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INFLUENCE OF MARINE-DERIVED NUTRIENTS FROM SPAWNING SALMON ON AQUATIC INSECT COMMUNITIES IN SOUTH-EAST ALASKAN STREAMS

By

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ABSTRACT

INFLUENCE OF MARINE-DERIVED NUTRIENTS FROM SPAWNING SALMON ON AQUATIC INSECT COMMUNITIES IN SOUTH-EAST ALASKAN STREAMS

By

JoAnna Lynn Lessard

Alaska is the last region along the Pacific coast of the United States that still enjoys large runs of spawning salmon. Salmon runs provide these oligotrophic systems with a huge pulse of nutrients from the ocean. The retention of these nutrients in streams potentially sustain this pulse of nutrients over many months. Annual nutrient delivery from salmon to Alaskan streams range into the millions of tons of carbon, nitrogen, phosphorous. These nutrients are termed marine-derived nutrients (MDN) and may be tightly linked to secondary production in streams. The most important link between MDN and production is in the production of juvenile salmon. In providing a positive feedback mechanism to ensure viability of subsequent generations, intermediate steps that connect MDN and juvenile salmon production include alterations of dissolved nutrients, biofilm production and alterations to the macroinvertebrate community. Changes due to MDN have far reaching implications in watersheds that receive salmon and may shape the dynamics of stream communities seasonally.

This research focused on aquatic insect community responses to MDN in multiple natural stream systems in southeast Alaska. The objectives were quantify insect abundance, biomass, functional group proportions, richness, diversity, growth and secondary production in relation to MDN inputs. These community attributes were studied to establish if stream communities with exposure to MDN are organized differently from non-anadromous streams in that region. This research will help to elucidate the effect that MDN has on stream insect communities and will also help to better understand the link between MDN and fish production.

Mayfly standing stock and secondary production was higher in control reaches. Chironomid production was higher in stream sections that do receive large annual runs of salmon. Richness, diversity and functional group composition was not impacted by MDN over most of the year. These results suggest that the disturbance of salmon spawning creates a dichotomy of response to MDN so that larger, univoltine taxa have lower population levels in salmon spawning areas. Smaller, multivoltine taxa, however, have higher populations levels, most likely due to their ability to recover and respond to MDN. The links between MDN and juvenile salmon production may be more simplified than many models predict.

This dissertation is dedicated to my parents, Kathy and Joe Lessard, who always celebrate my victories and help me through my disappointments.

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Chapter 1
Literature Review and Research Introduction

Introduction

Nutrient transfers along streams and rivers from headwaters to the mouth are a well-studied phenomenon. The utilization of terrestrially derived nutrients (e.g., nitrates, phosphorous, etc.) from run-off, erosion, and riparian litter are considered to be the drivers of stream productivity. Stream communities are hypothesized to be organized spatially (Cummins 1974, Vannote et al. 1980) and temporally (Kaushik and Hynes 1971, Cummins et al. 1989) to capitalize on the predictable influxes of these terrestrial nutrients.

Coastal stream that serve as spawning ground for anadromous salmon have an additional nutrient source that may cause organizational patterns that differ from streams that rely solely on nutrients from the watershed. The life history of salmon is fairly complicated and varies among the different species. The general scheme is for a salmon to be semelparous (die after spawning) spending part of its early life growing in natal streams before undergoing physiological changes needed to deal with salt water (i.e., smoltification). Smolts then migrate to the ocean where they grow to adult size by feeding on marine-based nutrients (e.g., marine plankton and fish) until finally returning to the stream where they were born to spawn and die. It is theorized that salmon evolved anadromy around 25 million years ago to take advantage of newly cooled and productive oceans where they could grow larger than if they remained in their comparatively un-productive natal streams (Lichatowich 1999). By completing this circle, the salmon create a nutrient pulse in the form of their excretion, eggs, sperm and carcasses that travels in the opposite direction of normal river continuum theory (i.e. Vannote et al. 1980).

The role that these marine-derived nutrients (MDN) play in coastal systems has been the object of study in recent years. It is of particular interest in the Pacific Northwest of the United States, where salmon runs are extinct or threatened in many streams along the coasts of Washington, Oregon and northern California (Lichatowich 1999, Gresh et al. 2000). It has been hypothesized that the salmon provide an essential nutrient source in these normally oligotrophic Northwestern systems and, by subsidizing the nutrient base in their spawning grounds, increase the viability and production of their own offspring fostering future generations of salmon (Kline et al. 1997, Lichatowich 1999). Without enough adults returning to spawn in these streams, salmon populations may spiral into extinction and the entire stream community may lose a nutrient source that it has relied on for thousands of years. Reversing this trend may be the key to saving salmon in the Pacific Northwest (Bilby et al. 2000, Stockner et al. 2000).

Alaska is one of the few areas in the United States where salmon runs remain at or near historic levels (Baker et al. 1996, Gresh et al. 2000). Southeast Alaska contains the 8.5 million hectare Tongass National Forest, most of which is pristine forest surrounding 5,200 anadromous salmon streams (Halupka et al. 1999). These streams collectively support hundreds of millions of spawning salmon that annually transport millions of kilograms of carbon, nitrogen, phosphorous, and other nutrients to freshwater streams (Larkin and Slaney 1997, Halupka et al. 1999). This represents a considerable nutrient load for one region when compared to streams in Washington, Oregon and California, which collectively receive only 11.8-13.7 million kg of salmon annually (i.e., 360,000-

418,000 kg N and 43,000-49,000 kg P) (Gresh et al. 2000). Because the runs in Alaska are still largely intact, this region provides the opportunity to study the structure and function of stream systems with the salmon runs in a relatively pristine state. Research on the role of MDN in stream ecosystems may elucidate conservation measures that should be taken and also help direct restoration attempts in areas where salmon are threatened.

Some impacts of salmon runs on stream communities have been investigated in recent years, and these studies have revealed varying responses to MDN enrichment (Cederholm et al. 1999). Some of this variation may be due to variability in the retention of salmon carcasses in streams due to differences in flow rates and abundance of debris jams and wood in stream channels (Cederholm and Peterson 1985, Cederholm et al. 1989). While there is variation in the level of response of stream communities to MDN enrichment, several patterns of community responses are evident.

Increasing the production of lower trophic levels is an important enrichment mechanism, because this provides the basis for higher production throughout the stream community. Several studies have shown increased production of biofilm (i.e. mixed assemblage of autotrophic and heterotrophic microbes set in a glycoprotein polysaccharide medium attached to stream substrates) in the presence of MDN (Schuldt and Hershey 1995, Cederholm et al. 1999, Peterson and Foote 2000). In Southeast Alaska, Wipfli et al. (1998) found biofilm production to be 15 times higher in a MDN enriched stream section compared to a non-anadromous upstream control section. Stable isotope research on streams in Washington showed that biofilm in the presence of MDN obtained up to 30% of nitrogen and 26.6% of carbon from salmon carcasses, demonstrating the utilization of MDN by biofilm in these systems (Bilby et al. 1996).

The subsequent consumption of MDN enriched biofilm by invertebrate scrapers and collectors is one way that MDN is transferred to the next trophic level. The increased abundance of biofilm has been shown to coincide with an increase in invertebrate abundance in enriched stream sections (Wipfli et al. 1998) and the disproportionate incorporation of MDN into invertebrate grazers (Schuldt and Hershey 1995). Beyond the indirect enrichment of invertebrates from feeding on biofilm and other insects that are enriched in MDN (Bilby et al. 1996), there is also the potential for direct enrichment. Several researchers have found insects associated with salmon carcasses themselves and also have found evidence for the direct consumption of carcass tissue by aquatic insects (Piorkowski 1995, Kline et al. 1997, Bilby et al. 2000, Merritt and Wallace 2001). While insects may feed on salmon flesh and benefit from these nutrients, it is unclear if the salmon flesh is the attractant or the associated microbes and fungi growing on the carcasses (Minakawa 1997). Most likely the salmon carcasses play a dual role as substrate and concentrated food resource directly and indirectly, and as such may be important ephemeral habitats.

Whatever the mechanism of enrichment (direct or indirect), invertebrate communities have been shown to respond to salmon runs in some important ways. Among these responses are short-term reductions in abundance and increased drift due to the high level of benthic disturbance created during large spawning runs (Minakawa 1997, Peterson and Foote 2000). As discussed earlier, increased insect density following salmon carcass decomposition has been documented (Minikawa 1997, Wipfli et al. 1998, Kline et al. 1997), as well as indications that insect richness and diversity may increase from salmon enrichment in central Alaskan streams (Piorkowski 1995). There is also evidence that growth rates of certain taxa increase in the direct presence of salmon tissue (Minakawa 1997, Chaloner and Wipfli 2002). Additionally, the source of nutrients for invertebrate biomass has been traced using stable isotope analysis and these studies reveal that MDN is an important contributor to the nutrition of many of the functional feeding groups of insects in stream systems (Schuldt and Hershey 1995, Bilby et al. 1996).

Macroinvertebrate communities often show temporal and spatial organization in response to nutrient sources. Stream shredders emerge and grow at times which take advantage of autumnal leaf fall and the associated microbial community in temperate regions (Kaushik and Hynes 1971, Anderson and Cummins 1979, Cummins et al. 1989). The vast amount of research that has been done on this phenomenon has concluded that shredder communities have evolved with the predictable influx of leaves and their subsequent conditioning, and that these factors drove the life history of shredders (Anderson and Cummins 1979,Cummins and Klug 1979). Different populations of the same insect species also have been shown to vary their growth rates in response to different nutrient levels in streams in the same geographic area (Anderson and Cummins 1979). Filtering insects often congregate below lake outlets capitalizing on the high quality seston in these areas (Wallace and Merritt 1980, Herlong and Mallin 1985, Richardson and Mackay 1991). Because of the plasticity of insect communities to mold themselves according to the productivity of the system, and the long historical relationship that exists between marine enrichment and stream communities in Alaska, it is possible that aquatic invertebrates in MDN enriched streams have systematically different communities from un-enriched streams in the same region.

MDN enrichment may allow these cold, oligotrophic streams to sustain a greater diversity and abundance of insect taxa compared to streams without salmon. The seasonal presence of large numbers of spawning salmon and carcasses may alter the diversity and abundance of taxa found in MDN enriched reaches on a seasonal basis as well. This could happen as invertebrate communities re-structure themselves first around the disturbance of spawning and then around the additional substrate and food resources created by the carcasses themselves. Insects may also exhibit different growth rates in enriched streams as the production of primary producers and microbes increase, which would lead to greater condition, survival, fecundity and abundance of these insects. This increase in diversity and abundance from MDN may provide the basis for increased fish production in these streams. Fish communities, and in particular juvenile salmon, may benefit initially from increased food during spawning in the form of salmon eggs and increased invertebrate drift and then all year as invertebrate production remains elevated due to the enrichment. The entire stream community may be structured seasonally around the salmon spawning run, which will provide insight into another mechanism for trophic linkages in stream ecology.

The objectives of this research were to:

1. Evaluate the effect of MDN on seasonal patters of aquatic insect abundance and biomass in southeast Alaskan streams.
2. Evaluate the effect of MDN on seasonal patters of aquatic insect diversity and richness in southeast Alaskan streams.

3. Evaluate the effect of MDN on annual secondary production of selected insect taxa in southeast Alaskan streams.
4. Evaluate the effect of spring carry-over of MDN on growth rates of selected insect taxa in southeast Alaskan streams.

I hypothesized, that natural stream systems that have a long history of natural MDN enrichment via salmon spawners will:

1) Have aquatic insect communities with greater standing stock abundance and biomass than streams that do not receive MDN.
2) Have aquatic insect communities with greater diversity and richness than communities that are not subsidized by MDN.
3) Have aquatic insects that show greater annual secondary production than aquatic insects living in non-anadromous streams
4) Have aquatic insects that show greater specific growth rates than aquatic insects living in non-anadromous streams

Study sites

This research was conducted in southeast Alaska in the Tongass National Forest. This area is described as having a maritime climate (average precipitation=1500-5000 mm, average July temperature=13°C) and dense coastal forest (Oswood et al. 1995). The primary areas of study were streams in and around the Juneau area (Figure 1) and in selected streams on Prince of Wales Island (Figure 1). The primary salmon runs in this region are pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) which spawn in this region typically in early autumn (August-September). These streams also receive runs from coho (*O. kisutch*), sockeye (*O. nerka*) and chinook (*O. tshawytscha*) salmon.

Juvenile coho, sockeye and chinook spend 1-3 years in their natal streams before migrating to the ocean while pink and chum salmon migrate out to estuary waters soon after emerging from the gravel as fry. Other common fish species found in these streams are dolly varden (*Salvelinus malma*), sculpin (*Cottus spp.*), cutthroat trout (*O. clarki*), and steelhead trout (*O. mykiss*).

This research was conducted in streams that we term "legacy" streams, because they are stream systems that have an anadromous section (connects to the ocean) and a non-anadromous section that has been cut off from salmon migrations over eons of time (since the little ice age) by a natural barrier (i.e. an impassable waterfall). Therefore downstream sections have a "legacy" of annual MDN inputs. This disconnection of stream sections allowed for the simultaneous comparison of the insect fauna that live in areas with (treatment sections) and without (control sections) exposure to MDN, while minimizing variation in other factors that could also impact insect communities (e.g. riparian cover, water temperature etc.). Within this "category" of streams (i.e. legacy) we have two general groups, the first being streams that receive large annual runs of salmon and the second are streams that typically receive low numbers of spawners. These studies will help us to understand if aquatic insect communities across multiple natural stream systems respond to the cycle of natural MDN enrichment in a generalized manner and also if there is some seasonality to their response. Specific experiments or studies will address select community attributes (e.g. growth, secondary production) to be studied in fewer systems but at a higher resolution than the studies across all streams. The combination of all these studies fills gaps in the literature on the effects of MDN on aquatic insect communities.

Chapter Introductions

Chapter 2: Influence of marine-derived nutrients from spawning salmon on stream macroinvertebrate communities in southeast Alaska.

The current literature on insect community responses (e.g. standing stock biomass) to MDN contains results from studies done either in mesocosms, from short-term experiments and/or from natural stream observations with little or no replication. Diversity, richness and functional group changes in association with MDN have not been examined thoroughly in any study.

This chapter focuses on broad seasonal community patterns across all seven study streams. Streams were sampled quantitatively and qualitatively in the spring (pre-run), late summer (during-run), and mid-Autumn (post-run) in each stream section (both above and below the barrier). Quantitative samples were used to examine trends in insect abundance, biomass, diversity and functional groups around the salmon runs, using the upstream sections as controls for each downstream treatment area. The qualitative samples were used to examine community richness patterns.

Chapter 3: Influence of marine-derived nutrients from spawning salmon on mayfly and midge secondary production in two southeast Alaskan streams.

One of the most important questions in research studies addressing MDN effects on streams is the influence on secondary production, as this is the intermediate link between the dissolved nutrients from salmon and fish production. Yet secondary production has never actually been measured in MDN studies in streams, instead it had been inferred from standing crop estimates.

In order to address the question of the influence of MDN on insect secondary production, I selected two legacy streams to sample through time for the majority of the growing season (May to October) in both stream sections (above and below the barrier). The selection of taxa for this study was based on 1) taxa commonly cited in publications as showing changes in standing crop from MDN, 2) taxa common in our study streams, and 3) taxa with different life histories. For these reasons, secondary production estimates were made for the five most common mayfly genera: *Baetis spp.* (Baetidae), *Epeorus spp.*, *Cinygmula spp.*, *Rhithrogena spp.* (Heptageniidae) and *Drunella spp.* (Ephemerellidae) and midges of the family Chironomidae. The richness of the midge community in each stream section was estimated over the study period, but production was calculated at the family level. This study determined what the influence of salmon is on the secondary production of insects and how the results vary for univoltine and multivoltine taxa.

Chapter 4: Growth of caddisflies (Limnephilidae: Trichoptera) in response to spring carry-over of marine-derived nutrients and food type in a southeast Alaskan stream.

Previous studies have shown that insects grow faster in the direct presence of MDN from salmon carcasses (Minakawa 1997,Chaloner and Wipfli in press). No studies, however, have addressed the influence of MDN carry-over on insect communities the following spring. In order for MDN to be of great importance to the overall production of their natal streams the nutrients must be incorporated into the community for a longer period than for the few weeks that carcasses are present.

I selected one legacy stream, Harris Creek, on Prince of Whales Island, to run a growth experiment in May, after winter snow melt and at least six months after salmon carcasses from the Autumnal pink and chum run would have disappeared. The experiment was run on three limnephilid caddisfly genera including a scraper (*Dicosmoecus atripes*) and two shredders (*Onocosmoecus sp.* and *Psychoglypha spp*) and simultaneously compared the growth rates of these genera in anadromous and non-anadromous stream sections. This experiment examined the effects of spring carry-over of MDN into the stream system and its effect on insect growth of different functional groups.

The following chapters, as introduced above, address one or more of the objectives and hypotheses listed in this introductory chapter. Separately, they address aspects of the influence of spawning salmon on aquatic insect community attributes that are currently lacking in the MDN literature. Collectively they provide strong empirical and experimental evidence for the dynamics of insect communities in southeast Alaskan streams and question the role that MDN plays as a nutrient subsidy to insects in these stream systems.

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Chapter 2

Influence of marine-derived nutrients from spawning salmon on aquatic insect community patterns in south-east Alaskan streams

Abstract

Studies investigating enrichment effects from spawning salmon, termed marine-derived nutrients (MDN), have shown positive relationships between insect abundance and biomass in artificial streams and in minimally replicated natural stream studies. To better understand these relationships, we sampled seven streams seasonally in southeast Alaska. Of the seven study streams four annually receive large runs of chum and pink salmon, while three had low or no salmon runs. All the streams selected had a natural waterfall barrier to salmon, which allowed for the simultaneous sampling of stream sections with similar habitat characteristics but with the separation of the influence of salmon and the barrier.

Nine modified-Hess samples were taken before, during and after the fall salmon run in each stream section of our seven study streams between 2001 and 2002. Qualitative samples for taxa richness also were taken in each stream section. Samples were analyzed for mean density, biomass (by taxon and functional feeding group), taxa richness and Shannon-Weiner diversity for each stream section (upstream and downstream) by period (pre, during and post) and run size (high and low).

High run streams had upstream sections with a greater abundance and biomass of mayflies (dominated by Baetidae, Heptageniidae and Ephemerellidae) during the run, and downstream sections had a greater abundance and biomass of Dipterans (dominated by Chironomidae). Diversity and richness were similar across stream sections and run size

within each period, except for during the run when both were significantly lower in downstream sections of high run streams. Functional feeding group patterns showed higher abundance and biomass of collector-gatherers (primarily Chironomidae) and shredders (primarily the nemourid *Zapada*) during the post spawning, carcass decomposition period. Overall, this study suggests that a positive relationship between MDN and stream insect abundance and biomass only exists for specific taxa with life history attributes that allow them to take advantage of the MDN enrichment.

