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Effects of Roadway-Related Physical and Chemical Habitat Alterations on Stream Ecosystems

Thomas Stuart Woodcock

EFFECTS OF ROADWAY-RELATED PHYSICAL AND CHEMICAL HABITAT ALTERATIONS ON STREAM ECOSYSTEMS

By

Thomas Stuart Woodcock

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Advisory Committee:

Alexander Huryn, Associate Professor of Aquatic Entomology, Advisor

Aria Amirbahman, Assistant Professor of Environmental Engineering

David Courtemanch, Maine Department of Environmental Protection

Christopher Cronan, Professor of Botany and Ecology

Francis Drummond, Professor of Insect Ecology and Entomology

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Thesis Advisor: Dr. Alexander Huryn

An Abstract of the Thesis Presented
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Roadways are an important feature of both rural and urban landscapes, and disturbances associated with them have a variety of effects on stream ecosystems. Organisms may be differentially affected by toxic substances, depending on such factors as sediment and water chemistry, toxin bioavailability, uptake and elimination processes, and tolerance mechanisms. The effects of heavy metal pollution and habitat alteration related to urbanization and industry were examined along a gradient of impact in Goosefare Brook, a small stream in southern Maine with a history of water quality impairment. The structure of invertebrate assemblages changed significantly along the gradient, and were related to both chemical pollution and habitat channelization. In contrast, litter processing rates showed small decreases along the gradient of pollution related to water and sediment quality. Whole-community secondary production showed a strong decrease related to metal concentrations, from 26.4 mgAFDM/m^2/y at the

reference station to 1.1 mgAFDM/m^2/y at stations receiving industrial discharges. Tolerant taxa played an increasing role in community energy flow along the gradient.

Subsequently, assessment of these same parameters in five streams that cross beneath the Maine Turnpike revealed that habitat alteration related to the roadway did not exceed system resistance to stress, and negative effects of the on litter processing and invertebrate production were not evident. Litter loss rate was greater at stations downstream of the highway (-0.0024 degree-day^{-1}) than upstream (-0.0022 degree-day^{-1}). Invertebrate secondary production in these streams was comparable to estimates from similar streams in the coastal plain of the eastern United States (3.5 to 15.3 mgAFDM/m^2/y). Significant differences in habitat, water and sediment chemistry, and biotic communities were evident among streams, although were not generally related to the presence of the roadway. Litter processing rates and secondary production were more strongly related to physical and chemical habitat variables than to the presence of the roadway. These studies have shown that pollution and habitat channelization can profoundly affect ecosystem function, and although stresses from the Maine Turnpike affect invertebrate population and community characteristics in small streams, they are not sufficient to consistently alter function in these systems.

DEDICATION

This work is dedicated to Dr. Stephen A. Marshall, who is responsible for directing my childhood interest in all creatures without backbones

and

To my parents, Marion and Andrew Woodcock, who encouraged it in the first place, in spite of all the jars, bottles, buckets, and escapees

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Chapter Summary

Roadways are an important feature of both urban and rural landscapes, and the pollutants and habitat disturbances associated with them have a variety of effects on stream systems. Both biotic and abiotic components may be impacted by physical habitat changes, such as channelization and sediment inputs, or by toxic effects from heavy metals, hydrocarbons, and other materials deposited by traffic and carried into the channel by drainage waters. Organisms may be affected differently depending on such factors as sediment and water chemistry, bioavailability, uptake and elimination processes, and tolerance mechanisms. These differential effects on individuals may result in effects on the success of populations, community structure, and ecosystem function. This paper will review the sources and mechanisms of deposition of roadway pollutants, and the effects of both physical and chemical alterations on stream systems at different levels of biological organization.

Introduction

As legislative measures such as the Water Pollution Control Act and the Clean Water Act exercise more effective control over point-source polluters, the relative importance of non-point sources as a threat to surface waters is increasing. A significant proportion of this pollution is generated by motor vehicles and deposited on or near road surfaces (Pratt and Coler 1976, Garie and McIntosh 1986, Landrum 1989, Tsihrintzis and Hamid 1997). Road systems are a major feature of both urban and rural landscapes, and the effects that they have on streams are varied and complex. These effects may be caused by physical alterations to the channel and riparian area, such as drainage improvement, channelization, and clearing of vegetation, or by chemical pollutants. Road networks and soil compaction affect the manner in which precipitation is routed through a catchment into stream channels, and the dissolved and particulate material transported by runoff (Booth and Jackson 1997, Jones et al 2000). This paper will review the physical alterations to the landscape, sources and deposition of chemical pollutants related to roads, and the effects of these stressors on streams at different levels of biotic resolution.

The prevalence of motorized vehicles, the wide variety of pollutants that they generate, and the importance of the quality and ecological integrity of surface waters makes control of roadway impacts a pressing concern. Physical alterations to the channel and riparian zone typically result in sediment inputs, increases in flow velocity, alteration of the hydrologic regime, and reduction in habitat complexity. Sources of chemical pollutants include wear and corrosion of automotive parts (Tsihrintzis and Hamid 1997),

fuel combustion (Pruell and Quinn 1988, Boxall and Maltby 1997), leakage of gasoline and lubricating fluids (Muller 1987, Maltby et al 1995a), and application of de-icing compounds (Demers and Sage 1990). A high proportion of the chemical pollutants sorb to particulate matter, which is carried by drainage waters and ultimately deposited in benthic sediments (Maltby et al 1995a, Trombulak and Frissell 2000).

Benthic organisms are crucial to the functioning of aquatic systems, because they link primary sources of energy and nutrient input to higher trophic levels (Anderson and Sedell 1979, Webster and Benfield 1986, Maltby et al 1995a). Although the toxicology of metals and hydrocarbons to aquatic invertebrates in a laboratory setting is fairly well-known, the interacting effects of the mixture of pollutants, altered habitat, and effects on the structure and function of lotic systems are not well understood. The extrapolation of laboratory toxicity tests to field situations is a difficult task, even when considered only at the population level. This is due to such factors as changing sensitivity at different aquatic life stages, synergistic or antagonistic effects of different water and sediment quality variables, and the interaction of organisms with their habitat and with other trophic levels (Wallace et al 1996, Clements 1997). However, these characteristics also make benthic organisms excellent indicators of water and sediment quality, because they are relatively sedentary, contain a variety of taxa with different life cycles and generation times, and usually represent several trophic levels (Rosenberg and Resh 1993). They also have the ability to concentrate pollutants to levels that are orders of magnitude higher than those present in the environment, making detection easier (Kalas et al 1980, Metcalfe et al 1988).

Pollutant Sources and Deposition

The construction and use of roads results in the deposition of a variety of pollutants that have the potential to enter surface waters (Table 1.1). Inputs of pollutants tend to occur during and following precipitation events, and concentrations in runoff are determined by several factors, including traffic volume and weather conditions (Davis and George 1987, Stotz 1987). The largest pulses in temperate climates occur at the time of snowmelt when a large volume of water carrying pollutants accumulated during the winter enters surface waters over a relatively short time period (Cline et al 1982, Lygren et al 1984). In small streams, the water chemistry may be dominated by runoff during these events (Harrison and Wilson 1985a).

Sediments

Roadways can affect stream habitat through alteration of the riparian zone or the channel itself, either directly (construction projects), or through general urbanization of the catchment. Roadway construction represents a major alteration to a catchment, because it is associated with clearing of vegetation, soil compaction, paving, and drainage improvement (Booth and Jackson 1997, Jones et al 2000). Construction activities typically result in the loading of large quantities of sediment into adjacent waterways, and for a short period thereafter as earthworks and fill areas settle and become re-vegetated (Barton 1977, Lenat et al 1981). The sediments mobilized during such activities may

Pollutant	Sources	References
Sediment & associated pollutants	Unpaved roads	Anderson and MacDonald (1998)
	Construction	Barton (1977), Burton et al (1976), Extence (1978)
	Stormwater	Bedient et al (1980), Boxall and Maltby (1995)
	Street dust	Grottker (1987)
Heavy metals (multiple)	Street dust	Ellis and Revitt (1982), Harrison et al (1981), Revitt and Ellis (1980), Ward et al (1977)
	Stormwater	Harrison and Wilson (1985a,b,c), Sansalone and Buchberger (1997), Wei and Morrison (1993)
	Various	Harrison et al (1985)
Lead	Stormwater	Bryan (1974), Hem and Durum (1973), Laxen and Harrison (1977), Solomon et al (1977)
	Street dust	Day et al (1975), Duggan and Williams (1977), LaBarre et al (1973)
	Exhaust	Hewitt and Rashed (1988), Little and Wiffen (1978)
Zinc	Stormwater	Christensen and Guinn (1979)
Hydrocarbons	Stormwater	Bomboi and Hernandez (1991), Boxall and Maltby (1997), Brown et al (1985), Fam et al (1987), Gavens et al (1982), Gjessing et al (1984b), Latimer et al (1990), MacKenzie and Hunter (1979), Whipple and Hunter (1979), Zurcher et al (1980)
	Exhaust	Ganley and Springer (1974), Miguel et al (1998), Westerholm et al (1988)
	Motor oil	Pruell and Quinn (1988)
	Various	Ellis et al (1985), Hamilton et al (1984), Larkin and Hall (1998)
Salt	Stormwater	Demers and Sage (1990), Hutchinson (1970), Kunkle (1972), Scott (1976, 1980), Shanley (1994)
General deposition	Stormwater	Bellinger et al (1982), Deletic and Maksimovic (1998), Ellis and Hvitved-Jacobsen (1996), Hedley and Lockley (1975), Hewitt and Rashed (1990, 1992), Hoffman et al (1985), Lygren et al (1984), Marsalek et al (1997), Shaheen (1975), Smith and Kaster (1983), Stotz (1987), Tsihrintzis and Hamid (1997, 1998), Whipple et al (1977, 1978)
	Street dust	Harrison and Johnston (1985)

Table 1.1. Summary of references dealing with the generation and deposition of roadway pollutants.

change the particle size distribution of the streambed, resulting in increases in fine materials and the embeddedness of larger particles (Luedtke et al 1976, Extence 1978, Cline et al 1982, Heliovaara and Vaisanen 1993, Maltby et al 1995a), turbidity (Burton et al 1976), and oxygen demand (Ellis and Hvitved-Jacobsen 1996).

Particulate inputs from 'street dust', although lesser in quantity than those released by construction, are an important concern where streams intersect established roads. During dry periods, dust accumulates on the road surface, most of which is located at the edge of the roadway and in gutters (Shaheen 1975, Grottker 1987). The primary components of street dust are common minerals and organic material derived from soils in the catchment (Harrison and Johnston 1985). Fine particulates are capable of sorbing more pollutants than coarser material, due to their larger surface area:mass ratio (Zurcher et al 1980). These particulates settle into aquatic sediments, and may become a source of pollutants in the water column as desorption of pollutants occurs over time (Peterson et al 1996). Some authors contend that the length of the interval since the previous precipitation event, referred to as the antecedent dry period, is an important factor in determining quantities of dust and pollutants on roadways (Tsihrintzis and Hamid 1998). Others have shown, however, that pre-storm dust levels may be re-established in as little as five hours, and hypothesize that wind conditions during the antecedent dry period are more important (Whipple et al 1977, Bedient et al 1980, Harrison and Wilson 1985b, Grottker 1987).

Channelization is the alteration of the shape or material of the stream channel or banks in order to increase drainage capacity, and is closely connected to sedimentation

(Stout and Coburn 1989). When a stream crosses a roadway, it typically passes through a culvert or bridge structure, and the banks are often cleared of vegetation. Areas near the roadway are lined with cobbles or other aggregates to assist drainage and decrease erosion. The channel may be deepened and/or widened to increase its stormwater carrying capacity (hydraulic smoothing *sensu* Booth and Jackson 1997), which in turn increases flow velocity and erosion potential within the channel (Ellis and Hvitved-Jacobsen 1996). Transport of particulate matter from the banks and paved surface to the channel, and its subsequent export at times of high flow, can change the nature and complexity of the benthic habitat.

Heavy Metals

Trace metals are naturally present in all aquatic ecosystems, some of which are essential in the nutrition of biota. The types and concentrations of metals present in part reflect the underlying geology in the catchment. However, as much as 75% of heavy metals entering surface waters in the United States can be traced to traffic-related sources (Tsihrintzis and Hamid 1997). The most common metals in road runoff are cadmium, chromium, copper, iron, manganese, nickel, lead, and zinc (Wilber and Hunter 1977, McHardy and George 1985, Davis and George 1987, Maltby et al 1995a). Levels of many of these metals have been shown to be positively correlated with traffic density (Davis and George 1987, Trombulak and Frissell 2000), and most are deposited within 20

meters of the road surface (Harrison et al 1981, Harrison and Johnston 1985, Lygren et al 1984).

Drainage waters are efficient at removing dust and associated pollutants from the road surface, and are considerably more important as a source of metal pollution to streams than is deposition from the atmosphere (Wilber and Hunter 1977, Harrison et al 1985, Hewitt and Rashed 1990). Deletic and Maksimovic (1998) found that while antecedent dry period was not correlated with the particulate content of runoff, it showed a relationship with maximum conductivity recorded for each event, suggesting that soluble materials can build up on the road surface through at least ten days of dry weather. Low-intensity storms tend to mobilize only the pollutant-rich fine particulate fraction, so storm intensity is not closely correlated to metal concentration in the runoff (Harrison and Wilson 1985a,c). During storm events, soluble materials are removed quickly, which is known as the "first-flush" effect, while sediments and associated materials must be physically dislodged and carried in suspension by the water (Harrison and Wilson 1985b, Ellis and Hvitved-Jacobsen 1996).

Spatial trends of metal concentrations in lotic sediments may indicate differences in metal inputs or differences in sediment sorption processes. Important sediment characteristics include size of sediment particles (Gibbs 1973, Shutes 1984), and content of organic matter, iron and manganese oxide and hydroxide minerals, certain clay minerals, and carbonates (Combest 1991, Carroll et al 1998, Chapman et al 1998). Metals in sediments are associated with various complexing or chelating functional groups on mineral surfaces, organic matter, or large hydrocarbon molecules such as particles of

asphalt. Oxygen-, nitrogen-, and sulfur-containing functional groups form complexes of varying stability with the metals (Cooper and Harris 1974, van Hattum et al 1993). Simple exponential models accurately describe downstream movement of metals, which decrease in concentration with distance from the input (Axtmann et al 1997, Trombulak and Frissell 2000). This suggests that characteristics of the solid rather than dissolved phase are more important in determining rates of metal transport in lotic systems. General information on road-related sources of pollutants is summarized below.

Lead

Despite the current use of unleaded gasoline, lead remains a potential problem in surface waters adjacent to roadways. Due to increased traffic volume and long residence time in soils adjacent to roadways, lead levels in aquatic systems remain a concern, in spite of reduction of gasoline lead levels (Harrison et al 1985, Marsalek et al 1997), although decreases have been reported in some areas (Sansalone and Buchberger 1997). Approximately 75% of lead emitted by vehicles is in aerosol form (Hem and Durum 1973), and it has been estimated that only 10% of this is deposited in the immediate vicinity of the road (Little and Wiffen 1978). Lead oxide is a product of tire wear (Tsihritzis and Hamid 1997). Lead found in roadway runoff is typically sorbed to particulate matter, or associated with organic carbon or metal hydroxides in sediments (Krantzberg and Stokes 1988).

Copper

Copper is a major component of brake pads, and significant quantities are deposited on the road surface in the form of brake dust (Hewitt and Rashed 1990, Tsihrintzis and Hamid 1997). Copper is also used in pipes in the engine and chassis, and may be deposited as wear or corrosion products of these parts (Ward et al 1977, Tsihrintzis and Hamid 1997). In aquatic systems, copper is typically sorbed to fine particulates, or associated with dissolved organic carbon (DOC) (Harrison and Wilson 1985a, Watts and Pascoe 1996).

Zinc

Zinc diethylcarbamate is used in the tire vulcanization process, and tire treads are approximately one percent zinc by weight (Hedley and Lockley 1975). Most zinc deposited on roadways is a product of tire wear (Christensen and Guinn 1979, Ellis and Revitt 1982, Smith and Kaster 1983). Zinc also occurs in some additives to lubricating fluids (Ward et al 1977) and as a corrosion product of galvanized metals. Recent increases in the use of galvanized automotive parts may further increase zinc deposition on roadways (Sansalone and Buchberger 1997). Galvanized metals are also frequently used in the construction of roadway structures such as culverts. Zinc typically exists in surface waters sorbed to fine particulates or associated with DOC (Harrison and Wilson 1985a).

Cadmium

Cadmium is deposited on the road surface as a product of tire wear (Smith and Kaster 1983, Hewitt and Rashed 1990). It is chemically similar to zinc, and is present as a contaminant of the zinc diethylcarbamate used in the vulcanization of tires, zinc-containing additives to lubricating oils, and coatings on galvanized metals (Ward et al 1977, Huebert and Shay 1992). Like zinc, it typically exists in surface waters sorbed to fine particulates or associated with DOC (Harrison and Wilson 1985a).

Chromium

Chromium is present on the road surface as corrosion products of vehicles (Maltby et al 1995a). Chromium may also come from the wear of certain moving parts, such as wheel bearings (Tsihrintzis and Hamid 1997). In oxic waters it typically exists as the chromate anion.

Nickel

Nickel is present as a trace component of lubricating oils and diesel fuels (Smith and Kaster 1983), and corrosion and wear products of some chromework (Ward et al 1977). Nickel may also come from the wear of certain moving parts, such as wheel bearings (Tsihrintzis and Hamid 1997). Nickel is highly mobile, and is significantly complexed only by organic material (Wang and Wood 1984, Powlesland and George 1986).

Iron and Manganese

Iron is present on the road surface as a corrosion product of vehicles, in the form of oxides (Maltby et al 1995a). Traffic-related deposition of manganese is not well understood (although Mn is a component of automobile batteries), but its common occurrence with iron necessitate its consideration with roadway-generated pollutants. Precipitates of iron and manganese act as "scavengers" by incorporating other metals into oxide coatings on sediment particles, or by removing them from solution through adsorption or co-precipitation (Helsel et al 1979, Harrison et al 1981, Dzombak and Morel 1990). Manganese in oxic systems is most commonly in the form of solid manganese dioxide, and found in association with iron hydroxides or DOC (Harrison and Wilson 1985a, Tessier and Campbell 1987).

Hydrocarbons

Hydrocarbons naturally occur in substantial quantities in surface waters, being derived from such sources as leachate from plant material, terpenoids from fossil fuel deposits, phytadienes from plankton, and other low molecular weight organic compounds from plankton, algae, and bacteria. Traffic-related sources include leaked lubricants and engine exhaust products (Shaheen 1975, Hamilton et al 1984, Fam et al 1987, Larkin and Hall 1998). Most surface waters adjacent to roadways show some elevated level of anthropogenic hydrocarbons. This material tends to be concentrated in the sediments, as

hydrocarbons in motorway runoff are typically associated with particulates (Gavens et al 1982, Muller 1987, Larkin and Hall 1998). Motor vehicles deposit aliphatic hydrocarbons as an unresolved complex mixture (UCM), with the major sources being crankcase oil, lubricating greases, and exhaust particulates (MacKenzie and Hunter 1979, Zurcher et al 1980, Hoffman et al 1982, Brown et al 1985). Whipple and Hunter (1979) suggest that physical force must be exerted by precipitation to dislodge sticky agglomerations of hydrocarbons, and for this reason hydrocarbon content of runoff is correlated with rainfall intensity. However, hydrocarbon films and odors have been observed in some polluted streams at base flow (Angino et al 1972), possibly due to desorption from previously deposited sediments.

When compared to aliphatics, polycyclic aromatic hydrocarbons (PAHs) have higher toxicity, affinity for sediment, and resistance to biodegradation (Yuan et al 2001, but see Maier et al 2000). They are mainly anthropogenic in origin, being formed during the incomplete combustion of fossil fuel, although there is some input from natural sources, including fires, weathering of natural petroleum seeps, and possibly biosynthesis (Brown and Starnes 1978, Wakeham et al 1980, Giesy et al 1983, Landrum and Scavia 1983). Lygren et al (1984) showed deposition rates of 100 to 200 μg/km/d of PAHs within 100 meters of a roadway. Accumulation rates of PAHs on the road surface are positively correlated with traffic density (Larkin and Hall 1998). Depending on their chemical characteristics, compounds may volatilize from the road surface, be oxidized or photo-oxidized (Hewitt and Rashed 1992), or remain until washed from the pavement by

runoff (Gjessing et al 1984a). Most biodegradation in aquatic systems occurs in the sediments (Li et al 1998).

The most common PAHs in roadway runoff are phenanthrene, pyrene, anthracene, benzo[*a*]anthracene, fluoranthene, and chrysene, although many other compounds exist in trace amounts (Fam et al 1987, Boxall and Maltby 1997, Marsalek et al 1997). PAHs are found in gasoline, but are broken down during combustion, and the PAHs in emissions are newly formed molecules (Grimmer et al 1981, Westerholm et al 1988). Pruell and Quinn (1988) found that unused motor oil was devoid of PAHs, but levels increased rapidly to approximately one percent by mass after standard use in a gasoline engine. PAHs in exhaust are less important (Marsalek et al 1997), and are found mainly in the solid component, known as GEET (gasoline engine exhaust tar) (Christensen et al 1997). Diesel engines do not cause accumulation of PAHs in lubricant (Grimmer et al 1981), although exhaust emission still occurs. Other sources of PAHs include asphalt and tar from road wear and leaked fuel (Gavens et al 1982, Fam et al 1987, Muller 1987, Maltby et al 1995a, Miguel et al 1998).

De-Icing Salt

Application of de-icing salt to roads can be a significant source of dissolved material in surface waters. In the northeastern United States, typical application rates range between 8-15t annually per lane kilometer (Demers and Sage 1990). Salt application became a widespread practice in Maine in the early 1950s (Hutchinson 1970),

and use increased to 54000t per year statewide by the mid-1980s (Pugh et al 1996). Chloride levels of 89000 ppm were recorded during winter, and 2700 ppm were recorded during spring thaw in a Toronto stream (Scott 1976, 1980). Bellinger et al (1982) recorded chloride levels of 37500 ppm in a small British stream, but noted that levels had returned to normal within four weeks of the cessation of salting. It is hypothesized that the extremely high winter levels recorded by Scott (1980) were due to the fact that only water from ice actually melted by the salt is entering the stream at sub-freezing temperatures.

Essentially all of the chloride ions added to roads ultimately enter surface and ground waters, while sodium ions are bound in the soil and may mobilize other soil cations (Huling and Hollocher 1972, Kunkle 1972, Crowther and Hynes 1977, Bellinger et al 1982). Kunkle (1972) discussed the process of chloride pollution by de-icing salt in rural Vermont streams. Chloride levels in the affected streams were lowest during spring snowmelt, presumably due to the high dilution factor, and peaked during summer base flow. Groundwater seeps contained 200ppm chloride or more, and caused stream concentrations to rise as a greater proportion of the flow was contributed by groundwater. Stream concentrations did not exceed 100ppm during the year, and control streams showed little seasonal variation in chloride content. It was speculated that salting may also be responsible for the elevated calcium levels observed in affected streams, as sodium may exchange with and mobilize calcium in the soil (Shanley 1994).

Biotic Effects

Most of the available information dealing with the effects of pollutants on biotic systems comes from toxicological studies conducted at the level of individual organisms, while progressively less is known about impacts on populations, the structure of communities, and ecosystem function (Table 1.2). Clements (1997) suggested that the higher the level of biological organization being examined, the greater the ecological scale of the impact, and the more difficult it is to gain knowledge of the nature and magnitude of that impact. Few studies have been performed on the effects of pollutants or habitat alterations in the field, and fewer still deal specifically with the effects of roadways and roadway-generated pollutants. This section presents a review of knowledge on the effects of roadways and roadway-generated pollutants at different biotic scales.

Effects on Individual Organisms

Sediment inputs to stream systems from roadways occur during construction as a result of erosion, and from the mobilization of street dust. Sediment characteristics such as particle size and embeddedness are important determinants of habitat suitability for individual organisms (Rice et al 2001). Addition of sediment can also affect aquatic organisms through 'smothering' and introduction of pollutants associated with the sediment particles (White 1976, Extence 1978, Lenat et al 1981, Landrum and Robbins 1990). Roadway-related sedimentation has been shown to increase the densities of pollution-tolerant burrowing organisms and fine-particle feeders, such as chironomids

Biotic Level	Pollutant	Organism	Reference
Organism	Heavy metals	Algae	Ferguson and Bubela (1974), McHardy and George (1985), Morrison and Florence (1988), Ozer et al (1994)
		Bivalvia	Anderson (1977a)
		Bryophyta	Wehr and Whitton (1983a,b)
		Chironomidae	Harrahy and Clements (1997), Krantzberg and Stokes (1988, 1989), Timmermans et al (1992a), Watts and Pascoe (1996)
		Culicidae	Rayms-Keller et al (1998)
		Decapoda	Giesy et al (1980)
		Isopoda	van Hattum et al (1993)
		Macrophytes	Jackson (1998), Mortimer (1985)
		Oligochaeta	Ankley et al (1994), Brkovic-Popovic and Popovic (1977)
		Various	Campbell and Stokes (1985), Chapman et al (1998), Gerhardt (1993), Hare (1992), Kiffney and Clements (1996), Lin and Chen (1998), Luoma (1989), Rehwoldt et al (1973), Smock (1983a,b), Spehar et al (1978), Tessier and Campbell (1987), Yang and Kong (1997)
	Cadmium	Amphipoda	Abel and Barlocher (1988), Duddridge and Wainwright (1980), McCahon and Pascoe (1988), Wright (1980), Wright and Frain (1981)
		Gastropoda	Wier and Walter (1976)
		Hirudinea	Wicklum and Davies (1996)
		Hyphomycetes	Abel and Barlocher (1984), Duddridge and Wainwright (1980)
		Trichoptera	Dressing et al (1982)
		Various	Clubb et al (1975), Thorp and Lake (1974), Williams et al (1985)
	Copper	Amphipoda	Borgmann (1998)
		Chironomidae	Gauss et al (1985), Kosalwat and Knight (1987a,b)
		Isopoda	Guidici et al (1987)
		Various	Arthur and Leonard (1970), Diks and Allen (1983), Darlington et al (1986), Meador (1991)
	Iron	Ephemeroptera	Gerhardt and Westermann (1995)
	Nickel	Algae	Wang and Wood (1984)
		Chironomidae	Powlesland and George (1986)
	Zinc	Mollusca	Wurtz (1962)
	PAHs	Algae	Warshawsky et al (1995)
		Amphipoda	Eadie et al (1982), Landrum and Scavia (1983)
		Chironomidae	Gerould et al (1983), Knezovich and Harrison (1988)
		Isopoda	van Hattum et al (1998)
		Various	Borchert et al (1997), Landrum and Robbins (1990), Suedel et al (1993)

Table 1.2. Summary of references dealing with the bioavailabilty and toxicology of pollutants commonly associated with roads.

Biotic Level	Pollutant	Organism	Reference
Organism	Road runoff	Algae	Dussart (1984)
	General study	Various	Reynoldson (1987)
Population	General study	Various	Buikema and Benfield (1979), Tolba and Holdich (1981)
	Heavy metals	Isopoda	Brown (1976, 1977)
		Chironomidae	Bisthoven (1998a,b,c), Groenenduk et al (1998), Wentsel et al (1978)
		Viviparidae	Gupta (1998)
	Cadmium	Isopoda	Guidici et al (1986)
		Chironomidae	Williams et al (1986)
Community	Heavy metals		Anderson (1977b), Anderson et al (1978), Clements et al (1988a, 1992), Clements (1994, 1999), Gachter and Geiger (1979), Kiffney (1996), Kiffney and Clements (1993, 1994b), Medley and Clements (1998), Poulton et al (1995), Reinfelder et al (1998), Timmermans et al (1992b), Wachs (1985), Waterhouse and Farrell (1985), Winner et al (1980), Yasuno et al (1985)
	Cadmium		Brown and Pascoe (1988), Selby et al (1985)
	Copper		Clements et al (1988b, 1989, 1990), Leland et al (1989)
	Zinc		Hoiland and Rabe (1992), Jones (1940, 1958), Kiffney and Clements (1994a)
	Aliphatic hydrocarbons		Rosenberg and Wiens (1976)
	PAHs		Giesy et al (1983)
	Road runoff		Davis and George (1987), Garie and McIntosh (1986), Pedersen and Perkins (1986), Pratt et al (1981), Shutes (1984)
	Sediment		Chutter (1969), Cline et al (1982), Lenat et al (1981), Luedtke and Brusven (1976), Luedtke et al (1976), Rier and King (1996)
	Salt		Chutter (1969), Crowther and Hynes (1977)
Ecosystem	Heavy metals		Burrows and Whitton (1983), Dixit and Witcomb (1983), Enk and Mathis (1977), Eyres and Pugh-Thomas (1978), Hakanson (1984), Mathis and Cummings (1973), Timmermans et al (1989), van Hassel et al (1980), van Hattum et al (1991)
	Organics		Thomann et al (1992)
	Road runoff		Stout and Coburn (1989), Maltby et al (1995a)

Table 1.2, continued

and oligochaetes, downstream of a roadway crossing (Barton 1977, Pedersen and Perkins 1986, Maltby et al 1995a). Certain molluscs may have respiration or egg development inhibited by deposition of particulate matter (Chutter 1969), and filter-feeding organisms such as hydropsychid caddisflies may have the efficiency of their filtering devices impaired (Higler and Tolkamp 1983). Organisms may be smothered, and those that require firm sites for physical attachment to the substrate (i.e. leeches, limpets) may be unable to survive (Extence 1978).

