different logging methods were studied including: 1) leaving a buffer strip along the stream margin; 2) clear-cutting with great care not to disturb the stream; and 3) clear-cutting without regard for the stream. Hartman et al. (1987) provided an excellent synthesis of published Carnation Creek studies up to 1986, describing changes in physical characteristics of the watershed and responses of fish to those changes. Hartman et al. (1996) followed up the review of published Carnation Creek results to 1996, and the implication for fisheries managers. In the review they describe how timber harvesting had negative impacts on macroinvertebrate densities. Densities of seven select taxa were lower in the clear-cuts and total macroinvertebrate densities were at 41-50% of prelogging and unlogged control levels. In an effort to determine how the distribution of macroinvertebrates is affected by interstitial detritus quality and quantity, Culp and Davies (1985) experimented with four different mixtures of detritus (no detritus, low hemlock, low alder, high alder) in the main channel of Carnation Creek. They found that total macroinvertebrate densities were higher in the low alder treatment and that total biomass of macroinvertebrates was greater in both alder treatments than in the no detritus and low hemlock treatments.

Alaska

The research focus of timber harvest effects on fisheries in Southeast Alaska has changed from the 1950s to the present (Gibbons et al., 1987; Murphy and Milner, 1997). Beginning in the 1950s, when timber harvesting began to flourish in southeast, research focused on harvesting effects on salmon spawning habitat. Post 1960, research switched focus to harvesting effects on rearing habitat. In the 1990s, with revision of the Alaska Forest Resources and Practices Act, streamside buffer strips were required to protect salmonid habitat, and research focus will likely be aimed at monitoring these buffer strips and their effectiveness. Research on the effects of timber harvesting on benthic macroinvertebrates has determined that changing light levels are important in Southeast Alaska streams. Increases in algal production following clear-cutting resulted in increased benthic invertebrate abundance, while the dominant functional feeding group (collector-gatherer) remains unchanged (Duncan and Brusven 1985). Research on effects of canopy type on benthic macroinvertebrate and detritus export from headwater streams, due to previous timber management in Southeast Alaska, (Piccolo and Wipfli, submitted) has shown streams with a young growth (35 yr old) red alder-dominated canopy exported significantly more macroinvertebrates than did streams with young growth (35 yr old) conifer-dominated canopy.

Table1 Review and summary of selected studies examining forest harvest effects on stream attributes

	Streamflow	Temperature	pH	Conductivity	Nutrients	Suspended Solids	D.O.C.	Woody Debris	Organic Matter	Allochthonous Input	Leaf Pack Processing	Periphyton	Benthic Invertebrates	Fish
Eastern United States Studies														
(Rishel *et al.* 1982)		X												
(Silsbee and Larson 1983)			X	X	X	X	X	X					X	
(Martin *et al.* 1985)					X				X			X	X	
(Noel *et al.* 1986)												X	X	
(Griffith and Perry 1991)			X	X	X						X		X	
(Garman and Moring 1993)													X	X
(Brown *et al.* 1997)													X	
Coweeta Hydrologic Laboratory														
(Webster *et al.* 1983)	X	X			X	X	X			X	X	X	X	
(Gurtz and Wallace 1984)													X	
(Wallace and Gurtz 1986)												X	X	
(Stone and Wallace 1998)													X	

Table1 (cont'd)

	Streamflow	Temperature	pH	Conductivity	Nutrients	Suspended Solids	D.O.C.	Woody Debris	Organic Matter	Allochthonous Input	Leaf Pack Processing	Periphyton	Benthic Invertebrates	Fish
California Study														
(Newbold *et al.* 1980)													X	
Alsea Watershed Study														
(Hall *et al.* 1987)	X	X				X								X
(Hansmann and Phinney 1973)												X		
(Connolly and Hall 1999)														X
H.J. Andrews Studies														
(Rothacher 1970)	X													
(Harr *et al.* 1982)	X													
(Hicks *et al.* 1991)	X													
(Lyford Jr. and Gregory 1975)												X		
(Hawkins *et al.* 1982)									X			X	X	
(Anderson 1992)													X	
(Thomas and Megahan 1998)	X													
(Johnson and Jones 2000)		X												

Table1 (cont'd)

	Streamflow	Temperature	pH	Conductivity	Nutrients	Suspended Solids	D.O.C.	Woody Debris	Organic Matter	Allochthonous Input	Leaf Pack Processing	Periphyton	Benthic Invertebrates	Fish
Washington State Studies														
(Bilby and Bisson 1987)	X	X										X		X
(Bilby and Ward 1991)								X	X					
(Bilby and Bisson 1992)	X	X			X		X		X	X		X	X	X
Carnation Creek Studies														
(Hartman *et al.* 1987)		X						X						X
(Hartman *et al.* 1996)		X			X							X	X	X
(Culp and Davies 1985)									X				X	
Southeast Alaska Studies														
(Gibbons *et al.* 1987)														X
(Murphy and Milner 1997)						X			X			X	X	X
(Duncan and Brusven 1985)										X			X	
(Piccolo and Wipfli submitted)									X				X	

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CHAPTER 2

BENTHIC INVERTEBRATE COMMUNITY STRUCTURE AS AFFECTED BY FOREST SUCCESSION AFTER CLEAR-CUT LOGGING ON PRINCE OF WALES ISLAND, SOUTHEAST ALASKA

INTRODUCTION

Clear-cut logging, a timber harvesting method in which the forest canopy is removed, is a disturbance that affects both physical and biological characteristics of adjacent streams and rivers. One of the major changes occurring after a clear-cut is the decrease of the allochthonous energy base (Duncan and Brusven 1985a) on which headwater streams and benthic macroinvertebrates are dependent (Vannote *et al.* 1980). The effects of the disturbance on benthic macroinvertebrates have either been studied before and after the harvest (Garman and Moring 1993; Hall *et al.* 1987; Hartman *et al.* 1996) or in comparative studies with a reference stream (Anderson 1992; Hawkins *et al.* 1982; Newbold *et al.* 1980). However, because the riparian vegetation is brought to a stage of secondary succession (Alaback 1984), it also has been studied as such (Stone and Wallace 1998) by comparing macroinvertebrate community structure in streams with riparian vegetation in different stages of succession (Haefner and Wallace 1981; Murphy *et al.* 1981).

Prince of Wales Island is the third largest island in the United States. It is located within the Tongass National Forest in the southeast panhandle of Alaska. The primary industries of the island are tourism, timber harvesting and sport and commercial fisheries. Because many streams and rivers on the island are located within Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) forests, they are subjected to forestry management practices such as clear-cut logging. Because timber harvesting is a disturbance that could adversely affect the fishing industry, the effects of clear-cutting on spawning and rearing habitats of commercial and sport fish species such as coho (*Onocorhynchus kisutch*), pink (*O. gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) salmon have been investigated (Murphy and Milner 1997; Duncan and Brusven 1985b). However, because the topography of Prince of Wales and southeast Alaska is mountainous, there are many small fishless headwater streams in the upland forests connecting to larger fish bearing streams that have received little attention. These small headwater tributaries can be important sources of fluvial organic matter to the larger streams and its biota, and potential sources of benthic invertebrates (Wipfli and Gregovich 2001) that are major food items for economically important fish species. Therefore, knowledge of the effects of timber harvesting on benthic macroinvertebrates in these headwater streams is important for the more effective management of both forest and aquatic resources.

Prince of Wales has been logged extensively since 1950 (Swanston 1967). As a result, there are streams within forest management conditions with differing types of dominant vegetation in different stages of forest succession. This study contrasted streams within four different forest management conditions. First, recent clear-cut (CC) conditions that were in their fifth year of regeneration had riparian vegetation comprised primarily of shrubs. Second growth areas varied in canopy composition. Canopy composition ranged between two extremes where either red alder (*Alnus rubra*) or coniferous trees were dominant along the riparian margin. This study contrasted the extremes, alder-dominated second growth (SA) and conifer-dominated second growth

(SC), in stands that had been regenerating between 35 and 40 years. Lastly, coniferous trees dominated the old growth (OG) condition, which has previously not been cut.

In addition to studying the effects of timber harvest based on forest succession, I also wanted to assess the effects of substrate type on macroinvertebrate response to timber harvest. Gurtz and Wallace (1984) concluded that more stable substrates were capable of mediating disturbance effects. Common substrates in these streams are large woody debris, cobble and gravel.

My overall objectives were to: 1) contrast headwater benthic invertebrate community structure between the four forest management conditions (CC, SA, SC, OG); and 2) evaluate which instream habitat (large woody debris, cobble or gravel) supported greater taxa richness, diversity, densities, and biomass of invertebrates.

METHODS

I. Study Sites

The study was conducted on 12 streams in the Maybeso Experimental Forest and the adjacent Harris River watershed in the Tongass National Forest, Prince of Wales Island, in southeast Alaska (Figure 1). Vegetation of the island is classified as a temperate rainforest with annual precipitation ranging between 150 to 500 cm, and air temperatures range from –20°C to 36°C (Duncan and Brusven 1985c; Harris et al. 1974). All stream sites were first order, high gradient, headwater streams of the Harris and Maybeso catchments, and they were sampled upstream of logging roads once between 7-15 July 1998 and once between 11-14 June 1999.

Riparian vegetation differed across management conditions. Vegetation in clear-cut condition was in its fifth year of regeneration with salmonberry (*Rubus spectabilis*) and Alaskan blueberry (*Vaccinium spp.*) as the dominant riparian species. The alder-dominated second growth condition, between 35 and 40 years old, consisted of dense red alder along the riparian margin with a mixture of some conifers and an understory of ferns and mosses. The conifer-dominated second growth condition, also between 35 and 40 years old, was predominantly Sitka spruce and western hemlock with some red alder and a fern understory. The old growth condition, that had never been cut, had similar vegetation to the conifer-dominated second growth, but the trees were more mature and less dense. There also was a more extensive understory comprised of devils club (*Oplopanax horridus*), skunk cabbage (*Lysichition americanum*) and ferns.