Introduction

Alaska is the last region along the Pacific coast of the United States that still receives large, annual runs of spawning salmon near historic levels (Baker et al. 1996, Gresh et al. 2000). Upstream migrations of adult salmon provide these normally oligotrophic systems with a huge pulse of nutrients from the ocean. These nutrients, which enter the stream in the form of salmon eggs, sperm, waste and ultimately the adult carcasses, are termed marine-derived nutrients (MDN) and have been hypothesized to be linked to the dynamics and structure of stream communities (algae to fish). Estimates of annual nutrient delivery from spawning salmon to Alaskan streams range in the millions of tons of carbon, nitrogen, phosphorous and other nutrients (Larkin and Slaney 1997, Halupka et al. 1999).

Theories on the role of MDN in coastal stream communities predict that this nutrient subsidy provides a positive feedback mechanism, linking adult anadromy and semelparity with juvenile salmonid production (Kline et al. 1997, Lichatowich 1999). Intermediate steps predicted to connect MDN and juvenile salmon include alterations of dissolved nutrients, biofilm production and alterations to the macroinvertebrate community (Wipfli et al. 1998, Cederholm et al. 1999, Chaloner et al. 2004). Stream community responses to MDN have far reaching implications in these watersheds affecting algal production to terrestrial vertebrate predators and have been suggested to be a key factor for salmon recovery programs throughout the Pacific Northwest (Bilby et al. 2000, Stockner et al. 2000, Gende et al 2002).

Aquatic macroinvertebrates are important organisms for studying the impact of MDN on the overall stream community because they integrate bottom-up pathways of enrichment to juvenile salmonids, and are good indicators of stream ecosystem structure and function. Previous studies have shown aquatic insect communities to respond to salmon runs in several important ways. Among these responses are short-term reductions in abundance and increased drift due to the disturbance created during large spawning runs (Minakawa 1997, Peterson and Foote 2000). Increased insect density following salmon carcass decomposition has been documented (Minikawa 1997, Wipfli et al. 1998, Kline et al. 1997), as well as indications that insect richness and diversity may increase from salmon enrichment in central Alaskan streams (Piorkowski 1995). These previous studies provide important insights into the potential impact of MDN from salmon on the invertebrate communities, but the majority of the evidence linking MDN and insect enrichment comes from artificial stream studies or short term, poorly replicated natural stream studies. No study has addressed the relationship of MDN and aquatic macroinvertebrate community dynamics across seasons or stream systems. The objective of this study was to evaluate the impact of MDN from spawning salmon on aquatic insect communities seasonally and across several natural stream systems. The community attributes I focused on were insect abundance and biomass, community richness and diversity, and functional feeding groups. Seasonal samples were directed at times of the year that would allow me to address the long-term effects of MDN into the spring (pre fall spawning run), the impact of the spawning disturbance (during the fall run) and the responses to the major nutrient subsidy (post fall salmon run and during carcass decomposition).

Study Sites

Southeast Alaska contains the 8.5 million hectare Tongass National Forest, most of which is pristine forest surrounding 5200 anadromous salmon streams (Halupka et al. 1999). Because the runs in Alaska are still intact, these streams provide the opportunity to study the structure and function of these systems around the salmon runs from a fairly pristine state. The primary salmon (*Oncorhynchus*) runs in terms of biomass entering the stream in this region are pink (*O. gorbuscha*) and chum salmon (*O. keta*), but these streams also receive runs from coho (*O. kisutch*), sockeye (*O. nerka*) and chinook (*O. tshawytscha*) salmon. Other common fish species are dolly varden (*Salvelinus malma*), sculpin (*Cottus spp.*), cutthroat trout (*O. clarki*), and steelhead trout (*O. mykiss*). Southeast Alaska is described as having a maritime climate (average precipitation=1500-5000 mm, average July temperature=13°C) and dense coastal forest (Oswood et al. 1995). Study streams were located in and around the Juneau-Douglas area (Figure 1) and in selected streams on Prince of Wales Island (Figure 1). Study streams around Juneau-Douglas were: Fish Creek (58°19'N, 134°35'W), Sheep Creek (58°16'N, 134°18'W), Salmon Creek (58°19'N, 134°27'W), Peterson Creek (58°28'N, 134°44'W), and Bessie Creek (58°35'N, 134°54'W). Study streams on Prince of Wales Island, near Hollis were: Harris River (55°27'N, 132°42'W) and Sata/Gulch Creeks, which are both tributaries to the Trocadero River (55°21'N, 132°52'W). Most study streams were systems that have an anadromous section (connects to the ocean) with healthy salmon runs and a non-anadromous section that had been cut off from salmon migrations for thousands of years (since the little ice age) by a natural waterfall barrier, which is enough time for adaptive changes due to MDN to have occurred. This disconnection of stream sections allowed for the simultaneous comparison of the insect fauna that occur in areas with and without exposure to MDN, while minimizing variation in other factors that could also impact insect communities (e.g., substrate, riparian cover etc.). To test this, we also selected stream systems with barriers but with lower reaches that didn't receive large salmon runs. Table 1 provides a description of the seven study streams.

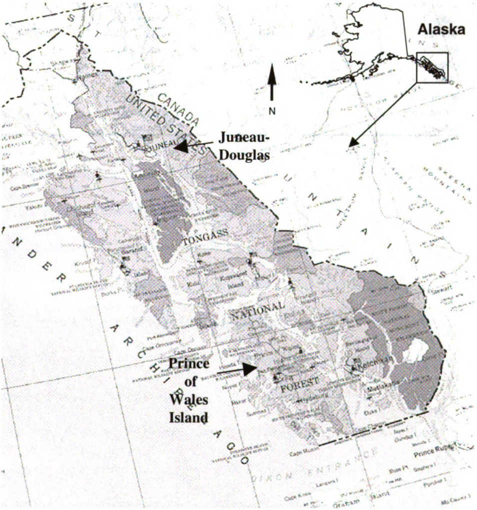

Figure 1. Map of southeast Alaska. Study streams were near Juneau-Douglas and on Prince of Wales Island.

Table 1. Location, spawning run size and physical habitat data for the seven study streams.

Stream	Location	Section	Run Size	Width (m)	Depth (cm)	Water Temp (°C)	Substrate	Riparian Canopy
Bessie	Juneau	Downstream	Low	6.7	24.9	10.6	Cobble	Conifer
		Upstream		4.7	39.5	10.6	Cobble	Conifer
Fish	Douglas Is.	Downstream	High	20.52	27.27	8.0	Cobble/Boulder	Conifer
		Upstream		11.93	35.38	8.0	Cobble/Boulder	Conifer
Harris	POW	Downstream	High	29.38	49.53	8.0	Cobble/Boulder	Conifer/Alder
		Upstream		13.56	33.80	9.0	Cobble	Conifer
Peterson	Juneau	Downstream	High	13.68	9.38	10.9	Cobble	Conifer/Alder
		Upstream		11.90	41.25	10	Cobble	Conifer
Salmon	Juneau	Downstream	High	11.38	26.58	7.3	Cobble	Conifer/Alder
		Upstream		9.72	30.89	6.30	Cobble	Conifer
Sata/Gulch	POW	Downstream	Low	8.70	30.42	N/A	Cobble	Alder
		Upstream		5.58	31.6	N/A	Cobble	Conifer/Alder
Sheep	Juneau	Downstream	none	12.5	45.0	8.0	Boulder/Cobble	Alder
		Upstream		8.9	46.8	6.5	Cobble	Alder

Methods

Streams were sampled between late May and early June before the large autumnal run of pink and chum salmon ("pre"), again in late August once the autumnal run had begun and spawning was occurring ("during"), and once more in late September-early October before snow fall but after decomposition of the salmon carcasses was well underway ("post"). I took three modified-Hess samples (0.04 m^2, mesh size 250 μm) from each of three riffle reaches from each stream section (upstream and downstream of the barrier) pre, during and post spawning for a total of 54 samples from each study stream. Samples were washed into labeled ziptop bags with 90% ethanol and transported to the laboratory. Hess samples were used for abundance, biomass, functional group and diversity estimates. For taxa richness, a field crew of three to four people took a combination of modified-Hess or D-net samples from all macro-habitats (riffle-cobble, run-gravel, pool-fines, submerged wood and vegetation, and detritus) in one reach (~100-300m long) in each stream section (upstream and downstream of the barrier). Richness samples were picked in the field from white pans and processed as above. Sampling was conducted for approximately two hours and was terminated when no new taxa were collected for at least 30 minutes.

Selected physical properties were measured from each stream section once, during the pre-run sampling period. Parameters measured included channel width, depth, water temperature, substrate, and riparian vegetation. All habitat parameters were measured at five transects in each stream section. Transects were selected randomly along a 300m reach. The pebble count method was used to analyze mineral substrate size (Kondolf and Li 1992). Riparian vegetation was assessed using the line intercept method from the stream bank out 30 m (Bonham 1989, Grubbs and Cummins 1994). Run size for each stream (high or low/no run) were determined from published data on these streams (Chaloner et al. 2004), communications with the Alaska Department of Fish and Game, and direct observations. The habitat data for the seven study streams is summarized in Table 1. Upstream were the control sites and refer to above the barrier while downstream are the treatment sites and refer to below the barrier and open to the ocean. There were four high run streams that consistently received large runs (i.e. thousands to hundreds of thousands) of salmon and three low or no run streams that received virtually no spawning run. All streams had similar temperatures and substrate, but there was variation in stream size (i.e. width) and riparian canopy.

In the lab, samples were picked and sorted under 10x magnification. Identification was done down to the lowest taxonomic unit possible, which was generic level for most orders. Species designations were confirmed by taxonomic experts. Insect abundance and total lengths (nearest 0.5 mm) were recorded for all taxa in each modified-Hess sample. Published length-weight regressions were used to calculate biomass (Benke et al 1999). Diversity was compared using the Shannon-Wiener diversity index. Functional feeding group designations were made using Merritt and Cummins (1996).

Data Analysis

The data were analyzed using repeated mixed model analyses with stream as a random effect, section within stream as the repeated factor (because each stream section was sampled three times pre, during and post spawning) and compound symmetric covariance structure. Density and biomass data were normalized with natural-log transformations that are referred to as ln_density and ln_biomass on all figure axes. For simplicity, however, the results and discussion will refer to these data as simply density and biomass. Trichopteran density and biomass, however, was too rare to be normalized with any transformation and so trichops were omitted from order and family level analyses, but were included in all the community comparisons (i.e. diversity, richness, and functional feeding groups). Separate repeated mixed models were run on the density and biomass of each insect order, the dominant families in each order, functional feeding groups, and also taxa richness and diversity. Each model tested the effects of section (upstream vs. downstream), period (pre, during and post), run size (high run vs. low/no run) and interactions of these three factors. Due to the high occurrence of significant ($\alpha < 0.05$) three-way interactions in these models, significant differences between stream sections (our primary treatment factor for the effects of MDN) were analyzed separately with regular (i.e., non-repeated) mixed models within period and run size.

Results

The results of the mixed modeling analyses by order are given in table 2 and figures 2 and 3. Density and biomass varied significantly by period and run size for Ephemeropterans, while significant three way interactions for Dipterans only existed for the density data, and for Plecopterans for the biomass data (Table 2).

Table 2. Results (p-values) of the repeated mixed modeling analysis by order. Period and section are abbreviated in the 3-way interaction term.

Order	Transformation	Section	Period	Run	Period*Section	Per*Sec*Run
Epemeroptera	ln_density	0.086	<0.0001	0.514	0.150	0.002
	ln_biomass	0.511	<0.0001	0.448	0.307	0.009
Diptera	ln_density	0.085	<0.0001	0.512	0.715	0.046
	ln_biomass	0.112	<0.0001	0.442	0.730	0.488
Plecoptera	ln_density	0.653	0.050	0.392	0.769	0.087
	ln_biomass	0.734	0.033	0.880	0.752	0.017

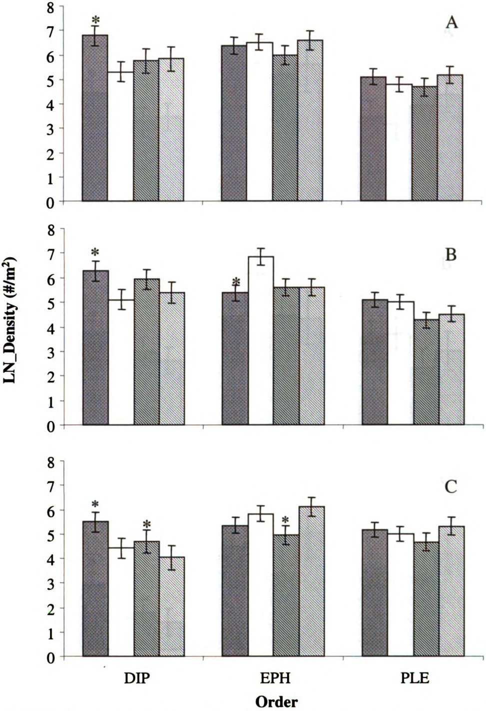

Figure 2. Natural log- transformed density means for each aquatic insect order by stream section and run size for each period (A=pre, B=during, and C=post spawning). Bars are: high run, downstream (▩), high run, upstream (□), low run, downstream (■) and low run, upstream (▨). An * denotes significant differences by stream section within run size.

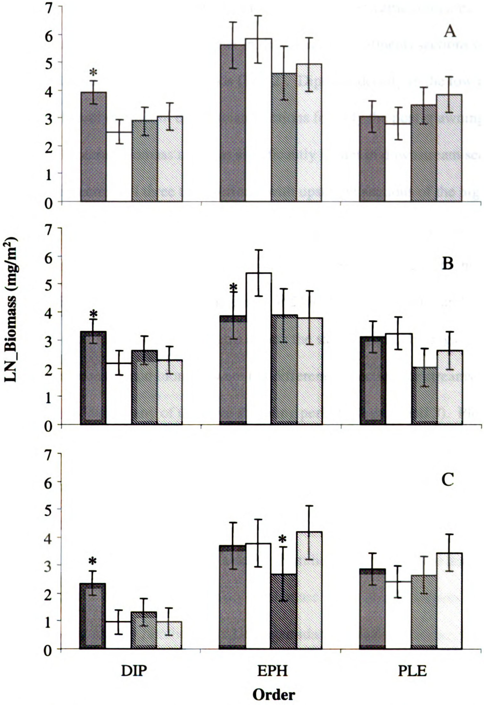

Figure 3. Natural log- transformed biomass means for each aquatic insect order by stream section and run size for each period (A=pre, B=during, and C=post spawning). Bars are: high run, downstream (▨), high run, upstream (□), low run, downstream (■) and low run, upstream (░). An * denotes significant differences by stream section within run size.

Dipteran density was on average higher in the high run streams compared to the low run streams, and was significantly higher in downstream (treatment) sections of the high run streams across all three time periods (Fig. 2). Dipteran density in the low run streams was significantly higher in downstream sections for only the post spawning time period (Fig. 2). Dipteran biomass also was significantly higher in downstream sections of high run streams across all three time periods, with upstream sections of the high run streams being similar to both sections of the low run streams (Fig. 3). On average, biomass of ephemeropterans was also greater in the high run streams compared to the low run streams (Fig. 3). Ephemeropteran density and biomass were significantly greater in upstream sections of high run streams during the salmon run only (Figs. 2 and 3). Plecopteran density and biomass were not different by section for streams in either run size category during any of the three sampling periods (Figs. 2 and 3). Plecopteran biomass was greater in both upstream and downstream sections in the high run streams during the salmon run.

To examine these data at a finer resolution, family level analyses were run on the dominant families in each order (Table 3). Families were considered dominant if they comprised 20% or more of the density or biomass in any stream section for any period. The dominant mayfly families were Heptageniidae (primarily *Epeorus*, *Cinygmula* and *Rhithrogena*), Baetidae (primarily *Baetis*) and Ephemerellidae (primarily *Drunella*). The dominant Dipteran family was Chironomidae (primarily Orthocladiinae, Tanytarsini and Tanypodinae). The dominant plecopteran family was Chloroperlidae (primarily *Sweltza* and *Suwallia*). A synoptic list of all taxa identified in each stream by section and period are given in Appendix A. The results of the repeated mixed analyses by family are shown in table 4 and figures 4 and 5.

Table 3. Dominant families in each order by stream section (upstream and downstream) and period (pre, during and post spawning). Percent of total density and biomass are given for each family.

			Upstream		**Downstream**	
Period	**Order**	**Family**	**% Density**	**% Biomass**	**% Density**	**% Biomass**
Pre	DIP	Chironomidae	91.1	77.9	90.7	73.9
	EPH	Heptageniidae	38.5	51.6	61.6	57.1
	EPH	Baetidae	52.4	25.2	35.6	38.6
	EPH	Ephemerellidae	1.9	22.1	1.4	3.9
	PLE	Chloroperlidae	66.1	76.4	92.3	95.3
	TRI	Rhyacophilidae	28.1	31.6	26.7	68.4
	TRI	Limnephilidae	23.4	13.5	26.7	1.2
	TRI	Glossosomatidae	25.0	39.1	6.7	5.1
During	DIP	Chironomidae	86.9	53.1	97.8	87.9
	EPH	Heptageniidae	39.9	51.8	30.0	41.0
	EPH	Baetidae	36.7	24.3	44.3	38.0
	EPH	Ephemerellidae	4.6	21.2	5.8	6.6
	PLE	Chloroperlidae	69.5	81.7	90.8	96.3
	TRI	Rhyacophilidae	19.2	43.9	12.1	22.0
	TRI	Limnephilidae	26.7	25.3	57.8	57.0
	TRI	Glossosomatidae	41.7	10.8	28.4	16.3
Post	DIP	Chironomidae	81.0	49.8	93.2	73.0
	EPH	Heptageniidae	44.6	83.8	65.1	79.1
	EPH	Baetidae	43.1	13.4	29.1	17.9
	EPH	Ephemerellidae	6.9	1.5	2.3	0.9
	PLE	Chloroperlidae	55.8	62.4	70.3	94.9
	TRI	Limnephilidae	39.6	71.8	20.9	37.1
	TRI	Lepidostomatidae	5.7	4.5	46.3	40.9
	TRI	Rhyacophilidae	39.6	71.8	9.0	9.8
	TRI	Glossosomatidae	30.2	15.3	20.9	10.7

Table 4. Results (p-values) of the repeated mixed modeling analyses by family. Period and section are abbreviated in the 3-way interaction term.