Bioavailabilty and Uptake

Metals and hydrocarbons from roadways are typically concentrated in sediments, although the nature and extent of sedimentary association is dependent upon the chemistry of the specific pollutant. Bioavailability is controlled by sediment characteristics such as particle size and organic matter content, and desorption from sediments into water or in the guts of consumers is typically required before uptake into animal tissues is possible. Therefore, bioavailability is a function of the chemical characteristics of the pollutant, the physical and chemical characteristics of the substrate, and behavioral and physiological characteristics of the organism in question.

Metals in aquatic systems exist in solution or weakly adsorbed to solids (readily available), adsorbed to organic material or metallic hydroxides (chemical change is often necessary for release), or in crystal lattice structures of minerals (unavailable) (Gibbs 1973). Cadmium, copper, nickel, and zinc tend to be in dissolved form or aqueous

complexes, while lead, iron, and chromium are associated with particles or occur as precipitates (Wang and Wood 1984, Powlesland and George 1986, Sansalone and Buchberger 1997). Sediment characteristics that reduce binding and enhance aqueous concentrations of metals tend to enhance bioavailability, because uptake from the aqueous phase is more efficient than from adsorbed or precipitated phases (Hare et al 1991). Bioavailable pollutants generally enter the body associated with food material, or via transport (passive or active) across the body wall. These pathways are independent and additive, and pollutants from different sources may ultimately be traced to different parts of the body (Hare et al 1991, Hare 1992, Gerhardt and Westermann 1995, Borgmann 1998, Reinfelder et al 1998).

Desorption of metals from sediments over time may pose a more serious problem than acute runoff events (Wei and Morrison 1993). Potentially bioavailable metals are those not bound in a mineral lattice, and include free ions, soluble organic and inorganic complexes, precipitates of varying solubility, those associated with organic and inorganic sediments and seston, and those associated with iron and manganese oxide precipitates (Burton 1991, Hansen and Maya 1997). The strength of metal bonding to particulates is more important to bioavailability than total metal concentration, and is influenced by characteristics of the sediment, including presence of iron and manganese hydroxide compounds, organic matter, carbonates, and size and composition of the mineral particles (Ramamoorthy and Kushner 1975, Luoma 1989, Combest 1991, Harrahy and Clements 1997, Yang and Kong 1997, Chapman et al 1998, Lin and Chen 1998).

Cuticular uptake of metals is generally low, although osmoregulatory structures such as chloride epithelia in Trichoptera and anal papillae in larvae of Diptera may actively transport ions into the body (Wachs 1985, Heliovaara and Vaisanen 1993). Some organisms have metal body burdens that reflect concentrations in the environment, while others accumulate metals to levels greater than those in the sediments. Much of the body burden is often not in the tissues, but associated with material in the gut, or adsorbed to the body surface (Smock 1983a). The general processes by which metals enter freshwater food webs is by sorption to sediments or association with biofilms which are ingested by organisms (Helsel et al 1979, Kiffney and Clements 1993), or through direct uptake from the water (Enk and Mathis 1977, Wright 1980, Heliovaara and Vaisanen 1993). Biofilms are an important factor in metal dynamics, as pollutants often sorb to them more readily than to mineral surfaces (Besser et al 2001). The metals may be sorbed to polysaccharides or proteins on the cell surface or taken into cells of biofilm organisms, but there remains the possibility of remobilization by sloughing or feeding activities of primary consumers (Crist et al 1981, Flemming et al 1996).

The bioavailability of PAHs in sediments depends mainly on the structural complexity of the molecules, which is positively correlated to affinity for sediment (Yuan et al 2001). The rate of desorption from sediments partially determines the fraction of the contaminant that is available in interstitial water or on particle surfaces. However, the physico-chemical processes governing these factors are ill-defined (Landrum 1989, Landrum and Robbins 1990). Invertebrates accumulate different PAHs to different levels, which are positively correlated with the octanol/water partitioning coefficient (K_{ow}) of

each compound (Giesy et al 1983, Maltby et al 1995b). However, the concentration of very large PAHs (five or more rings in the structure) in tissues has been observed to be lower, possibly because their sediment affinity is sufficiently strong that bioavailability is reduced (van Hattum et al 1998). Accumulation of organic contaminants by ingestion is limited by two rate processes. The first is the rate of sediment ingestion, and the second is desorption from particulates inside the gut, which may have different chemical conditions than the environment (Knezovich et al 1987, Landrum and Robbins 1990). Non-dietary routes are governed by separate rate processes, such as uptake across the body wall, and require separate consideration.

Toxicity

Although the factors affecting bioavailability and uptake of metals and hydrocarbons may be similar, the toxic effects of different pollutants vary considerably. The major mechanism of metal toxicity is the alteration of enzyme function (Enk and Mathis 1977), and the tolerance of a species is related to its ability to prevent the metal from being biochemically active in its tissues (Eyres and Pugh-Thomas 1978). Some metal tolerance is inherent in all aquatic organisms (Wurtz 1962, Dixit and Witcomb 1983, Krantzberg and Stokes 1989), and the ability to regulate metals required by the organism (micronutrients) is more common than the ability to regulate non-essential metals such as lead and cadmium (Anderson et al 1978, Krantzberg and Stokes 1989, Timmermans et al 1989). However, active elimination of non-essential metals has been

observed in some taxa (Timmermans et al 1992a, Heliovaara and Vaisanen 1993). High levels of cations (i.e.-H^+, Ca^{2+}, Mg^{2+}) may reduce the availability of cellular binding and uptake sites for metals, and therefore reduce the influx of metals into animal tissues (Wright 1980, Campbell and Stokes 1985, Mance 1987, Gerhardt 1993). The increased concentration of hydrogen ions may be responsible for some observed reductions in toxicity associated with low pH (Crist et al 1981, Campbell and Stokes 1985).

Many metal-tolerant insects have been shown to sequester metals by complexing them with high-sulfur metallothionein proteins and storing them in vesicles, by active deposition in the exoskeleton, or by active deposition onto the peritrophic membrane (Brown 1977, Kosalwat and Knight 1987a, van Hattum et al 1993). Other organisms form inorganic metal storage crystals with anions such as phosphate (Reinfelder et al 1998). When environmental metal levels are high, the production of metallothioneins by invertebrates may represent a large investment of energy, and is partly responsible for the smaller size at maturity that often occurs in metal-stressed organisms (Krantzberg and Stokes 1989, Timmermans et al 1992a).

Many organisms tend to show greater susceptibility to metal toxicity at smaller life stages (Williams et al 1986, Leland et al 1989). Later stages may show a higher apparent tolerance due to their lower surface area:mass ratio, meaning that they have the potential to absorb less metal per unit of mass across the body wall. This is known as the growth dilution effect (Darlington et al 1986, van Hattum et al 1991, Kiffney and Clements 1996). Other possible reasons for differential toxicity include higher metabolic rates of smaller organisms, which may increase uptake rates (van Hattum et al 1991), or

diets of finer-textured particles, which tend to have a higher pollutant concentration (Smock 1983b, Timmermans et al 1989). Toxicity may also increase with temperature as respiratory processes accelerate, resulting in accelerated rates of both uptake and elimination processes (Mance 1987, Hare 1992, van Hattum et al 1993).

Short-chain aliphatic hydrocarbons are toxic in aquatic environments due to their disruptive effect on plasma membranes (Boyles 1980, Gavens et al 1982). In contrast, many of the PAH compounds emitted by automobiles have been associated with carcinogenic and mutagenic activity in fish and other aquatic organisms, and some are acutely toxic to fish at the parts-per-billion level (Landrum and Scavia 1983, Boxall and Maltby 1995). Smaller molecules have comparatively lower toxicity, while those of larger size show greater evidence of carcinogenicity and propensity to accumulate in tissues (Larkin and Hall 1998). Prokaryotes able to metabolize PAHs do so using a dioxygenase enzyme system, and they are also broken down by some algae. Some of the metabolites formed by these processes, however, are also toxic and/or mutagenic (Warshawsky et al 1995). Chronic toxic effects occur due to binding of arene oxides, which are highly reactive breakdown products of PAHs, to genetic material (Landrum and Scavia 1983, Muller 1987). The presence of aryl hydrocarbon hydroxylase has been demonstrated in certain marine organisms, and confers a measure of resistance to PAH toxicity (Reynoldson 1987). However, the existence of a similar mechanism has not been confirmed in freshwater invertebrates.

De-icing compounds represent a special case, in that they are purposely applied to roadways, and due to their solubility are more mobile than any of the other pollutants

considered thus far. When introduced to water, de-icing salt dissociates into sodium and chloride ions, both of which are taken up by aquatic organisms under normal circumstances for osmoregulatory purposes. The effects of pulses of high salt concentration on stream organisms were investigated by Crowther and Hynes (1977). They concluded that benthic animals increased their propensity to drift when exposed to the pulses of salt (>1000ppm). Salt pulses in runoff events have been recorded to reach 89 000ppm (Scott 1980), but deleterious effects on the benthic community beyond an increase in drift have been poorly studied. Trout are even less tolerant to salt, the onset of toxic effects being seen at approximately 400ppm (Kunkle 1972).

Effects on Populations

Habitat changes associated with roadways can reduce or eliminate populations of organisms, and movement of organisms within and between populations may be restricted by roadway crossings. Dillon (1988) found that upstream movement of pleurocerid snails was impeded by a culvert, and differences in gene frequencies in the populations upstream and downstream provided further evidence that separation exists. Interference with the movement of adults has been observed in several populations of stoneflies, which fly upstream to oviposit and use the reflective surface of the water for navigation. Kjeldsen (1991) found that the darkness inside the culvert appeared to cause the adult insects to become disoriented, and few were observed flying over the obstruction to the other side. Changes in vegetation types in the riparian areas and wind

conditions within and above the culverts may also affect upstream navigation. There is clearly an added hazard in flying over a roadway to the stream on the other side. Movements of fish may also be impeded by culverts, due to difficulty in moving against the current (Warren and Pardrew 1998, Kahler and Quinn 1998).

When examining the effects of toxic substances on a population of stream invertebrates, the effects of chronic and acute stress on several different life stages must be considered (Smock 1983b, Williams et al 1986, Krantzberg and Stokes 1989). Resistance tends to be metal-specific, because metallothionein proteins are specific to certain metals or groups of metals, and can therefore be selected for separately within a population (Yamamura et al 1983). Much of the research on population effects of heavy metals has been conducted using isopods, which are known to be tolerant to pollution (Brown 1977, van Hattum et al 1993). However, genetic diversity and individual fecundity in these populations may be reduced by exposure (Brown 1977, Guidici et al 1986, van Hattum et al 1993), and isopods from impacted sites are significantly smaller and reach higher population densities than those from unimpacted sites (Tolba and Holdich 1981).

At sublethal levels of chemical stress, phenological problems may occur in populations of stream invertebrates. Insects must attain a certain minimum weight prior to emergence, which may account for phenological delays. Larvae of *Chironomus riparius* reared in copper-contaminated sediments were found to be significantly smaller than larvae from the same population reared in clean sediments (Watts and Pascoe 1996). Reduction in the size of adult females may result in reduced fecundity, and if size is

decreased below a certain threshold, emergence of adults will not occur (Giesy et al 1988, Gerhardt 1993, Watts and Pascoe 1996, Sibley et al 1997). *Aedes aegypti* larvae exposed to a sublethal dose of heavy metals take longer to mature and emerge, perhaps due to reduced rates of growth and development (Rayms-Keller et al 1998).

Effects on Communities

The effects of stresses from habitat changes and toxic substances on populations may lead to substantial changes in community composition. It has been shown that sediment input alone, as occurs when construction is ongoing, can alter community structure by encouraging organisms that are small, grow quickly, and can colonize the unstable sediment surface (Barton 1977, Extence 1978, Lenat et al 1981). Community response to pollutants is determined by sensitivity of its members, their recolonization ability, and variation in environmental conditions such as particle size and sediment organic matter content (Clements 1994). Loading with many chemical or physical impacts tends to lead to general declines in richness and abundance (Winner et al 1980, Slooff and de Zwart 1983). Community-level changes may not be related to direct toxic effects. For example, Kiffney (1996) found evidence that part of an observed population decline of *Hydropsyche* was due to the anomalous nets constructed by the organisms while under stress from heavy metal pollution. These nets required more frequent repairs, which resulted in increased predation by the stonefly *Hesperoperla* because *Hydropsyche* spent greater proportion of time outside the retreat conducting the repairs.

Biomagnification, or increasing pollutant body burdens at successive trophic levels, occurs when the rate of pollutant transfer from prey (ingestion + assimilation) exceeds the elimination capacity of the predator (Reinfelder et al 1998). This phenomenon has rarely been convincingly demonstrated with metals in aquatic systems, with the exception of methylmercury, but is more common with organic contaminants (Chapman et al 1998). Benthic organisms are an important link in transferring pollutants to fish, which may not otherwise receive much exposure due to lower contact with sediments (Eadie et al 1982, Landrum et al 1991). It is hypothesized that differences in tissue concentrations are more related to the feeding behavior of an organism than to its trophic position (van Hassel et al 1980, Smock 1983a, Wachs 1985, Timmermans et al 1989). Fine-particle consumers tend to consume greater concentrations of pollutants in their food than coarse-particle consumers, and engulfing predators consume not only chemicals in the tissues of their prey, but also those adsorbed to the animal's surface or to particulate matter in the gut (Mathis and Kevern 1975, Hare et al 1991). However, in many studies, predators are consistently the feeding group with the lowest metal concentrations (Burrows and Whitton 1983, Smock 1983a, Kiffney and Clements 1993), possibly due to more effective elimination mechanisms (Heliovaara and Vaisanen 1993). Conversely, grazing organisms are typically sensitive, and their elimination may result in a community with reduced grazing pressure and a consequent increase in biofilms (Leland et al 1989).

Effects on Ecosystems

Few studies have investigated the effects of pollutants on aquatic ecosystems, although work has been done examining the partitioning of heavy metals amongst biotic and abiotic compartments, such as sediment, water, and different trophic levels of aquatic food webs. While these studies do include interactions between organisms and the environment, they tend not to describe effects beyond the uptake of pollutants by individuals and transfer between trophic levels. The effects of pollutants on the subset of communities that processes leaf litter has special relevance in forested stream ecosystems. In these systems, processing of terrestrial detritus such as leaves is the key to the integrity of the biotic community, with allochthonous organic material supporting a substantial proportion of stream biomass (Kaushik and Hynes 1971, Fisher and Likens 1973, Wallace et al 1999). A major rate-limiting step is the transformation of this coarse particulate organic matter (CPOM) to fungal and macroinvertebrate biomass. Colonization of the detritus by fungi is required to render it palatable to invertebrates (Webster and Benfield 1986, Maltby et al 1995a). Roadway runoff may damage hyphomycete communities that make leaf detritus palatable to shredding organisms, or by reducing shredder abundance and richness, which interrupts the flow of energy to other detritivores (Vannote et al 1980) and higher trophic levels (Stout and Coburn 1989). However, Maltby et al (1995a) concluded that roadway runoff did not affect microbial decomposition of leaf litter, but macroinvertebrate feeding activity on the detritus was reduced.

Synthesis

The presence and use of road networks affects the biotic and abiotic characteristics of ecosystems at several scales. Stream reaches are partly dependent on resources and impacts from areas upstream in the catchment, and are affected by disturbances that alter energy inputs and transport (Vannote et al 1980). Changes in physical habitat conditions, such as substrate particle size and incident light, may occur over much smaller spatial and temporal scales than would naturally be present, and chemical pollution may change the characteristics of the biotic community by reducing or eliminating populations of sensitive taxa (Clements et al 1992, Kiffney and Clements 1994a). This loss of taxa results in a simplification of stream communities and food webs, which can in turn lead to changes in key ecosystem attributes, such as organic matter processing, total energy flow and energy pathways, and resistance to additional stresses (Fore et al 1996, Wallace et al 1996).

The proportional area of impervious surfaces in a catchment is a good indicator of the magnitude of the effects of urbanization, which affects both hydrology and the types of materials that enters streams (Arnold and Gibbons 1996, Booth and Jackson 1997). Modern roadways are designed to shed water as quickly as possible, without regard for impacts on adjacent surface waters (Mungur et al 1995, Ellis and Hvitved-Jacobsen 1996). Traffic releases petrochemicals, metals, de-icing salts, and a host of other materials (Davis and George 1987, Heliovaara and Vaisanen 1993, Maltby et al 1995a), and conventional water quality parameters such as oxygen demand and total suspended solids do not capture the complexity of this mixture (Hao 1996). The release of

contaminants is proportional to the quantity of traffic, and may arise directly from vehicles, from wear on the road surface, or purposely applied material such as salt. These chemicals may be deposited onto the road surface, deposited in the immediate vicinity of the road, or disperse into the atmosphere. Pollutants following one of the first two pathways are dissolved or re-suspended and discharged into surface waters with runoff (Hewitt and Rashed 1990). Most pollutants are associated with particulate matter, which may be incorporated into stream sediments. Thus, the concentration of the pollutant in the sediments may be much greater than in the water, rendering the benthic community particularly vulnerable to toxic effects.

The effects of road-related water and habitat quality degradation on individual organisms can be divided into lethal and sublethal types. Lethal effects prevent an organism from completing its life cycle in the habitat, although they may still interact in the food web and process organic matter. This may result in the loss of the population from the system, or changes in its genetic structure through the selection of individuals able to cope with the stress. Sublethal effects are more difficult to quantify using standard bioassessment procedures, and may include reduction in growth rates or individual body size and changes in behaviour or phenology, as the organisms expend energy in stress tolerance mechanisms (Wicklum and Davies 1996, Rayms-Keller et al 1998). These stresses, while not lethal to individual organisms, may eventually lead to the loss of the population if reduced body size, reduced fecundity, or alterations in life history results in problems to which the population cannot adapt (Watts and Pascoe 1996, Sibley et al 1997).

Both lethal and sublethal stresses act on individuals, but the additive results have implications for higher levels of ecological organization (Clements 1997). Lethal effects result in a decrease in abundance and biomass, and possibly elimination of the population. Sublethal effects may also decrease standing stock, for instance by decreasing growth rates and therefore the accumulation of biomass, or by stimulating drift (Crowther and Hynes 1977, Lugthart and Wallace 1992, Courtney and Clements 1998). However, sublethal effects generally reduce production by diverting energy from feeding and growth into pollution tolerance mechanisms, which may lead to a decrease in growth rate and production/biomass ratio (P/B). They are represented by increases in metabolic costs associated with respiration and tolerance mechanisms, such as the manufacture of metallothionein proteins in metal tolerance, with the result that less energy is devoted to tissue production (Wicklum and Davies 1996).

Continued urban expansion and increasing vehicular traffic are factors that contribute to non-point source impacts from roads on stream systems. The key to controlling these problems lies in minimizing the deposition of pollutants from vehicles and de-icing strategies, implementation of best management practices such as wetland conservation and pre-treatment methods to control the toxicity of runoff, and planning of transportation networks that are sensitive to the effects on habitat, channel structure, hydrologic regime, and drainage patterns of streams and their catchments. It is imperative that examination of effects at levels of organization greater than the individual organism be encouraged, in order to understand how surface waters and road networks may coexist with a minimum of impact on water quality and ecosystem integrity.

Chapter II

EFFECTS OF A HEAVY METAL POLLUTION GRADIENT ON LEAF LITTER PROCESSING AND INVERTEBRATE ASSEMBLAGES IN A HEADWATER STREAM

Chapter Summary

Leaf pack invertebrate assemblages and processing rates of red maple leaves were examined along a gradient of heavy metal pollution and habitat alteration in Goosefare Brook, a first-order coastal plain stream in southern Maine, U.S.A. Increasing metal concentrations were associated with runoff from roadways and an industrial operation. There was no significant difference in softening rate between stations in 1997, and only the most polluted station showed a decrease in 1998. Litter loss rates showed decreases associated with stress in both years. Both rates were slower in 1997, likely due to colder temperatures. The structure of invertebrate assemblages changed in response to stress, including decline in EPT richness and an increase in the proportion of collecting taxa. However, total shredder biomass was only weakly affected by pollution and channelization. Shredder biomass at all stations were dominated by *Tipula*, although the biomass of other shredder taxa showed a progression along the gradient of stress, from Plecoptera and Trichoptera to more tolerant Crustacea. Litter processing rates were related to water and sediment quality variables (metals, nutrients, alkalinity, specific conductance) rather than to characteristics of the invertebrate assemblages.

Introduction

In forested headwater streams, terrestrial detritus in the form of leaf litter supports the majority of consumer production (Fisher and Likens 1973, Cummins et al 1989, Wallace et al 1999). A major rate-limiting step in the functioning of these ecosystems is the incorporation of this leaf litter into fungal and invertebrate biomass. During this stage in litter processing, aquatic hyphomycete fungi assimilate carbon from the leaf tissues and obtain other nutrients from the water column (Suberkropp and Klug 1980, Gessner 1999). Due to the high C:N ratio of the structural polymers in leaves (i.e. cellulose, hemicellulose, lignin), an important part of the diet of detritivores is fungal biomass. Once colonized by fungi, leaf litter is processed by invertebrates that directly consume leaf tissue (shredders) into fine particulate organic matter (FPOM). This material is arguably an important energy source to other organisms in the community, and to communities downstream as transported particulate and dissolved organic matter (Anderson and Sedell 1979, Vannote et al 1980, Cummins et al 1989).

The processing rate of leaf litter is controlled by factors affecting leaching and physical fragmentation, such as fungal maceration and the activity of detritivores (Webster and Benfield 1986, Molinero et al 1996, Gessner 1999). Nutrient availability and temperature are also important environmental factors (Suberkropp and Klug 1980, Young et al 1994, Huryn et al 2002). Litter conditioned under increased dissolved nutrient concentrations has been shown to have increased nutrient levels (Suberkropp 1995, Molinero et al 1996), and accelerated rates of tissue softening (Suberkropp et al 1975, 1976, Webster and Benfield 1986). Presumably the reduction in nutrient limitation

results in increased growth of fungal decomposers, which in turn increases the rate of leaf tissue maceration (Suberkropp 1995, Suberkropp and Chauvet 1995). Within the limits of the thermal tolerance of the organisms, higher temperatures increase the rates of fungal and detritivore activity, which also results in increased litter breakdown rates (Suberkropp et al 1975, 1976, Webster and Benfield 1986).

Human activities may affect litter processing in streams by affecting any biologically mediated step. Pollutants have been shown to alter fungal communities that make leaf detritus palatable to shredding organisms (Maltby et al 1995a). Pollutants such as heavy metals may impair fungal growth and sporulation, and uptake and accumulation by fungi is potentially an important mechanism by which these pollutants reach higher trophic levels (Duddridge and Wainwright 1980, Abel and Barlocher 1984, 1988). The reduction of fungal productivity or cellulolytic activity could significantly slow the rate of energy flow to higher trophic levels, affecting the food web at its base. These communities may show reduced efficiency because certain microconsumers are eliminated by exposure to pollution, and/or because density of the shredders is reduced, which in turn may reduce the flow of energy to other functional feeding groups (Vannote et al 1980).

In view of the important role of leaf litter in the energetics of forested streams, the examination of litter processing rates and the biota associated with litter provides insight into an important ecosystem function. Measurement of litter processing rates may thus be useful in assessing anthropogenic impacts on stream systems, since it represents an integration of physical, chemical, biological, and microbiological factors (Stout and

Coburn 1989, Young et al 1994). This study examined the effects of a gradient of heavy metal pollution in a first-order Maine (U.S.A.) stream on leaf litter processing rates, and on the characteristics of invertebrate assemblages associated with leaf litter. A gradient design is useful in evaluating the ecological effects of stress, because it allows comparison of structure and function over a continuum of stress intensity (Cao et al 1997, DeLong and Brusven 1998). A decrease in litter processing rates along the gradient is anticipated, in addition to coincident changes in the macroinvertebrate assemblages associated with the leaf litter, including a shift from sensitive shredder taxa (Ephemeroptera, Plecoptera, Trichoptera) to tolerant taxa (Tipulidae, Chironomidae, and Malacostraca).

Study Site

Goosefare Brook is a small brownwater stream in the coastal plain region of southern Maine (43°32'N, 70°27'W). The stream drains the Saco Heath, a raised peatland, and flows east into the Atlantic Ocean. The study reach is the upper, first-order portion of the stream, within four kilometers of its source (Figure 2.1). The banks of the stream are forested with oak (*Quercus* spp.), hemlock (*Tsuga canadensis* (L.) Carr.), and red maple (*Acer rubrum* L.), and there is a thick understory of ferns and herbaceous plants. The channel form of the stream is low-gradient, meandering, and sandy, with frequent roots and woody debris incorporated into the streambed. The width of the stream channel varies from 1-3m, and discharge ranges from a summer base flow of

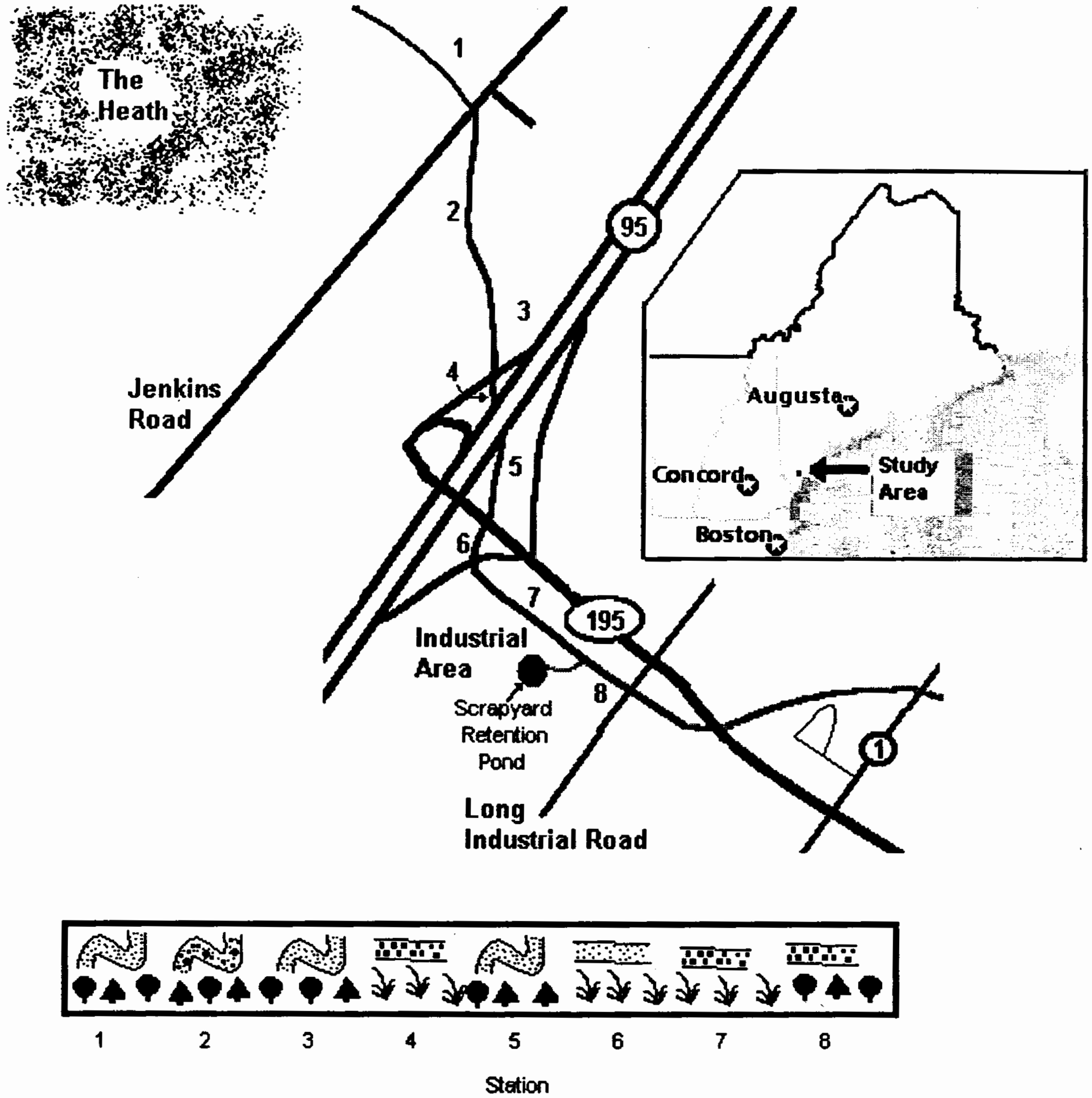

Figure 2.1. Schematic diagram of Goosefare Brook sampling stations, pollution sources, and habitat characteristics. Station habitat pictograms at the bottom of the diagram indicate channel shape (sinuous/unchannelized vs. straight/channelized), substrate texture (sand/clay vs. cobble/boulder), and riparian vegetation (forested vs. cleared). See also Table 2.1 for more detailed habitat variables.

approximately 10 L/s to 100 L/s in the spring. pH varies seasonally from circumneutral during the summer months to ≤4.0 in the autumn. In 1997 and 1998, water temperature ranged from ~0°C in the winter to a high of ~17°C in summer. During the periods of this study (October and November), temperatures ranged from ~0°C to ~4.2°C in 1997, and ~0°C to ~14.0°C in 1998 (Figure 2.2). Channelization to improve drainage has altered the channel form and riparian zone at several stations (Figure 2.1), with channelized reaches tending to have coarser substrate and higher flow rates (Figure 2.3). The main sources of pollution in the stream include runoff from paved highway surfaces and industrial sources (Table 2.1). Eight sampling stations were established in the study area. Station 1 serves as the reference station, being unaffected by known physical or chemical stressors, while each of the remaining seven stations were located downstream of a potential source of stress.