II. Physical Measurements

Physical measurements were taken in streams across the four management conditions in 1999. Water temperatures were taken simultaneously with Onset® Optic StowAway Temperature Loggers for a three week period. Discharge was measured using a Marsh-McBirney® flow meter by the velocity-area method described in Gore (1996). Nitrates were measured with a Hach® nitrate field test. The percentage of large woody debris, cobble and gravel habitats was quantified within 25m in each of the 12 streams. Algal AFDM on clay tiles was determined at two streams of each management condition using the methods in Steinman and Lamberti (1996).

III. Experimental Design and Analysis

The experimental design of the study was a split-plot design; management condition was the whole-plot factor, habitat was the sub-plot factor. Three streams were sampled upstream of logging roads in each of the four management conditions. Within each stream, three random macroinvertebrate samples were collected in 1998 while two random samples were collected in 1999, from each of the following habitats: 1) large woody debris, characterized by being of cedar origin, >10 cm diam. and conditioned (in the water long enough to be suitable for invertebrate colonization); 2) completely submersed riffle cobble (64-256 mm diam.); and 3) gravel between 2-16 mm diameter. A total of 108 samples were collected from the 12 headwater streams in 1998, and a total of 72 samples were collected from 12 headwater streams in 1999.

Results were tested for normality and log transformed or square root transformed where necessary. Multiple ANOVAs were generated contrasting richness, diversity, density and biomass, vs. management conditions (clear-cut, alder-dominated second growth, conifer-dominated second growth, and old growth) and habitat (large woody debris, cobble, gravel). ANOVAs were generated for the analysis of nitrates, discharge and algal AFDM vs. management conditions (SAS Institute 1996). Although results were transformed, they will be presented in untransformed fashion in graphs and tables.

IV. Macroinvertebrate Sampling

The large woody debris samples were randomly selected from the first six pieces encountered upstream of logging roads. Length and diameter measurements were taken to estimate surface area. Each piece of large woody debris was collected and placed in a 19

L bucket and pressure sprayed with water from a hand-pumped lawn sprayer to remove invertebrates. The macroinvertebrate sample was then rinsed through a 250-micron sieve and transferred into a 250-ml Whirl-Pak®, preserved in 80% ethanol, and returned to the lab for sorting under a dissecting scope. All invertebrates were picked from each sample, counted, identified to the lowest possible taxon, mostly generic level (except Chironomidae) using Merritt and Cummins (1996a). Chironomidae were subsampled and identified to subfamily.

Cobble samples were removed from submersed cobble of riffle areas. Each cobble habitat was selected from the center of each of the first three riffle areas encountered upstream of logging roads. Sample collection and processing were similar to that of large woody debris. The cobble were labeled and returned to the lab to estimate surface area. Surface area was determined by wrapping the cobble in foil paper, removing the foil, and tracing it onto paper. Surface area was calculated from the paper using a Li-Cor® portable leaf area meter Model-Li-3000.

Gravel core samples were collected from the center of each of the first three gravel areas encountered upstream of logging roads. Samples were collected with a core sampler (6 cm x 6 cm x 6 cm). The core sampler was inserted into the gravel area to a depth of 6 cm and the contents scooped out with a 250-micron mesh net. The entire sample was transferred into a whirl-pak and returned to the lab for processing as above.

Invertebrate density was estimated from abundance and surface area calculations for the large woody debris and cobble samples and was converted to number per $1 m^2$. Density was calculated from abundance and sample volume for the gravel core samples and was converted to number per $1 m^3$. Dry mass of invertebrates was estimated according to Benke et al. (1999). Richness was measured as total number of taxa present and diversity was measured using the Shannon-Weiner diversity index (Hauer and Resh 1996). Macroinvertebrates were designated a functional feeding group status (shredders, filtering-collectors, gathering-collectors, scrapers and predators) according to Merritt and Cummins (1996b). Dry mass of Oligochaeta were not determined and therefore omitted from biomass and functional group analysis.

RESULTS

I. Physical Measurements

Daily temperature maximums were greatest in the old growth condition and lowest in the conifer-dominated second growth. Daily temperature minimums were lowest in the conifer dominated second growth condition and highest in the old growth condition. Greatest differences in maximum and minimum daily temperatures were found in the clear-cut condition and smallest differences in daily temperatures were found in both conifer-dominated second growth and old growth conditions (Table 1).

Discharge was not significantly different across management conditions, and nitrate data were incomplete for comparisons across management conditions. Instream habitat quantification showed that cobble and gravel habitats comprised the greatest proportion of available habitat for invertebrate colonization (Table 2). The conifer-dominated second growth management condition had the largest proportion of large woody debris with 20.9%, followed by old growth (12.1%), alder-dominated second growth (5.4%) and clear-cut (3.3%) (Table 2).

Algal AFDM was greatest in the clear-cut (0.06 mg cm^{-2}) management condition. It was significantly greater than in the old growth (0.013 mg cm^{-2}) ($p<0.05$), alder-dominated second growth (0.015 mg cm^{-2}) ($p<0.05$), and conifer-dominated second growth (0.013 mg cm^{-2}) ($p<0.05$) (Figure 2).

II. Macroinvertebrate Richness and Diversity Among Management Conditions

A total of 38 genera were collected from representatives of the Ephemeroptera, Plecoptera, Trichoptera and Diptera from the headwater streams of the Maybeso and Harris River watersheds (Table 3). In addition, three subfamilies of Chironomidae were identified from 1999 subsamples. Orthocladinae comprised the largest percentage across the four management conditions, followed by Tanypodinae and Chironominae (Table 4).

Mean richness, or the total number of taxa collected, was lowest in the old growth management condition. It was significantly lower than in the clear-cut ($p<0.05$) and alder-dominated second growth ($p<0.05$) conditions in 1998 (Figure 3a). Mean richness in the old growth condition also was significantly lower than in the alder-dominated second growth ($p<0.05$) in 1999 (Figure 3b).

Mean Shannon-Weiner diversity was greatest in both alder and conifer-dominated second growth management conditions and significantly less in clear-cut and old growth during both years (Figure 4).

III. Macroinvertebrate Densities and Biomass Among Management Conditions

In 1998, mean densities of invertebrates (6590 m^{-2}) collected from large woody debris and cobble habitats in clear-cut management conditions were significantly greater than mean densities in old growth (1423 m^{-2}) ($p<0.05$) and conifer-dominated second growth (988 m^{-2}) ($p<0.05$). In addition, the old growth management condition had significantly lower mean densities ($p<0.05$) than the alder-dominated second growth (3131 m^{-2}) (Figure 5a). There were no significant differences in mean densities of invertebrates collected from large woody debris and cobble habitats among management conditions in 1999. Mean densities of invertebrates collected from gravel habitats were greatest in the clear-cut (416,667 m^{-3}) management condition and least in the old growth (93,364 m^{-3}); however, these differences were only significant in 1999 ($p<0.05$) (Figure 5b).

In 1998, mean dry mass of invertebrates collected from large woody debris and cobble habitats was greatest in the clear-cut (291mg m^{-2}) management condition and significantly greater than in the old growth (95mg m^{-2}) ($p<0.05$) condition. In addition, mean dry mass in alder-dominated second growth (225mg m^{-2}) also was significantly greater than in old growth ($p<0.05$) management (Figure 6a). In 1999, mean dry mass of invertebrates collected from the large woody debris and cobble habitats was greatest in alder-dominated second growth (644mg m^{-2}) conditions and significantly greater than in the old growth (195mg m^{-2}) ($p<0.05$) (Figure 6b). There were no significant differences in mean dry mass of invertebrates collected from gravel habitats among management conditions in 1998. However, in 1999, mean dry mass of invertebrates collected from gravel habitats in clear-cut (20,491mg m^{-3}) management conditions was significantly greater than mean dry mass in old growth (6,043mg m^{-3}) ($p<0.05$) and conifer-dominated second growth ($p<0.05$). In addition, the old growth management condition had significantly lower mean dry mass ($p<0.05$) than the alder-dominated (15,673mg m^{-3}) second growth (Figure 6c).

IV. Functional Feeding Group Proportions Among Management Conditions

The composition of macroinvertebrates changed functionally and taxonomically relative to the old growth condition in 1998 (Figure 7). The old growth management condition was characterized by a high percentage of predators (42%), followed by scrapers (30%), collector-gatherers (19%), shredders (9%) and absence of collector-filterers. The clear-cut condition had collector-gatherers as the dominant functional group. *Baetis* mayflies and Ostracoda comprised the largest proportion of biomass of this functional group in the clear-cut condition, whereas the mayfly *Paraleptophlebia* was dominant in the old growth. The dominant scraper also changed taxonomically, from *Drunella* mayflies in the clear-cut to *Cinygmula* mayflies in the old growth. In addition, the clear-cuts had a greater proportion of collector-filterers, represented by the caddisfly *Dolophiloides*, than the old growth. The alder and conifer-dominated second growth condition changed slightly with respect to old growth condition. Scrapers and predators were still the dominant functional groups present, but both second growth conditions had relatively fewer collector-gatherers and more collector-filterers than the old growth. Taxonomically, the dominant scraper in the conifer-dominated second growth was the mayfly *Ironodes*, while *Cinygmula spp.* was dominant in both old growth and alder-dominated second growth conditions.

In 1999, the functional feeding group characterization differed from 1998 (Figure 8). Collector-gatherers (48%) made up the largest proportion in the old growth condition, followed by predators (30%), scrapers (18%), shredders (4%) and the absence of collector-filterers. Due to large biomass of the predator stonefly *Sweltsa*, they were the dominant functional group in both clear-cut and conifer-dominated second growth managements. As in 1998, the alder-dominated second growth had predators and scrapers as the dominant functional groups. Taxonomically, the alder-dominated second growth had the mayflies *Paraleptophlebia* and *Baetis* as the dominant collector-gatherers, just as in the old growth condition, but different from the clear-cut and conifer-dominated second growth conditions where *Baetis spp*. and Chironomidae were dominant.