Family	Transformation	Section	Period	Run	Period*Section	Per*Sec*Run
Heptageniidae	ln_density	0.126	<0.0001	0.193	0.006	0.002
	ln_biomass	0.486	<0.0001	0.588	0.108	0.050
Baetidae	ln_density	0.132	<0.0001	0.890	0.064	0.001
	ln_biomass	0.546	<0.0001	0.353	0.295	0.002
Ephemerellidae	ln_density	0.076	0.002	0.223	0.112	0.047
	ln_biomass	0.607	0.131	0.408	0.111	0.347
Chironomidae	ln_density	0.102	<0.0001	0.640	0.344	0.131
	ln_biomass	0.093	<0.0001	0.335	0.192	0.705
Chloroperlidae	ln_density	0.968	0.132	0.541	0.687	0.018
	ln_biomass	0.984	0.010	0.843	0.605	0.034

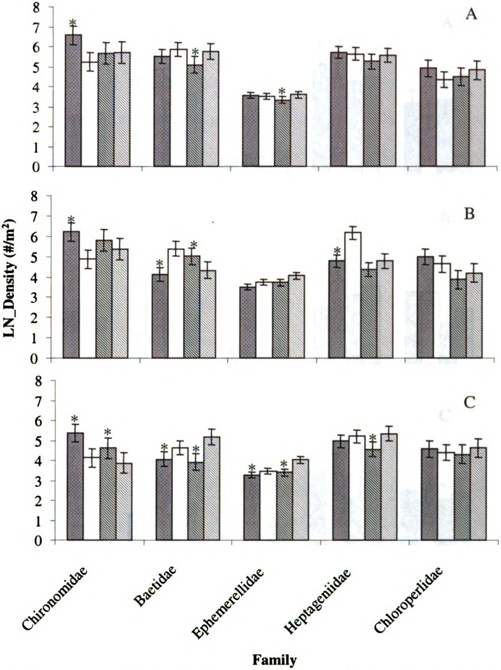

Figure 4. Natural log- transformed density means for each aquatic insect family, dominant in each order, by stream section and run size for each period (A=pre, B=during, and C=post spawning). Bars are: high run, downstream (▩), high run, upstream (☐), low run, downstream (■) and low run, upstream (▨). An * denotes significant differences by stream section within run size.

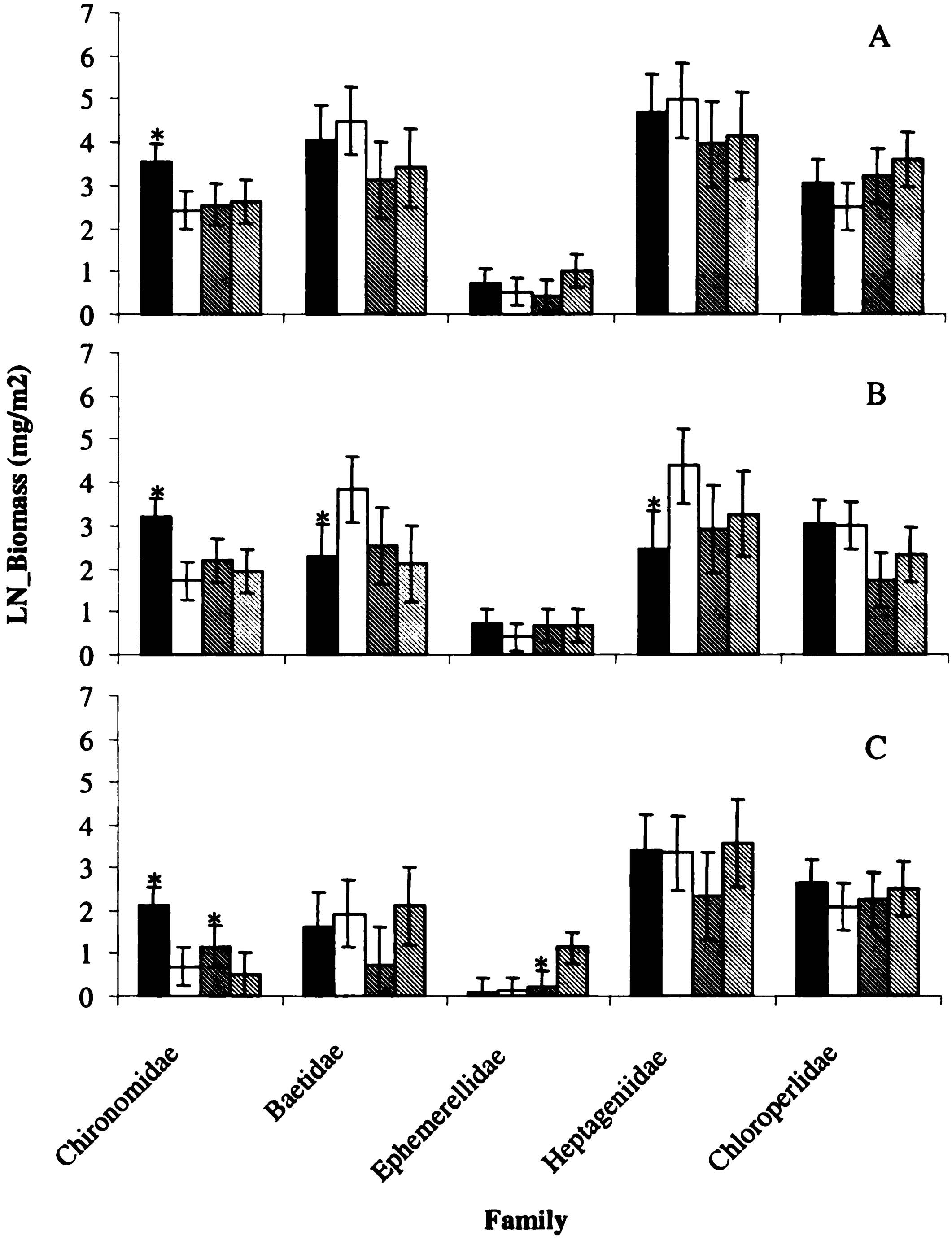

Figure 5. Natural log- transformed biomass means for each dominant aquatic insect family, by stream section and run size for each period (A=pre, B=during, and C=post spawning). Bars are: high run, downstream (■), high run, upstream (☐), low run, downstream (■) and low run, upstream (▨). An * denotes significant differences by stream section within run size.

Due to the high proportion of chironomids (50 to 97%) versus all other dipterans, the patterns for density and biomass by family were very similar to the order level analyses for Diptera, with greater density and biomass occurring in downstream sections of the high run streams in all three sampling periods (Figs. 4 and 5). Likewise, Chloroperlidae results were also very similar to what was shown for plecopterans, with no significant differences by stream section related to the salmon run (Figs. 4 and 5). Both baetid and heptageniid mayflies showed significant differences by stream section, with both density and biomass being greater in upstream (control) sections of the high run streams during the salmon run. Baetids and ephemerellids both had significantly lower densities in downstream sections of the high run streams post spawning, but this was also true in the low run streams.

When biomass and density data at both order and family levels are considered across sections and run size, the trend is for insect density and biomass to be higher before and during the run and at a minimum during the post spawning period (Figs. 2-5). These differences were greatest for the biomass data. This seasonal variation was consistent for both low and high run streams and both upstream and downstream sections, indicating factor(s) other than MDN enrichment influenced these communities post spawning.

I investigated the potential roles of stream size and riparian canopy (the only habitat parameters measured that showed variation across streams) on insect community abundance and biomass. Neither factor (width or riparian canopy), however, resulted in models with significant predictive power for insect density or biomass for any of the taxa in these streams. Since these factors did not interfere with the interpretation of the results in terms of salmon or MDN impacts, they will not be discussed further.

Mixed repeated analyses examining functional feeding groups by period, stream section and run size showed patterns similar to the family level analyses. Overall biomass declined in the autumn during the post-spawning time period. High run stream differences in density were seen for: 1) collector-gatherers, which were higher in downstream sections pre-spawning; 2) predators, which were higher in downstream sections during spawning; 3)and shredders, which were higher in downstream sections post-spawning (Fig. 6). High run stream differences in biomass were seen for collector-gathers, which were significantly lower in downstream sections during spawning and higher in downstream sections post-spawning (Fig. 7). Mixed analyses on taxa richness and Shannon-Weiner diversity resulted in significantly lower richness and diversity in downstream sections of high run streams during the spawning runs, with upstream sections of high run streams being more similar to both sections of the low run streams (Fig 8). There were no differences in diversity or biomass pre- or post-run in either high or low run streams.

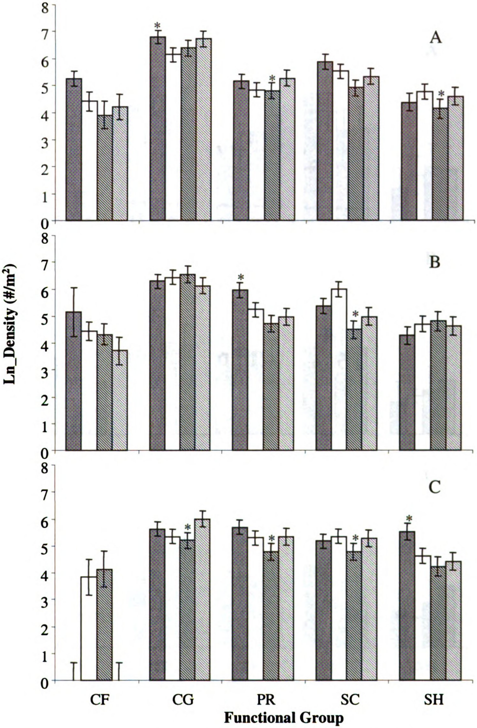

Figure 6. Natural log- transformed density means for each functional feeding group, by stream section and run size for each period (A=pre, B=during, and C=post spawning). Bars are: high run, downstream (▩), high run, upstream (☐), low run, downstream (▨) and low run, upstream (▧). An * denotes significant differences by section within run size.

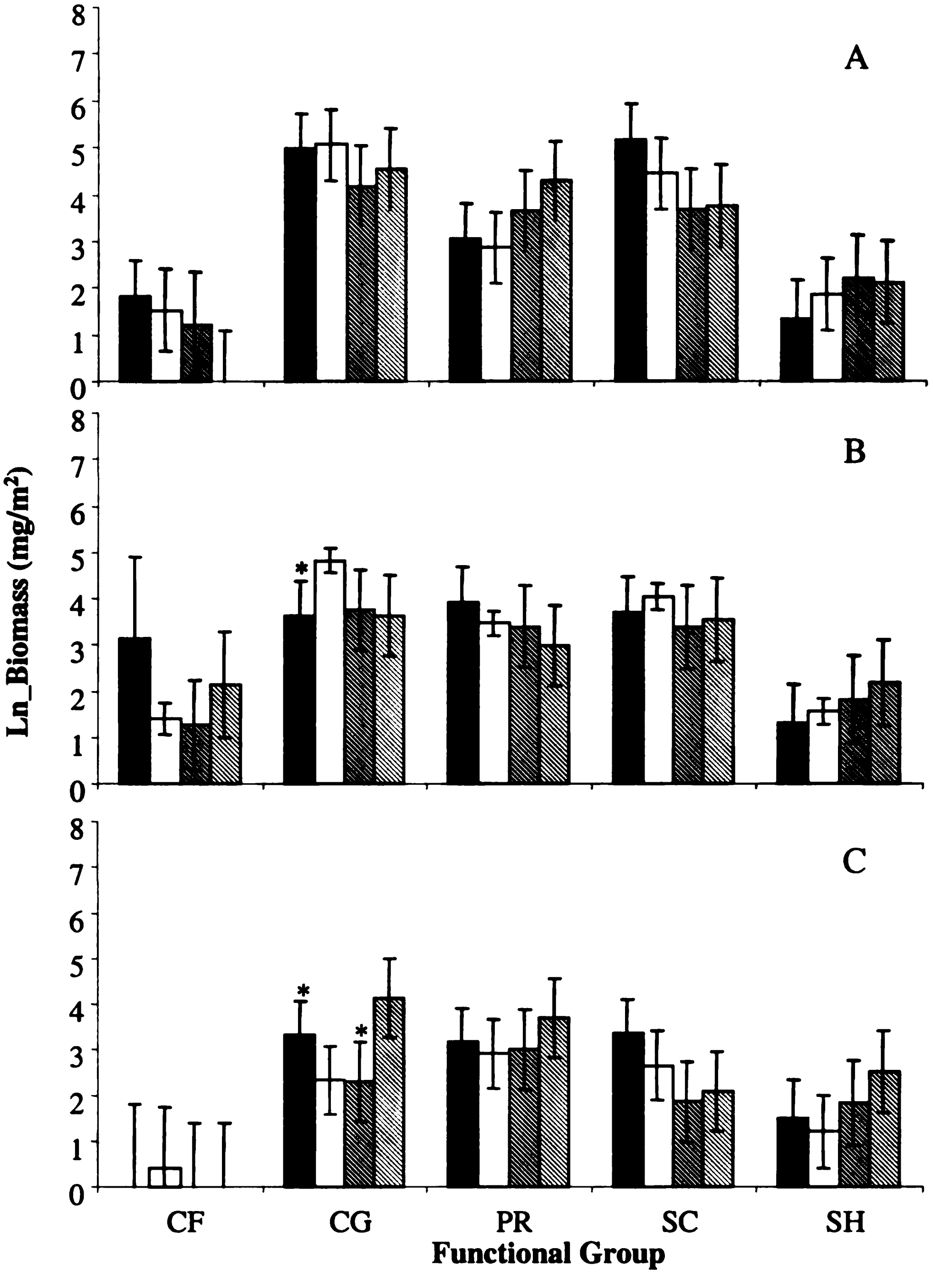

Figure 7. Natural log- transformed biomass means for each functional feeding group, by stream section and run size for each period (A=pre, B=during, and C=post spawning). Bars are: high run, downstream (▩), high run, upstream (□), low run, downstream (■) and low run, upstream (▨). An * denotes significant differences by section within run size.

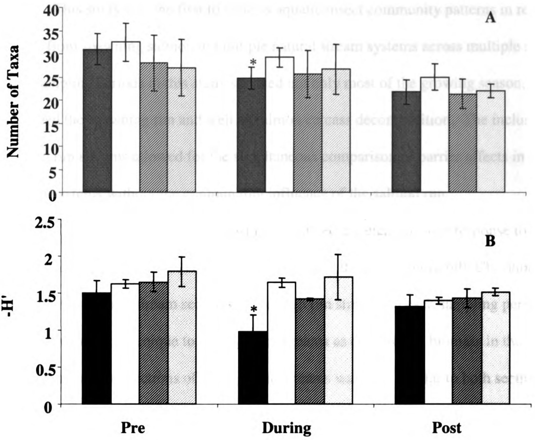

Figure 8. Mean taxa richness (A) and Shannon-Weiner diversity (B) by stream section, averaged across run size for each sample period (pre, during and post spawning). Bars are: high run, downstream (▩), high run, upstream (☐), low run, downstream (▨) and low run, upstream (▧). An * denotes significant differences by stream section within run size.

Discussion

This study was the first to address aquatic insect community patterns in relation to MDN from spawning salmon in multiple natural stream systems across multiple seasons. The sampling periods in this study spanned not only most of the growing season, but also included the spawning run and well as salmon carcass decomposition. The inclusion of low/no run streams allowed for the simultaneous comparison of barrier effects in similar stream systems without the confounding influence of the salmon run.

The order level analyses illustrate an immediate dichotomy in response to salmon. Dipteran density and biomass, which was driven by the dominant family Chironomidae, was greater in downstream sections of the high run streams in each sampling period. This appeared to be unique to the high run streams as chironomid biomass in the upstream (control) sections of the high run streams was very similar to both sections of the low run streams. Ephemeropterans, however, showed different trends with greater biomass and density in upstream sections of the high run streams during the run. These differences, however, were more likely due to a decrease in ephemeropterans in the downstream sections during the spawning run rather than an increase in upstream sections, because comparisons of pre-run and during-run data show that upstream sections were similar between these two time periods. The reduction in mayflies was due to the decrease of heptageniids and baetids in downstream sections. Salmon spawning activities as a disturbance to stream benthos is well documented (Hildebrand 1971, Peterson and Foote 2000, Minikawa 1997, Chaloner et al. 2004). Minikawa (1997) found decreases in chironomid midges, heptageniids and baetids during coho salmon redd excavation in a Washington stream. Chaloner et al. (2004), whose study included three of the streams sampled in this study (Fish Creek, Salmon Creek and Peterson Creek), found the same patterns during salmon spawning with higher biomass of chironomids in downstream sections, higher biomass of heptageniids in upstream sections, but, contrary to this study, they detected no difference in baetid biomass between sections.

The premise that MDN from salmon acts as a nutrient subsidy to stream communities, must assume that the preceding disturbance from spawning either left enough benthos intact to respond to the nutrient subsidy or the benthos can recover in time to take advantage of this subsidy. The light and temperatures in this region are at a maximum in the spring and summer. The primary salmon runs in these streams (pink and chum salmon), however, occur in the late summer and early fall, when flows are increasing due to autumnal spates, and temperatures and light are in sharp decline. Salmon MDN seem to be delivered at the time when the stream community, particularly aquatic macroinvertebrates, is least able to capitalize on them. Seasonal factors combined with the disturbance caused by the large salmon run sizes in this region, are likely important mortality factors for benthic organisms, as evidenced by the decline in many taxa during spawning in this and other studies (Peterson and Foote 2000, Minikawa 1997, Maier 2001, Chaloner et al. 2004). Minikawa (1997) noted a recovery of the chironomid densities approximately 45 days post spawning, while in these study streams chironomids did not exhibit a reduction during spawning. This indicated that chironomids in these streams are able to avoid the mortality factors associated with the benthic disturbance of spawning and therefore may have been able to take advantage of the MDN influx during decomposition. Chironomid standing stock densities and biomass were elevated, even during pre-spawning sampling periods, in downstream treatment sections above what was measured for both upstream sections of high run streams and both sections of low run streams. The nutrient enrichment by salmon may allow for greater fecundity and/or winter survival of midges in these streams, which would explain these differences remaining even 5-6 months after the carcasses have disappeared from the streams (i.e., the pre-run period). Another factor that may promote midge response to MDN is that, compared to mayflies, they seem to be less tied to bottom-up, algal mediated pathways in order to utilize MDN, because they have been shown to feed on the carcasses directly (Minakawa 1997, Chaloner and Wipfli 2002, Chaloner et al. 2002). By feeding on carcasses, midges would be less reliant on sunlight and temperature compared to epilitic biofilm feeders. Its reasonable for larger-bodied, univoltine, taxa like the heptageniid mayflies, to be most negatively affected by spawning. Unlike the small multivoltine chironomids, large univoltine fauna would be less able to escape the disturbance behaviorally and to re-colonize disturbed areas with new cohorts, before the salmon carcasses are decomposed and the MDN are lost to the ocean. Even if these mayfly taxa have larvae in the stream post-spawning, if their food is mediated by primary production they may be light and/or temperature limited in their growth during this part of the year, no matter how nutrient rich the waters are (Rosemond et al. 2000).