Methods

Leaf Litter and Macroinvertebrates

Leaves were collected post-abscission and pre-drop from a single red maple tree on the University of Maine campus in Orono. Approximately 8g (range ±0.1g) of air-dried leaves were placed in plastic mesh bags, after having been weighed to the nearest 0.01g and then moistened before placement in the bags to minimize breakage. Six litter bags were deployed at each of five stations in Goosefare Brook (3 to 7 inclusive) in 1997,

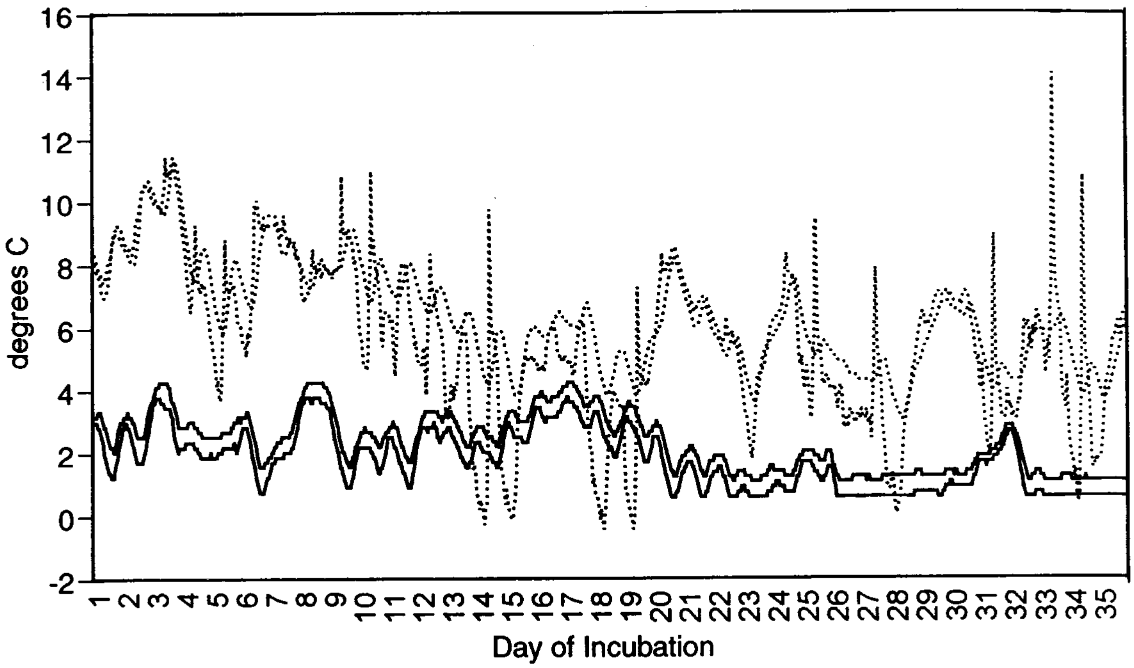

Figure 2.2. Hourly recorded temperatures during the period of litter bag incubation at Goosefare Brook Stations 3 and 5, 1997 (solid lines) and 1998 (broken lines).

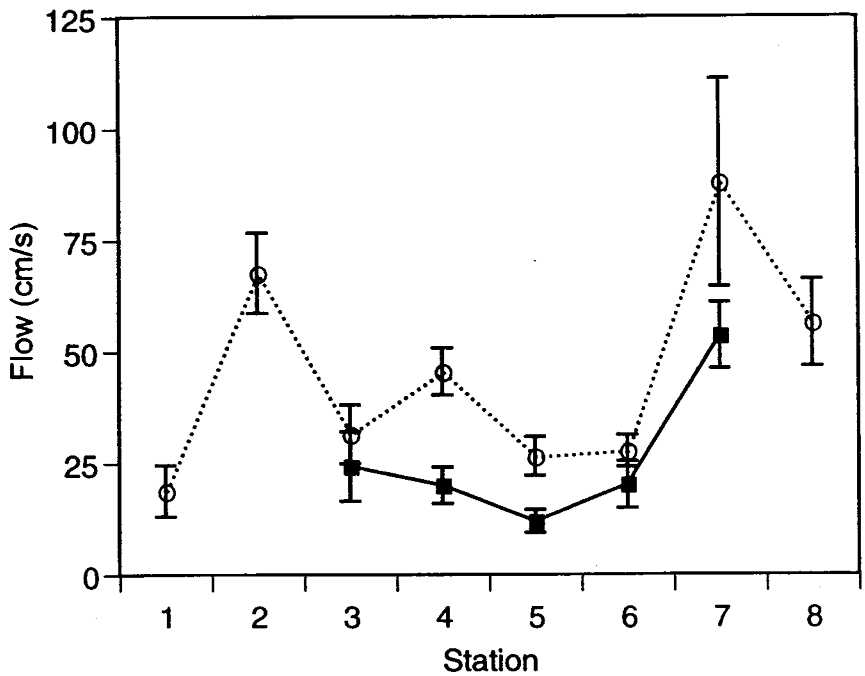

Figure 2.3. Mean flow velocity observed at litter bags at time of removal, 1997 (solid line) and 1998 (broken line). Error bars show ± 1 S.E.

1997		Station							
Parameter	Units	1	2	3	4	5	6	7	8
Specific Conductance	µS/cm	-	-	103	176	268	417	506	-
NO3-N	mg/L	-	-	0.31	0.32	0.29	0.27	0.25	-
NH4-N	mg/L	-	-	ND	ND	0.04	0.09	0.07	-
PO4-P	mg/L	-	-	0.004	0.003	ND	ND	ND	-
pH Oct/Nov	-	-	-	6.8/4.9	6.9/5.0	6.8/5.1	6.8/5.5	6.8/5.9	-
Alkalinity	$mgCaCO_3/L$	-	-	10.0	11.0	10.0	12.5	14.0	-
1998									
Specific Conductance	µS/cm	83	111	121	154	181	305	293	434
NO3-N	mg/L	0.18	0.21	0.30	0.35	0.35	0.32	0.32	0.26
NH4-N	mg/L	0.08	0.07	ND	ND	ND	ND	0.08	0.06
PO4-P	mg/L	0.014	0.007	ND	ND	ND	ND	ND	ND
pH	-	6.7	6.5	7.2	6.6	6.0	6.8	7.0	7.2
Alkalinity	$mgCaCO_3/L$	20.0	10.0	19.5	16.5	7.0	16.0	22.0	12.0

Table 2.1. Summary of water quality variables for Goosefare Brook sampling stations, 1997 and 1998. With the exception of pH, for which both values are shown, 1997 data represents the mean of two water samples taken at litter bag deployment and recovery. 1998 data from sample taken on November 6. ND indicates that concentrations were below detection limits.

and at all eight stations in 1998 (Figure 2.1). An extra set of six bags were transported with the others prior to their deployment, in order to evaluate loss due to handling (Benfield 1996), and were processed the same way as the others following collection to obtain initial penetrance and ash-free dry mass (AFDM). Each station consisted of a 10m reach. The bags were tied to 8" gutter nails which were driven into the stream substrate. The bags were incubated in the stream for 35d in both years; from October 10 to November 14 in 1997, and from October 23 to November 27 in 1998. This length of time was appropriate for streams in Maine, based on a targeted loss of 50% of the leaf material (Huryn et al 2002). Temperature was recorded hourly during this period using Optic StowAway temperature loggers (Onset Computer Corporation, Bourne MA) placed at Stations 3 and 5.

Recovery of the bags proceeded from the downstream end of the study reach, in order to disturb other bags as little as possible. Prior to its removal, flow was measured at the position of each litter bag using a Global flow meter (Global Water Instrumentation, Gold River CA). The bags were collected by quickly placing them inside a large plastic soil sampling bag held downstream. The litter bags were returned to the laboratory and their contents rinsed into a 500μm sieve. Invertebrates and debris were rinsed from the leaves and preserved in 95% ethanol for later sorting. Invertebrates were enumerated and identified to the lowest practical taxonomic level, typically genus (Wiederholm 1983, Thorp and Covich 1991, Merritt and Cummins 1996). Invertebrate length was measured to the nearest millimeter and biomass was calculated using published length-mass regressions (Benke et al 1999).

Leaf softness was measured with a penetrometer. As leaf tissue is macerated by fungi, the softness of the leaf tissue increases. This relative leaf softness is measured as "penetrance", defined as the weight required to push a standard blunt metal pin through a leaf (Young et al 1994). Penetrance is related to both fungal activity and the palatability of leaf detritus to detritivores (Suberkropp and Klug 1980). The penetrometer consisted of two heavy plastic blocks between which the leaf was placed in order to hold it flat. A pin supporting a dish was placed in a hole drilled through the blocks, so that the pin was supported by the leaf tissue. Lead shot was then slowly added to the dish until the leaf was penetrated, at which point the mass of the dish and the shot was obtained. The measurements were made near the center of the leaf, away from large veins and approximately half-way between the midrib and the leaf edge. In 1997, softness of five randomly selected leaves from each bag was measured, while in 1998 this sample size was increased to ten leaves, due to the high variability of the penetrance measurements observed in 1997.

Following the measurements of penetrance, the leaves from both incubated and breakage bags were placed in paper bags and dried in an oven at 60°C for three days. The leaves were again weighed (oven-dry mass), then ground in a blender and ashed in a muffle furnace at 550°C for 24h. AFDM was estimated as the difference between oven-dry and ash weights. The proportion of AFDM remaining was calculated by dividing the final AFDM by initial AFDM (corrected for handling loss). The initial value for penetrance calculations was the softness of freshly collected leaves prior to drying, obtained using the same method described above. Rate constants were expressed using

degree-days (>0°C) accumulated during the incubation period in order to facilitate comparisons between years (Young et al 1994, Huryn et al 2002). Rate constants for both leaf loss and leaf softening were calculated by fitting the data to a negative exponential decay model, where,

$$\text{rate} = [\ln(\text{final value}/\text{initial value})] / \text{accumulated degree-days}$$

Water and Sediment Chemistry

In 1997, water chemistry was assessed at each station using 500mL grab samples taken at the time of litter bag deployment, and again when the bags were recovered. All water samples were transported in rinsed, acid-washed amber plastic bottles, and stored on ice until their delivery to the Maine State Analytical Laboratory (5722 Deering Hall, University of Maine, Orono ME, 04469-5722) for analysis. The samples were analyzed for nitrate (NO_3-N), ammonium (NH_4-N), phosphate (PO_4-P), pH, alkalinity, specific conductance, and eight heavy metals (Cd, Cr, Cu, Fe, Mn, Ni, Pb, and Zn) following a nitric acid digestion.

Between May 1998 and April 1999, sediment samples were taken on nine dates at each station by pressing a length of 1" PVC pipe into the substrate to a depth of ~2cm and transferring the collected material to a rinsed, acid-washed amber plastic bottle. This was repeated nine times (left, right, and center of channel at three randomly determined locations within each station) and composited in a single bottle. All samples were stored

on ice until their delivery to the Maine State Analytical Laboratory. The water in the sample was analyzed for NO_3-N, NH_4-N, PO_4-P, pH, alkalinity, and specific conductance. Subsamples of the sediment were analyzed for organic carbon content and eight heavy metals (Cd, Cr, Cu, Fe, Mn, Ni, Pb, and Zn) using a two-stage extraction. The first extraction was performed using 1M ammonium acetate at pH 7, and measured aqueous and weakly complexed metals. The remainder of the sample was then digested in nitric acid. The sum of the metal concentration in the two extractions is the total metal concentration for the sample. Details of this methodology are described in Say and Whitton (1983). Concentrations of NO_3-N and NH_4-N were determined using an Aplkem flow injection analyzer (detection limit 0.05 mg/L). Concentrations of PO_4-P were determined using Dionex I.C. (detection limit 0.01 mg/L). Heavy metal concentrations were determined using flame AA, with a replicate performed every 9 samples. All results were checked against external standards bracketing the expected concentrations.

Invertebrate Assemblage Structure Metrics

A suite of metrics describing attributes of the invertebrate assemblages was used to examine longitudinal changes in the structure of assemblages occurring on the leaf packs. This suite included Raw Abundance, Taxa Richness, EPT richness, Berger-Parker Dominance, Shannon-Weaver Diversity, Total Biomass, %Ephemeroptera, %Plecoptera, %Trichoptera, %Chironomidae, %Scrapers, %Shredders, %Collector-Gatherers, %Filter-Feeders, %Engulfing Predators, and %Piercing Predators. All percentages were

calculated on the basis of biomass. The biomasses of important shredder genera were examined individually.

Statistical Analyses

Community metrics, measures of leaf decomposition (penetrance and leaf loss), and biomass were compared between the stations using one-way analyses of variance within each year. All proportional variables were arcsine-transformed (Neter et al 1996). Risk of type I error was set prior to the analyses at α=0.10 for all univariate ANOVAs (50 in total), and a Bonferroni correction was applied, so significance was accepted in each individual test if $p \leq 0.002$. While this α-value is greater than the traditional 0.05, it is reasonable in an ecosystem-level study due to the large number of variables tested, the high stochasticity in field studies, and the possibility that small changes at the scale of study could translate to significant changes in ecosystem function. A Tukey's post-hoc test was conducted for all analyses where a significant difference was detected (Neter et al 1996), and significance was accepted for a pairwise comparison when $p \leq 0.05$. In the case of the leaf decomposition parameters, an attempt was made to control for hydrological differences between the stations by using the flow at each leaf pack as a covariable.

Principal components analysis (PCA, Rencher 1995) of the physical and chemical variables (flow rate, nutrient and heavy metal concentrations, pH, alkalinity, specific conductance), and of biomass by taxon, were performed separately for 1997 and 1998 for

the purpose of data reduction. For the 1997 metal concentrations, the aqueous concentrations from samples taken in October and November were used, while in 1998 the exchangeable and total metal concentrations from one set of sediment samples were used. These samples were taken during the incubation period on November 6, 1998, and were assumed to best represent exposure during the study period. All variables used in the PCA were standardized prior to analysis. The principal components from the biotic, and physical and chemical analyses were used in a forward stepwise regression (F to enter $\geq$4.0) (Neter et al 1996), to evaluate relationships with each litter decomposition parameter in each year. The number of components used from each individual PCA was chosen by the number required to explain at least 85% of the variance in the data, up to a maximum of six.

Results

Water and Sediment Chemistry

The exchangeable and total metal levels show an increasing trend in mean annual value along the study reach (Figure 2.4). Significant increases in annual mean concentrations were determined using Kruskal-Wallis ANOVA, and are described in detail in CHAPTER III. Most of the increase is associated with the industrial inputs near Stations 7 and 8. Station 6 also has high metal concentrations, even though it is upstream of the industrial inputs. This is presumably because the channel has been excavated,

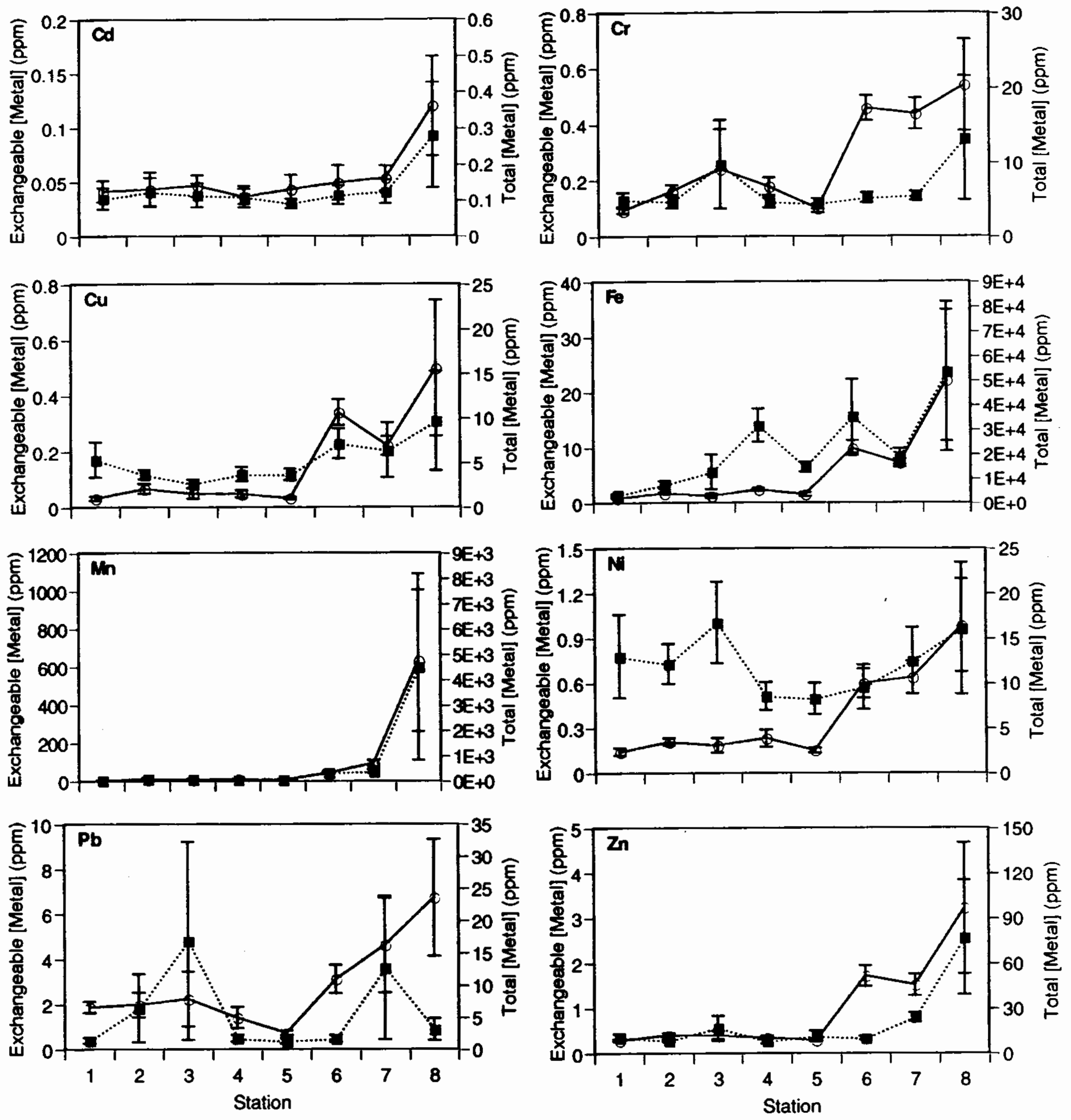

Figure 2.4. Total and exchangeable levels of eight metals in Goosefare Brook sediment samples (mean of nine composite sediment samples taken between May 1998 and April 1999). Annual concentrations of heavy metals are used in this figure for illustrative purposes. Broken lines denote the exchangeable metal fraction, solid lines denote total metals. Error bars show ±1 S.E. of the annual estimate.

exposing a substrate that is composed mainly of clay, which has a large surface area for metal sorption (CHAPTER III). The other six metals also show their highest average concentrations at this station, but spatial patterns of sedimentary concentration are more complex. With the exception of Cd, all metals showed a significant increasing downstream trend in exchangeable concentration, total concentration (Cr, Cu, Ni, Pb), or both (Fe, Mn, Zn – Figure 2.4). Significant increases along the gradient ranged from less than 4-fold for total Pb to more than 160-fold for total Mn. The largest increases in metal concentrations occurred between Stations 6 and 8. The major source appears to be related to industry, although there is also evidence of roadway inputs. A significant increase in zinc downstream of the galvanized culverts is also evident (CHAPTER III).

Fe is the most abundant metal in the study area, and also shows an increase in total sedimentary concentration along the gradient. However, there appears to be an interaction between habitat type and Fe concentration. An increase in Fe is associated with both the highway and industrial inputs, but the mean concentration is higher in the channelized habitats than in unchannelized habitats (Figures 2.1 and 2.4). Zn shows a marked increase in total concentration downstream of the first galvanized culvert (between Stations 5 and 6), but increases further downstream of the industrial input. However, the exchangeable Zn fraction is not elevated until the industrial effluent enters the stream. Cu and Cr show similar patterns to Zn, with exchangeable concentrations increasing more slowly than total concentrations. The total concentrations of Ni and Pb show an increase downstream of the industrial input, but the exchangeable fraction is more variable, and does not show a clear relationship to any known source. The peaks in

exchangeable fractions of Cr, Ni, and Pb at Station 3 are not readily explainable, since the station has similar habitat to others with natural channel form. It is possible that Ni and Pb, which are present in fuel additives and therefore in exhaust fumes (Smith and Kaster 1983, Hewitt and Rashed 1988, 1990), may be elevated at these stations due to aerial deposition. However, this does not explain the lower concentrations of these metals at Stations 4 and 5, which are also close to the highway.

Leaf Litter Processing

Penetrance is used as a measure of leaf softness, and higher values indicate tougher and therefore less conditioned leaves. Overall, leaf softening proceeded at a slower rate in 1997 than 1998 (Figure 2.5). This was likely due to higher temperature of the stream water in 1998, when 211°C degree-days were accumulated during the 35-day study period, compared to only 71°C degree-days accumulated in 1997 (Figure 2.2). There was no significant difference in the rate of softening between stations in 1997. In 1998, litter at Station 8 showed a significantly slower rate of softening compared with Stations 1 and 3.

In 1997, leaf loss was significantly lower at Station 7 compared with Stations 3, 4, and 5 (Figure 2.6). In 1998, the pattern is less clear. Leaf loss in 1998 was generally greater than in 1997, which may also be a result of temperature differences. A

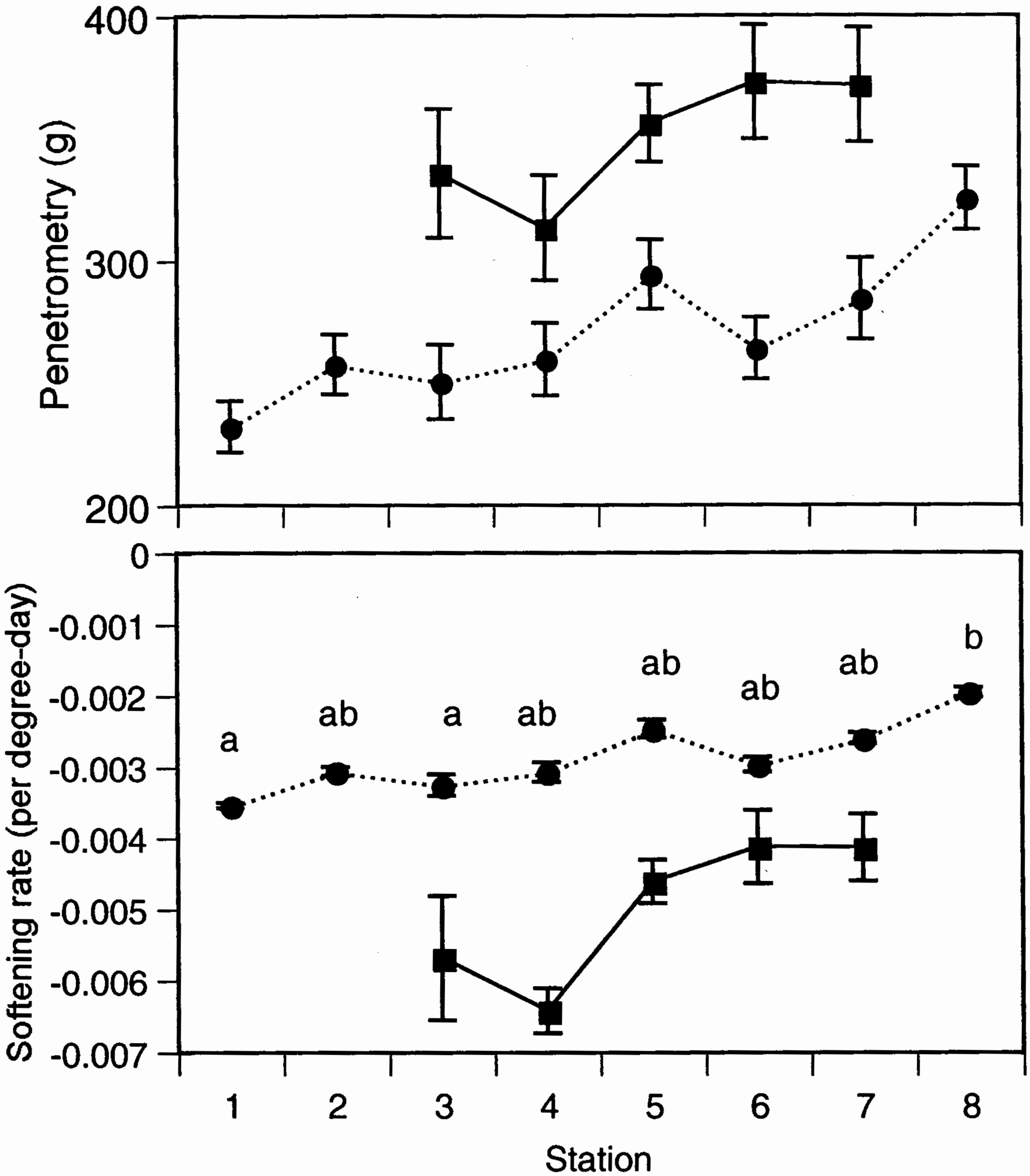

Figure 2.5. Leaf softening and leaf softening rate in Goosefare Brook as measured by penetrometry, autumn 1997 (solid lines) and 1998 (broken lines). Five stations were examined in 1997, and all eight stations in 1998. Error bars show ±1S.E. Stations sharing the same letter on the lower panel are not significantly different in total leaf softening or softening rate.