V. Macroinvertebrate Richness and Diversity Among Instream Habitats

Mean richness was greatest in the large woody debris habitat and least in the cobble habitat. Mean richness on gravel was significantly greater than on cobble habitats ($p<0.05$) only in 1998, while mean richness on large woody debris was significantly greater ($p<0.05$) than on gravel or cobble habitats in both years (Figure 9).

Mean Shannon-Weiner diversity was greatest in large woody debris habitats followed by gravel and cobble habitats on both years (Figure 10). Mean diversity on gravel habitats was significantly greater than on cobble habitat in 1998 ($p<0.05$) and 1999 ($p<0.05$). Mean diversity of invertebrates on large woody debris was significantly greater ($p<0.05$) than on cobble habitat both years.

VI. Macroinvertebrate Density and Biomass Among Instream Habitats

Mean invertebrate densities and biomass were not comparable between gravel and the other two habitats because of the differences in units; however, mean densities were significantly greater on large woody debris habitat (1998 - 5294m^{-2}; 1999 - 1893m^{-2}) than on cobble (1998 - 723m^{-2}; 1999 - 507m^{-2}) during both years (Figure 11). Mean dry mass of invertebrates from large woody debris (302mg m^{-2}) was greater than on the cobble (83mg m^{-2}) habitat; however, the difference was only significant in 1998 (Figure 12).

VII. Functional Feeding Group Proportions Among Instream Habitats

In 1998, the functional feeding groups on large woody debris included scrapers (38%) (primarily *Drunella* and *Cinygmula* mayflies), collector-gatherers (23%) (*Baetis* and *Paraleptophlebia* mayflies and Chironomidae), and shredders (18%) (stoneflies *Despaxia* and *Zapada*). Cobble habitats had a high proportion of scrapers (37%) (*Cinygmula* and *Ironodes* mayflies), and the caddisfly, *Arctopsyche spp.*, as the dominant collector-filterer (33%). In the gravel habitat, there were large proportions of predators (43%) (primarily *Sweltsa spp.* and the crane fly *Dicranota*), as well as scrapers (35%) (*Cinygma spp.* and *Cinygmula spp.*) (Figure 13).

In 1999, functional groups included for the most part, similar taxa from the previous year. On large woody debris there was a large proportion of scrapers (55%) followed by collector-gatherers (18%) and shredders (18%) (crane fly, *Tipula*). Cobble habitats had scrapers (60%) and collector-gatherers (25%) (mayfly *Epeorus*) in greatest proportions, while the gravel habitat had a large proportion of predators (55%) and collector-gatherers (28%) (*Baetis spp.*, *Paraleptophlebia spp.* and Chironomidae) (Figure 14).

DISCUSSION

I. Management Conditions

The results of this study showed that taxonomic and functional differences in macroinvertebrate composition occurred between harvested sites and old growth management conditions. The primary reasons for these changes may have been due to changes in the availability of food resources (e.g. algal AFDM, labile allochthonous inputs and fine particulates) in the harvested conditions. Anderson (1992) found that through the emergence of aquatic insects, streams in old growth management conditions had a greater number of taxa and evenness than from recent clear-cut and second growth deciduous riparian management conditions. In contrast, richness of macroinvertebrates in our old growth conditions was lower than in clear-cut and alder-dominated second growth conditions. Old growth conditions were lacking three taxa (*Micrasema spp.*, *Goeracea spp.* and *Prosimulium spp.*) that were present in the other management conditions. In addition, two dipterans (Thaumaleidae and *Limonia spp.*) were present only in the clear-cut condition, and *Neophylax spp.*, *Chyranda spp.*, *Rithrogena spp.* and Ptilodactylidae were present only in alder-dominated second growth. Vegetation in the old growth consisted primarily of more refractory coniferous allochthonous material, while all other management conditions have sources of more labile deciduous allochthonous inputs (i.e. red alder and salmonberry) that may be used more readily as a food source by the caddisfly shredders *Micrasema* and *Chyranda* and the crane fly shredder, *Limonia*. In addition, mean algal AFDM was greatest in the clear-cut management condition, which was similar to the findings of Murphy *et al.* (1986) who reported their clear-cut streams averaged 130% greater periphyton AFDM than in buffered and old growth streams, which they attributed to an increase in amount of light reaching the stream. Increased algal AFDM in the clear-cut condition may have resulted in a suitable food source for the caddisfly scraper, *Goeracea*, and the dipteran scraper, Thaumaleidae. Lastly, the presence of the black fly (*Prosimulium*) in managements other than the old growth suggested that the harvest resulted in greater fine particulates entering the stream through bank erosion, or lateral inputs from runoff and resuspension as Anderson and Sedell (1979) described. Webster et al. (1990) also showed that disturbed streams exported significantly more particulate organic matter than reference watersheds. My study was conducted upstream of logging roads in order to avoid any sedimentation effects caused by road construction, so fine particulates to the stream would have likely arisen from the harvest itself. However, our results also may have differed from those of Anderson (1992) because of greater taxonomic resolution in his study.

Although diversity of macroinvertebrates has been reported to be lower in harvested streams (Newbold *et al.* 1980), our results showed mean diversity was not lower in clear-cut streams than in old growth management streams. In addition to lower macroinvertebrate diversity, streams within harvested areas have generally been found to have greater macroinvertebrate densities throughout the lower United States (Hawkins *et al.* 1982; Silsbee and Larson 1983), in the Pacific Northwest (Murphy et al. 1981), and Alaska (Duncan and Brusven 1985b). However, Hartman *et al.* (1996) described negative impacts of harvesting on macroinvertebrate densities in Carnation Creek, a locality near Prince of Wales. In this study, large numbers of Chironomidae in the old growth condition and large numbers of midges and *Baetis spp.* in the clear-cut condition, as well as fewer taxa, were primarily responsible for lower diversity. The increase in densities after a harvest was largely due to large numbers of *Baetis spp.*, Chironomidae and the mayfly *Drunella* in clear-cut conditions. Similarly, Wallace and Gurtz (1986) reported increased numbers of *Baetis spp.* in their harvested streams and attributed it to increases in autochthonous production. The increase in macroinvertebrate densities in our alder-dominated second growth conditions were due to large numbers of *Zapada spp.* and *Micrasema spp.*, both of which are shredders and presumably using allochthonous inputs from the red alder riparian vegetation. Culp and Davies (1985) also found higher macroinvertebrate abundances in substrate patches with alder detritus as compared to hemlock detritus. I found that headwater streams of the Maybeso Experimental Forest and adjacent Harris River watershed had greater invertebrate densities following a harvest, with the clear-cut managements having the greatest densities. Second growth conditions had intermediate densities, and old growth had the lowest densities of invertebrates.

Mean biomass also was greater in harvested areas, particularly in the alder-dominated second growth and recently clear-cut management conditions. This greater invertebrate biomass in harvested areas may be the result of a greater amount of nutrient availability through increased litter processing rates (Stone and Wallace 1998), particularly alder litter which is processed quicker than conifer needles (Sedell *et al.* 1975). Stone and Wallace (1998) suggested that these processes could lead to increased production of macroinvertebrates in harvested streams.

Changes in the functional feeding group composition of streams have been shown to be the result of changes or differences in food availability (Vannote *et al.* 1980). It is probable that differences in macroinvertebrates between years may have resulted from different seasonal sampling times. Overall, larger proportions of scrapers were present in July than in June. Similarly, Duncan and Brusven (1985b) also found a tendency for increased scrapers from spring to summer in their studies in Prince of Wales Island. Large proportions of predators across management conditions may have resulted from an under representation in the non-predator fauna due to low sampling efficiency, since all available habitats (fine woody debris, root wads, mosses and bedrock) were not sampled in this study. Another possible reason for the presence of a large proportion of predators is a prey base with a rapid turnover in generation time. For example, large numbers of Harpactacoida copepods, with a presumably short generation times, were collected from all management conditions, primarily from large woody debris and gravel habitats where the predator *Sweltsa* were more commonly found.

Streams with alder-dominated second growth riparian vegetation had a functional and taxonomic similarity to old growth management conditions. However, alder-dominated second growth also had an abundant, richer and more diverse fauna. Therefore, streams in alder-dominated second growth conditions were potentially contributing a greater amount and variety of benthic invertebrates to larger fish-bearing streams.

II. Instream Habitats

In the event of a disturbance such as timber harvest, Gurtz and Wallace (1984) concluded that invertebrates responded by increasing their abundance on physically larger substrates that required more energy to move. In my study, the physical stability, structural complexity, and ability to retain organic matter resources for invertebrate consumption may have all been important. Invertebrate richness and diversity were greatest in the large woody debris followed by gravel and cobble substrates. This could have been due to a combination of physical stability and structural complexity of the substrates. Large woody debris is physically larger than either cobble or gravel substrates, and has greater structural complexity than cobble substrates, possibly allowing for a more stable habitat, greater variety of food resources and refugia for invertebrates. Wallace *et al.* (1995) showed an increase of coarse and fine particulate matter accumulation after log additions to a stream in North Carolina. In addition, large numbers of taxa have been found in association with wood as shown by Dudley and Anderson (1982) who recorded 56 taxa closely associated with woody debris and another 129 species as facultatively associated.

Gravel substrates also were areas of high numbers and biomass of invertebrates in my study streams. Gravel is more structurally complex than cobble. Cobble is generally smooth surfaced while the gravel habitat has interstitial spaces for refuge and detritus accumulation. Culp and Davies (1985) showed the importance of interstitial detritus in gravel substrates in determining the distribution of macroinvertebrates, with greater numbers of invertebrates associated with either high or low levels of red alder detritus than hemlock.