The biomass data for these streams supports the theory of seasonal production limitations, because biomass in all streams (high and low run) and sections (upstream and downstream) were lowest during the post-spawning period for all the dominant families and functional groups (except shredders). It was interesting that standing stock of mayflies in the post-spawning period were similar across stream sections. It doesn't appear that this similarity was due to downstream sections "catching up" to upstream population density and biomass, but rather during this time of the year mayfly populations in all stream sections were in decline. The most important factor, therefore, for predicting the influence of MDN on aquatic insects in stream systems may be the timing of the enrichment with the insect's life cycle. If in-stream insect production is reduced, due to emergence or diapausing stages predominating during salmon decomposition, the importance of MDN to these fauna would be severely limited. Only chironomid midges (which comprised most of the post-spawning collector-gatherers) and shredders (primarily *Zapada* stoneflies) maintained elevated densities and/or biomass during the post-spawning, salmon decomposition period. These may be the only aquatic insects that can be said to "benefit" from the influx of MDN and to then transfer these nutrients into higher trophic levels of the stream food webs. If this is the case, it would reduce the extent that MDN influences the stream communities as a whole, but it may not reduce the importance of MDN to production of fish, especially juvenile salmonids. Many studies have shown the high dependence of juvenile salmonids on chironomid larvae (Frolenko 1973, Loftus and Lenon 1977, Kaeriyama et al. 1978, Dauble et al. 1980, Armitage et al. 1995)

The fact that these streams overall, across run size and section, had very similar taxa richness and diversity values, implies how similar in general the insect communities are across study streams. The only factor that can be attributed to the decline in richness and diversity, during the salmon run was the spawning disturbance. However, while this may be considered a negative effect, it appears to be short-lived, as both richness and diversity were again similar post spawning. Piorkowski (1995) found marginal to significant increases in macroinvertebrate richness and diversity related to salmon enrichment in south-central Alaskan streams. In this study, however, the enrichment of MDN appeared to have no long-term effects in terms of stimulating richness or diversity of the aquatic insect communities.

In conclusion, it appears that the influence of salmon-mediated marine-derived nutrients on stream insect communities is more complicated and more simplistic than theories have often predicted. The complexity lies in the variation of the timing of salmon runs across salmon species and the coupled disturbance that must precede any natural enrichment. The primary runs in Southeast Alaska occur at the time of the year when stream productivity may be limited by factors other than nutrients and, therefore, would be less able to respond to MDN in all the complicated mechanisms that previous mesocosm studies have predicted. This may be very different for other regions or other spawning runs (i.e., summer spawners), and in streams where physical actors (e.g., spates) are not as pronounced. Due to the natural decline of most univoltine aquatic insect fauna, and the disturbance-mediated benthic community structure created in stream reaches containing salmonids, the influence of MDN on insect communities and the transfer of these nutrients into higher foods webs may be from only one or two families. Chironomidae (and possibly also the shredding nemourid *Zapada*) appear to be the only insects in these stream systems that respond to MDN in a detectable way, with their standing stock density and biomass. Therefore, if juvenile salmonids must rely on invertebrate-mediated access to MDN from spawners, it may be solely from these taxa. This research points to MDN as having no long term effect on overall stream richness, diversity or standing stock of any insect taxa or functional group, besides midges and shredders. Standing stock only provides a snap shot of these patterns, and so annual production studies should be conducted to better understand the dynamics of insect communities in these streams. This research provides strong evidence that conceptual models predicting the role of salmon and MDN in stream ecosystems must include disturbance as well as enrichment in order to better predict the mechanisms that will lead to better stream management and salmonid recovery programs.

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Chapter 3

Secondary production of mayflies and midges in response to spawning salmon in natural Alaskan streams

Abstract

Theories on the relationship between marine-derived nutrients (MDN) from spawning salmon link MDN with juvenile salmonid production via bottom-up pathways. Many studies have used short-term standing stock biomass of aquatic macroinvertebrates to infer relationships between MDN and secondary production in streams that receive spawners. No study, however, has actually measured secondary production in relation to MDN. To assess the relationship between MDN and aquatic insect production, we measured secondary production of the five dominant mayfly genera (Baetis spp., Drunella spp., Cinygmula spp., Epeorus spp., and Rhithrogena spp.) and chironomid midges throughout the primary growing season in two southeastern Alaskan streams. Both streams had upstream control reaches blocked from spawning salmonids by a waterfall barrier and downstream treatment reaches that received large spawning runs of pink and chum salmon. Four of the mayfly genera (Drunella spp., Cinygmula spp., Epeorus spp., and Rhithrogena spp.) had significantly greater production in upstream control sections. Secondary production of Baetis spp. was not significantly different between sections. Chironomid production was significantly greater in downstream treatment sections. Biomass of each taxon was maximized, however, in the spring and summer, before the primary time of MDN input. These patterns point to spawning disturbance and fish predation as the primary drivers of mayfly and midge production in

these streams. If this is a common pattern in this region, then in-stream secondary production mediated links between MDN and juvenile salmonid production most likely result from chiromonid midges.

Introduction

Nutrient transfers in lotic systems occur in a variety of ways. A well-known example is the utilization and transfer of terrestrially derived nutrients (e.g., leaf litter) from headwaters to downstream areas, which drives stream productivity and the spatial/temporal organization of stream communities (Kaushik & Hynes 1971, Cummins 1974, Vannote et al. 1980, Cummins et al. 1989). Nutrients also are transferred from marine systems into freshwater via fish migrations (Polis et al. 1997). Coastal streams that are spawning grounds for salmon receive these nutrients, termed marine-derived nutrients (MDN), in the form of salmon eggs, sperm, metabolic waste and adult carcasses. The role that MDN plays in stream systems has been the object of study in recent years. Most of these studies have dealt with either tracing MDN through surface-stream and riparian food webs, or comparisons of stream communities with and without salmon (Bilby et al. 1996, Kline et al. 1997, Wipfli et al. 1998, Cederholm et al. 1999, Chaloner et al. 2002a). These relationships are of particular interest in the Pacific Northwest of the United States, where salmon runs are extinct or threatened in many streams along the coasts of Washington, Oregon and northern California.

It has been suggested that salmon provide an essential nutrient source to the typically oligotrophic, anadromous streams of the Pacific Northwest region and, by subsidizing the nutrient base in their spawning grounds, increase stream productivity and the viability of their own offspring (Kline et al. 1997, Lichatowich 1999). There is evidence of the incorporation of MDN into stream communities (Schuldt and Hershey 1995, Bilby et al. 1996) and the short-term stimulation of primary production and increases in certain fauna (i.e. chironomid midges) (Kline et al. 1997,Wipfli et al. 1998, Wipfli et al. 1999, Chaloner et al. 2002a), however, the influence of MDN on the productivity of these streams remains unclear. In fact, while many studies discuss the implications of their results in terms of production, the influence of MDN on secondary production (i.e. accrual of biomass over time) has yet to be measured (Gende et al. 2002).

Alaska is one of the few areas in the United States where salmon runs remain at or near historic levels (Baker et al. 1996, Gresh et al. 2000). Southeast Alaska contains the 8.5 million hectare Tongass National Forest, with 5200 anadromous salmon streams that collectively support millions of spawning salmon (e.g. annual transport of over 100 million kg carbon, 10 million kg nitrogen, 2 million kg phosphorous and other nutrients to freshwater streams) (Halupka et al. 1999, Gresh et al. 2000). The objective of this study was to measure secondary production of selected aquatic insects to evaluate the influence of MDN on their annual production in these systems. By conducting research in Alaskan streams we were able to take advantage of the relatively pristine state of the MDN transfer cycle in streams in this region. This study also takes advantage of the fact that southeast Alaska contains many streams with reaches open to the marine environment that provide spawning habitat for annual migrations of salmon, but also have natural waterfalls that block salmon from reaches further upstream (i.e. natural control), and has done so for thousands of years.

In order for these nutrients to be of real importance to overall stream productivity, MDN must extend a significant distance upstream and be retained long enough for the bottom-up response of the fauna. We hypothesized that if MDN does provide an important nutrient subsidy to these streams, then aquatic insects living below the waterfall barriers (i.e., with MDN in the system) will exhibit higher annual production rates than aquatic insects living above the barriers (i.e., without MDN). To understand how MDN influences secondary production of different types of insects, we selected insects that are common and abundant in southeast Alaskan streams and have varied life histories (Table 1).

Table 1. List of taxa studied for secondary production. Taxa used were common in both study streams.

Order	Family	Genus	Dominant Species	Voltinism
Ephemeroptera	Baetidae	*Baetis*	*bicaudatus*	Bi-voltine
	Ephemerellidae	*Drunella*	*doddsi*	Univoltine
	Heptageniidae	*Epeorus*		Univoltine
		Cinygmula		Univoltine
		Rhithrogena		Univoltine
Diptera	Chironomidae[1]			Multivoltine

[1] Chironomids were grouped at the family level for secondary production analyses.

See table 4 for more detailed taxonomic information on midges.

Methods

Study Area

Fish Creek (58°19'N, 134°35'W) and Salmon Creek (58°19'N, 134°27'W) are both anadromous streams in the Juneau-Douglas area in Southeast Alaska. Both streams are characterized by the cool, clear, oligotrophic appearance, typical of streams in the Pacific Northwest. Fish Creek (watershed area= 36 km^2) is on Douglas Island and receives annual runs of salmon (Oncorhynchus) including: chum (O. keta), chinook (O. tshawytscha), coho (O. kisutch), and pink (O. gorbuscha). The largest runs are the pink and chum spawning migration, which normally take place between July and September. Salmon Creek (watershed area= 26 km^2) is located near downtown Juneau and receives pink, chum and coho salmon, with pink and chum also being the largest runs. Both study streams have natural waterfall barriers that block salmon migration from "upstream" reaches. Previous habitat sampling showed that upper and lower reaches were similar for both streams (e.g. substrate, canopy cover) (Chaloner et al. 2004, Lessard, unpublished data) (Table 2).

Samples of benthic invertebrates were taken using a modified Hess-sampler (0.04 m^2, mesh size 250 µm). On each sample date, nine samples were collected from riffle areas in each stream section (upper and lower) from each study stream. Benthos samples were collected in each stream approximately every two weeks from May to September, 2002 (18 May, 14 June, 29 June, 12 July, 28 July, 10 August, and 27 September) for a total of 252 samples. Samples could not be collected all year due to high flows and logistical constraints in the late fall and winter. The samples collected, however, should have captured most of the production for the year as light and temperature were at a

Table 2. Habitat data for study streams by section. Mean temperatures are in parentheses.

Stream	Section	Canopy	Substrate	Water Temp. (°C)	Mean Width (m)	Mean Depth (cm)
Fish Creek	Downstream	Conifer	cobble/boulder	5-12 (7)	20.5	27.3
	Upstream	Conifer	cobble/boulder	5-12 (7)	11.9	35.4
Salmon Creek	Downstream	Conifer/Alder	cobble/boulder	4-10 (7.3	11.4	26.6
	Upstream	Conifer	cobble/boulder	4-10 (7.3)	9.7	30.9

maximum, and our sample period extended through the major fall runs of pink and chum salmon and well into the period of carcass decomposition.

Samples were washed into labeled zip-top bags, fixed with 90% ethanol in the field and transported back to the laboratory for processing. In the laboratory, samples were picked under magnification and sorted. Insects were identified and measured for total length. Biomass (i.e., dry mass) was calculated using length-weight regressions from Benke et al. (1999). Preliminary data analysis revealed overlapping cohorts, therefore secondary production was calculated using the size-frequency method (Benke 1996). Cohort production intervals were estimated from either size frequency histograms of individual taxa or were taken from the literature. Standing stock biomass means and standards errors for each taxon, over the study period, were calculated using SYSTAT statistical software.

Results

Secondary production patterns between upstream and downstream sections were similar for both Fish Creek and Salmon Creek (Table 3, Fig.1). Baetis production was similar between upstream and downstream sections, where as the other mayfly genera (Drunella, Cinygmula, Epeorus and Rhithrogena) had consistently higher production in the upstream sections of both study streams (Table 3, Fig.1). Chironomid production showed the opposite trend with production rates over 800% and 600% higher in downstream sections of Fish and Salmon Creeks, respectively (Table 3, Fig. 2). The differences in production of each taxon by section represent not only a difference in number of individuals, but also differences in individual body size. Although maximum larval length of Baetis was similar between sections, all other mayfly taxa were larger in upstream sections, where as chironomids were larger in downstream sections (Table 3).

Chironomids were only analyzed for production at the family level, but the proportion of subfamilies and the number of dominant taxa were documented for each stream and stream section (Table 4). Overall, the Orthocladiinae comprised between 95% and 99% of the total midges in these streams, with the Tanytarsini making up the remainder of the Chironomidae. The richness of dominant chironomid genera tended to be higher in upstream sections, and overall it was higher in Salmon Creek.

Because the production patterns were similar across both study streams and genera within a family, we averaged the standing stock biomass data for each sample date across streams and genera. Figures 3 and 4 show the average standing stock biomass over time by stream section for the three mayfly families (Baetidae, Ephemerellidae and Heptageniidae) and one dipteran family (Chironomidae) studied.

Table 3. Standing stock biomass (dry mass), secondary production and maximum larval body lengths for five mayfly genera and chironomid midges from Fish Creek and Salmon Creek. Values are given for each stream reach (downstream and upstream). Percent difference is the difference in secondary production between stream reaches with positive values corresponding to higher production downstream and negative values to higher production upstream.

		Taxa					
	Fish Creek	Baetis spp.	Drunella spp.	Rhithrogena spp.	Epeorus spp.	Cinygmula spp.	Chironomidae
Downstream	Biomass (mg/m^2)	52.1	3	17.9	11.1	12.4	157.9
Upstream	Biomass (mg/m^2)	52.4	120	100.3	27.5	24.4	19.2
Downstream	Production (mg/m^2/year)	359.8	11.8	185.9	69.0	70.9	7548.3
Upstream	Production (mg/m^2/year)	325.3	600.0	1258.2	213.1	243.1	791.3
	% Difference	10.6	-98.0	-85.2	-67.6	-70.8	853.9
Downstream	P/B (1/y)	6.9	3.9	10.4	6.2	5.7	47.8
Upstream	P/B (1/y)	6.2	5.0	12.5	7.7	10.0	41.2
Downstream	Max Larval Length (mm)	6.5	5.0	5.0	5.3	5.8	7
Upstream	Max Larval Length (mm)	6	12.5	11	8	7	6
	Salmon Creek	Baetis spp.	Drunella spp.	Rhithrogena spp.	Epeorus spp.	Cinygmula spp.	Chironomidae
Downstream	Biomass (mg/m^2)	67.5	8.1	38.7	28.7	45.2	162.5
Upstream	Biomass (mg/m^2)	113.8	69.6	121.5	72.4	80.3	40.8
Downstream	Production (mg/m^2/year)	438.5	32.9	380.8	177.1	290.3	12612.6
Upstream	Production (mg/m^2/year)	445.3	175.4	1243.3	351.9	432.4	1682.4
	% Difference	-1.5	-81.2	-69.4	-49.7	-32.9	649.7
Downstream	P/B (1/y)	6.5	4.1	9.8	6.2	6.4	77.6
Upstream	P/B (1/y)	3.9	2.5	10.2	4.9	5.4	41.2
Downstream	Max Larval Length (mm)	8.5	11.5	9	7.5	7.5	12
Upstream	Max Larval Length (mm)	6.5	13.5	11	7.5	7.5	6

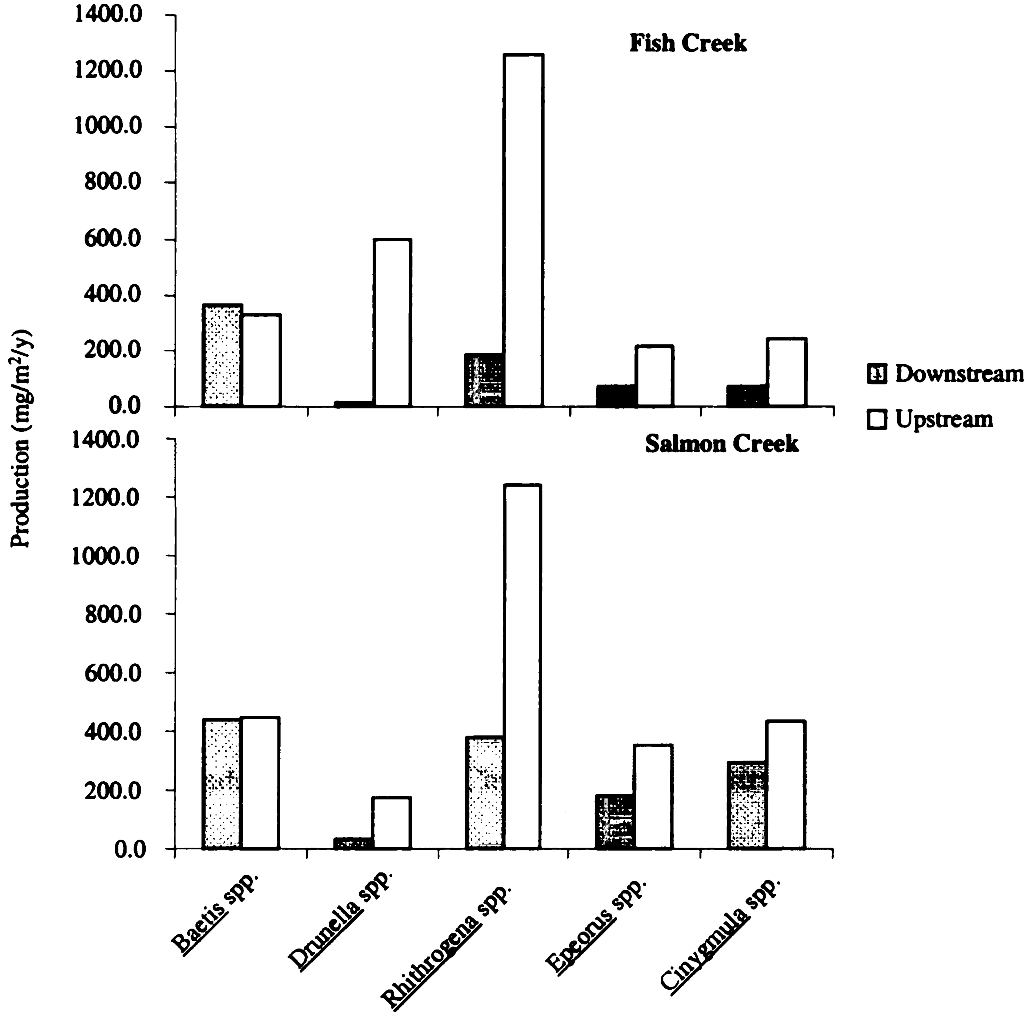

Figure 1. Secondary production of five mayfly genera for upstream (blocked from salmon) and downstream (open to salmon) sections of Fish Creek and Salmon Creek.