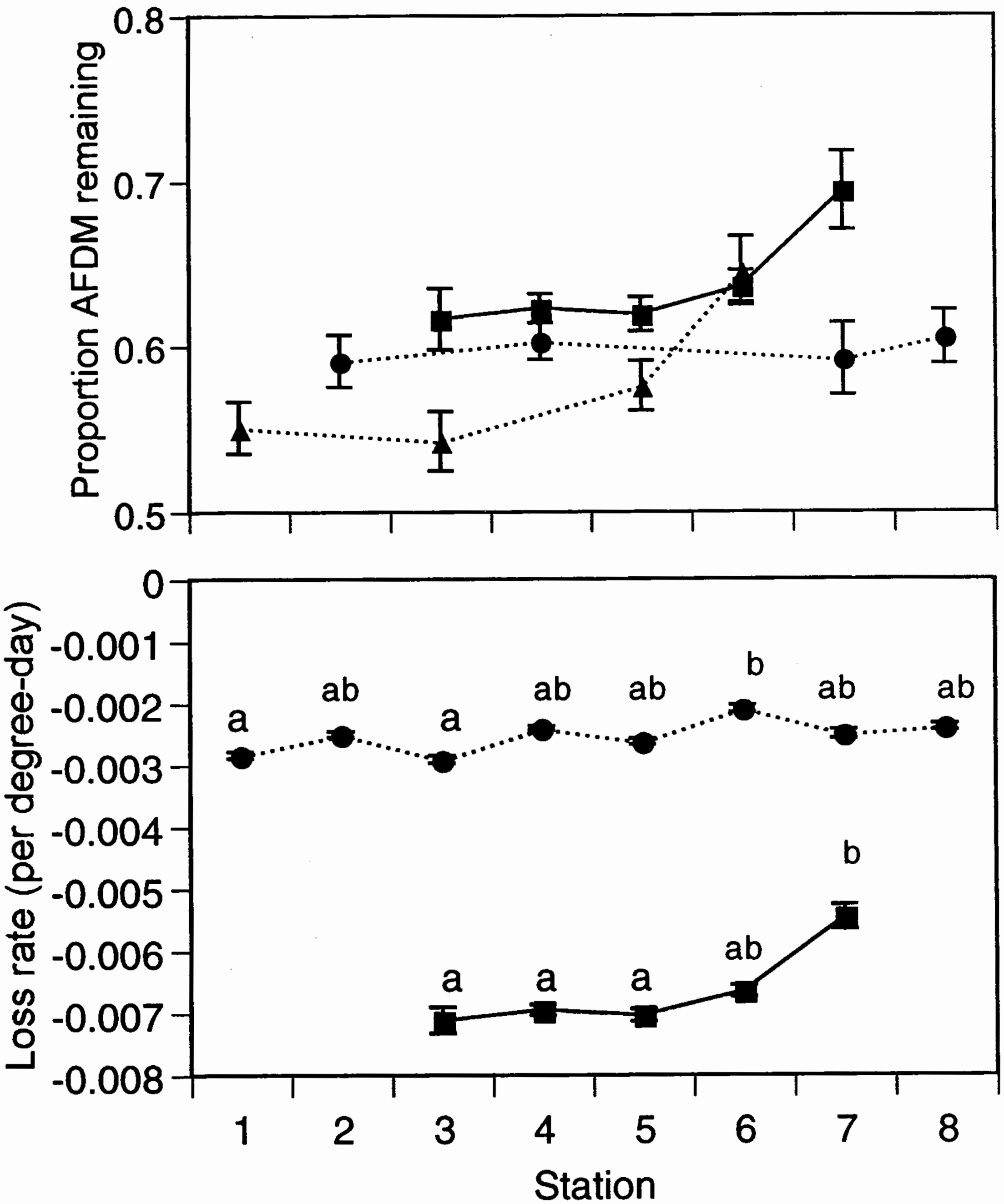

Figure 2.6. Leaf loss and leaf loss rate in Goosefare Brook, autumn 1997 and 1998. Five stations were examined in 1997 (solid lines), and all eight stations in 1998 (broken lines). Error bars show ±1S.E. Stations sharing the same letter on the lower panel are not significantly different in total leaf loss or loss rate. Separate lines connect channelized (●) and unchannelized (▲) stations in the upper panel.

comparison between the two years shows that although total softening and loss was greater over the 35 days in 1998 than in 1997, both processes proceeded more quickly per degree-day in 1997 (Figures 2.5 and 2.6). Although it has been shown that litter decomposition proceeds more slowly at colder temperatures (Suberkropp et al 1975, 1976, Webster and Benfield 1986), this suggests that temperature is not the only factor affecting this process.

Invertebrate Assemblage Structure

The metrics describing invertebrate assemblage structure showed significant changes along the pollution gradient (Figure 2.7). Total abundance and total generic richness did not show any significant differences in 1997. In 1998, however, Station 2 had a higher abundance than all other stations ($p<0.0001$), due to large numbers of Simuliidae and *Tvetenia*. Stations 7 and 8 had significantly fewer taxa than Stations 2, 4, and 5 ($p<0.0001$). In contrast, evenness (Berger-Parker dominance) showed no differences in 1998, but was significantly greater at Stations 6 and 7 than at Stations 3, 4, and 5 in 1997 ($p<0.0002$). EPT generic richness showed a significant decline downstream of the turnpike, and again downstream of the industrial inputs. This metric appeared to better reflect the gradient than did overall richness. As many as 12 EPT taxa were present in leaf packs at the less impacted stations, while only 3 were recorded below the industrial inputs. In 1997, Station 7 had significantly lower EPT richness than stations 3 and 4 ($p=0.001$). In 1998, Stations 7 and 8 again showed the lowest EPT of all stations.

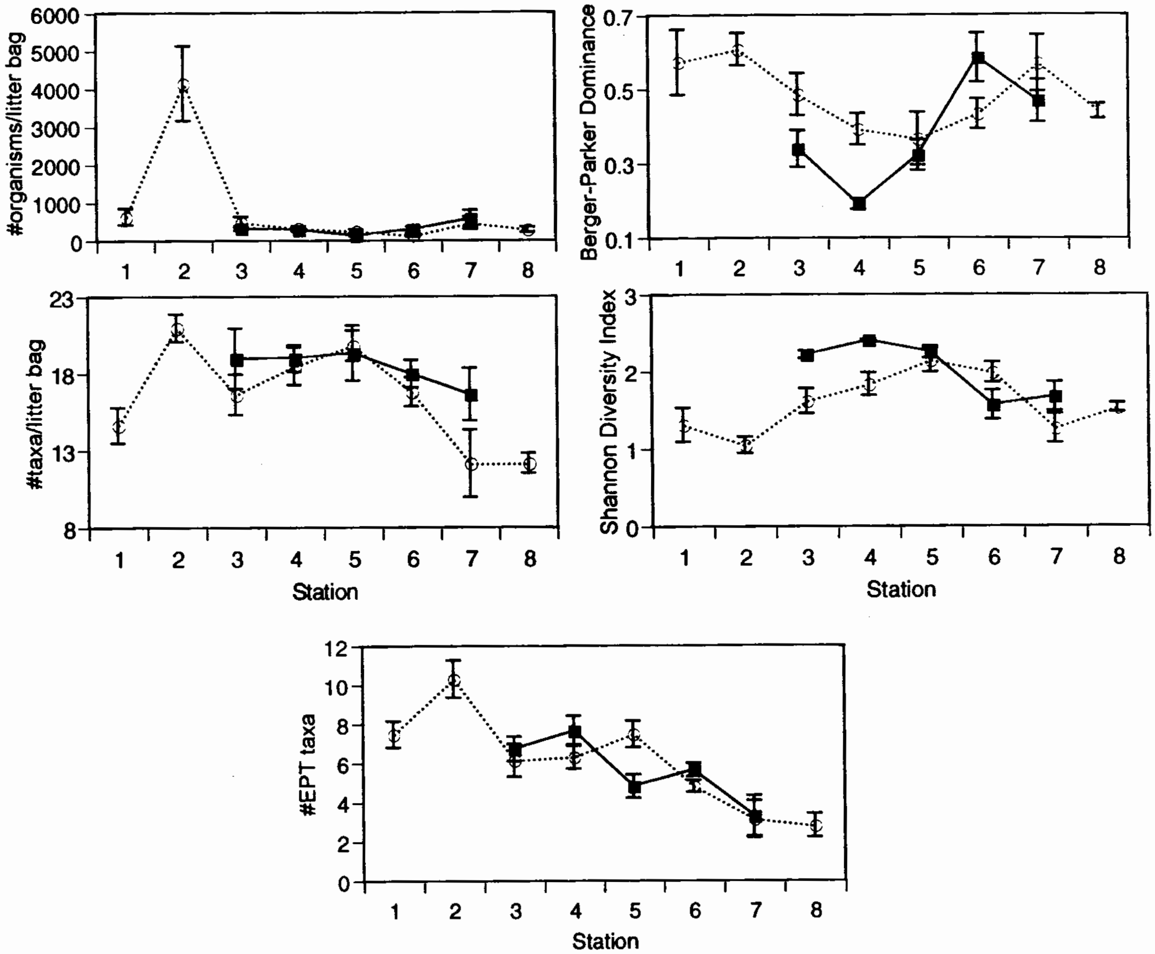

Figure 2.7. Litter bag assemblage metrics from Goosefare Brook sampling stations, 1997 (solid lines) and 1998 (broken lines). Error bars show $\pm$1S.E.

Station 6 also showed significantly lower EPT values than Stations 2 and 5 ($p<0.0001$). In 1997, the Shannon-Weaver Diversity index was significantly higher in the vicinity of the turnpike, with Stations 3, 4, and 5 greater than Stations 6 and 7 ($p<0.0003$). In 1998, the index shows its lowest values at the least- and most-impacted stations (1, 2, 7, and 8), and is greatest in the vicinity of the turnpike ($p<0.0001$).

Shredder biomass was uncorrelated with softening or loss in either year. Total invertebrate biomass per litter bag did not differ along the gradient in either 1997 or 1998, and no differences were seen in the proportions contributed by Plecoptera, Trichoptera, Ephemeroptera, or Chironomidae in 1997 (Figure 2.8). In 1998, however, significant differences were observed in the Plecoptera ($p<0.0002$) and Chironomidae ($p<0.0001$). The greatest proportion of assemblage biomass contributed by Plecoptera was seen at Station 1, which was greater than all other stations except 3. The Chironomidae showed an opposite pattern, with Station 8 having a greater proportion than all other stations except 2 and 6. The proportions of biomass contributed by different functional feeding groups (Merritt and Cummins 1996) also showed differences among stations (Figure 2.9). In 1997 the engulfing predators showed a precipitous drop in proportion of biomass downstream of the main artery of the turnpike (Stations 5, 6, and 7 – $p<0.0001$). In 1998, engulfing predators showed a similar pattern to 1997, with a peak in proportion of biomass at Station 4 ($p<0.002$). Although contributing little biomass overall, piercing predators showed an increasing trend, with Stations 7 and 8 higher than Stations 2 and 6 ($p<0.0001$). Filtering collectors contributed proportionally more biomass

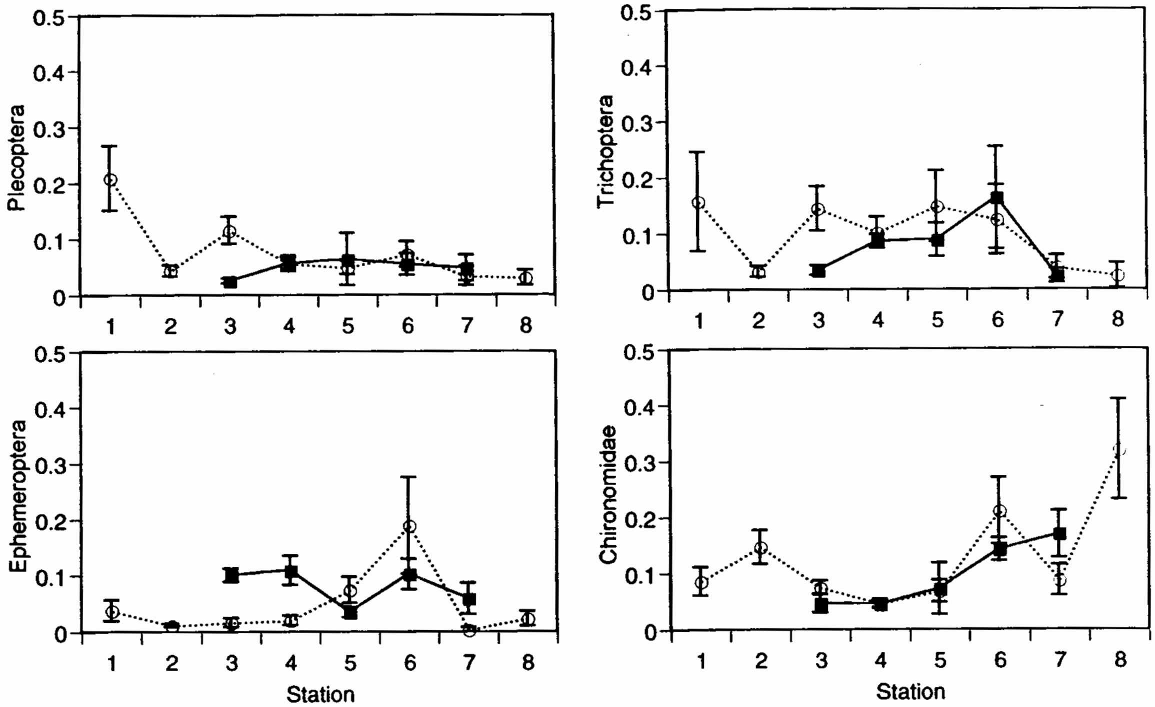

Figure 2.8. Proportion of biomass of major taxonomic groups in litter bag assemblages from Goosefare brook sampling stations, 1997 (solid lines) and 1998 (broken lines). Error bars show $\pm$1S.E.

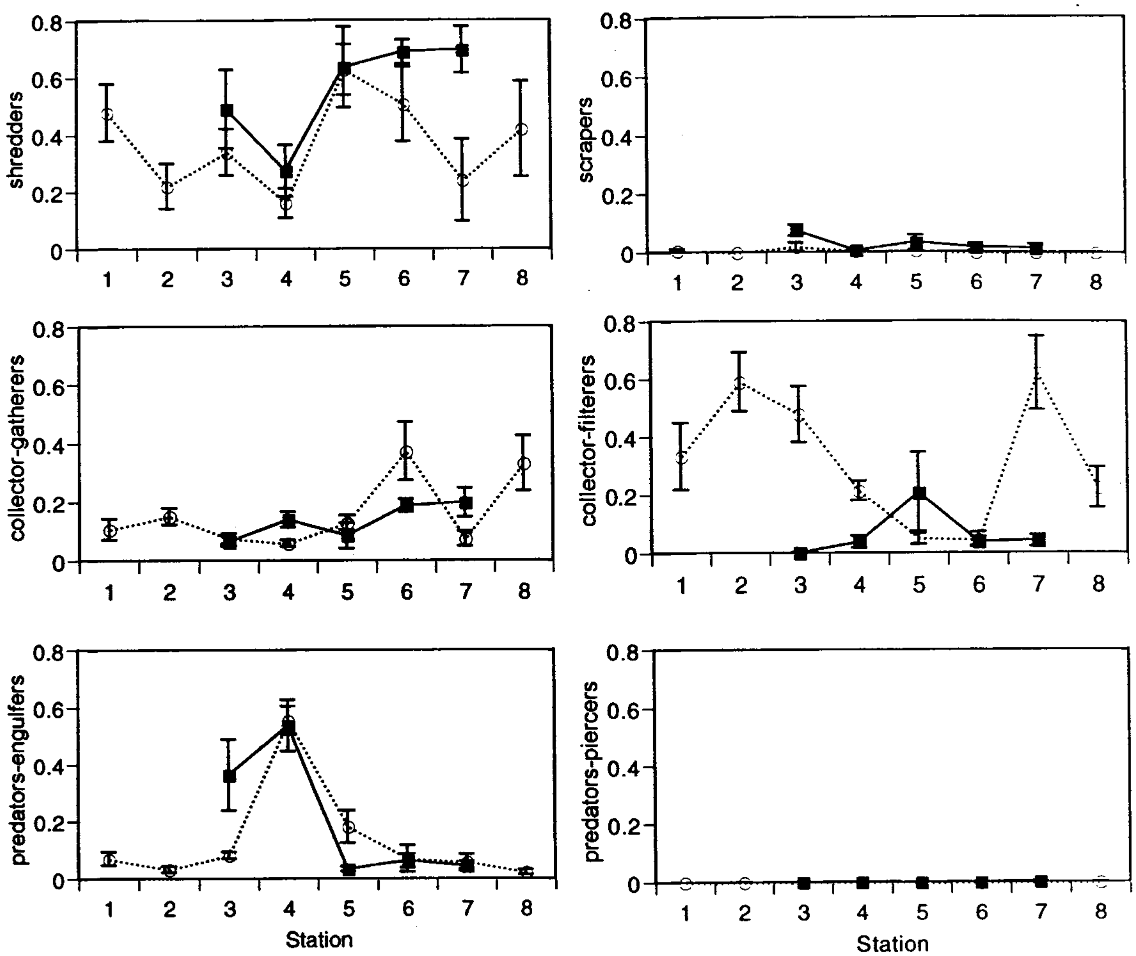

Figure 2.9. Proportion of biomass of functional feeding groups in litter bag assemblages from Goosefare Brook sampling stations, 1997 (solid lines) and 1998 (broken lines). Error bars show ±1S.E.

at Stations 1, 2, 3, and 7 than at 4, 5, 6, and 8 ($p<0.0001$). Gathering collectors contributed proportionally more biomass at Stations 6 and 8 than at all others ($p<0.0001$). Shredders formed a greater proportion of the assemblages in the unchannelized habitats at Stations 1, 5, and 6 compared with the channelized habitats at Stations 2, 4, and 7 ($p<0.0001$).

PCA of Physical, Chemical, and Assemblage Biomass Variables

Only physical/chemical principal components were admitted to the stepwise regression models of litter processing rates. In 1997, the first two components explained 88% of the variability in the physical and chemical data, but only 29% for biomass. Similarly, in 1998 67% of the variability in the physical and chemical data was explained by the first two principal components, but only 25% in the first two components in the analysis of biomass. No biomass principal components were admitted to any of the multiple regression models. The ten most influential variables in each of the components admitted to the models and their eigenvector coefficients are summarized in Table 2.2.

For the 1997 data, only the first physical-chemical principal component was admitted into the model of mean leaf loss at each station (model $r^2=0.77$). This demonstrates that the decreasing rates of leaf loss along the gradient in 1997 are related to increasing levels of metals and conductance, and to decreases in nutrient levels that occur downstream of the turnpike (Figure 2.10). The model of mean penetrance at each

	PHY1	c	PHY2	c	PHY3	c
1997	pH Nov	-0.28	Pb Oct	-0.54	-	-
	Fe Nov	-0.28	Ammonium Oct	-0.29	-	-
	Conductance Oct	-0.28	Zn Nov	-0.07	-	-
	Mn Oct	-0.28	Conductance Oct	-0.03	-	-
	Mn Nov	-0.28	Alkalinity Nov	-0.02	-	-
	Pb Oct	+0.05	Fe Oct	+0.24	-	-
	pH Oct	+0.12	Nitrate Nov	+0.25	-	-
	Phosphate Nov	+0.23	Phosphate Nov	+0.31	-	-
	Nitrate Nov	+0.23	Alkalinity Oct	+0.39	-	-
	Nitrate Oct	+0.28	pH Oct	+0.40	-	-
1998	Phosphate	-0.13	Nitrate	-0.53	Zn Exch	-0.32
	Alkalinity	-0.04	Ni Exch	-0.30	Fe Exch	-0.23
	Cr Tot	+0.29	Fe Exch	-0.19	Cd Tot	-0.11
	Cd Tot	+0.30	Conductance	-0.13	Nitrate	-0.10
	Mn Tot	+0.31	Cu Tot	-0.10	Mn Tot	-0.08
	Conductance	+0.31	Cd Tot	+0.09	Cr Tot	+0.15
	Ni Tot	+0.31	Mn Tot	+0.09	Cu Tot	+0.20
	Mn Exch	+0.32	Pb Tot	+0.38	Ni Exch	+0.37
	Zn Tot	+0.32	Ammonium	+0.40	Alkalinity	+0.44
	Fe Tot	+0.32	Phosphate	+0.48	pH	+0.56

Table 2.2. Most influential variables in the principal components analyses of standardized physical and chemical variables in the stepwise regressions of leaf litter decomposition parameters, Goosefare Brook, 1997 and 1998. PHY indicates physical and chemical principal components, and only those principal components that were significant in one or more of the stepwise regressions of litter decomposition parameters are shown. In the 1997 columns, 'Oct' and 'Nov' indicates the date of the water samples, in the 1998 columns, 'Tot' indicates total sedimentary metal concentration, and 'Exch' indicates the exchangeable concentration. 'c' denotes the eigenvector coefficient of the variable.

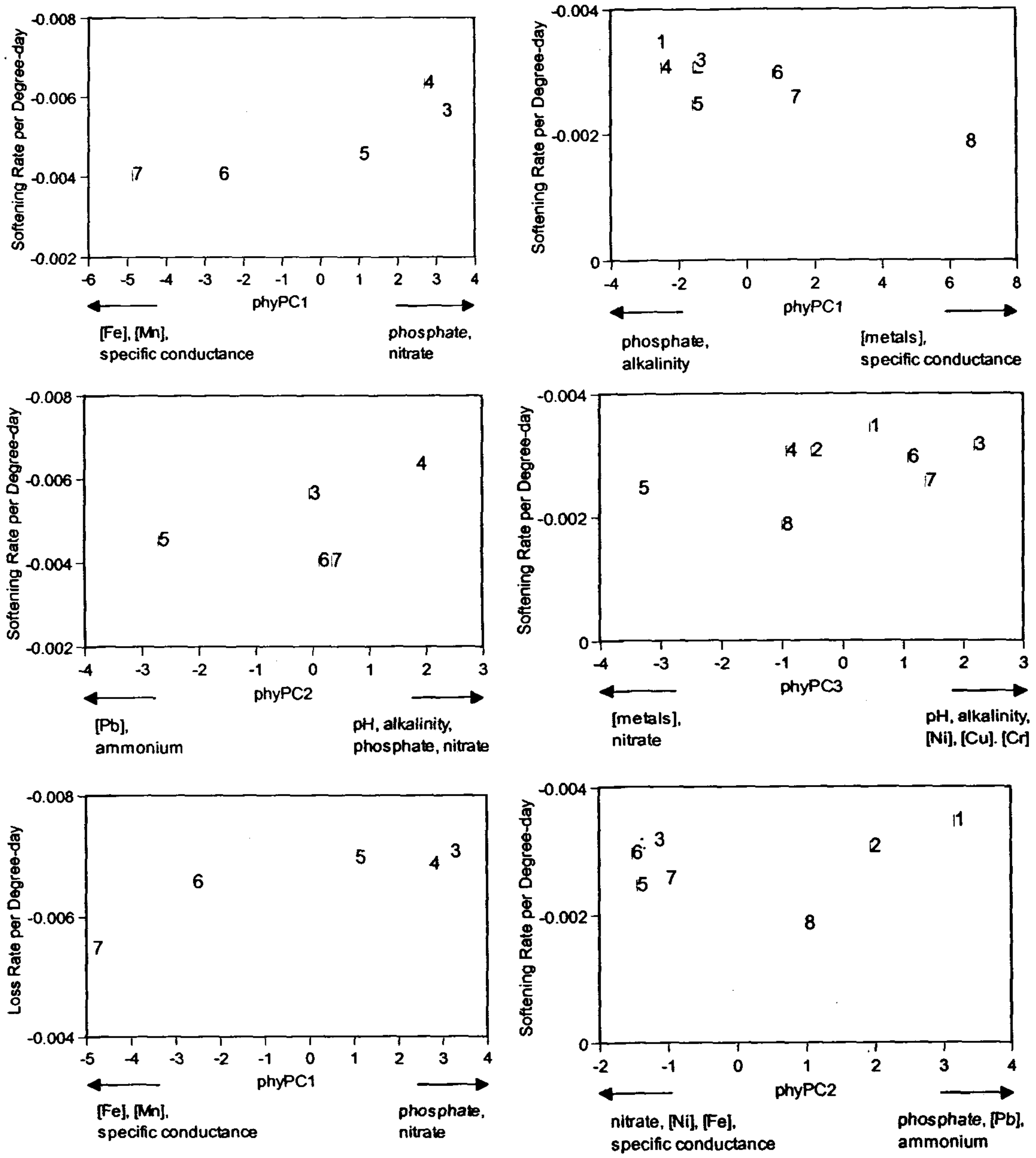

Figure 2.10. Litter softening and loss rates vs. physical/chemical principal components significant in the stepwise multiple regressions for 1997 (left) and 1998 (right). Labels on the X-axis indicate the most influential variables in the principal components, and numbers indicate sampling stations. No variables were admitted to the stepwise model describing leaf loss in 1998.

station admitted the first two physical-chemical principal components (model r^2=0.92), demonstrating the inverse response of litter softening rates to increasing metals and decreasing nutrients, particularly at Stations 6 and 7 (Figure 2.10). Physical-chemical PC2 explained differences between Stations 4 and 5, suggesting that Station 5 showed a slower softening rate correlated with higher Pb levels and changes in nutrient concentrations. Higher pH and alkalinity at Station 4 also had an effect on this component, although overall differences in these parameters were small (Table 2.1).

Much of the variation in penetrance in 1998 was explained by the first three physical-chemical principal components (model r^2=0.96), although no principal components were admitted to the regression of leaf loss (Figure 2.10). PC1 was the first admitted to the softening model, and showed that the reduction in softening at Stations 6 through 8 are related to the increase in metals, conductance, and pH, and a decrease in nutrients along the gradient. PC3 was the next term to enter the regression, and loaded on pH and alkalinity, Cr, Cu, and Ni in the positive direction, and negatively on nitrate, Zn, Fe, and Cd concentrations. It separates Stations 3, 6, and 7 from Station 5. PC2 loaded positively on phosphorus, ammonium, and Pb concentration, and negatively on Ni, Fe, nitrate, and specific conductance. It separates Stations 1 and 2 from those nearest the turnpike interchange. Station 8, having been separated from the other stations in PC1, has a low score on this component, although it is slightly positive due to Pb and ammonium concentrations.

Shredder Community Composition

The total invertebrate biomass per litter bag was not significantly different between stations in either year. At all stations, litter-feeding Diptera (mainly the crane fly larva *Tipula*) dominated shredder biomass (Figure 2.11). However, the shredder community showed significant changes in taxonomic composition as the level of pollution increased. Plecoptera, mainly the genera *Allocapnia*, *Paracapnia*, and *Amphinemura*, showed higher total biomass at Stations 1 and 2 than at the remaining stations in 1998. In 1997, only *Amphinemura* showed a significant difference in total biomass, with Station 3 being significantly higher than Stations 4 through 7 ($p<0.0001$). In 1998, with the addition of Stations 1 and 2, a difference was seen in all three genera. *Paracapnia* showed a decline to almost zero biomass downstream of Station 2, with Stations 1 and 2 significantly higher than Stations 4 through 8 ($p<0.002$). *Allocapnia* showed a similar pattern, with Stations 1 and 2 higher than all others ($p<0.0001$). *Amphinemura* showed a different pattern, having highest biomass at Stations 3 and 4 ($p<0.0001$).

Downstream of the stations associated with the turnpike interchange, the shredder community showed further changes in composition. In 1997, *Pycnopsyche* did not show a significant difference between stations, although *Lepidostoma* did, with higher biomass per litter bag at Stations 3 and 4 than at 5, 6, and 7 ($p<0.0001$). In 1998, however, both genera showed differences. *Lepidostoma* had greater biomass at Stations 3, 4, and 5 than at all others ($p<0.0001$). Similarly, *Pycnopsyche* showed its highest biomass per litter bag

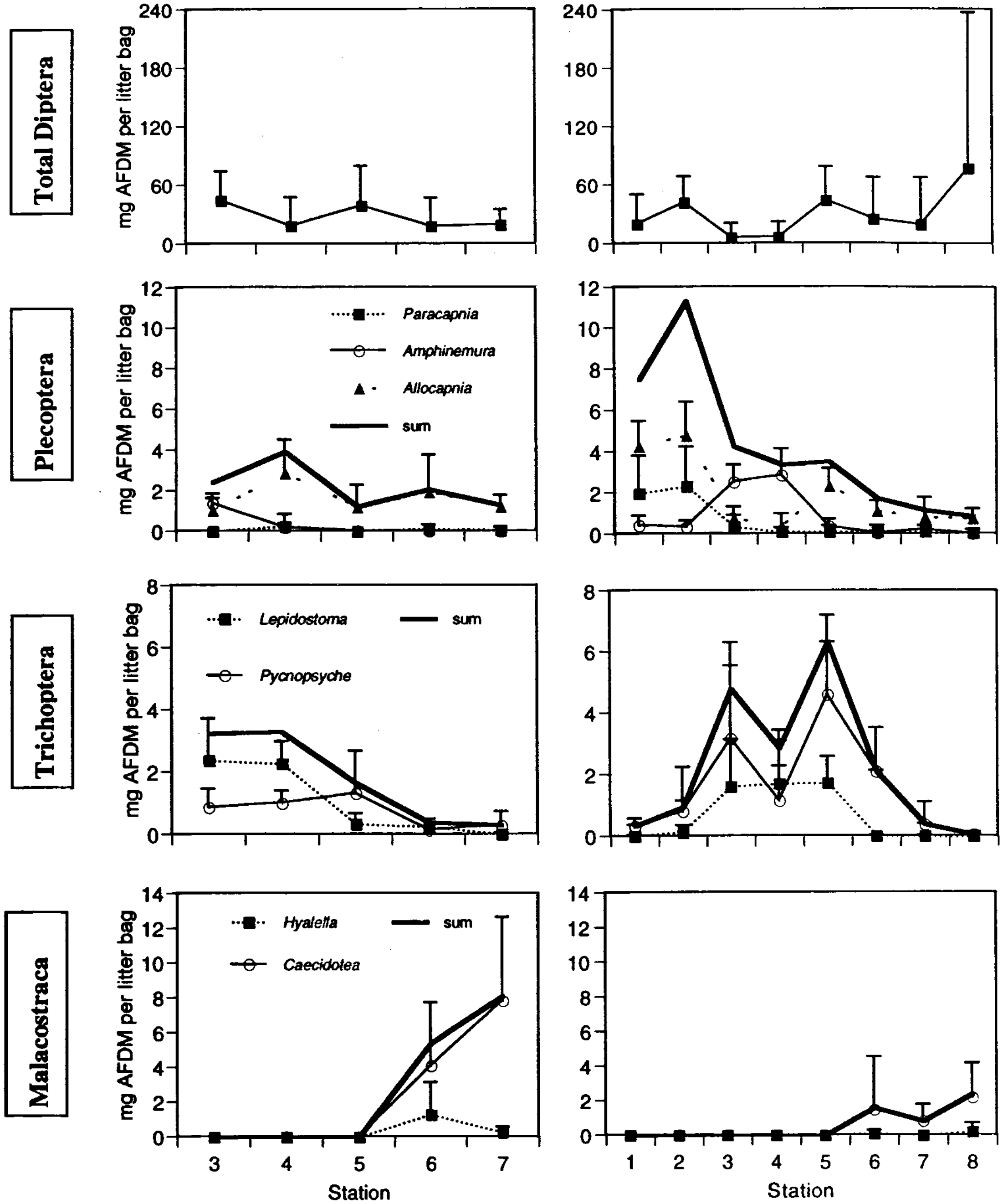

Figure 2.11. Shredder biomass by taxonomic group associated with leaf packs in Goosefare Brook, autumn 1997 (left) and 1998 (right). Plots show biomass of common shredder taxa along the pollution gradient. Diptera is predominantly (>95%) composed of *Tipula* (Tipulidae), with the remainder composed of *Brillia* (Chironomidae). Biomass is expressed as mg AFDM per litter bag. Error bars show +1S.E.

at Stations 3 through 6 ($p<0.0002$). Stations 3 and 5 have greater biomass than 1, 2, 7, or 8, while Stations 4 and 6 are not significantly different from these upstream and downstream areas, suggesting a decrease in *Pycnopsyche* in the channelized habitats. At the most impacted stations downstream of the industrial inputs, the dominant non-Diptera shredders were the Malacostracans *Caecidotea* and *Hyalella*, which were completely absent from litter bags upstream of Station 6.