All functional groups were represented in each of the three habitats under study. Scrapers made up a large proportion in each of the habitats; however, each habitat had a dominant functional group associated with it. Large woody debris had the highest relative proportion of shredders, reflecting on its ability to retain coarse particulates (i.e. leaf litter and detritus) (Bilby and Likens 1980). Cobble substrates had the highest relative proportion of collector-filterers suggesting their importance to this group even in the presence of stable large woody debris substrates. Gravel habitats had the highest proportion of predators, likely due to the presence of high abundances of Harpactacoida copepods and chironomid as a prey base.

Instream habitat quantification revealed that the sections of streams examined were comprised primarily of cobble and gravel substrates and the proportion of large woody debris present and available for macroinvertebrate colonization in old growth management conditions averaged 12.1% of the total habitat available. The proportion of large woody debris in clear-cut management conditions also was small (3.3%). Very few large pieces of wood remained in these streams after the harvesting event and the majority of the wood that was available was small and appeared to be slash from the harvesting event itself. Alder-dominated second growth conditions also had a small proportion of large woody debris (5.4%). Bilby and Ward (1991) compared woody debris inputs to streams from old growth, clear-cut and second growth forests and concluded that large woody debris inputs from second growth forests with red alder riparian stands were minimal. Surprisingly, conifer-dominated second growth conditions had the greatest proportion of large woody debris (20.9%); however, most of the large woody debris was larger in diameter than that of the current forest, suggesting that the origin of the wood was not from the second growth stand and was in the streams before the harvest or as a direct result of the harvest.

In addition to the functional importance of large woody debris in: 1) channel and pool formation (Keller and Swanson 1979); 2) the retention of organic matter (Bilby

1981); and 3) serving as a habitat for invertebrate colonization (Gurtz and Wallace 1984), it is important biologically as a food resource for invertebrates (Anderson et al. 1979; Kaufman and King 1987). Large woody debris contributed significantly to the richness, diversity, and abundance of macroinvertebrates in Southeast Alaskan headwater streams.

CONCLUSION

The results of this study suggested that forest succession after a timber harvest affected macroinvertebrate community structure in the upland forests of Southeast Alaska, as a result of changes in food availability relative to the old growth condition. First, canopy removal has led to increases in sunlight penetration to the streambed and consequently to higher autochthonous food resources which results in greater biomass and densities of scraper and collector-gatherer invertebrates in clear-cut management conditions. Secondly, in the alder-dominated second growth condition, provision of more labile allochthonous organic matter (i.e. red alder) has increased the abundance and number of different shredder invertebrates. Lastly, timber harvest has led to the presence of collector-filterer organisms in all harvested conditions. Although clear-cut conditions had the highest densities of invertebrates, alder-dominated second growth conditions had high densities of invertebrates in addition to a richer and more diverse fauna. Thus, management of upland forests in Southeast Alaska should provision for red alder riparian vegetation to maximize macroinvertebrate diversity and abundance.

The evaluation of instream habitats showed that large woody debris and gravel substrates were important to the contribution of high densities and biomass of invertebrates to upland Southeast Alaskan headwater streams. In addition, large woody debris also contributed to high taxa richness and diversity. Maintenance of both gravel and large woody debris substrates within these streams is advantageous for large numbers of benthic invertebrates that could potentially benefit the diet of downstream economically important fish communities.

There is a need for an alternative method to clear-cut harvesting of upland forests of Prince of Wales. The alternative must result in an abundant, richer and more diverse community of benthic invertebrates. Results of this study suggest that this could be achieved by opening up a portion of the canopy, having red alder along the riparian margin, and maintaining sources of wood to the streams. I would suggest selectively cutting a proportion of the riparian vegetation to potentially allow for: 1) greater sunlight penetration to stimulate autochthonous production; while 2) maintaining wood recruitment to the stream; and 3) planting of red alder saplings along the riparian margin for labile sources of allochthonous organic matter. This management strategy should positively influence invertebrate richness, diversity and abundance, without the loss of instream habitat.

Table 1. Average daily maximum, minimum and differences in streamwater temperature (°C) 1999.

	Old Growth	Clear-cut	Alder SG	Conifer SG
Ave daily max	10.44	9.96	9.13	7.71
Ave daily min	10.03	9.03	8.38	7.35
Ave max minus min	0.41	0.93	0.75	0.36

Table 2. Percentage of instream large woody debris, cobble and gravel habitats within management conditions. Do not equal 100 percent in cases where fine woody debris or bedrock substrates were present.

Management condition	large woody debris	cobble	gravel
Old Growth	12.1	46.3	40
Clear-cut	3.3	53.8	32.1
Alder SG	5.4	22.1	67.5
Conifer SG	20.9	24.1	34.2

Table 3. Checklist of taxa collected from upland forest headwater streams of Maybeso Experimental Forest and adjacent Harris River watershed Prince of Wales, Southeast Alaska.

Ephemeroptera	Plecoptera	Ryacophilidae
Baetidae	Nemouridae	*Rhyacophila*
Baetis	*Zapada*	Brachycentridae
Heptageniidae	*Visoka*	*Micrasema*
Cinygma		Limnephilidae
Cynigmula	Leuctridae	*Cryptochia*
Epeorus	*Despaxia*	*Chiranda*
Ironodes	Chloroperlidae	*Moselyana*
Rithrogena	*Sweltsa*	*Pseudostenophylax*
Ephemerellidae		*Psychoglypha*
Drunella	Trichoptera	Goeridae
Leptophlebiidae	Philopotamidae	*Goeracea*
Paraleptophlebia	*Dolophiloides*	Uenoidae
	Hydropsychidae	*Neophylax*
	Arctopsyche	Glossossomatidae
		Anagapetus

Table 4 (cont)

Coleoptera	Psychodidae	Non-insects
Ptilodactylidae	*Pericoma*	Turbellaria
	Simuliidae	Annelida
Diptera	*Prosimulium*	Oligochaeta
Thaumaleidae	Tipulidae	Copepoda
Ceratopogonidae	*Dicranota*	Harpactacoida
Atrichopogon	*Limonia*	Ostracoda
Probezzia	*Hexatoma*	Hydracarina
Chironomidae	*Pedicia*	
Chironominae	*Tipula*	
Orthocladinae	Empididae	
Tanypodinae	*Chelifera*	
Dixidae	*Clinocera*	
Dixa	*Oreogeton*	

Table 4. Percent distribution of Chironomidae subfamilies collected from large woody debris, cobble and gravel habitats in each management condition.

Habitat	Taxa	Old Growth	Clear-cut	Alder SG	Conifer SG
Large Woody Debris	Orthocladinae	59.3	91	85.6	83.4
	Tanypodinae	33.3	6.1	13.1	10.9
	Chironominae	7.5	2.9	1.3	5.7
Cobble	Orthocladinae	100	100	100	94
	Tanypodinae	0	0	0	2.7
	Chironominae	0	0	0	3.4
Gravel	Orthocladinae	100	86.2	80.2	95.9
	Tanypodinae	0	2.8	4	0
	Chironominae	0	11.1	15.8	4.1