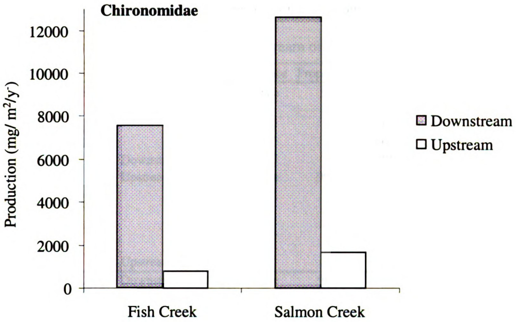

Figure 2. Secondary production of Chironomidae for upstream (blocked from salmon) and downstream (open to salmon) sections of Fish Creek and Salmon Creek.

Table 4. Dominant genera and the proportion of chironomid subfamilies or tribes in each stream and stream section (downstream or upstream of the waterfall barrier)

Stream	Section	Subfamily/Tribe	Proportion	Dominant Genera
Fish Creek	Downstream	Orthocladiinae	96.32	Corynoneura Cricotopus Eukiefferiella Orthocladius
	Downstream	Tanytarsini	3.68	Micropsectra
	Upstream	Orthocladiinae	99.29	Corynoneura Eukiefferiella Orthocladius Paraphaenocladius Tvetenia
	Upstream	Tanytarsini	0.71	Zavrelia
Salmon Creek	Downstream	Orthocladiinae	96.55	Brillia Corynoneura Eukiefferiella Orthocladius Thienemanniella Tvetenia
	Downstream	Tanytarsini	3.45	Cladotanytarsus Tanytarsus
	Upstream	Orthocladiinae	90.63	Corynoneura Eukiefferiella O. (Euorthocladius) Orthocladius Paraphaenocladius Paratrissocladius Psectrocladius Thienemanniella Tvetenia
	Upstream	Tanytarsini	9.38	Micropsectra Tanytarsus

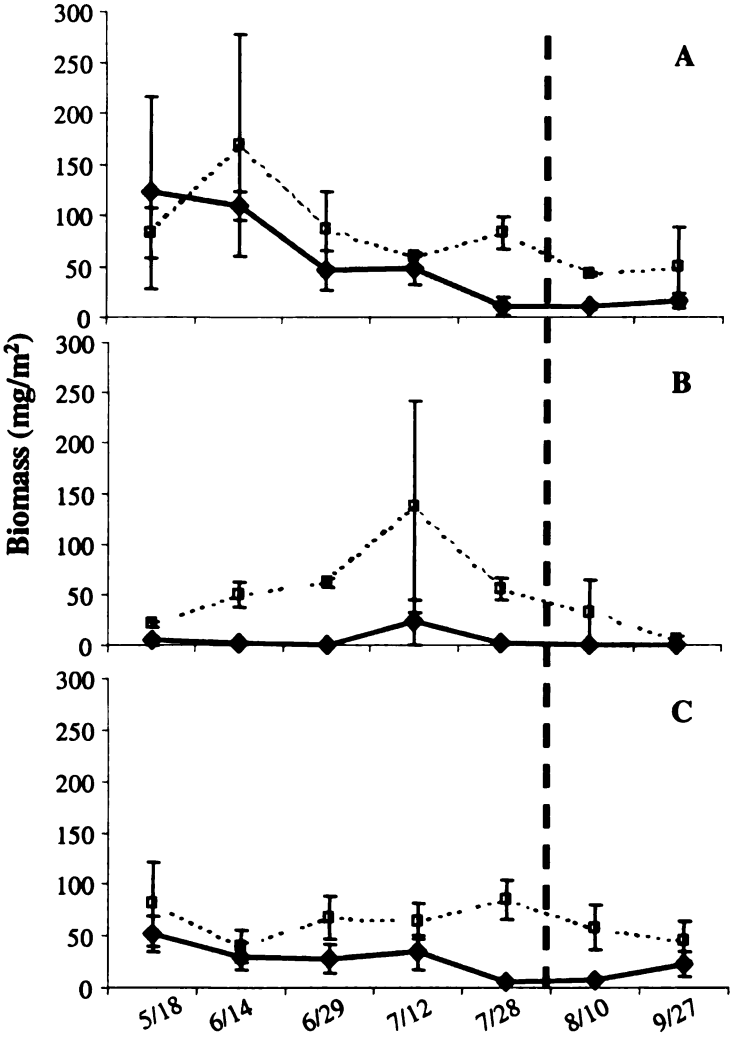

Figure 3. Standing stock biomass of mayfly families across sample dates. Means (+/- SE) for upstream (□) and downstream (◆) sections for Baetidae (A), Ephemerellidae (B) and Heptageniidae (C) are shown averaged across both study streams. The vertical dotted line represents when the spawning run began in downstream sections.

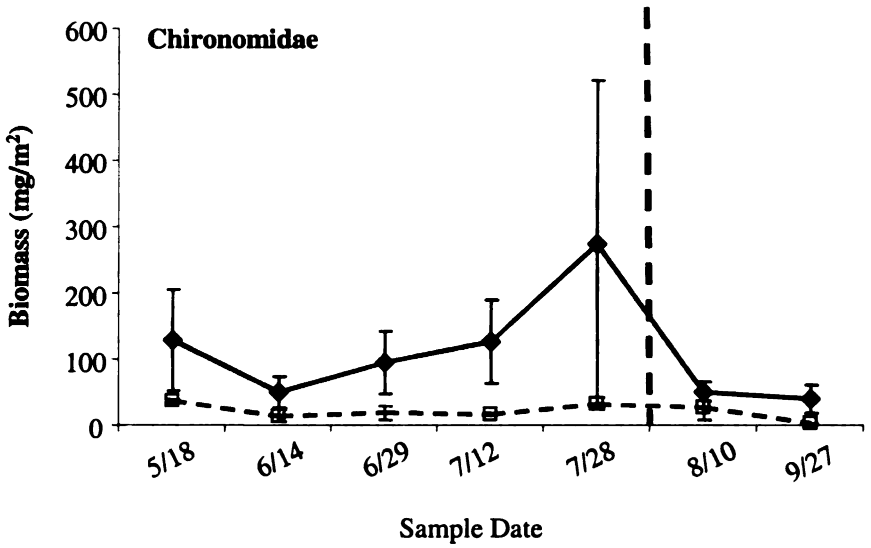

Figure 4. Standing stock biomass of chironomids across sample dates. Means (+/- SE) for upstream (□) and downstream (◆) sections are shown averaged across both study streams. The vertical dotted line represents when the spawning run began in downstream sections.

Mayfly biomass in both stream sections was similar early in the year and then diverged with biomass increasing at a greater rate in upstream versus downstream sections for both Ephemerellidae and Heptageniidae (Fig. 3). Baetidae showed a similar trend, but had greater variation and was not notably different on most sample dates. The Chironomidae showed the opposite trend, and had greater differences in biomass between sections in May with biomass increasing at a faster rate in downstream sections. All mayfly families showed a decline in standing stock biomass just before and during the salmon run in downstream sections. Upstream sections also showed a general decline in mayfly biomass after the run, but not as severe as in downstream sections (Fig. 3). Chironomid biomass peaked just before the run in downstream sections and then declined steeply during the run (Fig. 4). In late September, after the run and once carcass decomposition was well underway, biomass between stream sections was similar for each taxon.

Discussion

Theories about the linkages between nutrients transported by spawning salmon and juvenile salmonid production include many intermediate steps as these nutrients flow through stream communities to salmon fry via bottom-up processes (Kline et al. 1997, Lichatowich 1999, Gende et al. 2000). These theories have been bolstered by studies using stable isotopes to trace MDN into stream biofilm, aquatic insects, and resident fish (Bilby et al. 1996, Chaloner et al. 2002a). Studies looking at standing stock comparisons of selected taxa in both natural and artificial streams have found differences under various circumstances that also have implied a nutrient subsidy effect of MDN (Kline et al. 1997, Wipfli et al. 1998, Wipfli et al. 1999). However, the incorporation of MDN into stream communities and even higher standing stock biomass in salmon treatment areas does not automatically imply a stimulation of production for stream communities, as many studies have concluded. The nature of salmon spawning runs demands that prior to any real nutrient enrichment there is a large disturbance of the stream benthos (Minakawa 1997, Peterson and Foote 2000). It follows then, that this disturbance should increase with the number of spawners so that disturbance effects increase with enrichment potential. In order for enrichment influences of MDN in natural stream systems to be understood, it is necessary to consider the influence of the physical act of spawning, something mesocosm studies are unable to do. Similarly, pre/post standing stock studies of insect abundance and biomass do not give a realistic picture of what is occurring during the primary growing season. This study is the first to document secondary production differences in relation to MDN enrichment.

This study reveals the complex relationship between salmon and energy flow in streams. For larger sized, univoltine taxa such as ephemerellid and heptageniid mayflies, the influence of spawning disturbance appears to overshadow any potential enriching effect of the salmon. Upstream sections represent areas of refuge that allow for greater production than in downstream sections. Average biomass was initially higher in the spring in upstream sections for these mayflies, which may be due to higher numbers of adults laying eggs in this area. There are certain species of mayflies (e.g. Rhithrogena spp.) that have an over-wintering cohort, and these likely are severely reduced or even eliminated in downstream sections during the run. Both Drunella spp. and Rhithrogena spp. had large individuals sampled from upstream sections in May, where as only small individuals were sampled from downstream sections on the same date (Lessard, unpublished data). Because insect biomass naturally declined in both sections in the fall, even in upstream sections, there may have been selective processes over time that have driven insect life histories to have emergence periods occurring prior to the big salmon runs in this region. This type of influence on aquatic communities would be in direct opposition to MDN enrichment theories.

Chironomid patterns in these streams follow the predictions of MDN enrichment theories. Production was consistently much higher in downstream "treatment" sections of these two streams. This production primarily took place over the spring and summer, however, and similar to the ephemeropteran taxa, midge biomass declined during the run and remained low well into the carcass decomposition period. In fact, midge biomass was at a minimum during this period. For the midges to take advantage of salmon nutrients they would need to remain in the stream in adequate numbers to capitalize on this carcass decomposition period. There were several potential factors that could have influenced the midge patterns observed here. Although the focus of this research was not to determine which mechanism(s) were influencing these communities, it is still pertinent to discuss what could be driving these patterns. Midges may be able to avoid the disturbance of spawning by virtue of their small size allowing them to take advantage of hyporheic or interstitial spaces, thereby maintaining higher population levels in these areas, ultimately resulting in more individuals emerging and reproducing. However, this does not explain why midge populations are lower in upstream sections, where no spawning occurs. It may be that the lack of mayflies in downstream reaches reduces invertebrate competitive and predatory (Drunella are considered predators at larger sizes) interactions so that midges are able to grow and produce at much higher rates in downstream sections through the spring and summer. This seems contrary to other studies that have shown salmon spawning to increase drift and fish predation on insects, primarily midges (Peterson and Foote 2000). However, studies of fish predation effects on chironomid midges have found that the indirect effects of predatory fish on invertebrate midge competitors and predators, benefited chironomid populations more strongly than the negative direct effects of fish predation on the midges (Power et al. 1992, Batzer et al. 2000, Rosenfeld 2000). The indirect effects of spawning and predation on midges may be very important mechanisms in these systems as well. This is further supported by the fact that the fish community richness in downstream sections differ from upstream sections with sculpin, resident and ocean run Dolly Varden as well as juvenile salmonids occurring downstream and only Dolly Varden occurring upstream in these systems (J. Hudson, US Forest Service, Juneau, Alaska, unpublished data). Chironomids also have been identified in some streams as primary colonizers of salmon carcasses during decomposition (Chaloner et al. 2002b), so it may be that the midge community is temporarily diverted to the carcasses from other areas in the stream resulting in reduced densities on mineral substrates. This explanation could not be confirmed because carcasses were not sampled in this study. If midges are able to capitalize on MDN during carcass decomposition before winter, a net effect would be greater production of over-wintering cohorts the following year. Another closely related but distinct potential mechanism that could be driving the production patterns in these streams, would be based on the functional feeding groups that dominate each stream section. The upstream sections, that do not receive spawning runs, are assumed to be less disturbed over the year and so would support more consistent periphyton communities. It seems reasonable that scrapers (like heptageniids and ephemerellids) would do better in more stable habitats (i.e., upstream sections). The downstream sections, however, not only are less stable (due to spawning activities) but also contain decomposing salmon particles during the fall-winter period. This combination of unconsolidated sediments and high quality FPOM, should benefit collector-gatherers, such as midges of the tribe Orthocladiinae. Facultative collector-gatherers, such as baetids, would be expected to do fine under either scenario, and therefore would be expected to show little difference in their production between stream sections.

This research points to spawning disturbance, and possibly fish predation, as major driving forces organizing the benthic community so that areas upstream of salmon barriers support much greater production of univoltine, grazing, mayfly genera. It also suggests that this production of mayflies imposes constraints on the midge community in upstream sections that is released by the cycle of spawning and the presence of fish (resident species, juvenile salmonids and oceanic transient species) in sections open to the ocean. It is not clear if salmon impact midges by indirectly limiting invertebrate competitors and predators and/or stimulate midge production with the nutrients provided by the spawners. It is also not clear if the lower production of mayflies in spawning areas is due to increased predation by fish and/or the spawning disturbance. It seems likely that all these mechanisms may be acting simultaneously resulting in the production patterns seen in these streams. The link between MDN and juvenile salmonid production in these systems, therefore, may rely solely on chironomid production. Both pink and chum salmon have been shown to feed mainly on midges during their seaward migration (Frolenko 1973, Loftus and Lenon 1977, Kaeriyama et al. 1978). Chinook and coho juveniles are also known to feed predominantly on midges (Loftus and Lenon 1977, Dauble et al. 1980). The linkages between anadromy and juvenile salmon production may have less to do with enrichment than with spawning and fish community characteristics for streams in southeast Alaska. These factors need be considered and incorporated into MDN theory.

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Chapter 4

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Chapter 4

Spring growth of caddisflies (Limnephilidae: Trichoptera) in response to marine-derived nutrients and food type in a South-east Alaskan stream

Abstract

The short-term stimulation of production, due to marine-derived nutrients (MDN) from spawning salmon, for certain trophic levels in stream communities (e.g. algae and insect biomass) is well documented. The effect of these nutrients on the stream ecosystem as a whole, however, especially later in the year remains unclear. Trichopterans have been shown to feed on salmon and other fish carcasses and there is evidence for greater growth rates in the presence of salmon tissue. To address the question of long-term MDN subsidy on Trichopterans, we investigated the growth of three limnephilid caddisflies in the spring in the Harris River on Prince of Wales Island, Southeast Alaska. The Harris River has a natural waterfall barrier to salmon and receives large runs of pink and chum salmon each fall. We selected two shredding caddisflies (Onocosmoecus unicolor) and (Psychoglypha sp.) and one facultative scraper, (Dicosmoecus atripes) for our study. We had two objectives: 1) compare the spring growth of larval caddisflies in a stream section that receives a large autumn run of salmon with their growth in a stream section that is blocked from receiving salmon (due to an impassable waterfall), and 2) compare the growth of shredders with that of a facultative scraper when provided either leaves or biofilm on rocks as food.

Insects were placed in growth boxes 18 May 2001 with either conditioned alder leaves or rocks from the stream in the boxes. The boxes along with temperature loggers

were placed in both the salmon (below the waterfall) and non-salmon (above the waterfall) reaches. On 26 June 2001, 40 days later the boxes were removed. In-stream samples were taken of each caddisfly initially and at the end of the experiment to establish in-stream growth versus growth in the boxes. All larvae were coaxed from their cases from the rear with a blunt probe, measured for total wet length, dried and weighed.

Only D. atripes and Psychoglypha were growing during our experiment and both showed very high relative growth rates in the Harris River. We found a strong food effect with both Psychoglypha and O. unicolor being significantly larger in the leaf boxes and D. atripes being significantly larger in the rock boxes. Both D. atripes and Psychoglypha had significantly greater relative growth rates between food types (on biofilm on rocks and leaves respectively). These results support that D. atripes are most likely facultative scrapers at least in their first year of growth. None of these caddisflies showed differences in their final mean weights or relative growth rates between stream sections, indicating no effect of MDN on their spring growth in the Harris River. Further research on caddisfly growth in the fall and winter will help clarify if MDN has an influence on the life history of these species closer to the salmon run. This study questions the long-term influence of MDN on stream communities, particularly those parts that do most of their production in the spring, months after salmon carcasses are no longer visible.

Introduction

The utilization of terrestrially derived nutrients (e.g., leaf litter) is considered to be the driver of productivity and the spatial/temporal organization of many stream communities (Kaushik & Hynes 1971, Cummins 1974, Vannote et al. 1980, Cummins et al. 1989). Coastal streams, that are spawning ground for salmon, have an additional nutrient source termed marine-derived nutrients (MDN) in the form of salmon eggs, sperm, metabolic waste and adult carcasses. The role that these nutrients play in coastal systems has been the object of study in recent years. It has been suggested that the salmon provide an essential nutrient source to the typically oligotrophic anadromous streams of the Pacific Northwest of the United States and, by subsidizing the nutrient base in their spawning grounds, increase the viability of their own offspring (Kline et al. 1997, Lichatowich 1999). Most studies have dealt with tracing MDN through various surface-stream and riparian trophic levels or quantitative comparisons of stream communities with and without salmon (e.g. Bilby et al. 1996, Kline et al. 1997, Ben-David et al. 1998, Wipfli et al. 1998, Cederholm et al. 1999, Chaloner et al. 2002). There is ample evidence of the incorporation of MDN into stream communities (Schuldt & Hershey 1995, Bilby et al. 1996) and the short-term stimulation of primary production and increases in certain fauna (i.e. chironomid midges) (Kline et al. 1997,Wipfli et al. 1998, Wipfli et al. 1999, Chaloner et al. 2002). However, the long-term influence (i.e. through the winter and into the spring the following year) of MDN on the productivity of these streams is still unclear.

The importance of MDN to a stream community will depend on how far upstream the enrichment extends and the length of time these nutrients are retained in the system.

This is particularly true for insects not growing in the streams immediately following the major salmon run(s). Insect responses to enrichment take several forms including changes in population size, voltinism, fecundity and growth rates (e.g Anderson & Cummins 1979, Sweeney 1984, Arsuffi & Suberkropp 1986, Peterson et al. 1993).