Discussion

Community response to pollutants is determined by sensitivity of its members, their recolonization ability, and longitudinal variation in environmental conditions such as particle size and sediment organic matter content (Clements 1994). Loading with many chemical or physical impacts tends to lead to general declines in richness and abundance. In an artificial stream study, Kiffney and Clements (1994b) observed that pollution by multiple metals resulted in an overall reduction in macroinvertebrate abundance and diversity, and specifically decreased mayfly and stonefly populations, while increasing caddisflies and chironomids. In general, increasing pollutant levels have a decreasing rate of change on a community, as less tolerant taxa are eliminated and the resulting community is more resistant to further change (Clements 1997). The loss of taxa resulting from exposure to stress results in a simplification of stream communities and food webs. This can lead to changes in key ecosystem attributes, such as organic matter processing,

total energy flow and energy pathways, and resistance to additional stresses. These attributes are collectively known as biotic integrity (Fore et al 1996, Wallace et al 1996).

Habitat alteration by channelization or clearing of riparian vegetation related to road construction may result in a decrease in organic matter input and a decrease in litter retention due to reduced channel complexity and increased flow velocity. The channel is deepened and/or widened to increase its stormwater capacity, which in turn increases flow and erosion potential within the channel (Arnold and Gibbons 1996, Ellis and Hvitved-Jacobsen 1996, Booth and Jackson 1997). Channelization has been shown to reduce the amount of litter available to detritivores, as the increased flow, reduced complexity, and loss of retentive structures result in fewer naturally occurring leaf packs (Speaker et al 1984, Webster and Benfield 1986, Smock et al 1989). This is not accounted for by the design of the Goosefare Brook study, because litter bags were retained in the channel independent of retentive capacity. However, Gelroth and Marzolf (1978) observed a reduction in loss rates of leaves placed in channelized reaches when compared to unchannelized reaches in the same system, demonstrating that factors other than retention may affect the fate of leaf litter in channelized habitats.

Chemical pollution by nutrients or toxic substances presumably affects litter processing, although nutrients tend to accelerate processing, while toxins have the opposite effect. An insecticide application to a small stream reduced invertebrate biomass and halved the litter processing rate, demonstrating the effect that toxins may have on organic matter processing due to lethal effects on invertebrates (Chung et al 1993). Nelson (2000) did not find a reduction in processing in a high-altitude stream polluted by

Mn and Zn, suggesting that the level of toxic stress was insufficient to impair function, even though community structure was altered. No significant relationship between shredder abundance and litter processing was observed. A significant relationship between litter processing and land use was evident, but was attributed to elevated nutrient levels associated with agriculture and urbanization, rather than physical habitat changes. These studies suggest that flow rate and litter retention are only contributory factors to processing, and that physical and chemical stresses are also important, particularly if the shredder community is affected. In Goosefare Brook, changes were observed in the structure of the invertebrate community, with different detritivore taxa prominent in different parts of the habitat and pollution gradient. This did not translate into alteration of stream ecosystem function, as measured by litter processing rates. Rather, these rates were related to chemical habitat factors, including metal and nutrient concentrations, pH and alkalinity, and specific conductance.

Litter Processing

Litter loss rates showed decreases associated with increasing metal concentrations in both years, and also decreased in channelized habitats in 1998. The colder temperatures in 1997 may also have reduced differences observed in channelized habitats by decreasing shredder activity, thus increasing the relative importance of physical breakdown. Reduction in the leaf softening rate was not observed along the gradient of pollution in 1997, and minimal reduction was observed in 1998 when a greater range of

pollutant stress was examined. The softening rate at Station 8, which was channelized and had the highest sedimentary metal concentrations, was significantly slower than the unchannelized Stations 1 and 3 (Figure 2.5). While both processes were influenced by similar habitat factors (Figure 2.10), this suggests that litter softening is more resistant to stress than litter loss. Possible explanations of the decrease in nutrients in Goosefare Brook include uptake by observed blooms of iron bacteria, which were extensive downstream of the industrial inputs, or precipitation of nutrients with aqueous metals, as observed for phosphate by Duddridge and Wainwright (1980). The study of Huryn et al (2002) was conducted in streams with coarser substrate than Goosefare Brook, yet the role of nutrients and water chemistry was also prominent. That study showed loss rates comparable to those observed in Goosefare Brook in 1998, but not in the colder 1997.

Community Structure, Biomass, and Secondary Production

The effects of physical and chemical habitat characteristics on the rate of leaf litter processing are partially mediated through fungal and invertebrate assemblages, which may show decreases in biomass or richness associated with stress. Huryn et al (2002) found a significant relationship between shredder richness and leaf loss, but only a marginally significant relationship with shredder biomass. This supports the results seen in the laboratory study by Jonsson and Malmqvist (2000), in which the number and taxa of shredders present were less important than shredder richness in determining rates of litter loss. The relationship of litter processing rates to chemical habitat parameters such

as nutrients, pH, and heavy metal concentrations, rather than characteristics of the detritivore community, indicates that litter decomposition was controlled at a larger biotic scale than the measurements of community structure typically used in stream assessments. The changes in the structure of the biotic community that accompanied these ecosystem-level habitat changes are statistically significant (Figures 2.7-2.9, Figure 2.11), yet were apparently not related to processing rate of leaf litter.

In Goosefare Brook, alterations in the structure of the assemblages associated with the leaf packs in both a taxonomic and a functional context are evident, although few clear patterns exist that can be explicitly related to either physical or chemical habitat changes. In 1997, the proportion of biomass contributed by any of the taxonomic groups showed no changes in the portion of the pollution gradient studied (Stations 3 to 7), while in 1998 there was a replacement of Plecoptera with Chironomidae in the assemblage, and also a decline in Trichoptera at the most polluted stations (Figure 2.8). This is consistent with what was observed when biomass of individual shredder taxa was examined (Figure 2.11). The proportional biomass of shredders did not decline, although the biomass of individual shredder taxa changed significantly. Other groups, most notably the collector-gatherers, show changes in their importance in the assemblage, although most functional group changes show interaction between the pollution gradient and habitat (Figure 2.9). Perhaps the clearest trend is shown by the EPT metric, which shows consistent decline as these sensitive taxa are lost from the community (Figure 2.7).

At all stations the biomass of shredders in order Diptera, consisting almost entirely of larvae of *Tipula*, was not different between sampling years, and formed the

greatest proportion of shredder biomass (Figure 2.11). The Diptera at the most heavily polluted stations consisted of several large *Tipula* individuals, which accounted for more than 95% of the shredder biomass at Station 8. The mean biomass of each individual was more than twice the AFDM of *Tipula* individuals associated with leaf packs from the less impacted stations, although this difference was not statistically significant, possibly due to high variability and few specimens. The success of *Tipula* under stressful conditions is likely due to its inherent tolerance. To fully determine the influence of changes in shredder taxa on litter processing, differences in the feeding rates of the taxa under different levels of pollution stress needs to be examined. In this study, *Tipula* was dominant at all stations in terms of biomass, but other members of the shredder assemblage showed significant changes along the gradient. The progression from stoneflies through caddisflies to shredding crustaceans along the gradient represents apparent functional redundancy or replacement, although the loss of shredder richness has been shown to reduce litter processing rates (Jonsson and Malmqvist 2000). It is possible that the existence of competition for conditioned, accessible leaf litter prevents the pollution-tolerant shredder groups from dominating at less impacted sites.

A concurrent study of invertebrate secondary production in Goosefare Brook conducted in 1998-1999 provided further information about changes in the shredder community (CHAPTER III). Plecoptera and Malacostraca production showed a similar pattern to that seen in the litter bags, while Trichoptera did not, due to the high production of *Pycnopsyche* at Station 1 (Figure 2.12). *Tipula* also showed higher

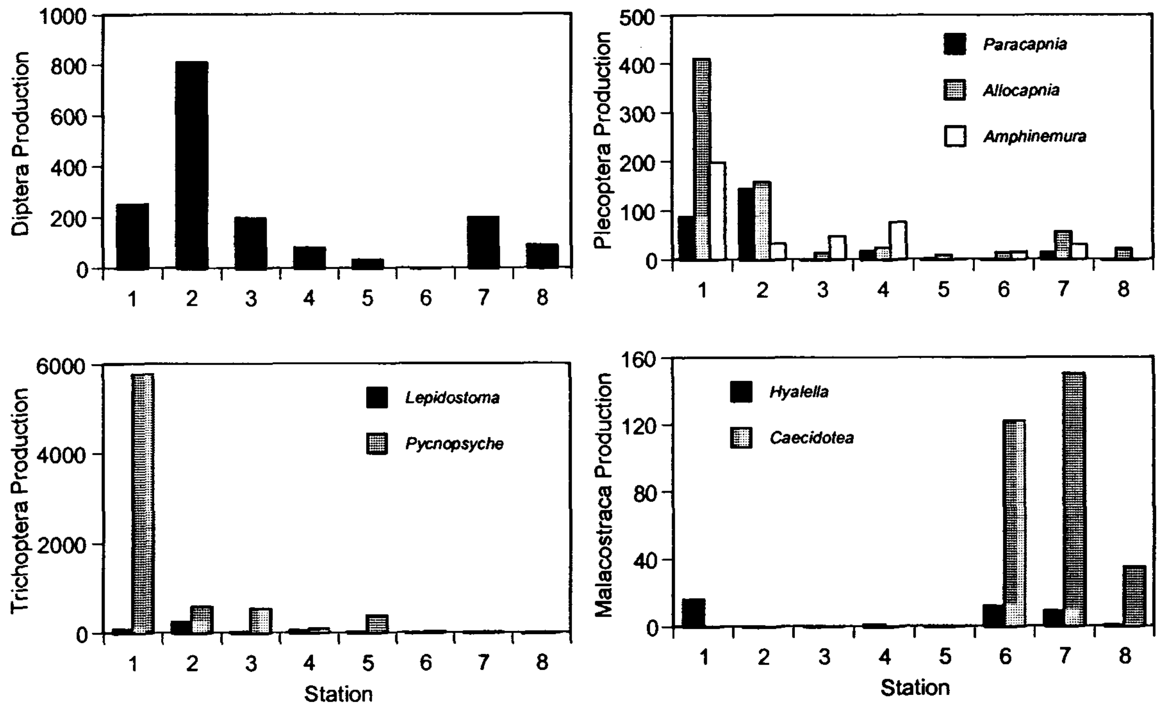

Figure 2.12. Annual secondary production of common shredder taxa in Goosefare Brook, 1998-1999. Values are expressed as mgAFDM/m^2/y.

production at the less impacted stations, although some increase was seen at Stations 7 and 8. However, *Tipula* did not dominate shredder production at any of the stations, whereas it accounted for most of the shredder biomass in the litter bags at all stations. It is possible that differences in life histories of the shredders contribute to the inconsistencies in annual production, since *Pycnopsyche* completes most of its growth subsequent to the litter bag incubation period, while the Plecoptera and Malacostraca are largest during the late autumn and winter. Also, a standard quantity of leaf litter was examined for each station in the litter bag study, while the production measurements depend on the quantity of leaves stored in the channel.

Ecosystem Effects and Assessment

The rate of energy flow in the ecosystem is the ultimate concern in the evaluation of impacts that affect processing rates of allochthonous organic matter. A decrease in the rate of decomposition could adversely impact many members of the community, whether it manifests as a decrease in litter softening, due to reduction in fungal growth or reproduction caused by the pollutants (Duddridge and Wainwright 1980, Abel and Barlocher 1984, 1988, Maltby et al 1995a), or reduction in litter loss due to alterations in the populations of shredders. Populations of invertebrates or fish that ultimately depend on detritivore activity for their own food source are also affected by factors that negatively impact litter processing, aggravating problems already being caused by pollutant toxicity. Rare taxa that are present in the community at low densities could

disappear entirely, or increase in abundance if they are tolerant. By reducing processing rates of leaf litter, all of these changes may ultimately lead to a decreased flow of energy in the system.

In Goosefare Brook, the gradient of pollution is potentially obscured by the channelization of the stream at some stations, although physical factors such as flow velocity were not found to be a strong predictor of litter processing rates. Elevated metal concentrations from runoff and industrial sources were associated with reduced softening and loss rates, although chemical variables other than pollution also appear to have an effect (Figure 2.10)

. The reductions in nutrient levels are not readily explicable based on the data, but have an interacting effect with increased metal concentrations in slowing litter processing. However, the increases in pH and alkalinity related to reduced processing rates may be caused by the passage of the stream through cement culverts near the roadway, and increased specific conductance may represent an increase in dissolved toxic substances that impair biotic processes. While more detailed study of the effects of water chemistry on these processes is necessary to identify specific mechanisms of impairment, the presence of a pollution gradient allows simultaneous comparison of many variables, in order to identify the sources and magnitude of stresses and their effects.

The examination of litter decomposition in Goosefare Brook demonstrates that stress-related changes in invertebrate communities are not necessarily accompanied by changes in ecosystem function. The apparent importance of different shredder taxa is dependent on the temporal scale of sampling (single-occasion litter bag samples versus

annual secondary production). The replacement of traditional bioassessment methods involving quantification of populations and translation of that information into metrics that represent the community is not likely to occur, due to concerns of cost, time, and ease of interpretation. However, the uncertainty in inferring functional characteristics from structual metrics necessitates the direct measurement of ecosystem-level responses (Schindler 1987, Clements 1997). It is essential to examine anthropogenic alterations to ecosystem function in order to develop an understanding of the true costs of disturbance and the benefits of conservation efforts.

Chapter III

EFFECTS OF A LONGITUDINAL GRADIENT OF PHYSICAL AND CHEMICAL HABITAT ALTERATION ON MACROINVERTEBRATE PRODUCTION IN A HEADWATER STREAM

Chapter Summary

In the analysis of aquatic ecosystems, functional variables are typically inferred from other measurements, such as water chemistry, suspended solid load, and community structural metrics. This study investigated the effects of physical and chemical habitat alterations on ecosystem function directly by examining patterns of macroinvertebrate secondary production and stored benthic organic matter along a gradient of heavy metal pollution and habitat channelization in Goosefare Brook, a first-order stream in southern Maine (U.S.A.). Whole-community invertebrate production decreased from 26.4 mgAFDM/m^2/y at the reference station to 1.1 mgAFDM/m^2/y at stations with the greatest levels of pollution. Production decreased along the pollution gradient for most taxa, although fewer taxa showed changes in response to habitat. Biomass turnover rates (P/B) were less affected by the stresses than production. Changes in functional structure of the community were evident at stations with channelized habitat, but overall production declined in a linear pattern that mirrored the increase in metals. Populations of taxa with documented pollution tolerance were more likely to maintain or increase production and P/B.

Introduction

Benthic organisms are important in the functioning of aquatic ecosystems because of their role in energy and nutrient processing (Webster and Benfield 1986, Maltby et al 1995a). Consequently, benthic invertebrate community structure is often analyzed to assess the effects of human activities on stream ecosystems (Rosenberg and Resh 1993). These analyses provide a wealth of information about water, sediment,and habitat quality because most benthic invertebrate communities contain a variety of taxa with diverse life cycles and generation times, representing several trophic levels and feeding behaviors (Rosenberg and Resh 1993). However, other ecosystem response variables such as primary and secondary productivity, nutrient and organic matter dynamics, and food web attributes are used less often in such assessments, but may provide greater understanding of ecosystem responses to stress (Wallace et al 1996, Shieh et al 1999). Although these parameters are rarely measured directly in stressed systems, they are sometimes inferred from less labor-intensive metrics based on instantaneous samples of biota, water chemistry, or suspended material.

The response of a population to chemical and physical habitat characteristics may be quantified using such parameters as mortality, growth, abundance, reproduction, development time, and standing stock biomass (Vannote et al 1980). Because it represents an integration of these attributes, secondary production is arguably an improved measure of the success of a population that provides a valuable process-oriented approach to bioassessment (Benke 1984, Lugthart and Wallace 1992).

Secondary production is the rate of formation of heterotrophic biomass (calculated as a product of population biomass and individual growth rate), and is an excellent indicator of the flow of energy through a given population or community (Benke et al 1988, Benke 1993). Measurement of production allows evaluation of growth and biomass turnover rates, which can improve understanding of the interaction of populations with each other and the environment through such processes as feeding and habitat use (Grubaugh et al 1997, Clements 1997).

A central goal of bioassessment is to understand the factors that control production of stream invertebrates, and the influence of human activities on these factors. Studies of process-level parameters have tended to focus on relatively undisturbed systems, and these measures have rarely been used in the ecological assessment of polluted systems. While some investigations of secondary production of macroinvertebrates affected by organic enrichment (Lazim and Learner 1986), agricultural land use (Sallenave and Day 1991), or acidity (Griffith et al 1993) have been conducted, and others have examined the effects of heavy metals on invertebrate biomass and community composition (Shieh et al 1999), none have examined whole-community production along a gradient of pollution and habitat alteration. A gradient design may be particularly useful in evaluating the ecological effects of stress, because it allows comparison of structure and function over a continuum of stress intensity (Cao et al 1997, DeLong and Brusven 1998).

This study investigated the effects of physical and chemical habitat alterations on ecosystem function by examining patterns of macroinvertebrate secondary production

and stored benthic organic matter along an impact gradient in Goosefare Brook, a first-order stream in southern Maine (U.S.A.). Stressors to this system include non-point sources of pollution in the form of road runoff from the Maine turnpike, point-source industrial discharges, and physical habitat alterations related to the presence of road crossings. Goosefare Brook provides an excellent opportunity to determine the nature and magnitude of human impacts on stream function, and to establish the relationship of process-level measurements to accepted methods of evaluating biotic integrity of small streams.

Study Site

Goosefare Brook is a small brownwater stream on the coastal plain of southern Maine. The study reach (Figure 3.1) is the first-order portion of the stream, within four kilometers of its source (43°32'N, 70°27'W). The stream drains the Saco Heath, a raised peatland, and flows east into the Atlantic Ocean. The banks of the stream are forested with oak (*Quercus* spp.), hemlock (*Tsuga canadensis* (L.) Carr.), and red maple (*Acer rubrum* L.), and there is a thick understory of ferns and herbaceous plants. The width of the stream channel varies from 1-3m, and average discharge ranges from a summer base flow of approximately 10 L/s to 100 L/s in the spring. Temperature was recorded hourly at two stations using Optic StowAway temperature loggers (Onset Computer Corporation, Bourne MA). During the study period, water temperatures ranged from

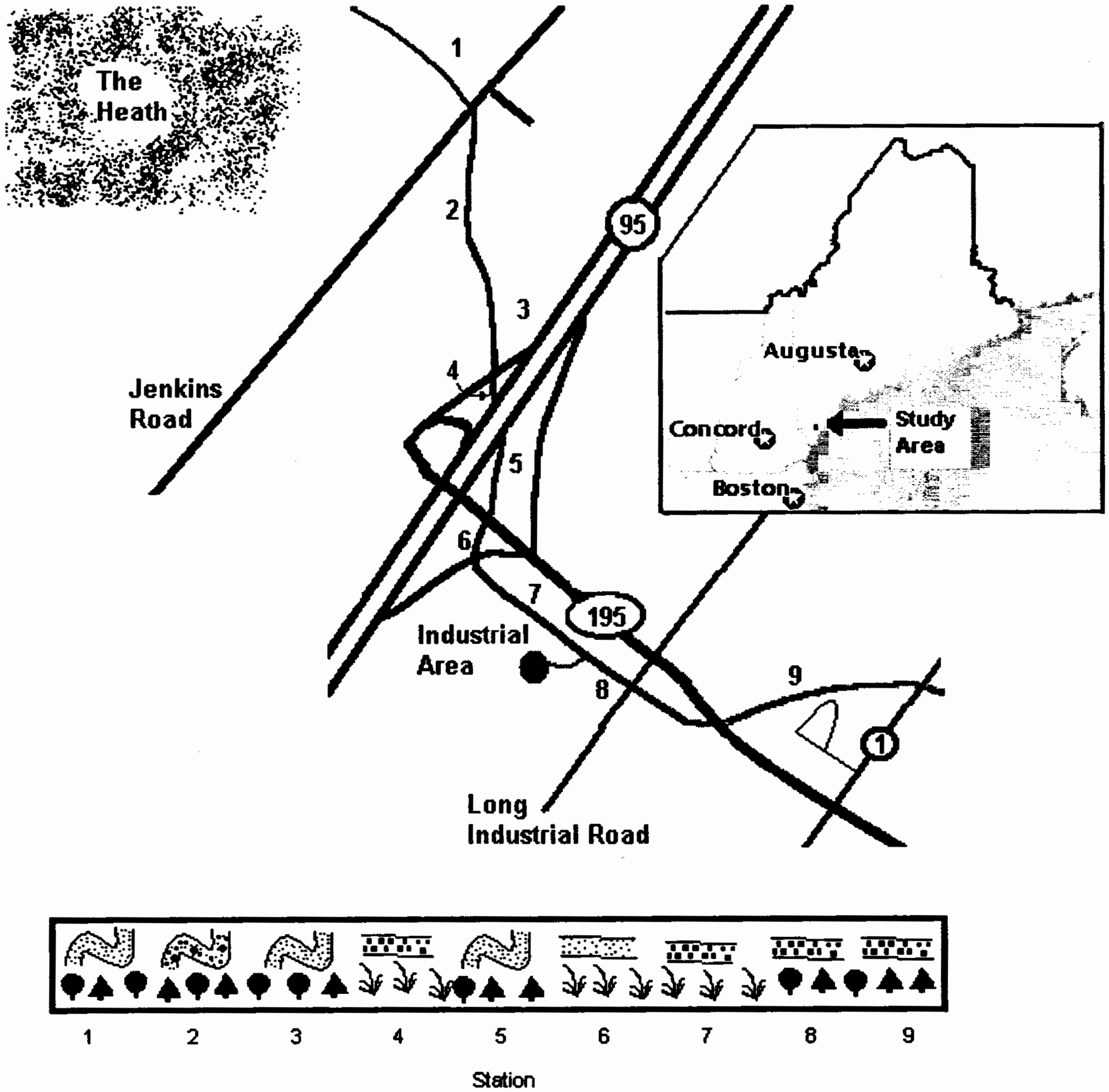

Figure 3.1. Schematic diagram of Goosefare Brook sampling stations, pollution sources, and habitat characteristics. Station habitat pictograms at the bottom of the figure indicate channel shape (sinuous vs. straight/channelized), substrate texture (sand/clay vs. cobble/boulder), and riparian vegetation (forested vs. cleared). See also Table 3.2 for more detailed habitat variables.

~0°C in the winter to a high of 20.2°C in summer. The annual mean was 7.5°C (Figure 3.2), and the accumulated annual degree-days (>0°C) was ~2207°C (April 7, 1998 to April 7, 1999). The channel form of the stream is low-gradient, meandering, and sandy, with frequent roots and woody debris incorporated into the streambed. In 1997, and subsequently in 1999 and 2000, pH was circumneutral during the summer months, but dropped to 4.0 or less in autumn as organic acids entered the stream from the Saco Heath. Inexplicably, this seasonal pattern did not occur in 1998.

The proportion of urban land use within the catchment doubles along the study reach (New England GAP Online Data, see CHAPTER III), although the level of urbanization does not exceed the threshold level determined to cause serious impact to Maine streams (Morse et al, *unpublished data*). Major alterations to the channel and riparian area have occurred in several places within the study reach due to drainage improvement, channelization, and clearing of riparian vegetation (Figure 3.1). Nine sampling stations were established in the study area. Station 1 serves as the reference station, being unaffected by known physical or chemical stressors from human activities, while each of the remaining eight stations is located downstream of a potential source of stress. Major chemical impacts on water and sediment quality occur in the form of runoff from paved highway surfaces and industrial sources located downstream of Interchange 5 of the Maine Turnpike (I-95).

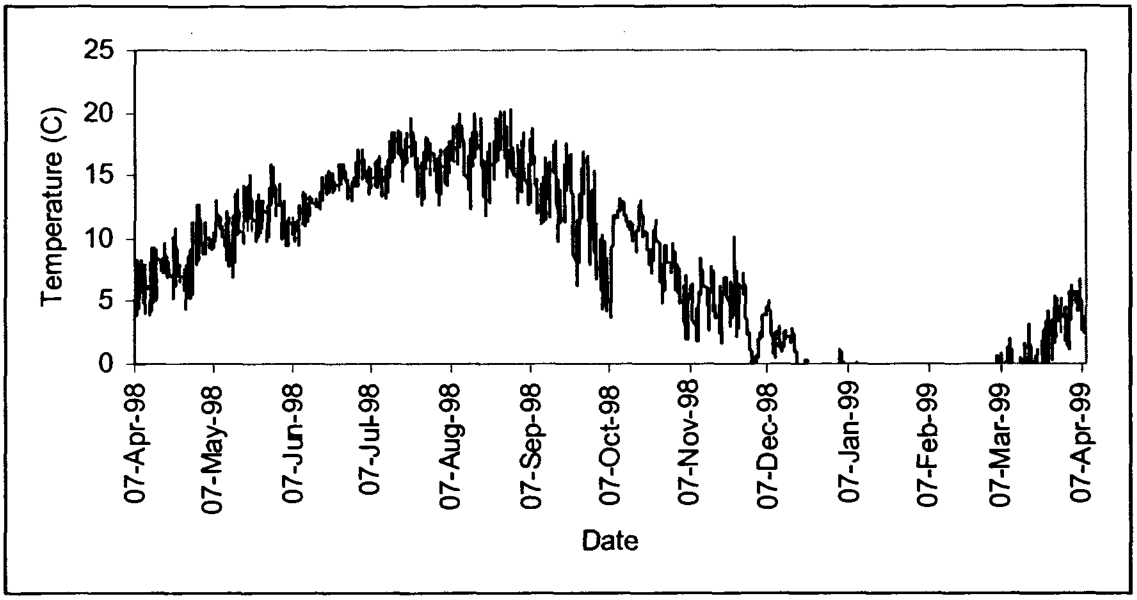

Figure 3.2. Hourly temperature record in Goosefare Brook, 1998-1999. The plot is an average value recorded by two data loggers, located at station 3 (upstream of Maine turnpike) and station 5 (downstream of Maine turnpike). Values recorded by the two loggers were typically <1°C apart.