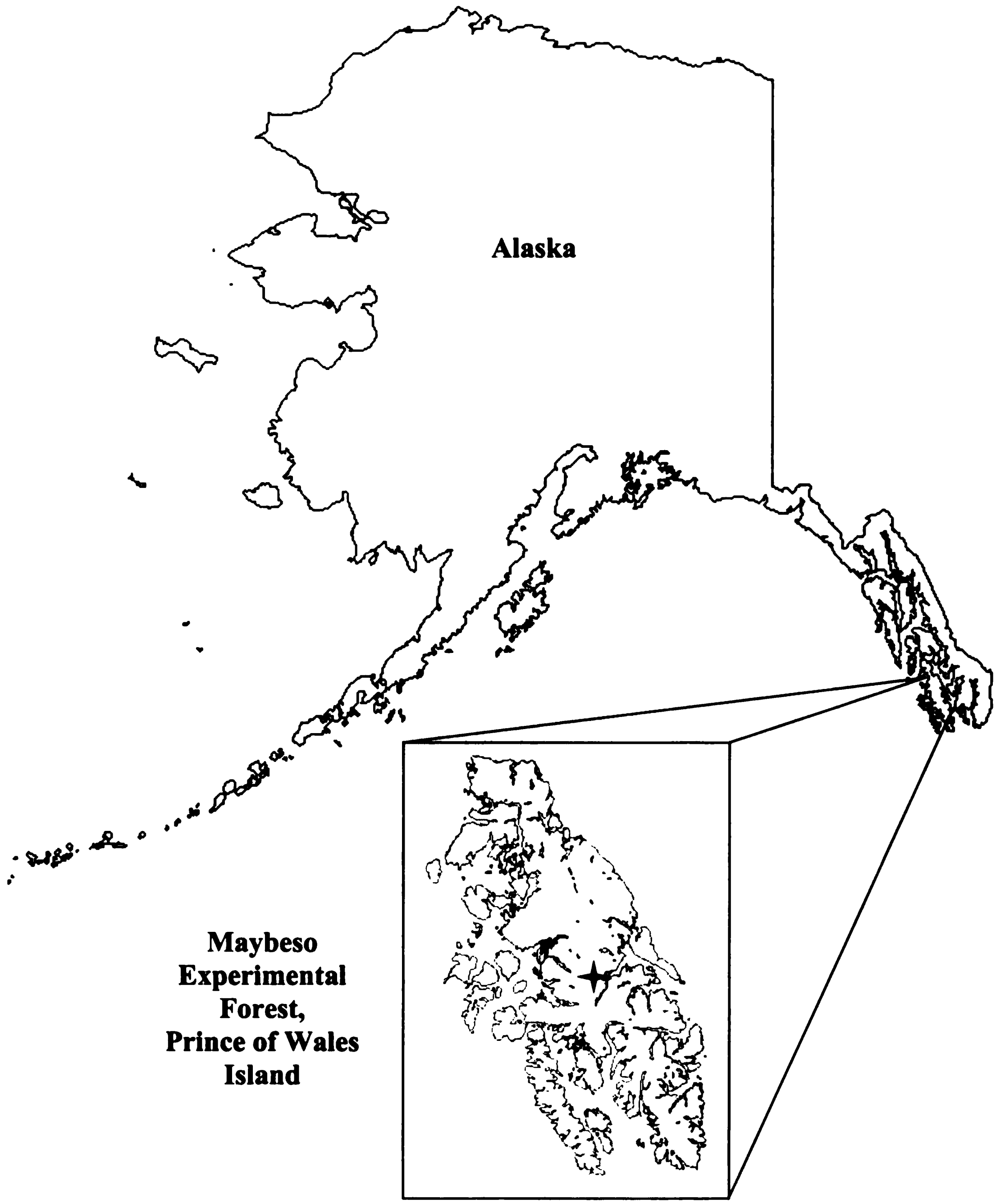

Figure 1. Maybeso Experimental Forest, Prince of Wales Island, Southeast Alaska

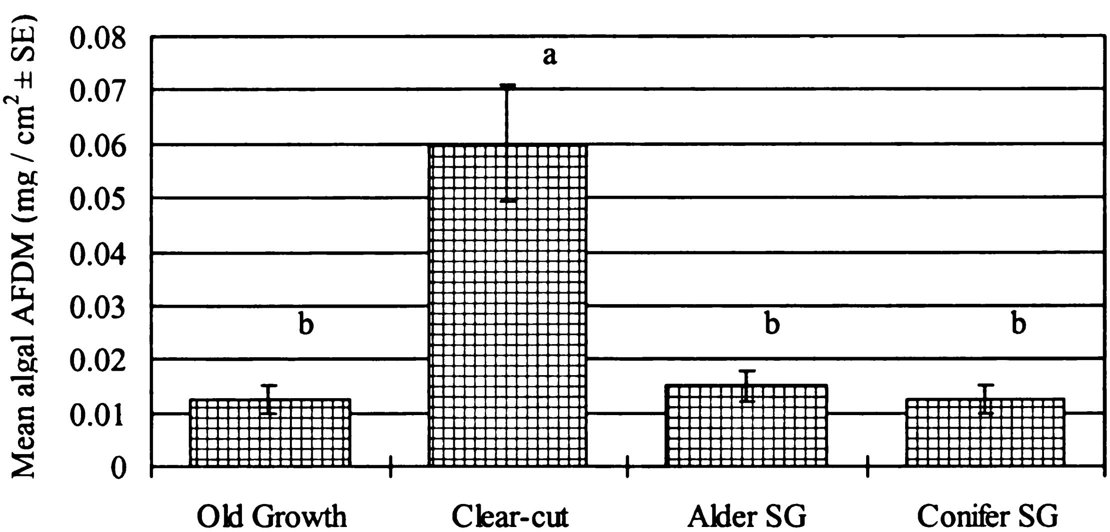

Figure 2. Mean algal AFDM among management conditions 1999. Means with different letters are significantly different ($p<0.05$).

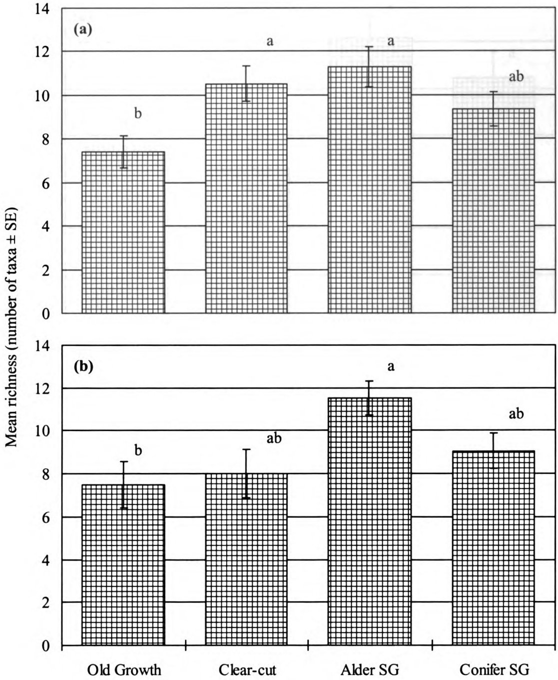

Figure 3. Mean richness of invertebrates among management conditions from (a) 1998 and (b) 1999. Means with different letters are significantly different ($p<0.05$)

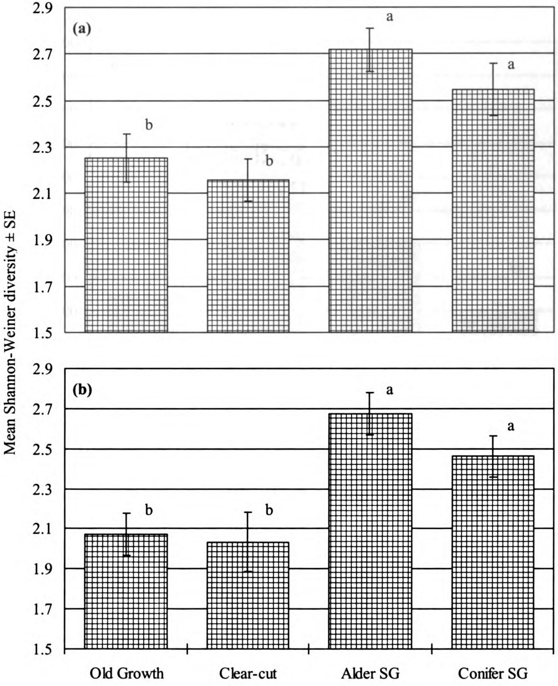

Figure 4. Mean Shannon-Weiner diversity of invertebrates among management conditions from (a) 1998 and (b) 1999. Means with different letters are significantly different ($p<0.05$).

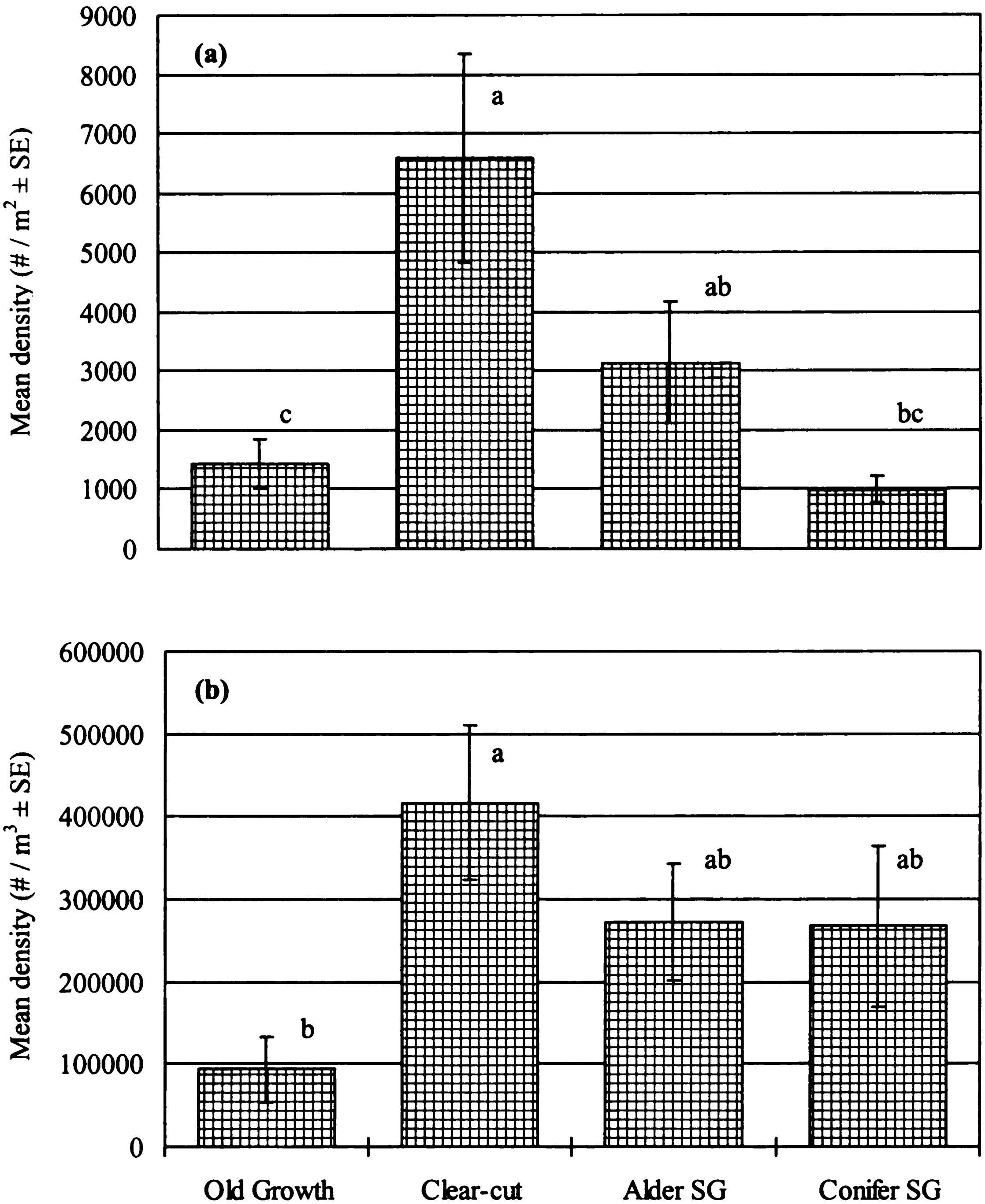

Figure 5. Mean densities of invertebrates among management conditions from (a) large woody debris and cobble habitats 7-15 July 1998; and (b) gravel habitats 11-14 June 1999. Means with different letters are significantly different ($p < 0.05$).