Several studies as well as observations by the authors, have indicated that Trichopterans are attracted to and feed on salmon and other fish carcasses (Brusven & Scoggan 1969, Chaloner et al. 2002). Minakawa (1997) found greater growth in Trichopterans directly feeding on MDN (i.e. salmon carcasses). The indirect influence of MDN on insect growth, however, is poorly understood. The objectives of this study were to: 1) address the question of long-term MDN subsidy (via indirect pathways) by comparing the spring growth of caddisflies above and below a natural barrier to salmon (i.e. impassable waterfall) in one stream in Southeast Alaska; and 2) compare the growth of selected caddisflies who are known to have different feeding modes (i.e., shredding and scraping) on two food sources, leaves and biofilm (defined as a matrix of algae, bacteria, fungi, protozoans and other organic matter). We hypothesized that if MDN does in fact provide an important long-term nutrient subsidy to these streams, then organisms grown below the waterfall barrier (i.e. with MDN in the system) would exhibit higher growth rates than organisms grown above the barrier (i.e. without MDN). The mechanism for increased growth was assumed to be greater food quality in the downstream section. We also hypothesized that when provided with either leaf litter or biofilm on rocks as food, shredders would grow better on leaves and scrapers would grow better on biofilm. The organisms selected have at least a one-year life cycle and in some circumstances take two years before metamorphosis, therefore, they have the ability to integrate the influence of MDN over the entire year. The timing of this study, however, was to determine if MDN influences caddisfly growth in the spring, eight months after the autumn salmon run.

Methods and materials

Study site

Harris River is an anadromous salmon stream on Prince of Wales Island, which is approximately 45 miles west of Ketchikan in Southeast Alaska. It receives annual runs of coho (Oncorhynchus kisutch) pink (O. gorbuscha) and chum (O. keta) salmon. The largest runs are the pink and chum spawning migration, which normally take place between late July and early September. Harris River received an estimated 920,000 chum and pink salmon the autumn of 2000. previous to the experiment (Alaska Department of Fish &Game, pers. comm.). Harris River has a natural waterfall that blocks salmon migrations from "upstream" reaches, and has done so since the last ice age. Preliminary habitat sampling showed that reaches above and below the waterfall (termed upper and lower Harris) were of similar mean depth (~40 cm), had similar bottom substrate (primarily small-large cobble and boulders) and riparian vegetation (mixtures of conifer and alder trees, shrubs, ferns and herbaceous plants), but lower Harris was wider and had less wood debris than upper reaches (Lessard, unpublished data).

Study Organisms

The limnephilid caddisflies we selected were Onocosmoecus unicolor (Banks), Dicosmoecus atripes (Hagen) and Psychoglypha sp. (Banks), all of which are fairly common fauna in anadromous streams of southeast Alaska. All three of these genera have also been associated with fish carcasses (Brusven & Scoggan 1969, Chaloner et al. 2002). These species, however, vary in their primary modes of feeding. Both O. unicolor and Psychoglypha sp. are considered obligate shredders (Wiggins & Mackay 1978, Merritt & Cummins 1996), while D. atripes larvae are facultative scrapers and shredders as early instars and shredders-predators during later instars (Wiggins & Richardson 1982, Gotceitas & Clifford 1983). While all species were found in both stream sections of the Harris River, preliminary sampling revealed that downstream of the barrier there was a greater abundance of O. unicolor and D. atripes while upstream there were more Psychoglypha sp.

Growth study

The experiment was initiated on 18 May 2001 during which time caddisflies were sampled from both upper and lower Harris River. Due to the lack of a large enough population of all three taxa in both reaches, all O. unicolor and D. atripes used in the experiment were from the lower reach and all Psychoglypha sp. used were from the upper reach. There also were some apparent instar differences among the D. atripes larvae: two general groups of 2nd-3rd instars, and 3rd-4th instars. Because of this, each of these size class groups was grown separately and the number of individuals varied between 5 and 10 per growth box (Figure 1). O. unicolor and Psychoglypha had only one size class.

Insects were captured from cobble, side areas and pools using D-frame nets. After sampling each reach, caddisflies were sorted and placed into growth boxes (modified 25x18x5 cm Tupperware ® containers with the top, sides and bottoms cut out and replaced with 2mm plastic mesh).

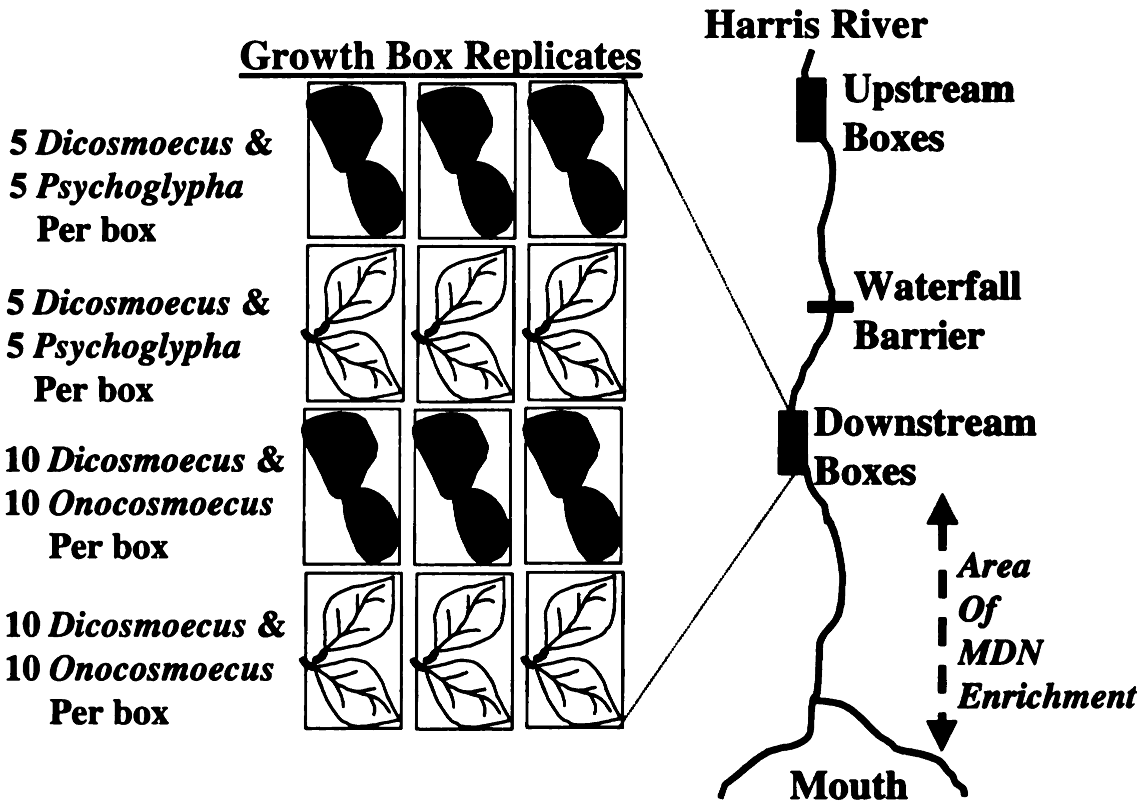

Figure 1. Schematic of growth experiment conducted in the Harris River. Identical set-ups were used in upstream and downstream sections. Box cartoons show the combinations of food type (conditioned alder leaves and rocks from the stream) and taxa that were put in each box, and replicated three times.

Food for the growth boxes consisted of either 12 conditioned (incubated in the stream for 2 weeks) red alder leaves (Alnus rubra Bong) or biofilm on 4-5 small rocks from the stream, both were inspected and had any insects removed before being put into the growth boxes. Caddisflies from each section (D. atripes and O. unicolor from downstream, Psychoglypha from upstream) were grown in both sections (above and below the waterfall) and on both food types (conditioned leaves or biofilm on rocks). Each box contained D. atripes and either O. unicolor or Psychoglypha, so that one of the obligate shredders and the facultative scraper were in each box. Five 3rd-4th instar D. atripes and 5 Psychoglypha were placed in each of 6 boxes (3 filled with leaves and 3 filled with rocks), while 10 O. unicolor and 10 2nd –3rd instar D. atripes were placed in another 6 boxes (3 filled with leaves and 3 filled with rocks). There were a total of 12 boxes placed in each stream section (Figure 1) which were cable tied to rebar (metal rods ~1.25 cm diameter) imbedded in the stream bottom in a slow flow area near the stream bank. Onset® temperature loggers were also placed in each stream section and set to take hourly readings. The remaining organisms from the stream samples of each caddisfly (30-50 per taxa) were used to obtain an initial population mean wet length and dry weight for each. These samples were brought back to the lab, coaxed from their cases from the rear with a blunt probe, measured to the nearest 0.5 mm, oven dried (30°C for four days) and weighed using a Cahn-Electrobalance (to the nearest 0.01 mg).

Throughout the experiment boxes were monitored to ensure no tampering or sedimentation had occurred. The rocks were changed twice and the leaves once in the boxes and conifer needles also were added. This was done to provide case making material and ensure access to food would not lead to a growth box effect not representative of in-stream growth. On 26 June, after 40 days, the experiment was terminated. All insects were removed from the boxes, counted and kept separate for processing. At this time another large, in-stream sample (20-30) of each caddisfly was taken from the Harris River to obtain a final in-stream population mean wet length and dry weight for each. All insects (from growth boxes and upstream and downstream in-stream samples) were brought back to the lab alive and processed the same way the initial samples were (i.e., coaxed from cases, measured for length, dried and weighed). The temperature loggers were also removed and the data downloaded.

Instar determinations were made by measuring the width of the head, dorsally across the eyes, using an ocular micrometer at 70x to the nearest 0.05 mm (Wiggins & Richardson 1982, Gotceitas & Clifford 1983, Wiggins & Richardson 1986). Descriptive statistical calculations, regressions and Mann-Whitney U tests were all computed using Systat statistical software. Growth box effects were examined by comparing average final weights in the boxes in each section versus average final weights of free-living larvae in the stream. MDN effects on these caddisflies were determined by comparisons between stream sections (i.e., above versus below). Food preferences were determined by comparing growth on leaves versus biofilm on rocks. Statistical significance was determined using $\alpha=0.05$ for independent comparisons and bonferroni adjustments to alpha were made for any multiple comparisons.

Results

Both D. atripes and Psychoglypha showed significant growth during the experiment and had similar final mean weights in the boxes as in the stream (i.e. no growth box effect) (Figure 2).

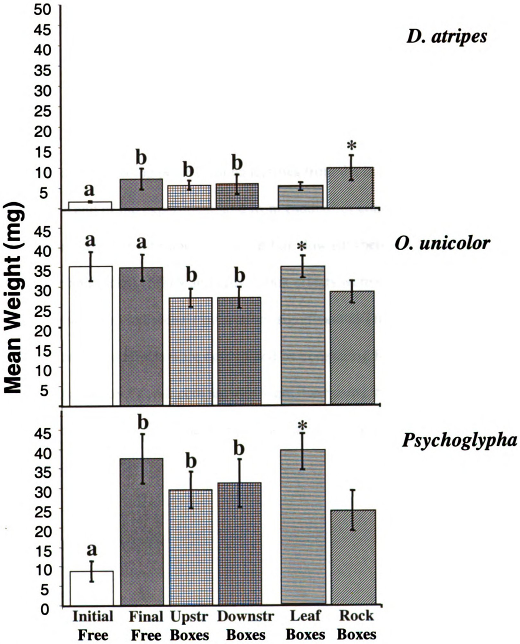
Mean Weight (mg)
D. atripes
O. unicolor
Psychoglypha
50
45
40
35
30
25
20
15
10
5
0
a
b
b
b
*
a
a
b
b
*
a
b
b
b
*
Initial Free
Final Free
Upstr Boxes
Downstr Boxes
Leaf Boxes
Rock Boxes

Figure 2.

Figure 2. Mean dry weight mg (+/- SE) of caddisflies from the in-stream samples (Free) initially and at the end of the experiment, and from caddisflies confined to the boxes divided by stream section (upstr=above the waterfall, downstr=below the waterfall) and food type (leaves and rocks). MDN and growth box effects were determined by comparing free and boxed individuals by section (significant differences indicated by different letters) and food effects were determined by comparing food types (significantly higher values indicated by *). All comparisons were done using the Mann-Whitney U test with bonferroni adjustments made for multiple comparisons when appropriate.

O. unicolor were not growing at all in the stream during this time and were significantly smaller in the boxes than in the stream ($\chi^2_{df=1}$=13.349, p<0.0001). None of the caddisfly taxa showed any differences in growth between stream sections (i.e. no MDN effect). All three taxa, however, showed varied growth by food type with both O. unicolor and Psychoglypha growing significantly more on leaves ($\chi^2_{df=1}$=10.829, p=0.001; $\chi^2_{df=1}$=10.763, p=0.001, respectively) and D. atripes growing significantly more on biofilm on rocks ($\chi^2_{df=1}$=14.578, p<0.0001) (Figure 2).

The upstream reach accumulated 282 degree-days (°C) throughout the 40-day experiment, while downstream accumulated 215 degree-days (°C). Normalizing for temperature, that is comparing relative growth rates per degree-day [calculated as: 100*(mean initial weight-mean final weight) /(mean initial weight * #of degree-days)] revealed similar results. O. unicolor and Psychoglypha had significantly greater growth rates on leaves ($\chi^2_{df=1}$=10.98, p=0.001; $\chi^2_{df=1}$=10.345, p=0.001, respectively), and D. atripes had a significantly greater growth rate on biofilm ($\chi^2_{df=1}$=14.295, p<0.0001) (Figure 3). Again, there was no MDN effect found when above and below mean growth rates were compared for each caddisfly taxa.

Nearly all the boxes had some loss (assumed to be mortality) of caddisflies (Figure 4). A greater percentage of D. atripes compared to the other two taxa were lost during the experiment in both stream sections, but significantly more D. atripes survived in boxes from the downstream reach ($\chi^2_{df=1}$=4.669, p=0.031). Psychoglypha was the only taxon that showed a food effect on mortality, with a significantly greater percentage surviving on leaves ($\chi^2_{df=1}$=8.539, p=0.003).

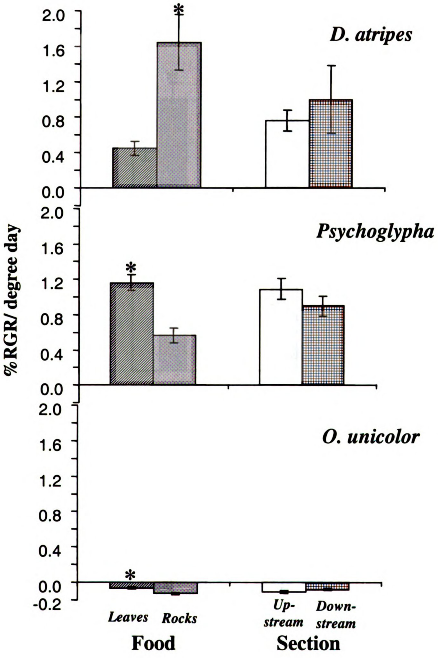

Figure 3. Mean % relative growth rate/ degree day (° C) (+/- SE) for caddisflies grown in growth boxes averaged by food type and stream section. An * indicates significantly greater %RGR from the Mann-Whitney U tests.

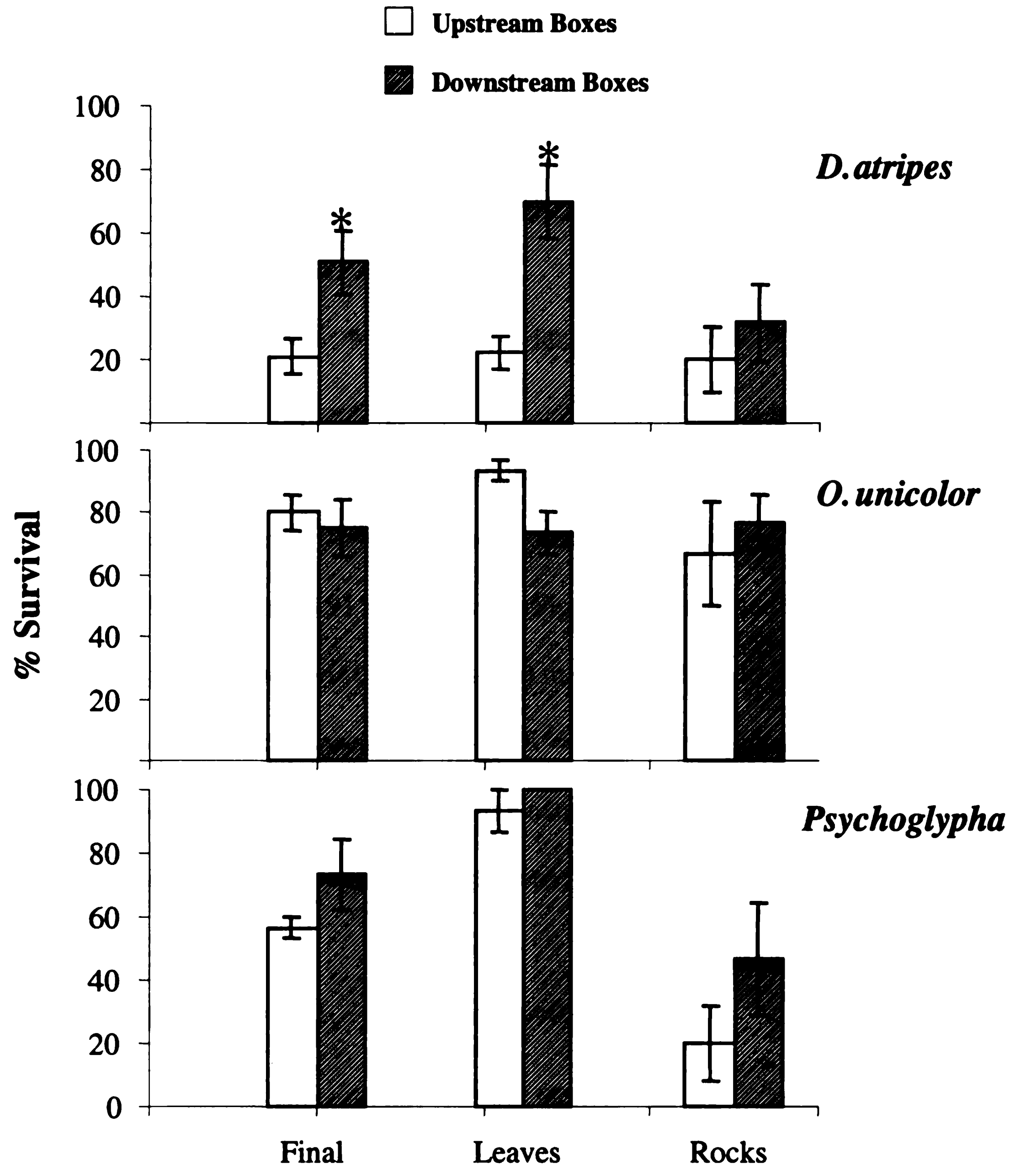

Figure 4. Mean % survival (+/- SE) of caddisflies in the growth boxes at the end of the experiment by stream section (averaged across food type). Survival at the end of the experiment is also shown by food type in each section (Leaves and Rocks). Significant differences between stream sections (i.e., each pair of bars), determined using the Mann-Whitney test, are indicated by an *.