Methods

Benthic Sampling and Invertebrate Production

Three benthic samples were taken from each station at randomly determined points (one each from the left, right, and center of channel) nine times between May 1998 and April 1999. Flow was measured using a Global flow meter (Global Water Instrumentation, Gold River CA) as close as possible to each point prior to sampling. An Ekman dredge ($0.0225m^2$) was used for sand, silt, and clay substrata, while a Surber sampler ($0.09m^2$, mesh size 250μm) was used for cobble/boulder substrata. Percent coverage of clay, sand, pebble, cobble, and boulder was estimated for each sample, and expressed using the modified Wentworth scale (ϕ - Cummins 1962). Samples were preserved in 10% formalin and returned to the laboratory, where they were rinsed through a 250μm sieve. Invertebrates were removed from the sample, preserved in 95% ethanol, and identified to the lowest practical level, typically genus (Wiederholm 1983, Thorp and Covich 1991, Merritt and Cummins 1996). Chironomids were morphotyped, and a subsample of each group was slide-mounted for generic identification. Body length of invertebrates was measured, and biomass was calculated using published length-mass relationships (Benke et al 1999). If an equation was not available for a taxon, the most similar taxon possible was substituted. Biomass was estimated as ash-free dry mass (AFDM).

Production was calculated using the size-frequency method (Benke 1984, 1993). Estimates were corrected for the cohort production interval (CPI) of each taxon (Benke 1979) and for unequal sampling intervals (Krueger and Martin 1980). The CPI estimate for each taxon was obtained empirically using length-frequency histograms of data collected in this study, or on the basis of published life history data from the most climatically comparable area available for each taxon. If low population density of a taxon made direct calculation impractical, production was estimated by multiplying mean interval biomass by the average annual production divided by mean interval biomass (P/B) of that taxon at all stations where calculations were possible, or by an assumed P/B of 5 (Benke 1984) if no station yielded a sufficient number of specimens.

Water and Sediment Chemistry

Sediment samples were taken at each station during benthic sampling by pressing a length of 1" PVC pipe into the substrate to a depth of ~2cm and transferring the collected material to a rinsed, acid-washed amber plastic bottle. This was repeated nine times (left, right, and center of channel at the same locations as the benthic samples) and composited in a single bottle. All samples were stored on ice until their delivery to the Maine State Analytical Laboratory (5722 Deering Hall, University of Maine, Orono ME, 04469-5722) for analysis. The water in the sample was analyzed for nitrate (NO_3-N), ammonium (NH_4-N), phosphate (PO_4-P), and pH, alkalinity, and specific conductance. A subsample of the sediment was analyzed for organic carbon content using a Leco TC/TN

analyzer. The remaining sediment was analyzed for eight heavy metals (Cd, Cr, Cu, Fe, Mn, Ni, Pb, and Zn) using a two-stage extraction. The first extraction was performed using 1M ammonium acetate at pH 7, and measured aqueous and weakly complexed metals. The remainder of the sample was then digested in nitric acid. The sum of the metal concentration in the two extractions is the total metal concentration for the sample. Details of this methodology are described by Say and Whitton (1983). Concentrations of NO_3-N and NH_4-N were determined using an Aplkem flow injection analyzer (detection limit 0.05 mg/L). Concentrations of PO_4-P were determined using Dionex I.C. (detection limit 0.01 mg/L). Heavy metal concentrations in sediment were determined using flame AA, with a replicate performed every 9 samples. All results were checked against external standards bracketing the expected concentrations.

Heavy metals obviously do not represent the totality of pollutants generated by either the roadway or industrial sources that affect Goosefare Brook. Other pollutants are deposited on highways, such as aliphatic and aromatic hydrocarbons (Fam et al 1987, Boxall and Maltby 1997) and de-icing salts (Demers and Sage 1990), that were not quantified in this study. The effects observed in the stream that are related to runoff from paved roadway surfaces are therefore not entirely due to toxicity of metals, but also include lethal and sublethal effects from these other stressors.

Benthic Organic Matter

From September 1998 to April 1999, organic matter in each benthic sample was separated into categories (wood, leaves, moss, macrophytes, and miscellaneous particulate organic matter), dried, and burned to obtain AFDM of organic habitat components. This period was chosen to bracket the maximum input of leaf litter.

Statistical Analysis

Exchangeable and total sediment metal content were compared between stations, as were those parameters expected to influence sedimentary metal concentrations (iron, manganese, organic carbon content, mean ϕ) (Combest 1991). Due to concerns of non-normality and inconstant variance between stations, observations for each concentration were ranked, and analyzed using Kruskal-Wallis analysis of variance. If significant differences were present, an *a posteriori* multiple comparison test was performed to determine differences between stations (Conover 1980).

Forward stepwise regressions (F to enter $\geq$4.0) were performed on measurements pooled from all stations to relate each metal variable to the sediment characteristics (Neter et al 1996). Transformation of the data was not required, because a diagnostic examination of residuals from univariate regression of each parameter revealed no serious deviations from normality or constant variance. Forward stepwise regressions were also used to relate interval standing stock biomass to exchangeable and total concentrations of metals, and to habitat characteristics (organic matter, flow, and particle

size), after transforming (ln(x+1)) all variables to satisfy assumptions of normality and constant variance.

Approximate 95% confidence intervals were calculated for annual secondary production using a bootstrapping technique (Huryn 1996). This procedure allows estimation of uncertainty in the data set, and also allows estimation of the probability distribution underlying the calculated parameters. The length-frequency data for each taxon that was sufficiently abundant were randomly resampled with replacement and the production calculation performed 1000 times. In cases where CPI estimation from the length-frequency histogram was unclear, a minimum and maximum value were estimated from the data. A CPI was then randomly chosen for each calculation in the bootstrapping procedure, such that these lowest and highest values respectively represented the 5th and 95th percentiles of a normal distribution. Total production and its associated error, and that of functional feeding groups, were estimated by summing the estimated vectors of all members of the group, producing a single vector of 1000 estimates for the entire group. Taxa for which the bootstrapping procedure was impractical typically represented a small proportion of total production, and a vector of 1000 identical values representing each taxon was added to the group mean when calculating confidence intervals of total feeding group and community production.

Canonical Correspondence Analysis (CCA, Rencher 1995) was used to investigate the relationship of invertebrate secondary production to sedimentary metal content and physical habitat variables. Only those variables that showed significant

between-station differences were used in the analyses. All variables were normalized prior to analysis.

Results

Sedimentary Metals

With the exception of Cd, all metals showed a significant increasing downstream trend in exchangeable concentration, total concentration (Cr, Cu, Ni, Pb), or both (Fe, Mn, Zn – Figure 3.3). The largest increases in metal concentration occurred between Stations 6 and 8. The major source appears to be related to the industry, although there is also evidence of roadway inputs. A significant increase in Zn downstream of the galvanized culverts is also evident. The total concentrations of Fe and Mn are the most common variables admitted to the stepwise regressions examining possible factors involved in sediment metal retention (Table 3.1). This is not surprising because many metals readily sorb to precipitates of iron and manganese (Dzombak and Morel 1990, Combest 1991, Lin and Chen 1998), and thus the correlation may be a combination of coincident input and increased retention by these precipitates.

Habitat Parameters and Benthic Organic Matter

Specific conductance followed a continuous increasing trend along the gradient (Table 3.2), with significant increases occurring at Stations 4, 5, and 8, which correspond

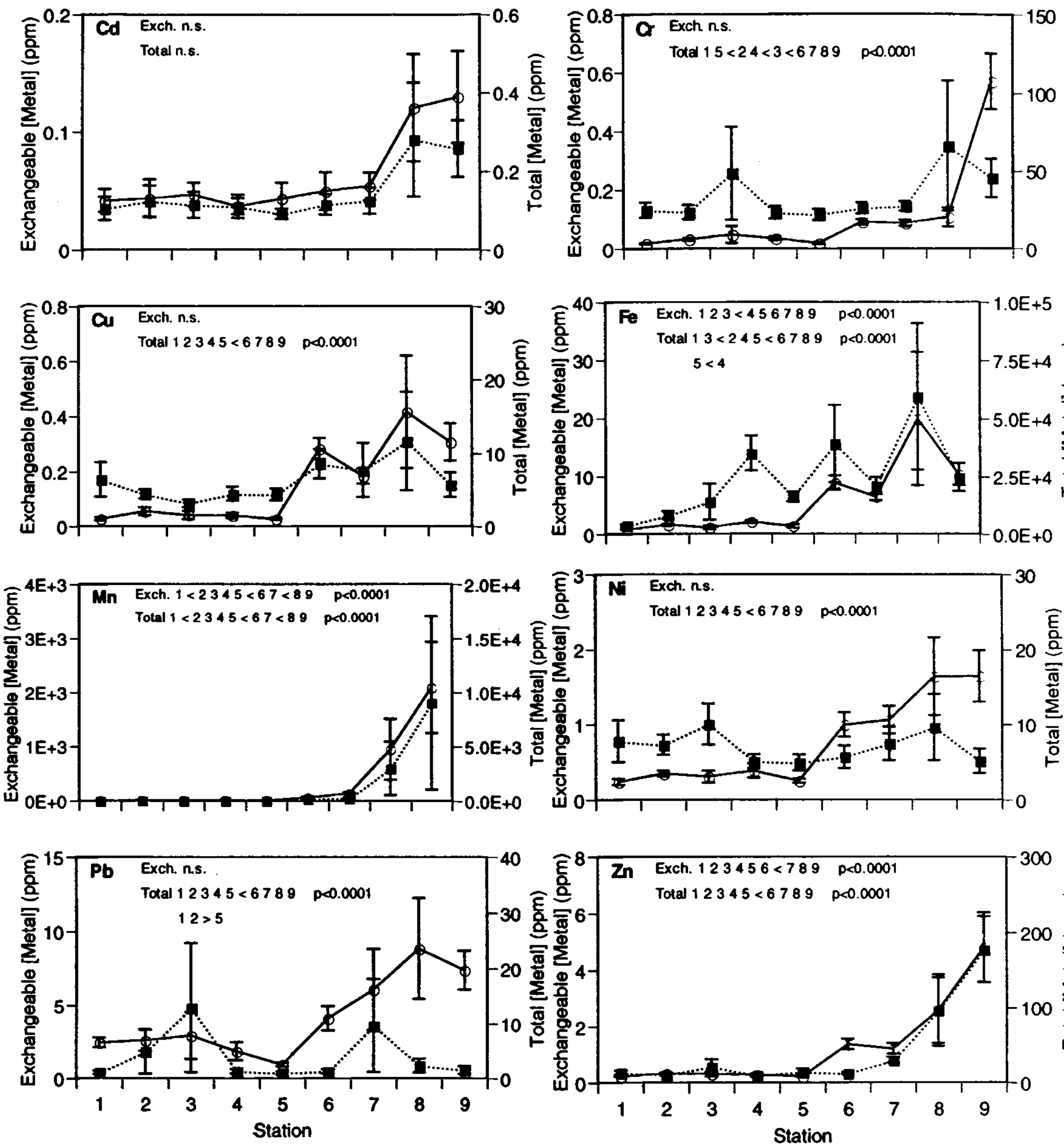

Figure 3.3. Total and exchangeable levels of eight metals in Goosefare Brook sediment samples, mean of nine composite samples taken between May 1998 and April 1999. Broken lines denote the exchangeable metal fraction, solid lines denote total metals. Error bars show ± 1 S.E. of the annual estimate. Concentrations expressed as mg/kg of sediment. Significant differences between stations, as determined by Kruskal-Wallis ANOVA, are presented for all concentrations measured ('n.s.' indicates no difference was found).

Exchangeable	Total Fe	Total Mn	Organic C	Mean ϕ	r^2
Cd	<0.0001	0.029	0.015	-	0.701
Cr	<0.0001	-	-	-	0.555
Cu	<0.0001	-	-	-	0.595
Ni	<0.0001	-	-	-	0.280
Pb	-	-	-	-	-
Zn	0.0001	<0.0001	-	0.002	0.844
Total					
Cd	-	<0.0001	-	-	0.387
Cr	-	<0.0001	-	0.039	0.479
Cu	<0.0001	0.0001	-	-	0.924
Ni	<0.0001	0.048	-	0.040	0.694
Pb	<0.0001	-	-	-	0.555
Zn	0.0006	0.011	-	-	0.917

Table 3.1. Variables admitted into univariate multiple regressions of metal concentrations on sediment characteristics. Numbers given are p-values of the sediment characteristic if admitted to the model, while the correlation coefficient is given for the entire model.

Parameter	Units	Station								
Water Quality		1	2	3	4	5	6	7	8	9
Specific Conductance	µS/cm	96 (10)	91 (7)	99 (7)	187 (14)	281 (38)	313 (31)	337 (39)	478 (50)	440 (44)
NO3-N	mg/L	0.20 (.03)	0.24 (.03)	0.30 (.03)	0.34 (.03)	0.26 (.03)	0.29 (.04)	0.28 (.06)	0.28 (.05)	0.17 (.02)
NH4-N	mg/L	0.12 (.02)	0.15 (.02)	0.07 (.02)	0.13 (.06)	0.10 (.03)	0.10 (.01)	0.11 (.01)	0.11 (.02)	0.13 (.02)
PO4-P	mg/L	0.03 (.02)	0.01 (.01)	0.01 (.0)	0.01 (.0)	0.10 (.09)	0.12 (.11)	0.03 (.02)	0.01 (.0)	0.01 (.0)
Mean pH	-	6.9 (.09)	6.8 (.11)	6.9 (.08)	6.6 (.10)	6.5 (.16)	6.9 (.14)	6.9 (.14)	6.9 (.14)	7.2 (.05)
Alkalinity	mgCaCO$_3$/L	20.1 (2.2)	17.4 (2.6)	19.4 (1.9)	14.3 (1.5)	16.1 (3.2)	26.1 (3.4)	24.4 (3.4)	26.6 (4.3)	54.1 (4.8)
Habitat										
Mean Flow	cm/s	12 (2)	19 (4)	20 (4)	26 (3)	14 (3)	10 (4)	40 (6)	44 (6)	31 (6)
Particle size	mean ϕ	2.0 (0.0)	0.06 (.27)	2.3 (.29)	-1.9 (.25)	1.9 (.05)	6.7 (.79)	-4.3 (.40)	-4.2 (.48)	-5.3 (.40)
Organic C	%	2.1 (.7)	2.2 (.7)	0.6 (.2)	0.4 (.1)	0.5 (.2)	0.4 (.1)	0.6 (.2)	1.5 (.5)	2.5 (.7)
Wood	gAFDM/m^2	438 (113)	232 (60)	349 (90)	143 (37)	296 (77)	69 (18)	26 (7)	81 (21)	0 (0)
Leaves	gAFDM/m^2	38 (10)	98 (25)	3 (.8)	11 (3)	14 (4)	9 (2)	11 (3)	7 (2)	2 (.5)
Misc. POM	gAFDM/m^2	555 (143)	223 (58)	164 (42)	31 (8)	186 (48)	67 (17)	21 (6)	41 (11)	7 (2)

Table 3.2. Water quality and physical habitat data for Goosefare Brook sampling stations, 1998-1999. Water quality measurements were taken from water included in sediment samples. Values repesent the mean of all measurements taken during the year, and standard error is shown in parentheses as a measure of variability within the year. Sedimentary metal concentrations are found on Figure 3.3.

to the stream entering the turnpike interchange, crossing the main artery of the turnpike, and receiving industrial effluent, respectively (Figure 3.1). Phosphate (PO_4-P) and alkalinity showed some longitudinal variation, but no clear correlation with potential sources of impact. There was no significant pattern in annual means of nitrate (NO_3-N), ammonium (NH_4-N), or pH along the gradient of impact.

Physical habitat parameters also showed significant differences, but were related to habitat type rather than to position along the gradient. Flow velocity and particle size (ϕ) differed between channelized and unchannelized stations (Table 3.2), and were strongly correlated with each other (r^2=0.88). Stored particulate organic matter (POM), wood, and leaves showed a decreasing trend along the gradient, although higher levels were evident in unchannelized habitats. Organic carbon content of the sediment showed peaks at either end of the gradient. The high levels at Stations 1 and 2 are due to stored POM, while the higher levels at Stations 8 and 9 are due to accumulations of iron bacteria (T.S. Woodcock, *personal observation*), similar to those described by Vuori (1995) for systems with high iron levels. Total stored organic matter was lower in channelized habitats than in unchannelized habitats. Channelized habitats had significantly less wood than unchannelized habitats, suggesting a lower retentiveness for other types of organic matter (Smock et al 1985). However, benthic organic matter storage showed a more linear change along the gradient of impact than physical habitat variables, such as particle size and flow velocity.

Macroinvertebrate Biomass and Community Structure

A total of 151 invertebrate taxa were identified from Goosefare Brook. Sufficient data were obtained to support bootstrapped production estimates for 70 taxa. Per-sample richness was significantly higher at Stations 1 (reference station) and at Stations 2, 4 and 7 (channelized habitat), but did not show a distinct correlation to the pollution gradient (Figure 3.4). However, counts of all taxa collected over the entire year are were fairly constant, with no obvious decreases except at Station 8. Exchangeable and total concentrations of all metal species examined (mean value for sampling interval) were negatively correlated with the interval macroinvertebrate biomass pooled across all stations and sampling events. The forward stepwise regression showed four variables admitted to a model predicting standing stock biomass from metal concentration (model r^2=0.76) (Figure 3.5).

Secondary Production and Functional Structure

Organisms for which direct calculation of production was possible contributed a mean of ~70% of the community production at each station (Appendix A). Total community secondary production decreased downstream along the gradient of impact, and the stations exhibited four distinct levels of decreasing production depending on their location, as determined by comparison of whole-community 95% confidence intervals (Figure 3.6). Station 1 formed the first level, and represents the apparent reference condition. Stations 2 and 3 are located between Jenkins Road and the turnpike. Stations 4

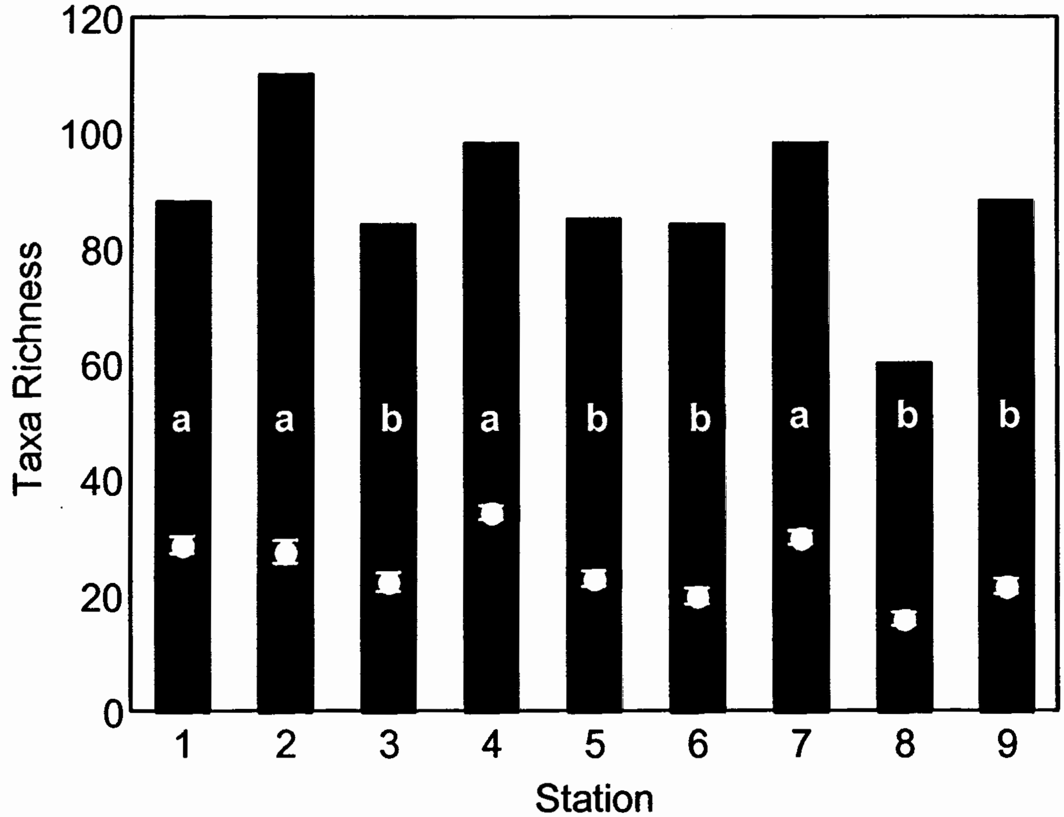

Figure 3.4. Macroinvertebrate taxonomic richness in Goosefare Brook, 1998-1999. Bars denote total number of taxa collected at the station in all 27 samples taken during the course of the year. Points within the bars show mean richness per sample, ± 1SE. Stations with mean interval richness that is not significantly different share the same letter.

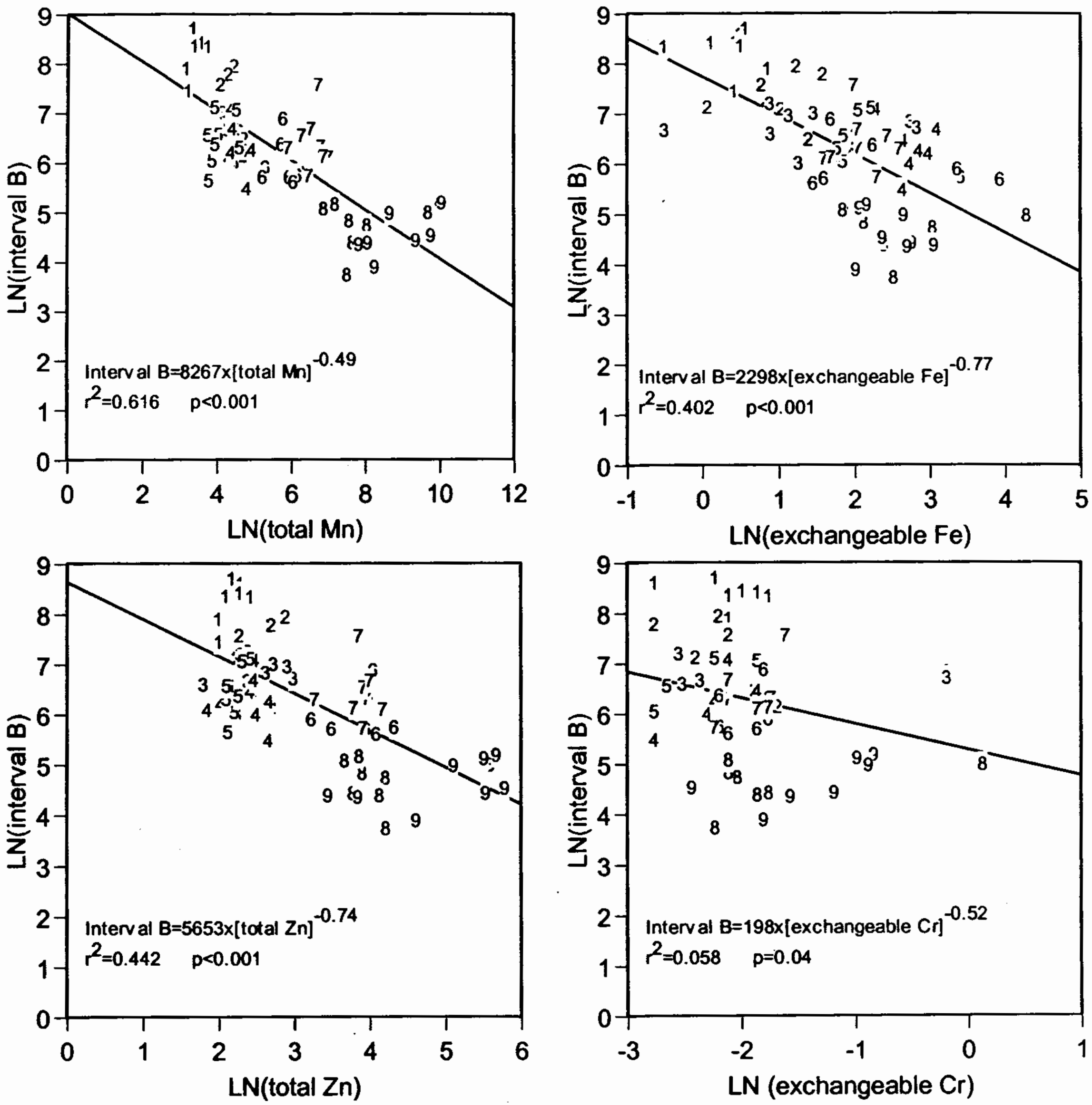

Figure 3.5. Single-variable regression models of metal concentrations and biomass (B) for each sampling interval, based on admission to a forward stepwise multiple regression model including all exchangeable and total metals. Interval B expressed as mgAFDM/m^2, metal concentrations as mg/kg. All variables were ln(x+1) transformed prior to analysis. Data points are numbered by station, and equations are based on untransformed data.

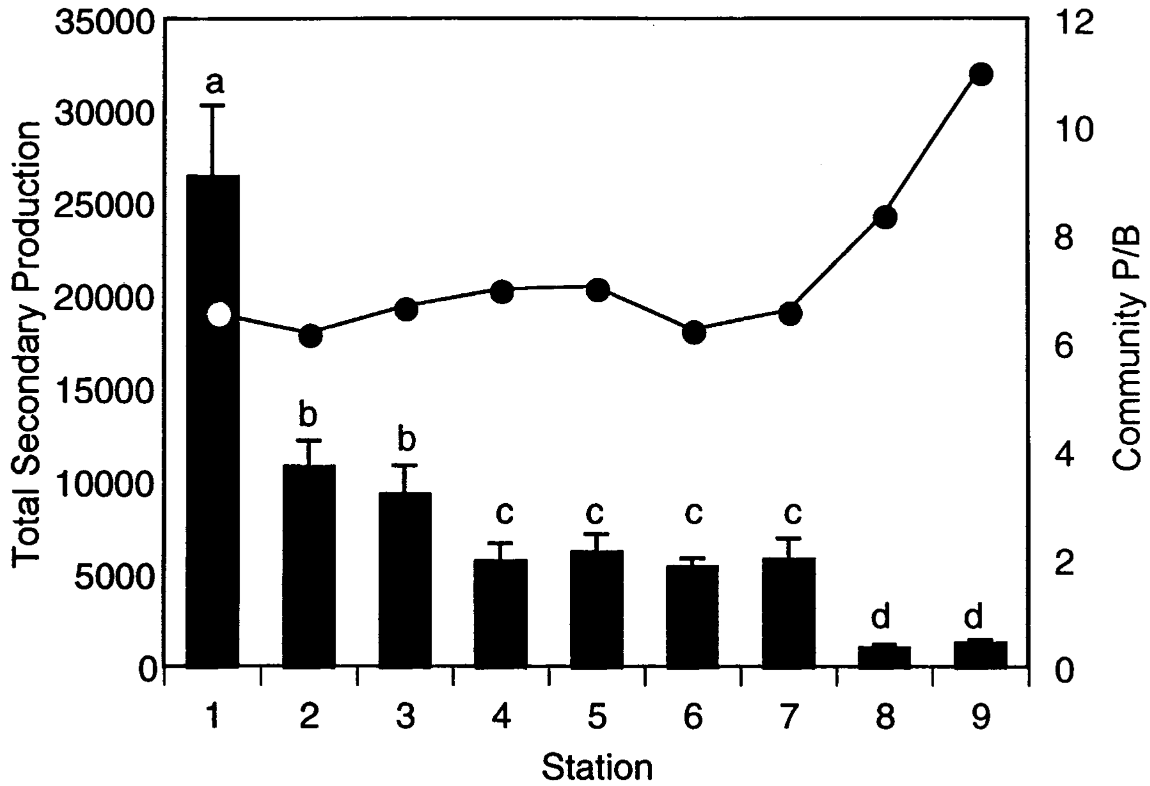

Figure 3.6. Total community secondary production (bars) and biomass turnover (P/B-line) for Goosefare Brook, 1998-1999. Secondary production is expressed as mg AFDM/m^2/y (+95% confidence interval). Production at stations sharing the same letter are not significantly different from one another, as determined by comparison of bootstrapped 95% confidence intervals.

through 7 are associated with the interchange, while the final level occurred at Stations 8 and 9, which received industrial effluent. The group formed by Stations 8 and 9 show an increased whole-community biomass turnover, due to the increasing proportion of small, fast-growing collector taxa (chironomids) in the community (P/B - Figure 3.6) (Kedzierski and Smock 2001). The linear decrease in total community production along the gradient was not clearly related to flow velocity or particle size (Figure 3.7). Flow velocity and particle size both tended to be greater in the channelized habitats, and thus had multimodal patterns along the study reach. Benthic organic matter, however, had a more linear decrease along the study reach, and was correlated with total production in addition to interval biomass.