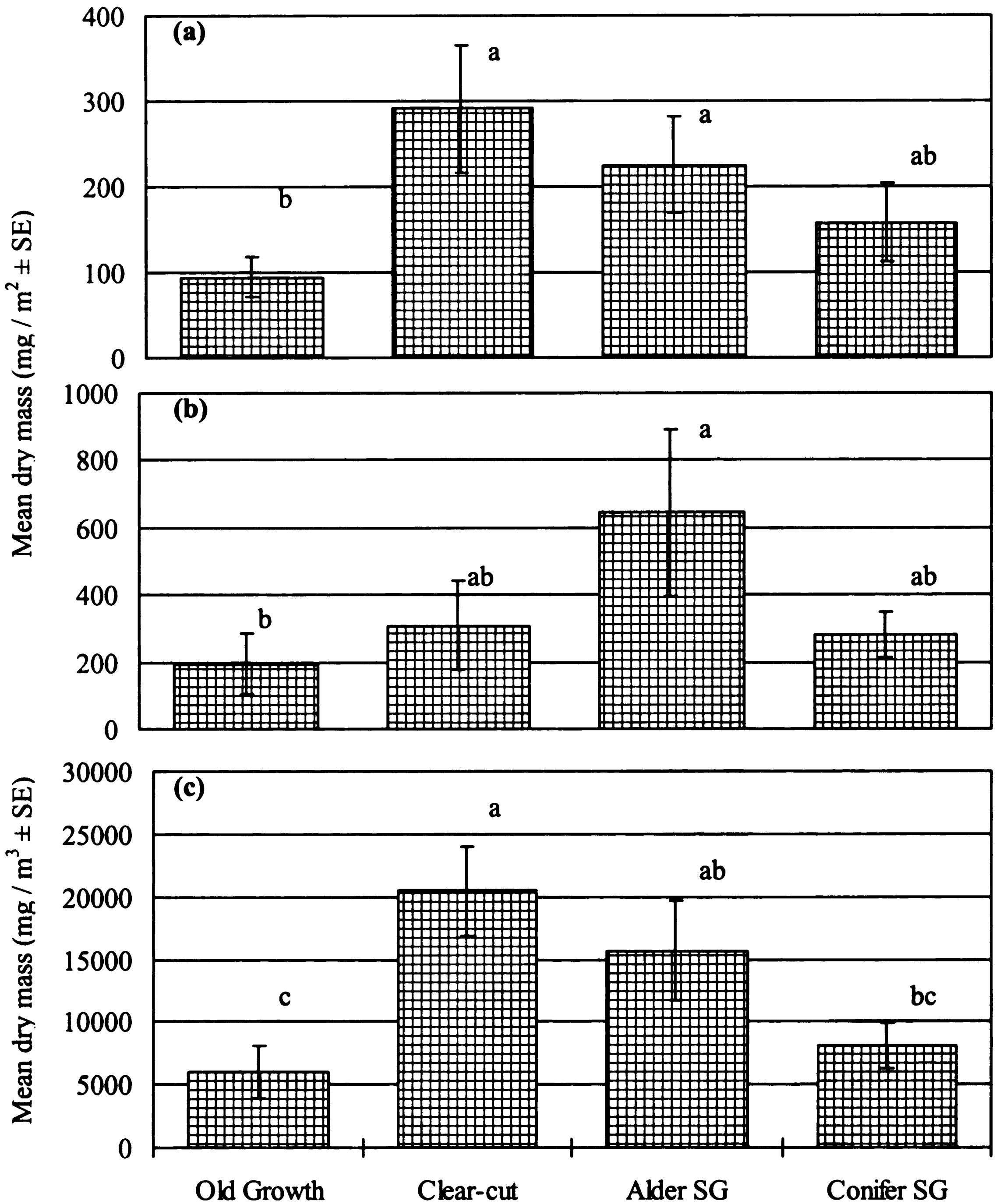

Figure 6. Mean dry mass of invertebrates among management conditions from (a) 1998 large woody debris and cobble habitats; (b) 1999 large woody debris and cobble habitats; and (c) 1999 gravel habitats. Means with different letters are significantly different ($p<0.05$).

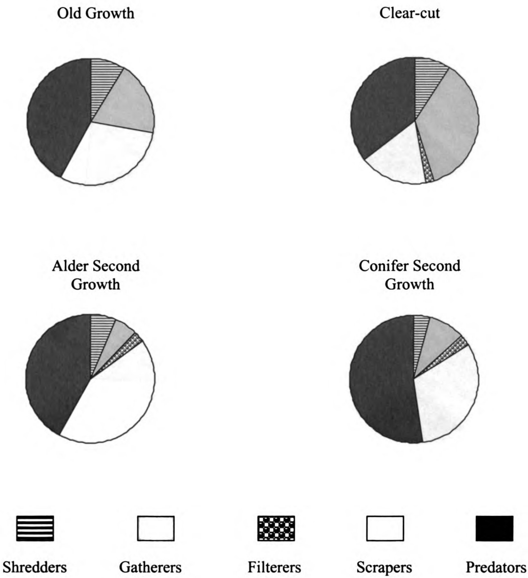

Figure 7. Percentage of functional feeding groups, based on biomass, present among management conditions 7-15 July 1998.

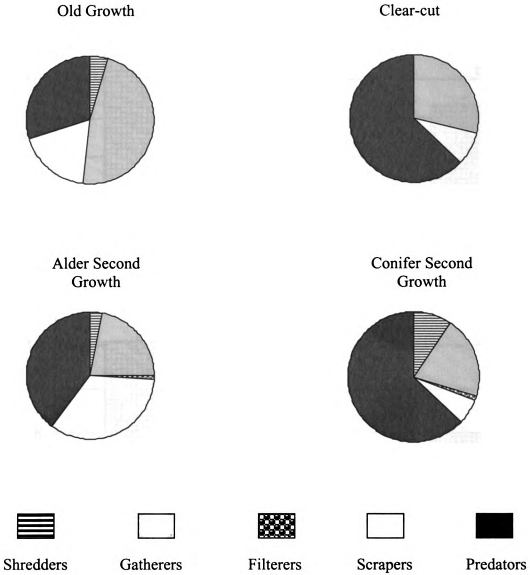

Figure 8. Percentage of functional feeding groups, based on biomass, present among management conditions 11-14 June 1999.

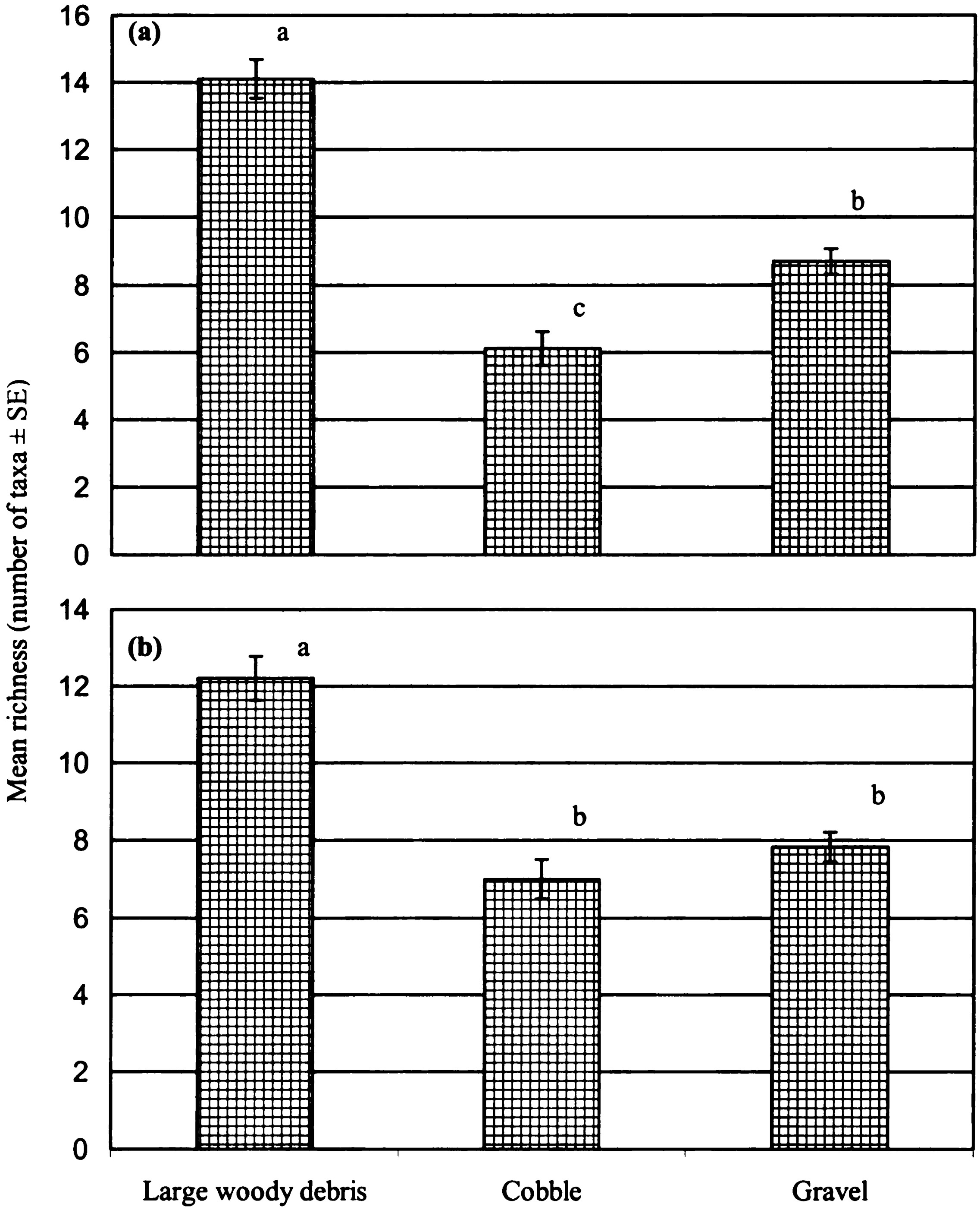

Figure 9. Mean richness of invertebrates among habitats from (a) 7-15 July 1998 and (b) 11-14 June 1999. Means with different letters are significantly different ($p<0.05$).