Comparisons of mean % RGR/degree-day versus % mortality in the growth boxes, revealed significant negative models for D. atripes and Psychoglypha, but the high degree of variation made these relationships quite weak, especially for D. atripes (Adjusted R^2= 0.19 and 0.45, p=0.022 and 0.010 respectively) (Figure 5). There was no relationship between mean % RGR/degree-day and % mortality for O. unicolor (Adjusted R^2= 0.00, p=0.895) (Figure 5).

The large number of animals handled during this experiment enabled us to develop strong wet length-dry weight relationships for D. atripes and Psychoglypha (Adjusted R^2= 0.95 and 0.91 respectively) (Figure 6). However, the small range in sizes for O. unicolor (due to their lack of growth) made it difficult to establish a good length-weight equation for this species (Adjusted R^2=0.49). Preliminary analysis revealed that the length-weight data were not linear so a natural log transformation was performed to produce a linear fit. The regression equations for these data were:

D. atripes (n=221) $\mathrm{Ln}(w)=0.421L-1.865$ [1]

Psychoglypha (n=62) $\mathrm{Ln}(w)=0.331L+0.04$ [2]

O. unicolor (n=126) $\mathrm{Ln}(w)=0.269L+1.716$ [3]

Where Ln(w), is the natural log of the dry weight (mg) and L is the total wet length (mm).

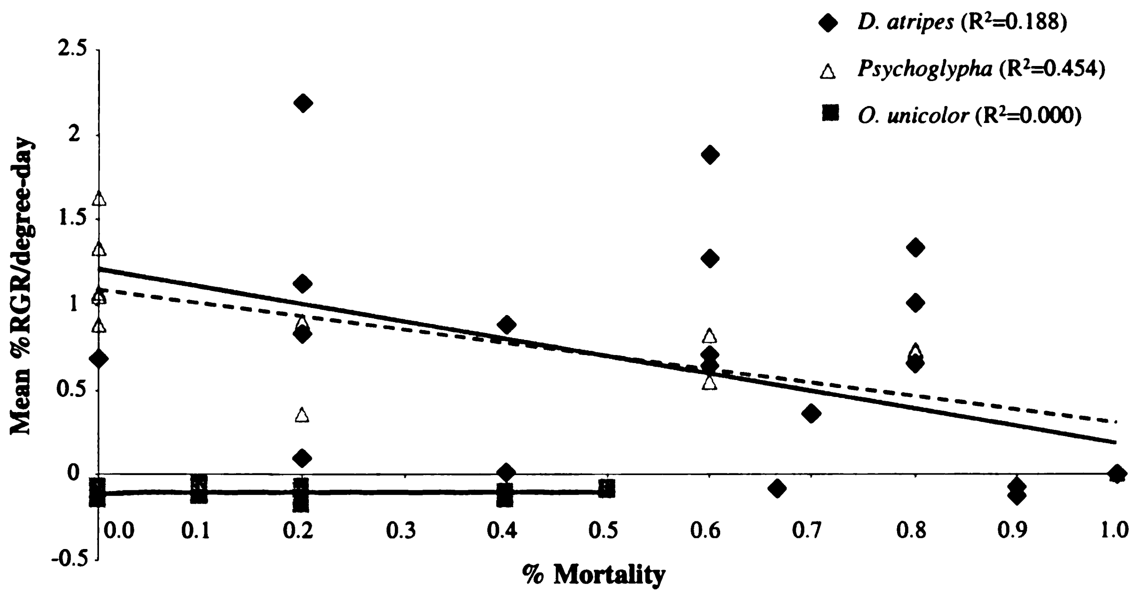

Figure 5. Mean % relative growth rate/ degree day (° C) versus % Mortality in the growth boxes for each caddisfly. The lines are the results of the regressions and the symbols are from the data for each taxa. Adjusted R^2 values for each model are given in the legend.

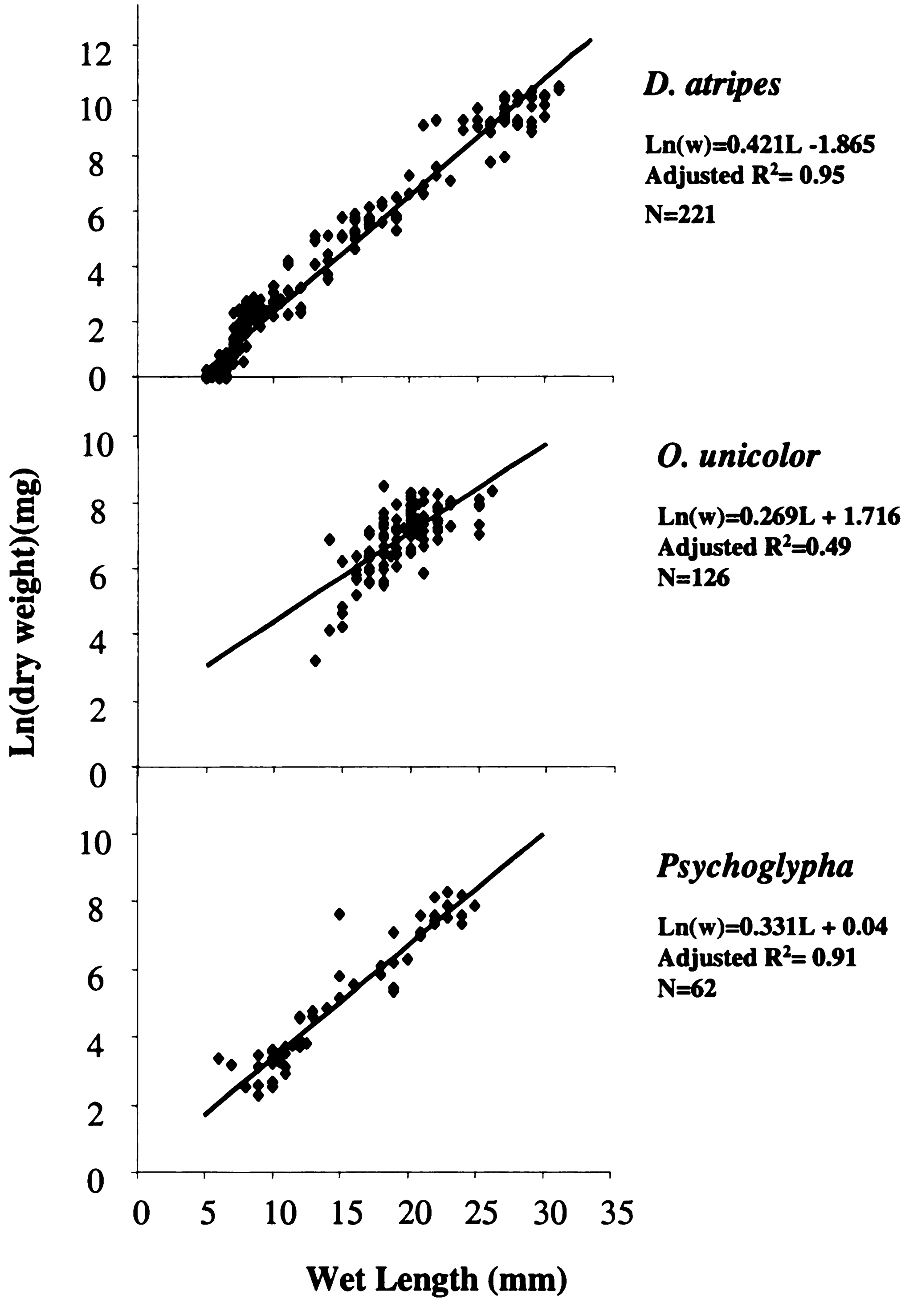

Figure 6. Wet length-dry weight relationships for the three caddisflies. Lines are the results of the regression equations shown to the right of each graph and diamonds are the individual data points from in-stream samples of each taxa.

Discussion

There was no detectable influence of MDN on the spring growth of these three limnephilid caddisflies in Harris River. O. unicolor hatch in the fall and grow quickly to fifth instars and then remain at that stage over the winter and spring, pupating and emerging during the summer (Wiggins & Richardson 1986, Irons 1988). Head capsule width measurements revealed that the Harris River's population of O. unicolor larvae were fifth instars throughout our experiment. There were not enough O. unicolor found above the waterfall to make in-stream above and below comparisons of weights. However, the presence of such a large population of this species in areas that receive salmon might be related to MDN. The life cycle of this species is timed to obtain the greatest advantage from the salmon with most larval growth occurring in autumn during salmon carcass decomposition (Irons 1988). Chaloner et al. (2002) found Onocosmoecus to be one of the most common invertebrate taxa associated with salmon carcasses after spawning runs in Southeast Alaskan streams. However, this also is the primary time for deciduous leaf fall so this shredder's life history may be keyed to the salmon, leaf litter inputs or both.

D. atripes also were found in greater numbers downstream. D. atripes was the only taxon that showed mortality variation between stream sections, with significantly more surviving in the downstream boxes. It is possible that niche partitioning in this stream relegates D. atripes and O. unicolor to downstream reaches and Psychoglypha to upstream areas, with further separation temporally of D. atripes and O. unicolor larval growth periods. However, the growth boxes did not support this hypothesis because more D. atripes were lost in boxes with O. unicolor, their natural physical companion, but these boxes also had twice as many and younger D. atripes individuals in the boxes. Lamberti et al. (1995) found evidence for density dependent growth of the scraping D. gilvepes in laboratory streams. In our experiment there was a weak negative relationship between %mortality and %growth for D. atripes, so it appears that boxes that lost more individuals were somehow also systematically poorer environments for growth. Due to the complexity of this experiment, however, and the number of potentially interacting factors, we were not able to determine inter- or intra-specific competitive interactions in the stream or in our growth boxes.

D. atripes' main growth period is during the spring and early summer (Wiggins & Richardson 1982, Gotceitas & Clifford 1983), and while they grew significantly during our experiment we were not able to detect an influence of MDN on the spring growth of this species either. Because D. atripes when supplied conditioned leaves grew less than when supplied biofilm in the boxes, this species is most likely a scraper, at least as earlier instars. Other feeding and growth studies on late and middle instar D. atripes larvae concluded that this species is a shredder and sometimes a predator (Wiggins & Richardson 1982, Mihuc & Mihuc 1995). Our data support those of Gotceitas & Clifford (1983), in Alberta, Canada who found in the first year of their life cycle D. atripes utilize algae as their main food source

During the second sampling period we found several very large D. atripes larvae that had switched their case making from organic to mineral. Head width analysis revealed that during our original sampling we had primarily 2nd and 3rd instars and during the second sampling we had 3rd, 4th, and 5th instars (Wiggins & Richardson 1982). D. atripes larvae have been shown to have two-year life cycles in cold streams (Gotceitas &

Clifford 1983). D. atripes in the Harris River also appeared to have a two year life-cycle which accounted for 5th instars being found during the second sampling. Second year D. atripes larvae over-winter as diapausing fifth instars attached in large aggregations under large boulders, and then become active again in the spring (Gotceitas & Clifford 1983). Dicosmoecus larvae were shown to be important processors of fish carcasses in a study of squawfish eradication in Idaho (Brusven & Scoggan 1969). Since D. atripes larvae remain in this stream throughout the spawning run and carcass decomposition, before the winter diapause, the importance of MDN to this species may occur during that time (i.e. between its first and second year of development) rather than at the beginning of the life-cycle.

Psychoglypha sp. are shredding caddisflies limited to the western montane regions of North America (Denning 1970, Wiggins & Mackay 1978, Merritt & Cummins 1996). Not much is known of the life history of this genus except that they are cold adapted and adults have been found between late fall and early spring in southeast Alaska and from April to August in the Yukon (Ellis 1978, Wiggins & Parker 1997). Growth studies of Psychoglypha sp. found that these caddisflies grew differently on varying food quality and exhibited high relative growth rates (0.51% body weight/degree day) on the highest quality food (Arsuffi & Suberkropp 1986). Psychoglypha in our study grew on average at a similar rate on the biofilm and at over twice that rate on the stream-conditioned alder leaves, indicating the generally high growth achieved by this taxon in the Harris River. These high growth rates were similar between stream sections and slightly higher in upstream sections, which again points to the lack of importance of MDN to the spring growth of this caddisfly. Psychoglypha also were associated with squawfish decomposition in Idaho (Brusven & Scoggan 1969), indicating the potential for a direct relationship between MDN and this caddisfly. The dominance of Psychoglypha sp. above the barrier, however, and their high growth rates upstream and probable emergence prior to salmon decomposition indicates less of a reliance on these nutrients for this caddisfly.

Conclusions

Salmon have an obvious effect on anadromous stream communities, from the huge disturbance caused by their numbers and spawning activity to the pulse of nutrients released following this activity and ultimately to the stream fish community by the addition of their offspring (Kline et al. 1997, Minakawa 1997, Wipfli et al. 1998, Peterson & Foote 2000). Initial post-spawning increases, however, are mainly due to the incorporation of salmon metabolic waste, sperm, and eggs into stream communities, all of which are temporary forms of MDN. The question is how is the community impacted the rest of the year? Is this enrichment retained in the system long enough to impact fauna that are not active in the stream during the initial autumn MDN pulse?

Once spawning has ended and salmon begin dying off, the retention of these blocks of MDN (i.e. carcasses) are now a function of hydrologic retention and stream structure (e.g. wood debris, surface topography), as are all sources of CPOM (coarse particulate organic matter)(Speaker et al. 1984, Cederholm & Peterson 1985). Retention would have to involve sequestration of nutrients in the surface and subsurface community and the slow release and cycling of these nutrients throughout the year. The easiest slow release mechanism to visualize would be from the burial and subsequent aerobic and/or anaerobic decomposition of whole carcasses and pieces, an area yet to be researched. A more difficult and complicated mechanism would be from the stimulation of production of autumnal flora and fauna that would cycle these nutrients via the surface and hyporheic food web at a magnitude and rate that allows for the benefit of other organisms months later. To our knowledge no research has been able to trace nutrients through a stream system for that long.

By comparing growth of these caddisflies on both biofilm on rocks and fungi on leaves we were able to look indirectly at variations in food quality between stream sections as well as establishing which food type each taxa preferred. This study revealed strong food preferences for all three caddisflies, which followed what was hypothesized. This study also suggests that MDN enrichment in Harris River may not have extended into subsequent generations of caddisflies and therefore growth of larvae in the spring was not different between areas with and without salmon. Further research in this area should continue, as well as studies on these insects in the fall and winter to help clarify if MDN has a role in their growth and life history more proximal to the large salmon input. The MDN story seems to be much more complicated than the typical model that links salmon enrichment, stream productivity and ultimately a positive feedback for juvenile salmon survival via direct and indirect pathways. The complications come from the coincidental disturbance that precedes MDN enrichment, varied life histories of aquatic insects, and the lack of knowledge of the fate of MDN in streams over longer periods of time. The links to fish production may take place over the few months directly following the large salmon run and therefore the influence on the stream community as a whole may be more limited than many hypotheses predict.

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APPENDICES

APPENDIX A

Appendix A. Taxa list for the major insect orders in each stream by period (pre, during and post) and section (D=downstream of barrier, U=upstream).

Study stream abbreviations are: B=Bessie, F=Fish, H=Harris, P=Peterson, Sa=Salmon, S/G=Sata/Gulch, and Sh=Sheep. Taxa not taken to species

(e.g. Orthocladiinae richness) were documented with counts of distinct taxa.

				Study Stream							Pre Section		During Section		Post Section	
Order	Family	Genus	Species	B	F	H	P	Sa	S/G	Sh	D	U	D	U	D	U
Coleoptera	Amphizoidae	Amphizoa							+			X				
	Curculionidae	Lixus							+				X			
	Dytiscidae	Agabus							+					X		
	Dytiscidae	Hydaticus			+						X					
	Dytiscidae	Hydrovatus		+										X	X	
	Dytiscidae	Liodessus					+					X				
	Dytiscidae	Oreodytes				+			+			X			X	
	Dytiscidae	Uvarus				+					X	X		X		
	Elmidae	Narpus				+					X			X		X
	Elmidae	Stenelmus							+				X			
	Empididae	Oreogeton							+				X			
	Hydrophilidae	Ametor		+	+		+		+			X				X
	Melyridae	Endeodes			+							X				
	Staphylinidae				+	+					X	X				
Diptera	Athericidae	Atherix			+											X
	Blephariceridae	Agathon	comstockae		+						X	X				
	Blepharoceridae	Agathon	aylmeri grp					+				X				
	Ceratopogonidae	Dasyhelea								+					X	
	Ceratopogonidae	Probezzia		+		+	+					X	X	X		X
	Chaoboridae	Eucorantha	underwoodi									X				
	Chironomidae	Chironomini		+		+	+	+	+		X	X		X	X	X
	Chironomidae	Orthocladiinae	1	+	+	+	+	+	+	+	X	X	X	X	X	X
	Chironomidae	Orthocladiinae	2	+	+	+	+	+	+	+	X	X	X	X	X	X
	Chironomidae	Orthocladiinae	3	+	+	+	+		+	+	X	X	X	X	X	X
	Chironomidae	Orthocladiinae	4		+	+		+			X	X	X	X	X	X

Appendix 1. (Cont'd)

						Study Stream					Pre Section		During Section		Post Section	
Order	Family	Genus	Species	B	F	H	P	Sa	S/G	Sh	D	U	D	U	D	U
	Chironomidae	Orthocladiinae	5		+	+					X	X	X	X	X	X
	Chironomidae	Orthocladiinae	6			+						X				
	Chironomidae	Tanypodinae		+		+	+	+	+		X	X	X	X	X	X
	Chironomidae	Tanytarsini		+		+	+	+	+	+	X	X	X	X	X	X
	Deuterophlebiidae	Deuterophlebia	inyoensis		+						X	X	X	X		
	Empididae	Chelifera		+	+	+		+	+		X		X	X	X	X
	Empididae	Clinocera							+							X
	Empididae	Oreogeton		+	+	+	+	+	+		X	X	X	X	X	X
	Empididae	Wiedemannia		+												X
	Simulidae	Helodon Onychodactylus complex			+						X	X	X	X		
	Simulidae	Simulium near Canonicolum			+						X	X	X			
	Simuliidae	Prosimulium		+		+	+		+	+	X	X	X	X	X	
	Simuliidae	Simulium		+		+	+	+	+		X	X	X	X		X
	Syrphidae	Syrphus				+									X	
	Tipulidae	Antocha			+	+		+			X	X	X	X	X	
	Tipulidae	Dicranota		+	+	+	+	+	+	+	X	X	X	X	X	X
	Tipulidae	Erioptera				+					X					
	Tipulidae	Hesperoconopa			+			+			X				X	
	Tipulidae	Hexatoma		+	+	+	+	+	+			X	X	X	X	X
	Tipulidae	Limonia		+				+				X			X	
	Tipulidae	Tipula		+											X	
Ephemeroptera	Ameletidae	Ameletus		+	+	+	+	+	+	+	X	X	X	X	X	X
	Ameletidae	Ameletus	velox		+							X				
	Baetidae	Baetis	bicaudatus	+	+	+	+	+	+	+	X	X	X	X	X	X
	Ephemerellidae	Caudatella	heterocaudata					+			X	X				
	Ephemerellidae	Caudatella	jacobi		+						X	X				X
	Ephemerellidae	Caudatella	orestes	+	+	+	+	+	+	+	X	X	X	X		X
	Ephemerellidae	Drunella	coloradensis	+	+			+	+	+	X	X	X	X		X
	Ephemerellidae	Drunella	doddsi	+	+	+	+	+	+	+	X	X	X	X	X	X
	Ephemerellidae	Drunella	flavilinea					+				X		X		