Taxa can be assigned to functional feeding groups based upon their major sources of nutrition (Merritt and Cummins 1996). All feeding groups showed a significant decrease in production along the gradient of impact (Figure 3.8). Scrapers and piercing predators accounted for a small proportion of the production at all stations, and both showed a significant decline, particularly downstream of the turnpike. Engulfing predator production was significantly higher in unchannelized habitats, reflecting the abundance of *Lanthus* and *Cordulegaster* (Odonata) on sand. Production by shredders and FPOM collectors (gatherers and filterers) dominated other primary consumers at all stations. Absolute shredder production declined downstream of the reference station. The proportion of shredder production declined downstream of Station 2, suggesting that energy flow through this group may be impaired even at a relatively low level of stress. Gathering and filtering collectors declined in total production, but made up an

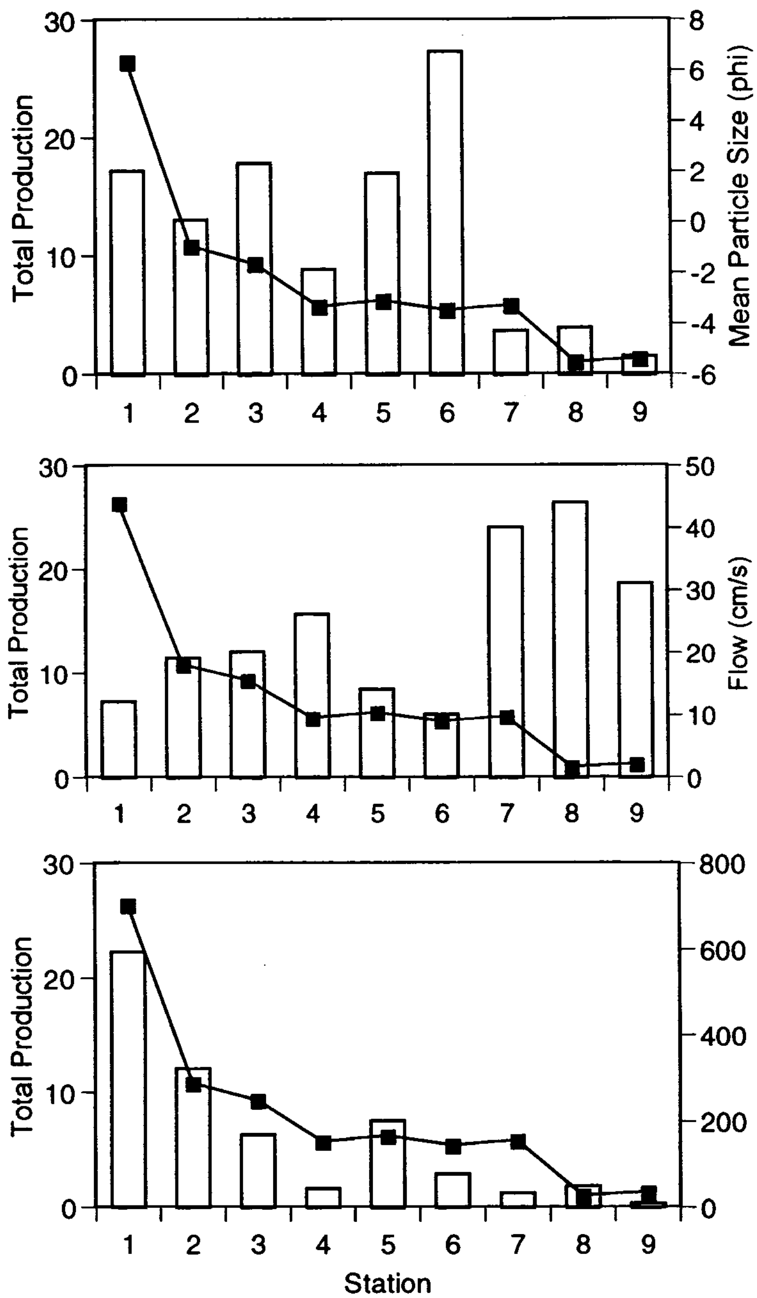

Figure 3.7. Plots of total macroinvertebrate production (lines) against physical habitat variables (bars) for Goosefare Brook, 1998-1999. All masses are expressed as g AFDM/m^2/y.

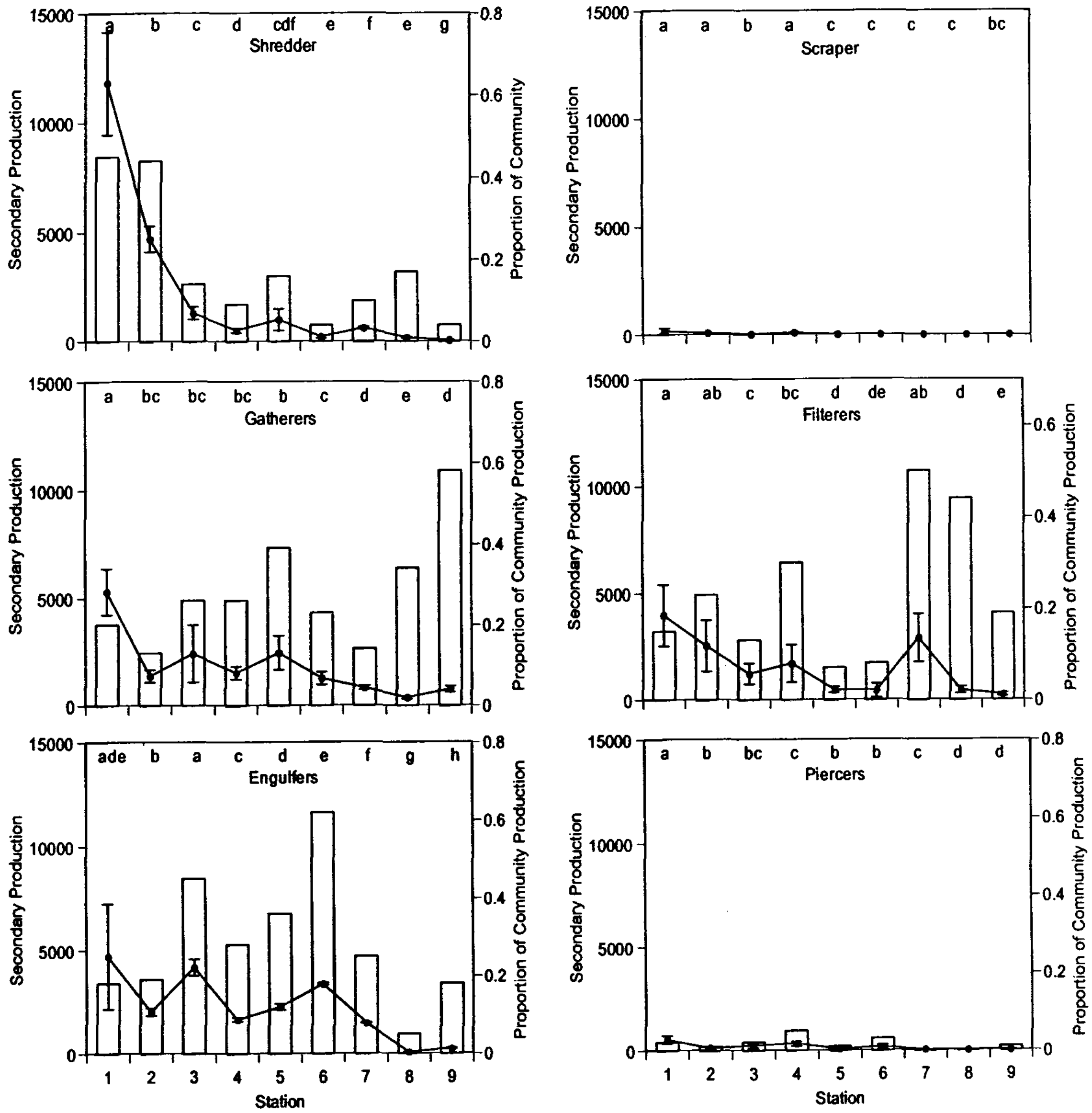

Figure 3.8. Secondary production of functional feeding groups at Goosefare Brook sampling stations, 1998-1999. Bars denote the proportion of total community production accounted for by that functional group, while lines show total production ($\pm$ 95% confidence interval). Stations sharing the same letter are not significantly different from one another in total P (mgAFDM/m^2/y, as determined by comparison of bootstrapped 95% confidence intervals). The proportion of scraper production is not shown, since at all stations it was <1% of the total. Y-axes are the same in all panels in order to show relative importance of the feeding groups.

increasingly greater proportion of the community along the gradient of stress. An interaction with habitat is apparent, with gatherers dominating the collector community in slow-flowing habitats and filterers in fast.

Canonical Correspondence Analysis provides further information about the interacting effects of habitat and sediment quality on secondary production. In the CCAs of production data, the habitat variables used were mean ϕ, flow, sediment organic carbon content, leaves, wood, and particulate organic matter. The sedimentary metal concentrations used were total Fe, Mn, Cr, Cu, Ni, Pb, and total and exchangeable Zn, based on significant differences in the Kruskal-Wallis analysis. The resulting plots of the taxa and stations in multivariate space were similar, with the two axes accounting for 62.2% of variability in the habitat CCA (Figure 3.9), and 65.2% in the metals CCA (Figure 3.10). In the habitat CCA, the flow vector is oriented opposite to small particle size and organic matter retention. In the metals CCA, all metal vectors oriented toward the downstream stations, and in the direction of large particle size and fast-flowing habitats. This shows that there is a correlation between altered habitat and pollutant load, although the less polluted stations (2 and 4) are closer to the origin, and do not have metal levels as high as stations 7 and 8. The position of Station 9 is somewhat anomalous, and may be a result of the boulder/bedrock channel form not being comparable to the others either in organic matter or metal retention.

Examination of the arrangement of production by taxon in multivariate space reflects the patterns seen in the distribution of functional feeding groups. Shredders show a tendency to cluster in areas of the highest organic matter (Station 1), although the

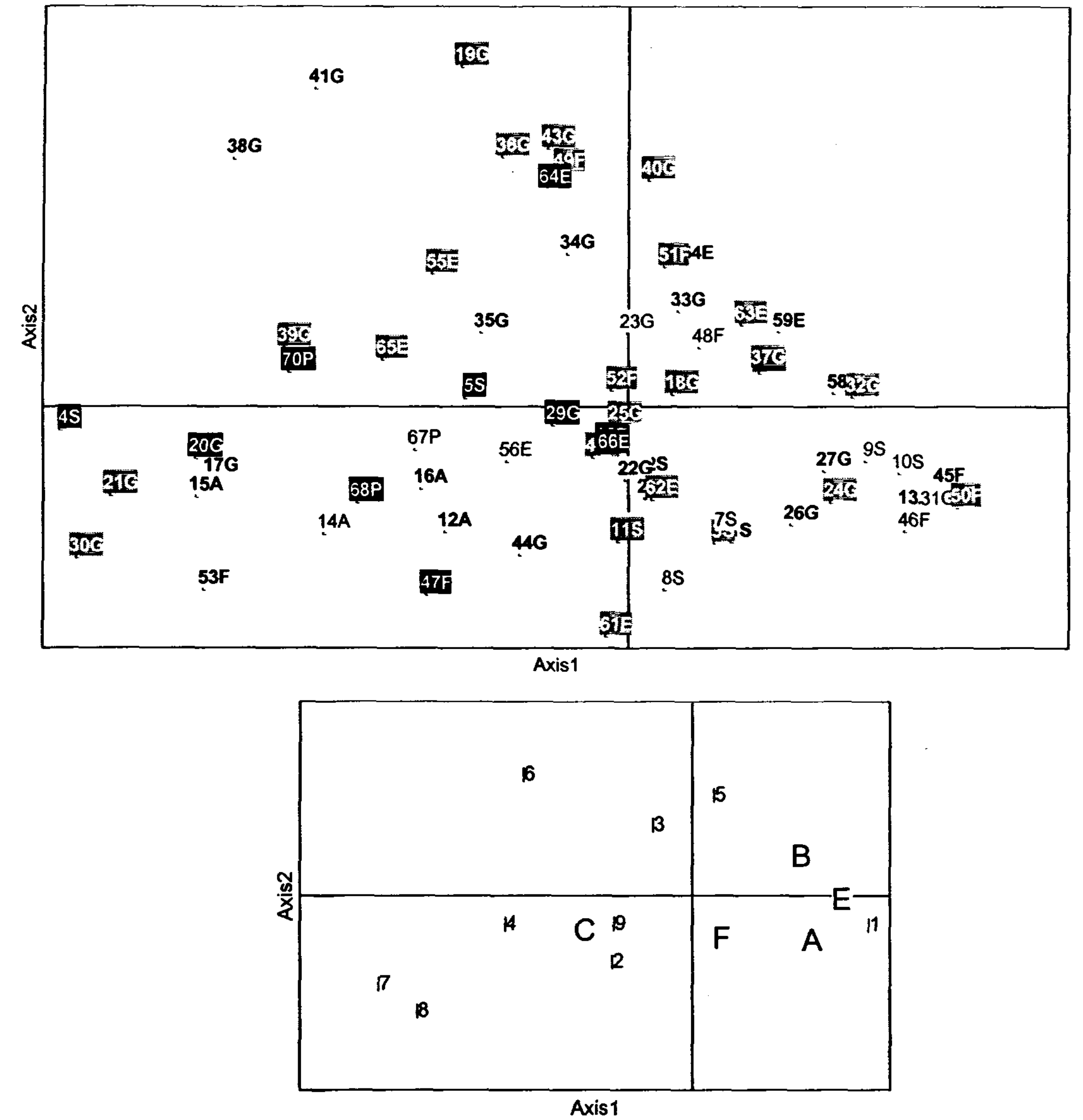

Figure 3.9. Canonical Correspondence Analysis plots of annual secondary production by taxon, as explained by habitat parameters. Codes denote the position of each taxon, its NCBI score (Lenat 1993 – normal type 0.0-2.5, bold type 2.6-5.0, grey hilight 5.1-7.5, black hilight 7.6-10.0) and its functional feeding group (S-shredder, A-scraper, G-gatherer, F-filterer, E-engulfing predator, P-piercing predator – taxon codes are listed in Appendix II). In the lower panel, explanatory vectors stretch from the origin to the code for that parameter (actual vectors are not included in order to minimize obscuring of data points). The codes are sediment organic carbon content (A), particle size (B), flow (C), wood and particulate organic matter (E), and leaves (F). Numbers in the lower panel show the position of each station relative to these habitat parameters.

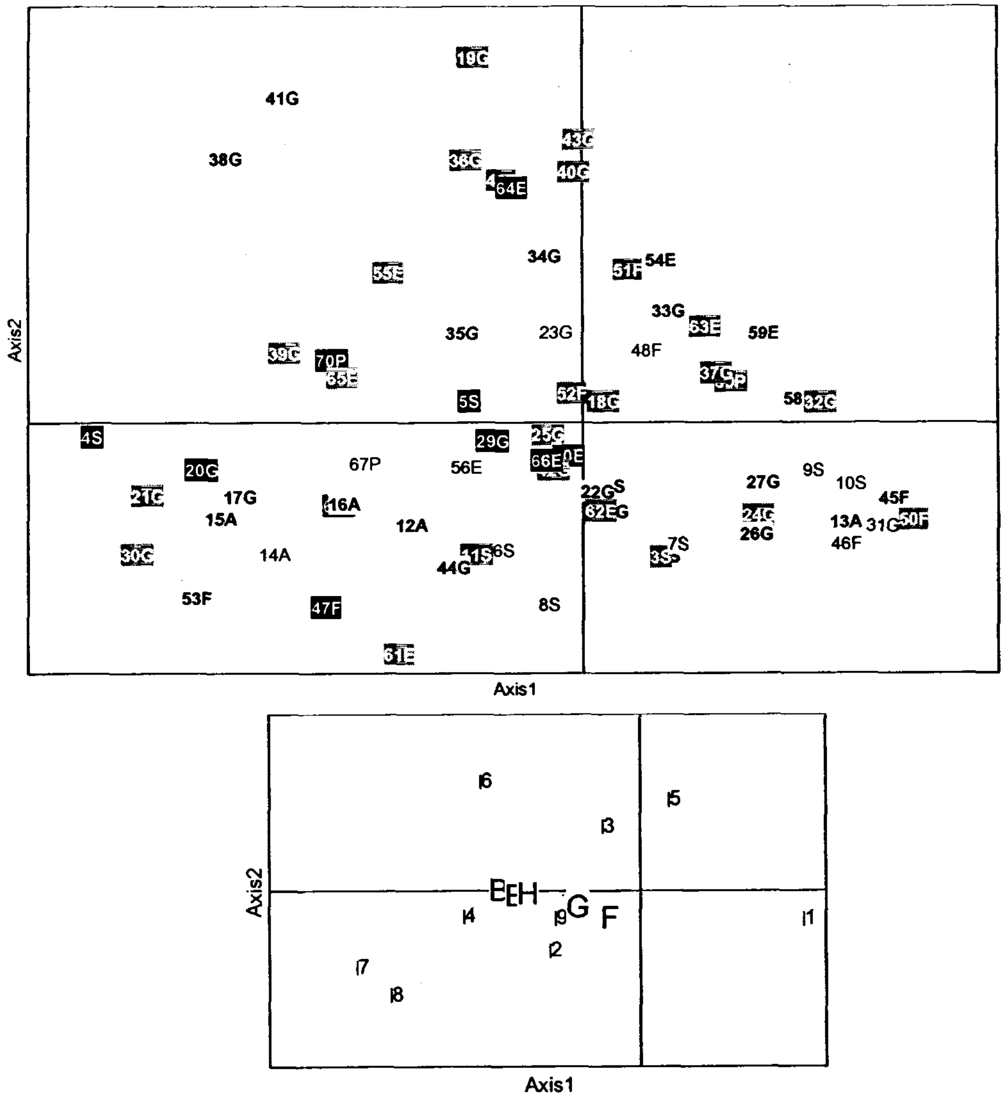

Figure 3.10. Canonical Correspondence Analysis plots of annual secondary production by taxon, as explained by sedimentary metal concentrations. Codes denote the position of each taxon, its NCBI score (Lenat 1993 – normal type 0.0-2.5, bold type 2.6-5.0, grey hilight 5.1-7.5, black hilight 7.6-10.0) and its functional feeding group (S-shredder, A-scraper, G-gatherer, F-filterer, E-engulfing predator, P-piercing predator – taxon codes are listed in Appendix II). In the lower panel, explanatory vectors stretch from the origin to the code for that parameter (actual vectors are not included in order to minimize obscuring of data points). The codes are Fe, Mn (B), Cu, Cr, Ni (E), Pb (F), and exchangeable (G) and total (H) Zn. Combination of vector labels is necessary due to coincident vectors representing correlated metals. Numbers in the lower panel show the position of each station relative to these habitat parameters.

pollution-tolerant shredder *Caecidotea* has a downstream bias. Scrapers, filterers, and gatherers (i.e. *Diplocladius*, *Eukiefferiella*) cluster at channelized stations at the downstream end of the pollution gradient. Pollution-tolerant slow-water gatherers (i.e. *Cryptochironomus*, *Paratendipes*, *Psectrocladius*) cluster near Station 6. In addition, a shift in production from coarse particle feeders to fine particle collectors is evident along the gradient.

Comparisons of pollution tolerance among taxa were made using the North Carolina Biotic Index (NCBI - Lenat 1993), in which taxa are assigned scores between 0 (most sensitive) and 10 (most tolerant). For the purposes of this study, these scores were assigned to four groups (0-2.5, 2.6-5.0, 5.1-7.5, and 7.6-10.0), represented by the colour codes in Figures 3.9 and 3.10. The replacement of intolerant taxa by others in the same functional feeding group represents some level of redundancy within each group, although a change in function must occur with the decrease in shredder production. Production of all taxa in the most tolerant group cluster at stations with channelized habitat, increased sedimentary metal concentrations, or both. Members of the most sensitive group cluster near Station 1, although they are more dispersed across the plots than the tolerant taxa. Those taxa with intermediate tolerance levels do not show clear relationship with either habitat or metals.

Discussion

The response of community structure to pollutants is determined by sensitivity of its members, their recolonization ability, and longitudinal variation in environmental conditions such as particle size and sediment organic matter content (Clements 1994). Loading with many chemical or physical impacts tends to lead to general declines in richness and abundance. Many studies have documented the relationships of community structure to chemical pollution (Clements et al 1988a, 1990, Clements 1994, Kiffney and Clements 1994a) and land use (Casper 1994), typically observing decreased mayfly and stonefly abundance and richness, an increase in collector-gatherers such as chironomids, and an overall reduction in macroinvertebrate abundance and diversity. Similar changes were observed in Goosefare Brook, with a decrease in sensitive EPT taxa, an increase in the role of collectors, and a general decline in invertebrate productivity. This decline in community production is important in characterizing the response of Goosefare Brook to pollution stress.

Estimates of whole-community production in lotic systems are typically 5-10 $g/m^2/y$, and values greater than 100 $g/m^2/y$ or less than 3 $g/m^2/y$ are rare (Huryn and Wallace 2000). Production estimates for a 1^{st} – 7^{th} order southern Appalachian river continuum varied between 5 and 154 $g/m^2/y$, with higher order streams having higher production and less stored organic matter than the headwaters (Grubaugh et al 1997). Few whole-community production estimates are available for low-gradient coastal plain

streams in the United States, and none in the northeast. Such streams have been found to be very productive in the warm southeast, particularly those with abundant snag habitats (Benke et al 1984, Benke 1998). The northernmost estimates previously available for low-gradient sandy streams are from Virginia. In a second-order stream, Smock et al (1985) found habitat-weighted production values up to 4.11 $g/m^2/y$. Kedzierski and Smock (2001) estimated 41 $g/m^2/y$ in an unlogged reach of a low-gradient stream. These estimates show that the productivity of these systems vary over an order of magnitude. Goosefare Brook has a comparable level of production at the reference station (26.4 $gAFDM/m^2/y$), despite latitudinal differences.

Production in Goosefare Brook sharply decreases with increasing intensity of human activity. This decline in productivity over such a short distance indicates an ecological impairment due to human activities in the catchment. While considerable changes in production may be expected over a gradient of several stream orders (Wohl et al 1995, Grubaugh et al 1997), the ~96% reduction observed within 4km of the 1st order reach of Goosefare Brook was not expected and is not likely attributable to naturally occurring changes. Furthermore, the studies of Wohl et al (1995) and Grubaugh et al (1997) show that community productivity tends to increase in higher stream orders within a system, rather than decrease as it does in Goosefare Brook. When production at each of the 9 stations is compared with 58 whole-community production estimates from around the world (Figure 3.11, data summarized from Benke 1993) it is apparent that secondary production in Goosefare Brook drops from average productivity to remarkably low

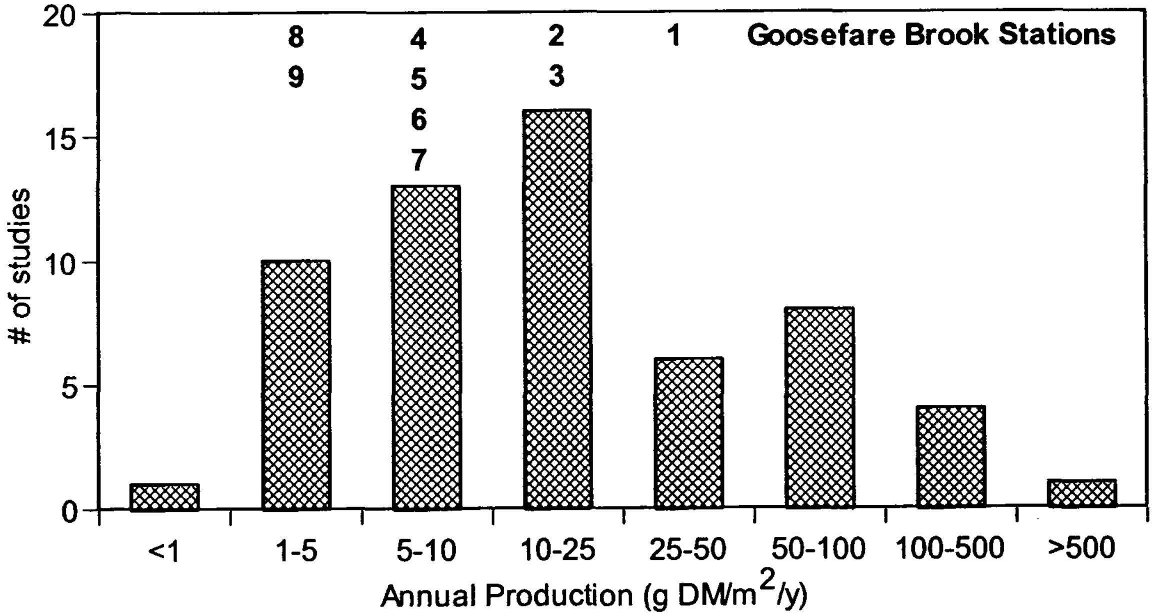

Figure 3.11. Summary of worldwide whole-community production estimates from Benke (1993), showing the location of Goosefare Brook sampling stations. A conversion factor was used to express all values as dry mass (DM) for the purposes of this comparison (DM=1.11 x AFDM, Benke 1993).

productivity over a short distance, and this reduction is correlated with the gradient of sedimentary metal concentrations.

Changes in the roles of functional feeding groups are also evident over the gradient of impact (Figure 3.8). All functional feeding groups show a significant linear decline in total secondary production along the gradient, demonstrating the general effects of toxic substances on most organisms. However, the proportions contributed to the whole-community estimate by shredders decreases, while the proportions of both gathering and filtering collectors increases. These changes show an interaction with habitat, particularly for the collectors, with gatherers contributing proportionally more production in unchannelized habitats, and filterers more in channelized habitats. The loss of shredders, increasing production by collectors and predators, and decrease in stored organic matter are similar to patterns observed along gradients of habitat less affected by human activities over several stream orders (Wohl et al 1995, Grubaugh et al 1997). Nevertheless, the changes in the proportional roles of the functional feeding groups is more often accompanied by an increase in whole-community production at higher stream orders (Benke 1993), rather than the decrease evident in Goosefare Brook along the gradient of stress.

Stress Tolerance and Control of Production

Effects of stress may be grouped into lethal and sublethal categories. Both act on individuals, but the additive results have implications for higher levels of ecological organization (Clements 1997). Lethal effects result in a decrease in abundance and biomass, and possibly elimination of the population. Sublethal effects may also decrease standing stock, for instance by decreasing growth rates and therefore the accumulation of biomass, or by stimulating drift (Crowther and Hynes 1977, Lugthart and Wallace 1992, Courtney and Clements 1998). However, sublethal effects generally reduce production by diverting energy from feeding and growth into pollution tolerance mechanisms. These tolerance mechanisms may involve increases in metabolic costs associated with respiration and the manufacture of metallothionein proteins required in metal tolerance, with the result that less energy is devoted to tissue production (Wicklum and Davies 1996).

A decrease in P/B for a given population suggests a sublethal effect on production of individuals by that stress, because energy that would otherwise be used for growth is diverted into the tolerance response of the organism (Wicklum and Davies 1996). An increase, particularly in tolerant taxa, is more difficult to explain. It is possible that the population is released from competition for resources by effects on less tolerant taxa, allowing higher growth rates. Bootstrapped confidence intervals for production and P/B were compared along the pollution gradient and between channelized and unchannelized

habitats, and the organisms were recorded as increasing, decreasing, or unchanged with respect to that stress (Figure 3.12). Production decreased along the gradient for most taxa, including all taxa in the most sensitive group, although tolerant taxa typically remained the same or increased (Figure 3.12a). Fewer taxa showed changes in response to habitat, and these changes were less closely related to tolerance. Biomass turnover rates (P/B) were less affected by pollution stress than production, although again tolerant taxa were more likely to have increased values than sensitive taxa (Figure 3.12b). Evidence suggests that the pollution gradient is a more important determinant of production than habitat changes, and more of the difference is attributable to lethal effects than sublethal effects.

Mean development times of taxa at each station were examined by calculating production-weighted mean CPI values (Figure 3.13). Only those taxa listed in Appendix A were included in this calculation. These values were calculated by multiplying the proportion of community production contributed by each taxon by its CPI (Table A.2), and summing the result to obtain a mean CPI. This shows an increase in the role of taxa with short life cycles at the most polluted stations, although taxa with short life cycles were also important at the reference station. At the reference station, however, these taxa included *Polypedilum* and fast-growing shredders such as *Allocapnia*, *Amphinemura*, and *Pycnopsyche*, while tolerant fast-growing chironomids such as *Diplocladius*, *Eukiefferiella*, *Orthocladius*, *Cricotopus*, and *Rheocricotopus* dominated Stations 8 and 9. Station 6 has a high CPI value due to high production of *Cordulegaster*.