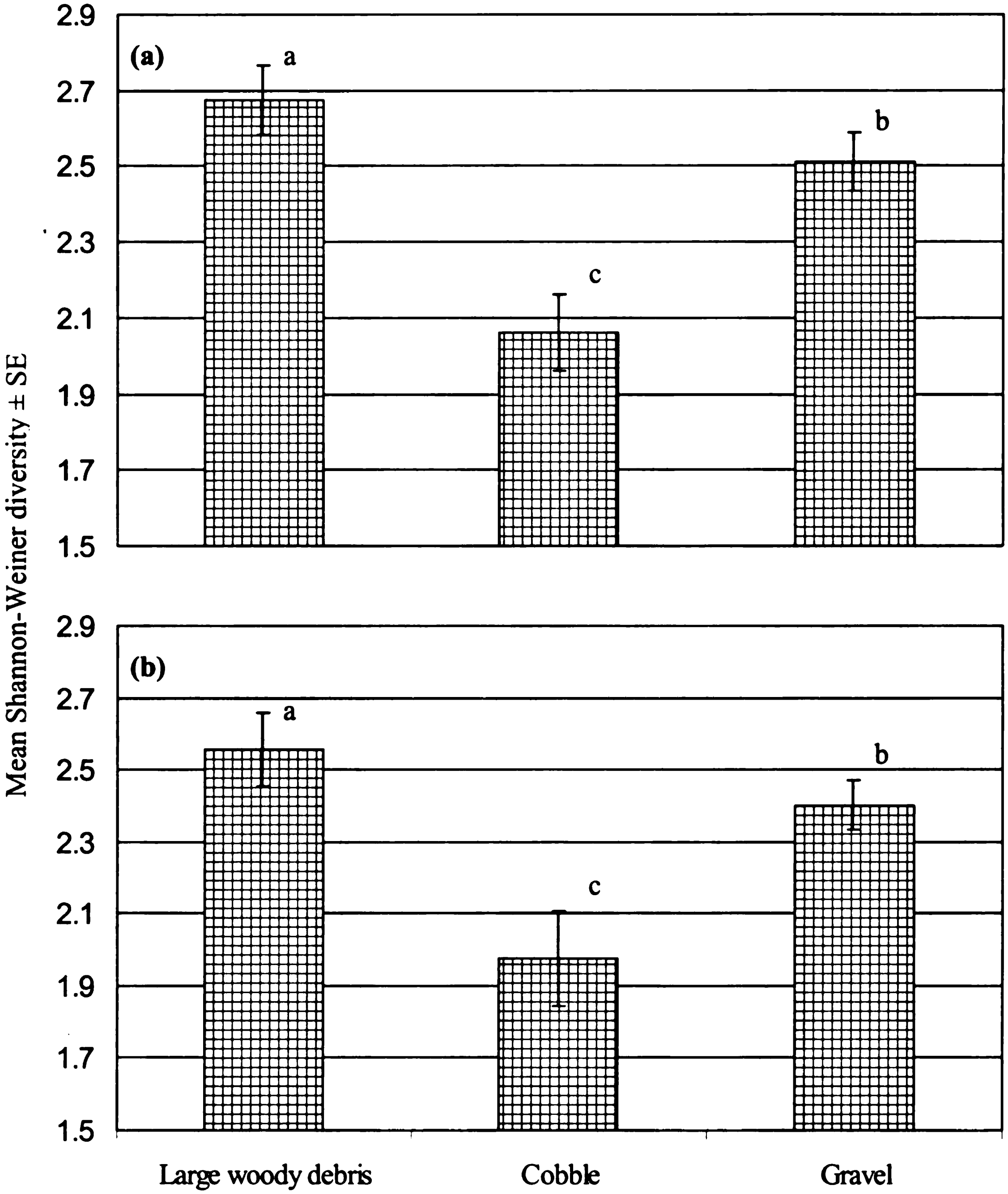

Figure 10. Mean Shannon-Weiner diversity among habitats from (a) 7-15 July 1998 and (b) 11-14 June 1999. Means with different letters are significantly different ($p<0.05$).

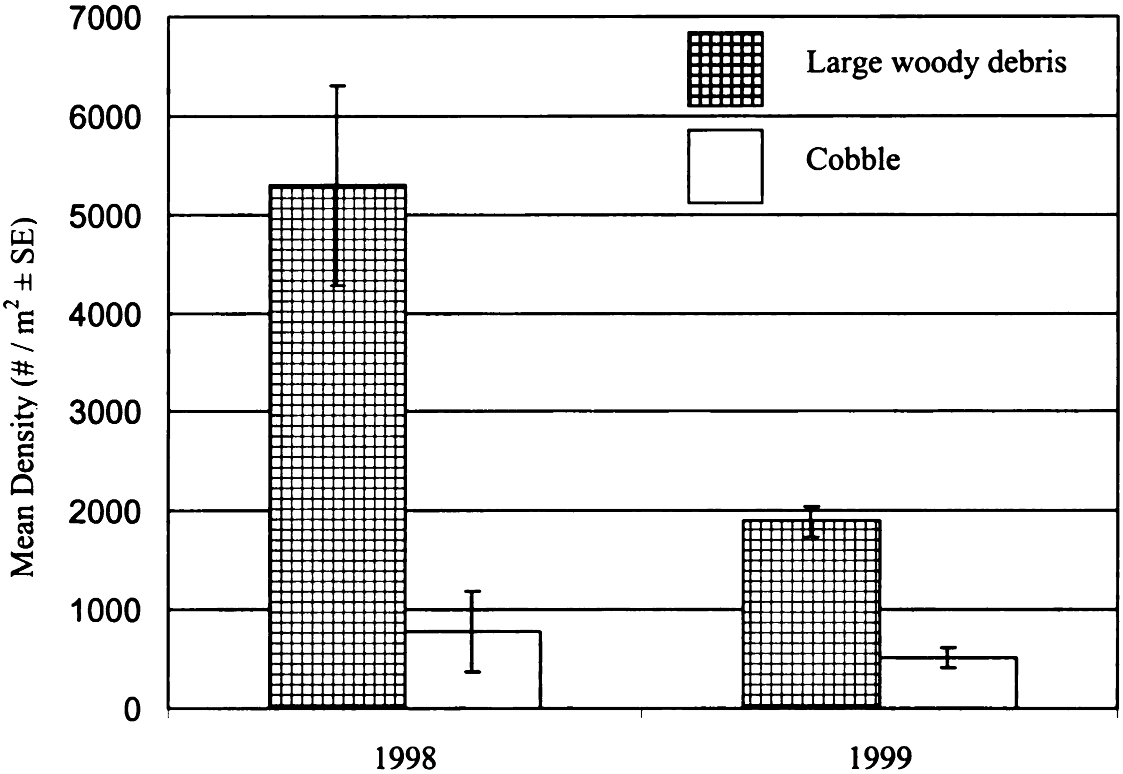

Figure 11. Mean densities of benthic invertebrates on large woody debris and cobble habitats across all management conditions. 7-15 July 1998 and 11-14 June 1999.

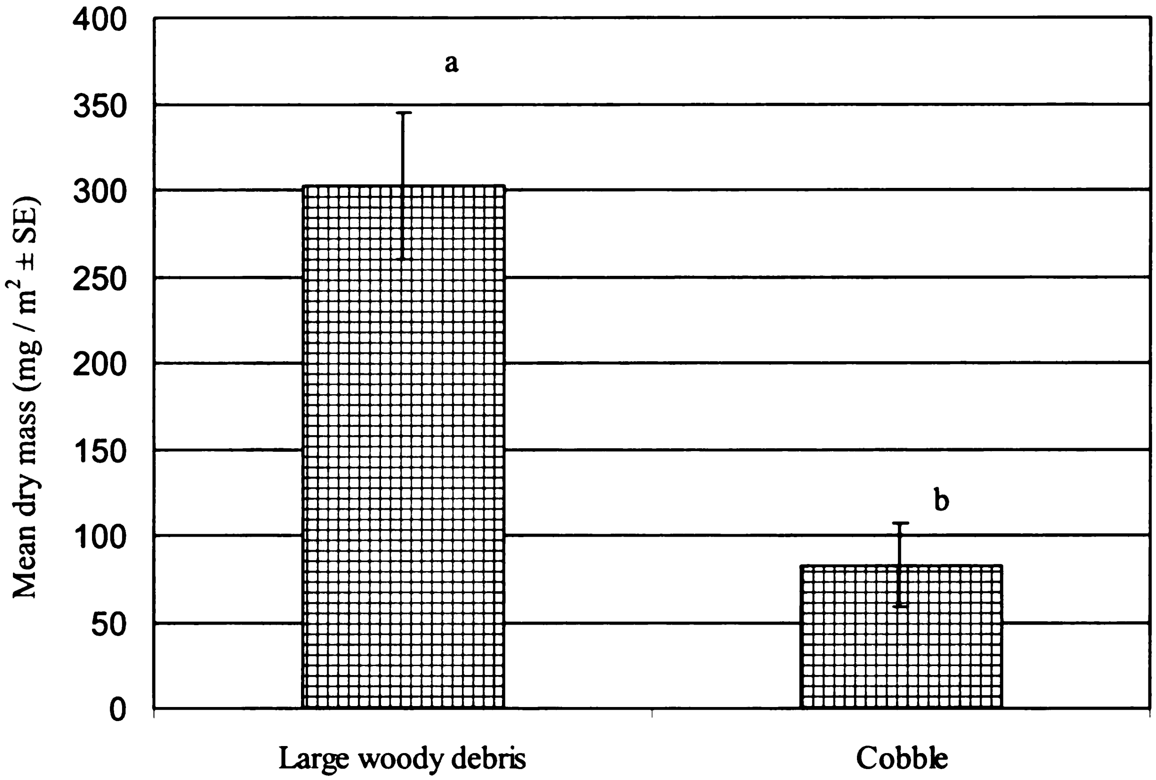

Figure 12. Mean dry mass of invertebrates among large woody debris and cobble habitats. 7-15 July 1998. Means with different letters are significantly different ($p<0.05$)