Appendix 1. (Cont'd)

											Pre		During		Post	
						Study Stream					Section		Section		Section	
Order	Family	Genus	Species	B	F	H	P	Sa	S/G	Sh	D	U	D	U	D	U
	Ephemerellidae	Drunella	grandis	+	+	+		+			X	X	X		X	X
	Ephemerellidae	Drunella	spinifera			+	+				X	X	X			X
	Ephemerellidae	Ephemerella				+					X					
	Ephemerellidae	Seratella			+	+	+		+			X	X	X	X	X
	Heptageniidae	Cinygma		+		+	+	+	+		X	X		X		X
	Heptageniidae	Cinygmula		+	+	+	+	+	+	+	X	X	X	X	X	X
	Heptageniidae	Epeorus		+	+	+	+	+	+	+	X	X	X	X	X	X
	Heptageniidae	Heptagenia			+						X					
	Heptageniidae	Iron	deceptivus		+											
	Heptageniidae	Iron	longimanus		+						X		X			
	Heptageniidae	Ironodes							+			X				
	Heptageniidae	Ironopsis			+							X			X	X
	Heptageniidae	Rhithrogena		+	+	+	+	+	+	+	X	X	X	X	X	X
	Leptophlebiidae	Paraleptophlebia		+	+	+	+	+	+		X	X	X	X	X	X
Plecoptera	Capniidae	Capnia			+	+		+	+	+	X	X	X			X
	Chloroperlidae	Haploperla								+					X	
	Chloroperlidae	Kathroperla		+	+	+		+	+		X	X		X		X
	Chloroperlidae	Kathroperla	perdita		+						X	X				X
	Chloroperlidae	Paraperla							+		X					X
	Chloroperlidae	Plumiperla	diversa		+						X	X		X		
	Chloroperlidae	Suwallia		+	+	+	+	+	+	+	X	X	X	X	X	X
	Chloroperlidae	Suwallia	forcipata		+								X			
	Chloroperlidae	Sweltza		+	+	+	+	+	+	+	X	X	X	X	X	X
	Chloroperlidae	Utaperla							+		X					
	Leuctridae	Despaxia		+	+	+	+	+	+	+	X	X	X	X	X	X
	Leuctridae	Despaxia	augusta		+						X					
	Leuctridae	Perlomyia		+				+		+	X	X				X
	Nemouridae	Amphinemoura							+					X		X
	Nemouridae	Nemoura						+	+	+	X	X		X	X	X
	Nemouridae	Ostracerca				+		+				X			X	X

Appendix 1. (Cont'd)

				Study Stream							Pre Section		During Section		Post Section	
Order	Family	Genus	Species	B	F	H	P	Sa	S/G	Sh	D	U	D	U	D	U
	Nemouridae	Podmosta							+		X	X				
	Nemouridae	Prostoia						+					X			
	Nemouridae	Shipsa							+						X	
	Nemouridae	Visoka						+					X			
	Nemouridae	Zapada	cinctepes	+	+		+	+	+		X			X	X	X
	Nemouridae	Zapada	oregonensis	+	+	+	+	+	+	+	X	X	X	X	X	X
	Perlidae	Hesperoperla	pacifica				+				X	X		X		X
	Perlodidae	Arcynopteryx			+									X		
	Perlodidae	Isoperla						+		+			X	X		
	Perlodidae	Megarcys	signata		+	+		+	+	+	X	X	X	X	X	X
	Perlodidae	Rickera	sorpta	+							X			X		
	Taeniopterygidae	Taeionema			+					+	X		X		X	X
Trichoptera	Apataniidae	Apatania				+							X	X	X	
	Apataniidae	Moselyana						+					X	X		X
	Brachycentridae	Micrasema		+		+	+	+	+		X			X	X	X
	Glossosomatidae	Glossosoma		+	+	+		+	+	+	X	X	X	X	X	X
	Hydropsychidae	Arctopsyche			+	+		+		+		X	X	X		X
	Hydropsychidae	Arctopsyche	grandis									X				
	Hydropsychidae	Parapsyche		+	+	+	+	+	+		X	X	X	X		X
	Lepidostomatidae	Lepidostoma			+	+	+		+		X	X	X		X	X
	Limnephilidae	Cryptochia				+										X
	Limnephilidae	Dicosmoecues		+	+	+	+	+	+				X			
	Limnephilidae	Dicosmoecus	atripes			+					X		X			
	Limnephilidae	Ecclisocosmoecus		+		+		+				X	X	X		X
	Limnephilidae	Ecclisocosmoecus	scylla										X			
	Limnephilidae	Ecclisomyia		+	+	+	+	+	+	+	X	X	X	X	X	X
	Limnephilidae	Grensia						+						X		
	Limnephilidae	Lenarchus						+				X				
	Limnephilidae	Onocosmoecus	unicolor		+	+			+	+	X	X				
	Limnephilidae	Psychoglypha		+	+	+	+	+	+	+	X	X	X	X	X	X

Appendix 1. (Cont'd)

											Pre		During		Post	
						Study Stream					Section		Section		Section	
Order	Family	Genus	Species	B	F	H	P	Sa	S/G	Sh	D	U	D	U	D	U
	Philopotamidae	Dolophilodes							+	+		X	X			
	Philopotamidae	Wormaldia		+				+						X		
	Polycentropodidae	Polycentropus				+	+		+		X	X		X		
	Rhyacophildae	Rhyacophila		+	+	+	+	+	+	+	X	X	X	X	X	X
	Uenoidae	Neophylax		+					+		X	X				
	Uenoidae	Oligophlebodes								+	X	X				

APPENDIX B

Appendix B

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.: 2004-04

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

Influence of marine-derived nutrients from spawning salmon on aquatic insect communities in south-east Alaskan streams

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

Entomology Museum, Michigan State University (MSU)

Other Museums: none

Investigator's Name(s) (typed)
JoAnna L. Lessard

Date 8/25/04

*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 B

Voucher Specimen Data

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Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Adults ♀
Dip 1: Athericidae, Atherix sp.	Fish Creek, Juneau, AK		x		
Dip 2: Blephariceridae: Agathon comstockae	Fish Creek, Juneau, AK		x		
Dip 3: Ceratopogonidae: Probezzia sp.	Bessie Creek, Juneau, AK		x		
Dip 4: Calliphoridae	Harris Creek, Prince of Wales Isle., AK		x		
Dip 5: Chaoboridae: Eucorantha underwoodi	Sata/Gulch Creek, Prince of Wales Isle., AK		x		
Dip 6: Chironomidae: Chironomini	Peterson Creek, Juneau, AK		x		
Dip 7: Chironomidae: Orthocladiinae #1	Bessie Creek, Juneau, AK		x		
Dip 8: Chironomidae: Orthocladiinae #2	Bessie Creek, Juneau, AK		x		
Dip 9: Chironomidae: Orthocladiinae #3	Bessie Creek, Juneau, AK		x		
Dip 10: Chironomidae: Orthocladiinae #4	Harris Creek, Prince of Wales Isle., AK		x		
Dip 11: Chironomidae: Orthocladiinae #5	Harris Creek, Prince of Wales Isle., AK		x		
Dip 12: Chironomidae: Orthocladiinae #6	Harris Creek, Prince of Wales Isle., AK		x		
Dip 13: Chironomidae: Tanypodinae	Harris Creek, Prince of Wales Isle., AK		x		
Dip 14: Chironomidae: Tanytarsini	Harris Creek, Prince of Wales Isle., AK		x		
Dip 15: Deuterophlebiidae: Deuterophlebia inyoensis	Fish Creek, Juneau, AK		x		
Dip 16: Empididae: Chelifera sp.	Harris Creek, Prince of Wales Isle., AK		x		
Dip 17: Empididae: Clinocera sp.	Fish Creek, Juneau, AK		x		
Dip 18: Empididae: Oreogeton sp.	Bessie Creek, Juneau, AK		x		

(Use additional sheets if necessary)

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Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Adults ♀
Dip 19: Empididae: Weidemannia sp.	Bessie Creek, Juneau, AK		x		
Dip 20: Simuliidae: Helodon, Onychoclatylus complex	Fish Creek, Juneau, AK		x		
Dip 21: Simuliidae: Prosimulium sp.	Bessie Creek, Juneau, AK		x		
Dip 22: Simuliidae: Simulium near canonicolum spp.	Fish Creek, Juneau, AK		x		
Dip 23: Syrphidae: Syrphus sp.	Harris Creek, Prince of Wales Isle., AK		x		
Dip 24: Tipulidae: Antocha sp.	Fish Creek, Juneau, AK		x		
Dip 25: Tipulidae: Dicranota sp.	Sata/Gulch Creek, Prince of Wales Isle., AK		x		
Dip 26: Tipulidae: Erioptera sp.	Harris Creek, Prince of Wales Isle., AK		x		
Dip 27: Tipulidae: Hesperoconopa sp.	Salmon Creek, Juneau, AK		x		
Dip 28: Tipulidae: Hexatoma sp.	Fish Creek, Juneau, AK		x		
Dip 29: Tipulidae: Limonia sp.	Salmon Creek, Juneau, AK		x		
Dip 30: Tipulidae: Tipula sp	Bessie Creek, Juneau, AK		x		
Eph 1: Ameletidae: Ameletus velox	Fish Creek, Juneau, AK		x		
Eph 2: Ameletidae: Ameletus sp.	Fish Creek, Juneau, AK		x		
Eph 3: Baetidae: Baetis bicaudatus	Fish Creek, Juneau, AK		x		
Eph 4: Ephemerellidae: Caudatella heterocaudata	Salmon Creek, Juneau, AK		x		
Eph 5: Ephemerellidae: Caudatella jacobi	Fish Creek, Juneau, AK		x		
Eph 6: Ephemerellidae: Caudatella orestes	Harris Creek, Prince of Wales Isle., AK		x		

(Use additional sheets if necessary)

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Eph 7: Ephemerellidae: Caudatella spp.	Fish Creek, Juneau, AK		x		
Eph 8: Ephemerellidae: Drunella coloradensis	Fish Creek, Juneau, AK		x		
Eph 9: Ephemerellidae: Drunella doddsi	Fish Creek, Juneau, AK		x		
Eph 10: Ephemerellidae: Drunella grandis	Fish Creek, Juneau, AK		x		
Eph 11: Ephemerellidae: Drunella spinifera	Harris Creek, Prince of Wales Isle., AK		x		
Eph 12: Ephemerellidae: Drunella spp	Fish Creek, Juneau, AK		x		
Eph 13: Ephemerellidae: Ephemerella spp.	Harris Creek, Prince of Wales Isle., AK		x		
Eph 14: Ephemerellidae: Seratella spp.	Fish Creek, Juneau, AK		x		
Eph 15: Heptageniidae: Cinygma spp.	Bessie Creek, Juneau, AK		x		
Eph 16: Heptageniidae: Cinygmula spp.	Bessie Creek, Juneau, AK		x		
Eph 17: Heptageniidae: Epeorus spp.	Bessie Creek, Juneau, AK		x		
Eph 18: Heptageniidae: Heptagenia spp.	Fish Creek, Juneau, AK		x		
Eph 19: Heptageniidae: Ironodes spp.	Cable Creek, Prince of Wales Isle., AK		x		
Eph 20: Heptageniidae: Rhithrogena spp.	Bessie Creek, Juneau, AK		x		
Eph 21: Leptophlebiidae: Paraleptophlebia spp.	Bessie Creek, Juneau, AK		x		
Eph 22: Siphlonuridae: Siphlonurus spp.	Cable Creek, Prince of Wales Isle., AK		x		
Plec 1: Capniidae: Capnia promota	Fish Creek, Juneau, AK				x
Plec 2: Capniidae: Capnia spp.	Cable Creek, Prince of Wales Isle., AK		x		

(Use additional sheets if necessary)

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Plec 3: Chloroperlidae: Kathroperla perdita	Fish Creek, Juneau, AK		x		
Plec 4: Chloroperlidae: Plumiperla diversa	Fish Creek, Juneau, AK		x		
Plec 5: Chloroperlidae: Suwallia forcipata	Fish Creek, Juneau, AK		x		
Plec 6: Chloroperlidae: Suwallia spp.	Fish Creek, Juneau, AK		x		
Plec 7: Chloroperlidae: Sweltsa spp.	Fish Creek, Juneau, AK		x		
Plec 8: Leuctridae: Despaxia augusta	Fish Creek, Juneau, AK		x		
Plec 9: Leuctridae: Paraleuctra spp.	Fish Creek, Juneau, AK		x		
Plec 10: Leuctridae: Perlomyia spp.	Sata/Gulch Creek, Prince of Wales Isle., AK		x		
Plec 11: Nemouridae: Amphinemoura spp.	Cable Creek, Prince of Wales Isle., AK		x		
Plec 12: Nemouridae: Nemoura spp.	Salmon Creek, Juneau, AK		x		
Plec 13: Nemouridae: Ostracerca spp.	Harris Creek, Prince of Wales Isle., AK		x		
Plec 14: Nemouridae: Podmosta spp.	Sata/Gulch Creek, Prince of Wales Isle., AK		x		
Plec 15: Nemouridae: Shipsa spp.	Sata/Gulch Creek, Prince of Wales Isle., AK		x		
Plec 16: Nemouridae: Visoka spp.	Salmon Creek, Juneau, AK		x		
Plec 17: Nemouridae: Zapada cinctipes	Fish Creek, Juneau, AK		x		
Plec 18: Nemuoridae: Zapada oregonensis	Fish Creek, Juneau, AK		x		
Plec 19: Perlidae: Hesperoperla pacifica	Peterson Creek, Juneau, AK		x		
Plec 20: Perlodidae: Arcynopteryx spp.	Fish Creek, Juneau, AK		x		

(Use additional sheets if necessary)

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		Eggs	Larvae	Nymphs	Adults ♀
Plec 21: Perlodidae: Isoperla spp.	Salmon Creek, Juneau, AK		x		
Plec 22: Perlodidae: Megarcys signata	Fish Creek, Juneau, AK		x		
Plec 23: Perlodidae: Rickera spp.	Bessie Creek, Juneau, AK		x		
Plec 24: Taeniopterygidae: Taenionema spp	Fish Creek, Juneau, AK		x		
Trich 1: Apataniidae: Apatania spp.	Harris Creek, Prince of Wales Isle., AK		x		
Trich 2: Apataniidae: Moselyana spp.	Salmon Creek, Juneau, AK		x		
Trich 3: Brachycentridae: Micrasema spp.	Bessie Creek, Juneau, AK		x		
Trich 4: Glossosomatidae: Glossosoma spp.	Bessie Creek, Juneau, AK		x		
Trich 5: Hydropsychidae: Arctopsyche grandis	Fish Creek, Juneau, AK		x		
Trich 6: Hydropsychidae: Arctopsyche spp.	Fish Creek, Juneau, AK		x		
Trich 7: Hydropsychidae: Parapsyche spp.	Fish Creek, Juneau, AK		x		
Trich 8: Lepidostomatidae: Lepidostoma spp.	Cable Creek, Prince of Wales Isle., AK		x		
Trich 9: Limnephilidae: Cryptochia spp.	Harris Creek, Prince of Wales Isle., AK		x		
Trich 10: Limnephilidae: Dicosmoecus atripes	Bessie Creek, Juneau, AK		x		
Trich 11: Limnephilidae: Ecclisocosmoecus scylla	Fish Creek, Juneau, AK		x		
Trich 12: Limnephilidae: Ecclisomyia spp.	Bessie Creek, Juneau, AK		x		
Trich 13: Limnephilidae: Onocosmoecus unicolor	Fish Creek, Juneau, AK		x		
Trich 14: Limnephilidae: Psychoglypha spp.	Fish Creek, Juneau, AK		x		

(Use additional sheets if necessary)

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Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Number of: Larvae	Number of: Nymphs	Number of: Adults
Trich 15: Philopotamidae: Dolophilodes spp.	Gulch Creek, Prince of Wales Isle.,AK		x		
Trich 16: Philopotamidae: Wormaldia spp.	Bessie Creek, Juneau, AK		x		
Trich 17: Polycentropodidae: Polycentropus spp.	Cable Creek, Prince of Wales Isle., AK		x		
Trich 18: Rhyacophilidae: Rhyacophila spp.	Bessie Creek, Juneau, AK		x		
Trich 19: Uenoidae: Neophylax spp.	Sata/Gulch Creek, Prince of Wales Isle., AK		x		
Trich 20: Uenoidae: Oligophlebodes spp.	Sheep Creek, Juneau, AK		x		
Col 1: Amphizoidae: Amphizoa spp.	Gulch Creek, Prince of Wales Isle.,AK		x		
Col 2: Curculionidae: Lixus spp.	Sata/Gulch Creek, Prince of Wales Isle., AK				x
Col 3: Dytiscidae: Agabus spp.	Sata/Gulch Creek, Prince of Wales Isle., AK		x		
Col 5: Dytiscidae: Hydrovatus spp.	Bessie Creek, Juneau, AK		x		
Col 6: Dytiscidae: Ilybius spp.	Cable Creek, Prince of Wales Isle., AK		x		x
Col 7: Dytiscidae: Oreodytes spp.	Cable Creek, Prince of Wales Isle., AK				x
Col 8: Dytiscidae: Uvarus spp.	Harris Creek, Prince of Wales Isle., AK				x
Col 9: Elmidae: Narpus spp.	Cable Creek, Prince of Wales Isle., AK		x		
Col 10: Elmidae: Stenelmis spp.	Sata/Gulch Creek, Prince of Wales Isle., AK				x
Col 11: Hydrophilidae: Ametor spp.	Bessie Creek, Juneau, AK				x
Col 12: Melyridae: Endeodes spp.	Fish Creek, Juneau, AK				x
Col 13: Staphylinidae	Harris Creek, Prince of Wales Isle., AK				x

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		Number of:			
Species or other taxon	Label data for specimens collected or used and deposited	Eggs	Larvae	Nymphs	Adults ♀
Coll 1: Entomobryiidae: Sinella spp.	Harris Creek, Prince of Wales Isle., AK		x		
Coll 2: Onchyiuridae: Lophognathella spp.	Sata/Gulch Creek, Prince of Wales Isle., AK		x		
Coll 3: Sminthuridae	Peterson Creek, Juneau, AK		x		

(Use additional sheets if necessary)

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