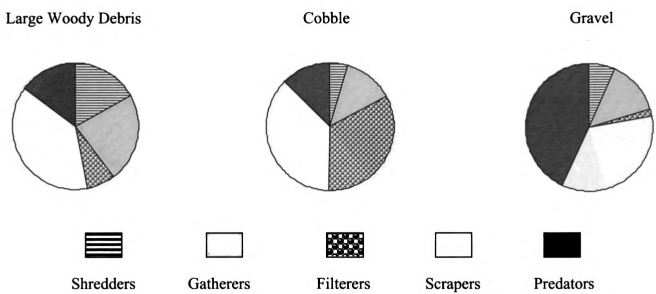

Figure 13. Percentage of functional feeding groups, based on biomass, present among instream habitats 7-15 July 1998.

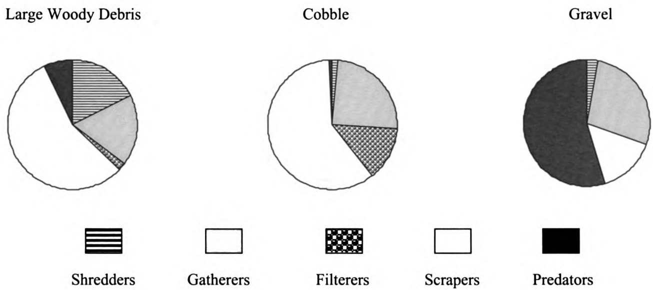

Figure 14. Percentage of functional feeding groups, based on biomass, present among instream habitats 11-14 June 1999.

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APPENDIX

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.: 2001-05

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

BENTHIC INVERTEBRATE COMMUNITY STRUCTURE AS AFFECTED BY FOREST SUCCESSION AFTER CLEAR-CUT LOGGING ON PRINCE OF WALES ISLAND, 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)
OSVALDO HERNANDEZ

Date 20, IV 2001

*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

Page 1 of 5 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										
Baetidae *Baetis spp.*	Harris Catchment	14, VII 1998		4						MSU
Heptageniidae *Cinygma spp.*	Harris Catchment	13, VII 1998		2						MSU
"	Harris Catchment	12, VI 1999		1						MSU
"	Maybeso Catchment	14, VI 1999		1						MSU
Heptageniidae *Cinygmula spp.*	Harris Catchment	14, VII 1998		1						MSU
"	Harris Catchment	13, VII 1998		1						MSU
"	Harris Catchment	14, VII 1998		2						MSU
Heptageniidae *Epeorus spp.*	Harris Catchment	14, VII 1998		1						MSU
"	Harris Catchment	13, VII 1998		1						MSU
"	Harris Catchment	12, VI 1999		2						MSU
Heptageniidae *Ironodes spp.*	Harris Catchment	14, VII 1998		1						MSU
"	Harris Catchment	13, VII 1998		2						MSU
"	Maybeso Catchment	7, VII 1998		1						MSU
Heptageniidae *Rithrogena spp.*	Harris Catchment	11, VI 1999		1						MSU
"	Harris Catchment	11, VI 1999		1						MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

OSVALDO HERNANDEZ

Date 20, IV 2001

Voucher No 2001-05

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

Curator [signature] Date 4/23/2001

Appendix 1.1

Voucher Specimen Data

Page 2 of 5 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									
Ephemerellidae *Drunella spp.*	Harris Catchment	14, VII 1998		1						MSU
"	Harris Catchment	14, VII 1998		3						MSU
Leptophlebiidae *Paraleptophlebia spp.*	Harris Catchment	14, VII 1998		1						MSU
"	Harris Catchment	12, VI 1999		1						MSU
"	Harris Catchment	13, VII 1998		1						MSU
"	Harris Catchment	7, VII 1998		1						MSU
PLECOPTERA										
Nemouridae *Zapada spp.*	Harris Catchment	14, VII 1998		3						MSU
Nemouridae *Visoka spp.*	Harris Catchment	14, VI 1999		1						MSU
Leuctridae *Despaxia spp.*	Harris Catchment	14, VII 1998		2						MSU
"	Maybeso Catchment	7, VII 1998		1						MSU
Chloroperlidae *Sweltsa spp.*	Maybeso Catchment	7, VII 1998		2						MSU
"	Harris Catchment	14, VII 1998		1						MSU
TRICHOPTERA										
Philopotamidae *Dolophiloides spp.*	Harris Catchment	14, VII 1998		1						MSU
"	Harris Catchment	13, VII 1998		3						MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

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

Curator Date

Appendix 1.1

Voucher Specimen Data

Page 3 of 5 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									
Hydropsychidae *Arctopsyche spp.*	Maybeso Catchment	14, VI 1999		2						MSU
"	Maybeso Catchment	14, VI 1999		1						MSU
"	Harris Catchment	11, VI 1999		1						MSU
Rhyacophilidae *Rhyacophila spp.*	Harris Catchment	14, VII 1998		4						MSU
Brachycentridae *Micrasema spp.*	Harris Catchment	14, VII 1998		1						MSU
"	Maybeso Catchment	7, VII 1998		3						MSU
Limnephilidae *Cryptochia spp.*	Harris Catchment	14, VII 1998		1						MSU
"	Maybeso Catchment	7, VII 1998		3						MSU
Limnephilidae *Chyranda spp.*	Maybeso Catchment	14, VI 1999		1						MSU
Limnephilidae *Moselyana spp.*	Maybeso Catchment	14, VI 1999		1						MSU
Limnephilidae *Pseudostenophylax spp.*	Harris Catchment	12, VI 1999		1						MSU
"	Harris Catchment	12, VI 1999		1						MSU
Limnephilidae *Psychoglypha spp.*	Harris Catchment	13, VII 1998		1						MSU
"	Maybeso Catchment	14, VI 1999		1						MSU
Goeridae *Goeracea spp.*	Maybeso Catchment	7, VII 1998		3						MSU
"	Harris Catchment	14, VII 1998		1						MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

OSVALDO HERNANDEZ

Date 20, IV 2001

Voucher No 2001-05

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

Curator Date

Appendix 1.1

Voucher Specimen Data

Page 4 of 5 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									
Uenoidae *Neophylax spp.*	Maybeso Catchment	7, VII 1998		2						MSU
"	Maybeso Catchment	14, VI 1999		2						MSU
Glossossomatidae *Anagapetus spp.*	Maybeso Catchment	14, VI 1999		3						MSU
COLEOPTERA										
Ptilodactylidae	Maybeso Catchment	7, VII 1998		5						MSU
DIPTERA										
Thaumaleidae	Harris Catchment	12, VI 1999		1						MSU
"	Harris Catchment	14, VII 1998		1						MSU
Ceratopogonidae *Atrichopogon spp.*	Maybeso Catchment	7, VII 1998		1						MSU
"	Harris Catchment	18, VII 1998		1						MSU
"	Harris Catchment	12, VI 1999		2						MSU
Ceratopogonidae *Probezzia spp.*	Maybeso Catchment	7, VII 1998		2						MSU
"	Harris Catchment	14, VII 1998		1						MSU
Chironomidae	Harris Catchment	12, VI 1999		10						MSU
Dixidae *Dixa spp.*	Maybeso Catchment	7, VII 1998		1						MSU
"	Harris Catchment	14, VII 1998		1						MSU
"	Maybeso Catchment	14, VI 1999		1						MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

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Appendix 1.1

Voucher Specimen Data

Page 5 of 5 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									
Dixidae *Dixa spp.*	Harris Catchment	18, VII 1998		1						MSU
Simuliidae *Prosimulium spp.*	Maybeso Catchment	7, VII 1998		1						MSU
"	Harris Catchment	14, VII 1998		1						MSU
"	Harris Catchment	13, VII 1998		2						MSU
Tipulidae *Dicranota spp.*	Harris Catchment	14, VII 1998		4						MSU
Tipulidae *Limonia spp.*	Harris Catchment	14, VII 1998		1						MSU
Tipulidae *Hexatoma spp.*	Harris Catchment	12, VI 1999		1						MSU
"	Maybeso Catchment	14, VI 1999		2						MSU
Tipulidae *Pedicia spp.*	Harris Catchment	11, VI 1999		1						MSU
Tipulidae *Tipula spp.*	Harris Catchment	11, VI 1999		1						MSU
Empididae *Chelifera spp.*	Harris Catchment	13, VII 1998		1						MSU
"	Maybeso Catchment	7, VII 1998		3						MSU
Empididae *Clinocera spp.*	Harris Catchment	14, VII 1998		4						MSU
Empididae *Oreogeton spp.*	Harris Catchment	12, VI 1999		1						MSU
"	Harris Catchment	12, VI 1999		3						MSU

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

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Date 20, IV 2001

Voucher No 2001-05

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Curator Date