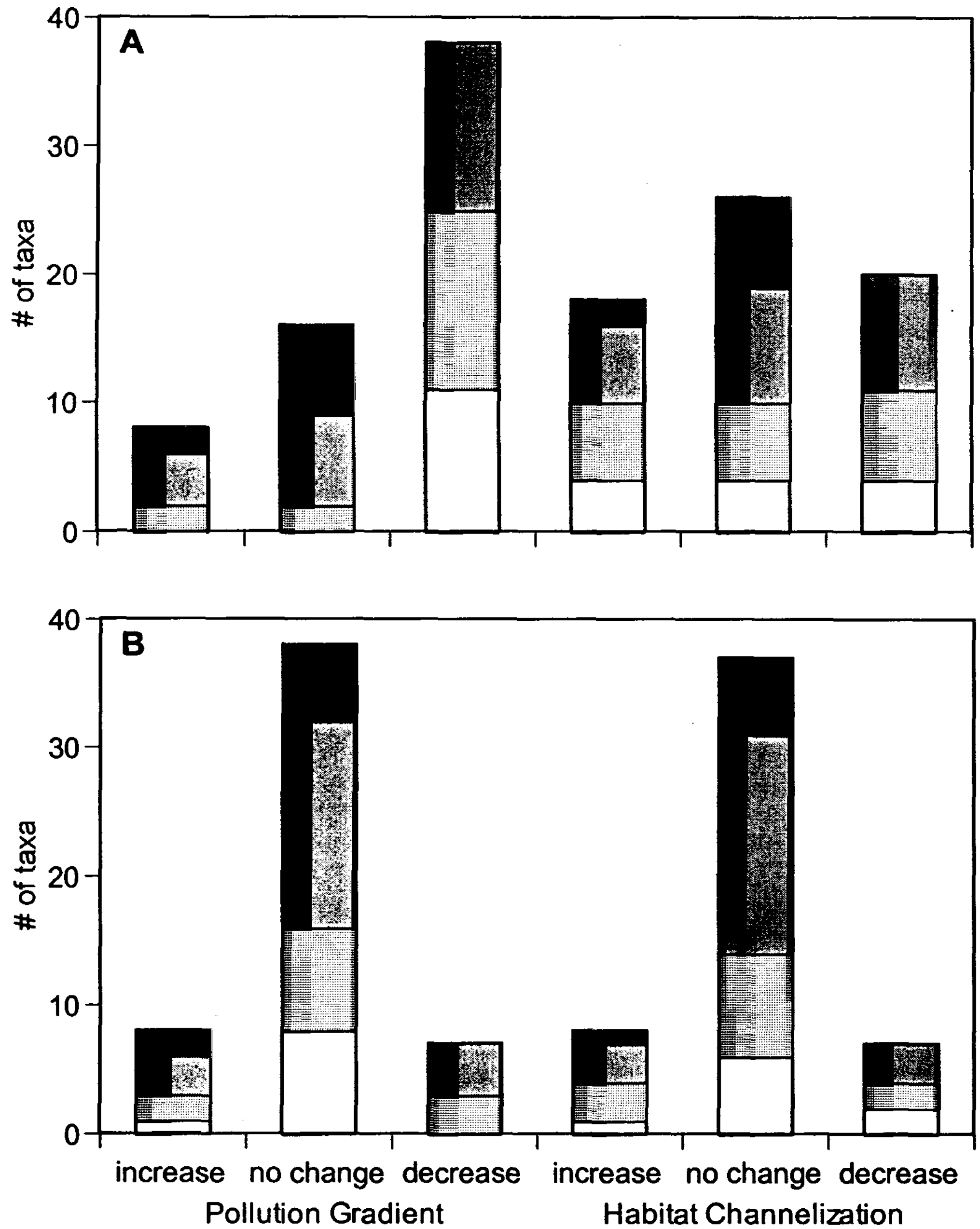

Figure 3.12. Number of invertebrate taxa showing significant change in annual production (A) and annual P/B (B) associated with increasing pollution and channelization of habitat. Production differences were determined by comparison of bootstrapped 95% confidence intervals, P/B differences were determined qualitatively for those taxa showing significant production differences. Taxa are grouped by NCBI score (Lenat 1993 – white 0.0-2.5, stipple 2.6-5.0, dark grey 5.1-7.5, black 7.6-10.0).

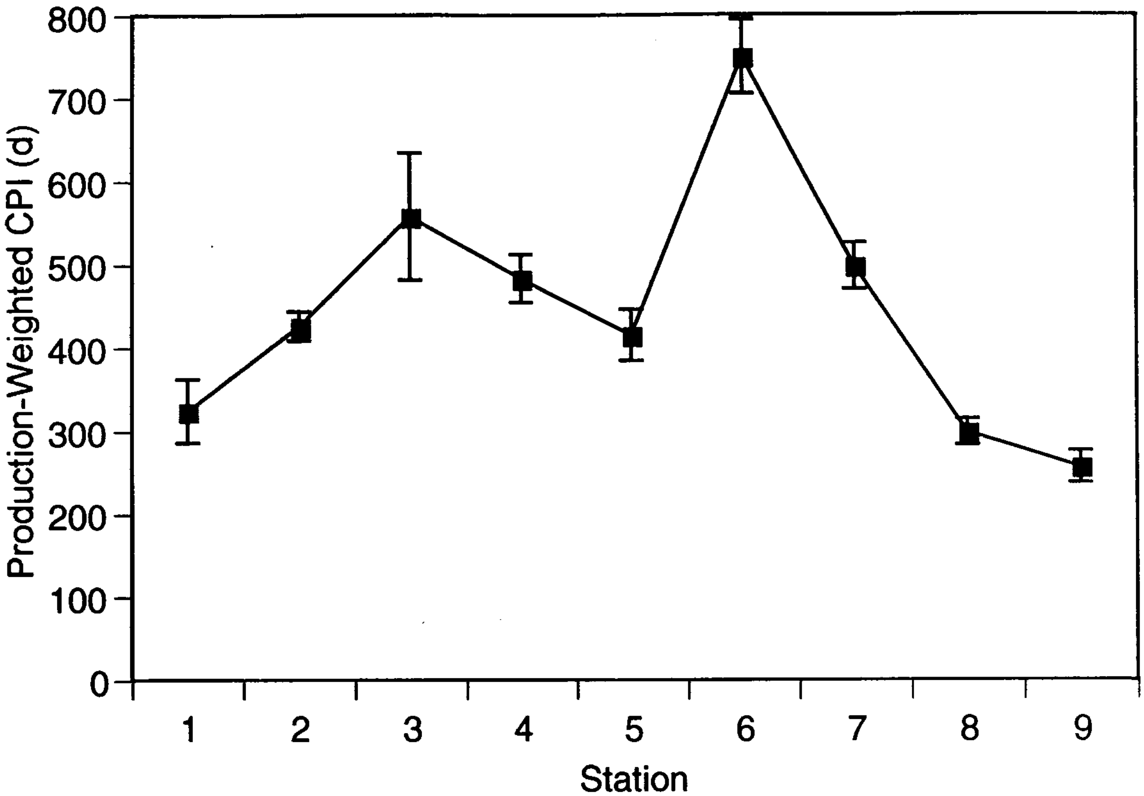

Figure 3.13. Production-weighted mean cohort production interval (CPI) for invertebrate communities in Goosefare Brook, 1998-1999. Error bars indicate 95% confidence intervals, calculated using the bootstrapped vectors from the production analysis.

Habitat and Sediment Quality

Sediment inputs, flow velocity, and changing substrate particle size are important factors in structuring biotic communities in streams (Rice et al 2001), as are pollutants associated with sediment inputs from roadways (Garie and McIntosh 1986, Davis and George 1987). Two general patterns in response variables are evident along Goosefare Brook. The first is a simple linear pattern, which implies that the response variable is closely related to the pollution gradient, because most heavy metal concentrations show a fairly steady increase from upstream to downstream (Figure 3.3). The second is a non-linear pattern, which suggests an interaction with other factors, such as channel form. For example, specific conductance (Table 3.2), most sedimentary metals (Figure 3.3), total production (Figure 3.6), stored organic matter (Figure 3.7), and shredder production (Figure 3.8) show a linear pattern, while Fe concentration (Figure 3.3), taxa richness (Figure 3.4), and production of gatherers, filterers, and predators (Figure 3.8) show a complex pattern with respect to the gradient that suggests an interaction with habitat characteristics. Therefore, the simple gradient pattern of whole-community production suggests that chemical pollution rather than channel alteration is controlling this parameter. Alteration of habitat may also act as an environmental filter on the community, further reducing the production of taxa that characterize the reference site.

The amount of stored organic matter in a system is a potentially important determinant of production, and the observed decrease along the gradient in Goosefare Brook may limit the amount of invertebrate production that can be supported. However, a shift in functional feeding group composition and an increase in production is normally

associated with decreasing stored organic matter over long stream continua (Vannote et al 1980, Wohl et al 1995, Grubaugh et al 1997). It is also possible that very fine POM (<250μm) was important at polluted stations, which would be consumed by the small gatherers (i.e. chironomids) that dominate these communities, and is underestimated with the sieve size used in this study (Wallace and Grubaugh 1996). The importance of this factor in explaining the production decrease in Goosefare Brook is thus questionable.

Understanding effects of stress on the growth and biomass of organisms is important because it allows the consideration of the effects of stress on ecological function. Consideration of the interaction of habitat, organic matter, and chemical contaminants leads to a better understanding of effects of human activities on stream function than do quantifications based strictly on abundance or diversity. In Goosefare Brook, the impairment of biotic integrity is manifested not only as a shift in community composition and richness, but also as a significant decline in total production, an increase in biomass turnover, and a change in functional structure. All of these changes suggest a shift in the manner in which organic matter is processed and energy flows in the system. The communities at the most impacted stations showed a drastic decrease in total energy flow, even though many tolerant taxa maintained or even increased their annual production.

Clements (1997) hypothesized that as pollutant levels increase in a system, there is a decreasing rate of change in the community, as less tolerant taxa are eliminated and the resulting community is more resistant to further change. Evidence for this hypothesis is provided in Goosefare Brook by the non-linear association of total biomass with metal

concentrations (Figure 3.5), suggesting that progressively higher metal levels are needed to cause a decrease in biomass as the community becomes more tolerant. The intercorrelation of metal concentrations in Goosefare Brook is due to their apparent commonality of sources, and coprecipitation and adsorption processes in the stream sediments (Figure 3.10) (Dzombak and Morel 1990, Combest 1991). The change in the community takes the form of an asymptotic change in composition along the gradient, offset somewhat by the increases in the tolerant taxa. The reduced role of less tolerant taxa due to exposure to stress results in a simplification of stream communities and food webs. In turn, this may then lead to changes in key ecosystem properties, such as rates of organic matter processing, total energy flow and energy pathways, and resilience to additional stresses, which are collectively known as biotic integrity (Fore et al 1996, Wallace et al 1996).

The example of Goosefare Brook shows that the changes in community structure observed in polluted systems result in functional changes in the ecosystem. Human activities may decrease production by decreasing biomass and/or growth rates in Goosefare Brook through lethal and sublethal effects, or reduction of food and suitable habitat due to channelization. These effects range from the shifts in the pathways of energy flow observed at stations exposed to moderate physical or chemical stress, to the loss of most taxa and decrease in production under severe stress. However, the shifting prominence of different taxa along a continuum of stress shows that while simple metrics may be able to detect impairment, the nature of the change in a functional context is not so easily measured. Consideration of the interaction of habitat, food resources, and

chemical contaminants rather than simple metrics alone is needed to further understanding of the effects of stress on stream function.

Chapter IV

EFFECTS OF ROADWAY CROSSINGS ON LEAF LITTER PROCESSING AND INVERTEBRATE ASSEMBLAGES IN SMALL STREAMS

Chapter Summary

The effects of the Maine Turnpike (Interstate 95) on leaf litter processing were examined in five first- and second-order coastal plain streams in southern Maine, U.S.A. Invertebrate assemblages and red maple leaf softening and loss rates were compared at 53 stations upstream and downstream of the turnpike. Litter softening rate was not affected by the roadway, and litter loss rate was significantly faster at downstream stations (-0.0024 degree-day^{-1}) than at upstream stations or those nearest the roadway, which were not different from each other (-0.0022 degree-day^{-1}). Litter softening and loss rates were more strongly related to physical and chemical habitat variables than shredder assemblage characteristics, and habitat variation among streams was greater than within streams. Among-stream differences were observed in most community structural metrics and biomass of important shredder taxa, but effects of the roadway were rarely consistent among streams. This study suggests that while the presence of the Maine Turnpike may influence stream habitats, the effects of roadway drainage are insufficient to overcome within-stream variability in litter processing and leaf pack invertebrate assemblage structure.

Introduction

In forested headwater streams, terrestrial leaf litter supports the majority of consumer production (Fisher and Likens 1973, Cummins et al 1989, Wallace et al 1999). A major rate-limiting step is the incorporation of leaf litter into tissue of hyphomycete fungi, a process known as conditioning (Cummins and Klug 1979, Suberkropp and Klug 1980, Rossi 1985). During their growth, these fungi assimilate carbon from the leaf tissues and obtain other nutrients from the water column (Sinsabaugh et al 1985). Due to the high C:N ratio of the structural polymers in leaves (i.e. cellulose, hemicellulose, lignin), an essential part of the diet of detritivores is fungal biomass. Conditioned leaf litter is processed by invertebrates that directly consume leaf tissue (shredders) into fine particulate organic matter (FPOM), which is consumed by other feeding guilds (collectors) in the community and in reaches downstream (Anderson and Sedell 1979, Vannote et al 1980).

The breakdown rate of leaf litter is controlled by factors affecting leaching and fragmentation, such as microbial maceration and the activity of detritivores (Webster and Benfield 1986, Molinero et al 1996, Gessner 1999). Nutrient availability and temperature are also important factors determining the rate of litter decomposition (Suberkropp and Klug 1980, Young et al 1994). Elevated concentrations of aqueous nutrients have been shown to accelerate rates of litter softening, indicating faster fungal growth (Suberkropp 1995, Suberkropp and Chauvet 1995). Within the physiological limits of the organisms, higher temperatures tend to increase the rate of fungal respiration and growth and the

activity levels of detritivores, also increasing litter processing rates (Suberkropp et al 1975, Suberkropp et al 1976, Webster and Benfield 1986).

Physical and chemical stress from human activities may affect litter processing in streams by altering habitat or impairing biological activity. Watershed land use has been shown to be related to litter processing rates and composition of invertebrate assemblages associated with leaf litter (Stout and Coburn 1989, Huryn et al 2002). Pollutant contamination from roadways has been shown to alter the structure of fungal assemblages that make leaf detritus palatable to shredding organisms (Maltby et al 1995a). Fungal growth and sporulation may be affected by exposure to pollutants such as heavy metals, and uptake and accumulation by fungi is a potentially important mechanism by which pollutants reach higher trophic levels (Duddridge and Wainwright 1980, Abel and Barlocher 1984, 1988). The reduction of fungal productivity or cellulolytic activity could significantly slow the rate of energy flow to higher trophic levels, affecting food web structure and function. Changes in channel form and the character of the riparian vegetation may affect litter retention due to decreases of woody debris and increased flow velocity (Speaker et al 1984), and may to alter detritivore communities in the affected reach (Stout and Coburn 1989, Sponseller and Benfield 2001).

In view of the important role of leaf litter in the energy dynamics of forested streams, the examination of litter processing rates and the biota associated with litter provides insight into an important ecosystem function. Measurement of litter processing rates may thus be useful in assessing anthropogenic impacts on stream systems, since detritus processing represents an integration of physical, chemical, biological, and

microbiological factors (Stout and Coburn 1989, Young et al 1994). These communities may show reduced efficiency because certain microconsumers are eliminated by exposure to pollution, and/or because density of shredders is reduced, which in turn reduces the flow of energy to other functional feeding groups (Vannote et al 1980).

This study was conducted to examine the effects of roadway disturbance and non-point source pollution on detrital dynamics. It was expected that physical and chemical habitat alterations associated with the roadway may result in impairment of fungal conditioning of litter, due to direct toxic effects of runoff on the fungi and physical changes such as altered substrate and changes in the flow regime. Together with decreased food quality of the litter, these alterations would result in changes in the structure of shredder assemblages, which in turn would translate into decreased processing rates. This study assessed the effects of physical habitat alteration by roadway crossings and chemical stresses from roadway runoff on leaf litter processing rates and invertebrate assemblages in five small streams in Maine (U.S.A.).

Study Sites

The five streams in this study were first- or second-order reaches that cross beneath the Maine Turnpike in York and Cumberland counties in the southern part of the state. The streams are located in the coastal plain of southern Maine, and are generally low gradient and sandy, with large quantities of woody debris. The streams were selected on the basis of having similar habitats and channel form on either side of the roadway.

With one exception, five 50m study reaches were selected in each stream on either side of the roadway as part of an ongoing study on the effects of roadway crossings on stream ecosystems (Figure 4.1). The exceptions were the five downstream reaches in Goosefare Brook (Stations 6-10), which were 25m each.

The study streams have riparian areas forested predominantly with oak (*Quercus* spp.), hemlock (*Tsuga canadensis* (L.) Carr.), and red maple (*Acer rubrum* L.), and there is a thick understory of ferns and herbaceous plants. Clearing of vegetation has occurred near the roadway to some degree, and some of the forest at Ward Brook is in early successional state (*Alnus* spp). Detailed discussion of land use and riparian habitat is given in CHAPTER V. Three of the streams drain bog areas (Cascade, Goosefare, and Stevens Brooks), while Ward Brook and Branch Brook do not. Important physical and chemical habitat descriptors are presented in Table 4.1.

Methods

Leaf Litter and Macroinvertebrates

Leaves were collected post-abscission and pre-drop from a single red maple tree on the University of Maine campus in Orono. Approximately 8g (range $\pm$0.1g) of air-dried leaves were placed in plastic mesh bags, after having been weighed to the nearest 0.01g and then moistened before placement in the bags to minimize breakage. Six litter bags were deployed at each station (Figure 4.1). An extra set of twelve bags were

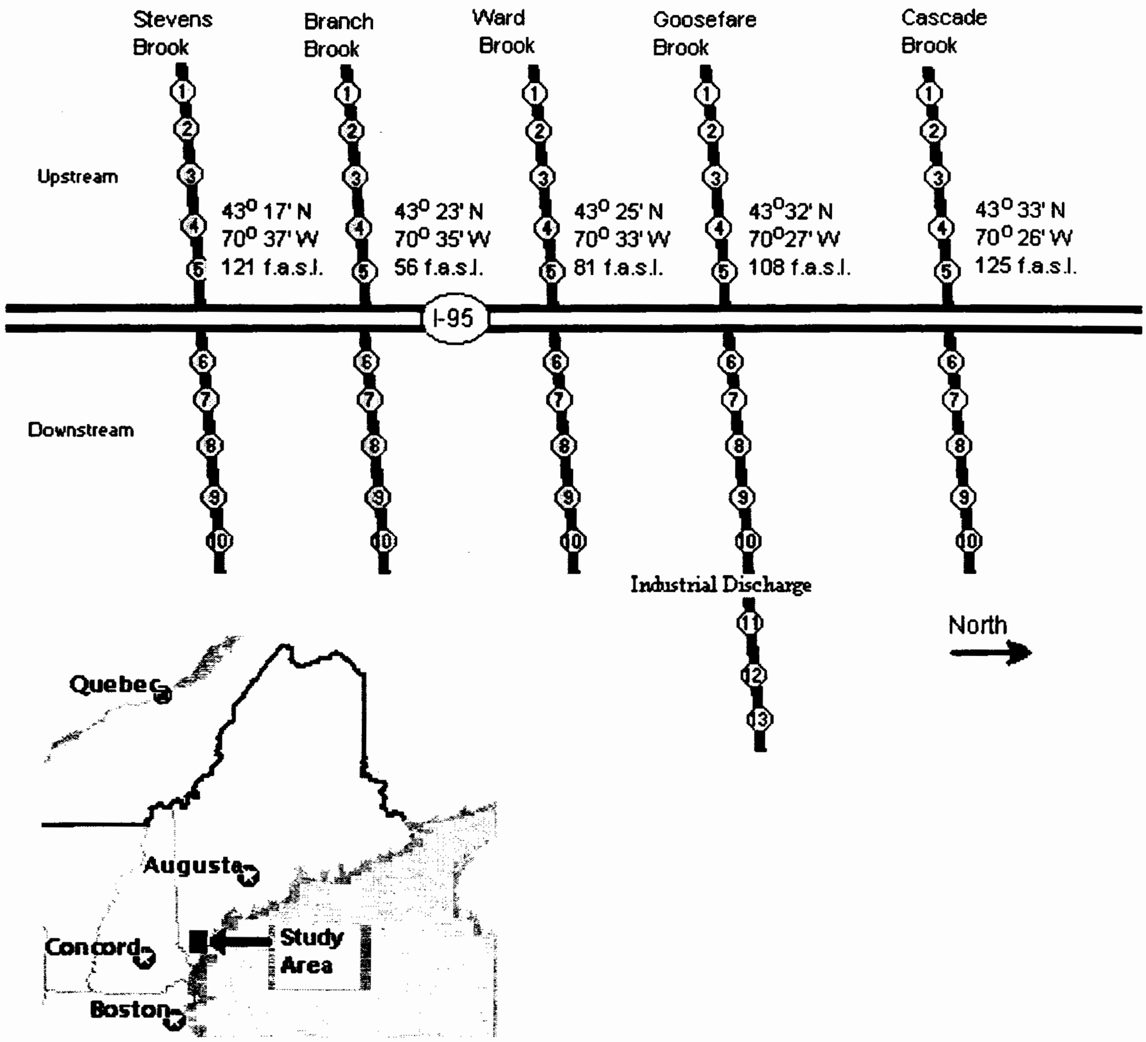

Figure 4.1. Schematic diagram of the study design. Latitude, longitude, and elevation in feet above sea level are given for the point at which the road and stream cross. Inset shows the location of the study sites in Maine. The study area encompasses from Turnpike mile marker 15 (Stevens Brook) to mile marker 36 (Cascade Brook).

Parameter	units	Cascade		Goosefare			Ward		Branch		Stevens	
		U	D	U	D	I	U	D	U	D	U	D
Habitat												
Bankfull Width	m	3.8	6.4	2.5	2.3	2.4	4.6	5.9	6.5	7.2	3.1	3.1
Depth	cm	8.0	25	14	23	23	34	18	39	38	6.0	3.7
Flow	cm/s	1.0	1.0	13	8.6	5.2	9.8	37	40	59	1.0	1.0
Particle Size	mean ϕ	-0.43	-0.86	2.0	1.7	1.1	2.2	1.0	1.0	0.17	-0.28	-0.24
Min temperature	°C	4.0	4.3	5.1	6.2	6.2	5.5	5.0	10.6	7.9	6.4	7.3
Max temperature	°C	10.4	10.7	11.3	10.9	10.9	10.1	10.5	12.7	11.0	11.0	10.6
Degree-days	°C	212.9	214.8	216.1	222.4	222.4	210.8	212.6	312.4	253.4	229.1	238.3
Water												
pH	-	6.3	6.4	5.8	6.1	6.3	6.8	6.5	6.5	6.5	4.6	5.5
Conductance	µS/cm	83.9	118	80.6	167	423	62.7	72.4	53.8	57.3	43.3	97.5
Dissolved O_2	ppm	10	10	9	9	10	11	10	10	11	10	10
NO_3-N	ppm	0.11	0.09	0.29	0.27	0.27	0.04	0.05	0.13	0.13	0.01	0.02
NH_4-N	ppm	0.022	0.028	0.030	0.043	0.043	0.014	0.048	0.013	0.017	0.023	0.031
PO_4-P	ppm	0.004	ND	ND	0.012	0.012	ND	ND	0.003	ND	ND	0.0
Alkalinity	mgCaCO3/L	48	49	18	21	21	18	20	15	16	2.0	9.0
DOC	ppm	22	21	13	12	12	7.3	7.3	3.0	3.4	18	16

Table 4.1. Water quality and physical habitat characteristics of the study streams, 1999-2000. Values given are mean annual measurements recorded upstream (U) and downstream (D) of the Maine turnpike. Values in Goosefare Brook are also provided downstream of industrial inputs (I). ND indicates that concentrations were below detection limits.

transported with the others prior to their deployment, in order to evaluate loss due to handling (Benfield 1996). The litter bags were placed near the upstream end of each study reach, and an effort was made to place the litter bags near retentive structures, where natural litter accumulations existed. The bags were tied to 8" gutter nails which were driven into the stream substrate. The bags were incubated in the stream for 28d (October 21 to November 18). This length of time was appropriate for streams in Maine, based on a targeted loss of 50% of the leaf material (Huryn et al 2002). Temperature was recorded hourly during this period using Optic StowAway temperature loggers (Onset Computer Corporation, Bourne MA).

Recovery of the bags proceeded from the downstream end of the study reaches, in order to disturb other bags as little as possible. The bags were collected by placing them inside a plastic bag held downstream, as quickly as possible to minimize escape of invertebrates. The litter bags were returned to the laboratory, and their contents rinsed into a 500μm sieve. All leaves were rinsed of invertebrates and debris, which were preserved in 95% ethanol. Invertebrates were enumerated and identified to the lowest practical taxonomic level, typically genus (Wiederholm 1983, Thorp and Covich 1991, Merritt and Cummins 1996). Invertebrate length was measured to the nearest millimeter and biomass calculated using published length-mass regressions (Benke et al 1999).

As leaves are macerated by fungi, the softness of the leaf tissue increases. Relative leaf softness is measured as "penetrance", defined as the weight required to push a standard metal pin through a leaf (Young et al 1994). Penetrance is closely related to both fungal activity and the palatability of leaf detritus to detritivores (Suberkropp and

Klug 1980). The penetrometer consisted of two heavy plastic blocks between which the leaf was placed in order to hold it flat. A pin supporting a dish was placed in a hole drilled through the blocks, so that the pin was supported by the leaf tissue. Lead shot was then slowly added to the dish until the leaf was penetrated, and the mass of the dish and the shot was obtained. The measurements were made near the center of the leaf, away from large veins and approximately half-way between the midrib and the leaf edge. This procedure was repeated for ten randomly selected leaves per litter bag.

Following the measurements of penetrance, the leaves from both incubated and breakage bags were placed in paper bags and dried in an oven at 60°C for three days. The leaves were again weighed (oven-dry mass), then ground in a blender and ashed in a muffle furnace at 550°C for 24h. Ash-free dry mass (AFDM) was estimated as the difference between oven-dry and ash weights. The proportion of AFDM remaining was calculated by dividing the final AFDM by initial AFDM (corrected for handling loss). The initial value for penetrance calculations was the softness of freshly collected leaves prior to drying, obtained using the same method described above. Leaf loss and leaf softening rate constants are expressed using degree-days (>0°C) accumulated during the incubation period in order to account for temperature differences among streams (Young et al 1994, Huryn et al 2002). Rate constants were calculated by fitting the data to a negative exponential decay model (Huryn et al 2002), where,

$$\text{rate} = [\ln(\text{final value}/\text{initial value})] / \text{accumulated degree-days}$$

Physical and Chemical Habitat Parameters

An ongoing study at the same stations provided physical habitat, sediment chemistry, and water chemistry data. Physical habitat characteristics, including substrate particle size, depth, flow, and bankfull width, were taken from the uppermost transect of a detailed habitat assessment conducted on the study reaches (CHAPTER V). On nine dates during the year, two water samples were taken in each stream (upstream and downstream of the turnpike) and analyzed for nitrate (NO_3-N), ammonium (NH_4-N), phosphate (PO_4-P), alkalinity, and dissolved organic carbon (DOC), and *in situ* measurements of pH, specific conductance, and dissolved oxygen (DO) were made using YSI hand-held meters (Yellow Springs Instrument Co., Yellow Springs OH). All water samples were stored on ice until their delivery to the Maine State Analytical Laboratory for analysis (5722 Deering Hall, University of Maine, Orono ME, 04469-5722).

Sediment samples were taken on three dates during the year, using the following procedure. A length of 1" PVC pipe was pressed into the substrate to a depth of ~2cm, and the collected material transferred to a rinsed, acid-washed amber plastic bottle. This was repeated twelve times (left, right, and center of channel at four randomly determined locations within each study reach) and composited in a single bottle. All sediment samples were stored on ice until their delivery to the Maine State Analytical Laboratory. The sediment was analyzed for eight heavy metals (Cd, Cr, Cu, Fe, Mn, Ni, Pb, and Zn) using a two-stage extraction. The first extraction was performed using 1M ammonium acetate at pH 7, and measured aqueous and weakly complexed metals. The remainder of the sample was then digested in nitric acid. The sum of the metal concentration in the two

extractions is the total metal concentration for the sample. Details of this methodology are described in Say and Whitton (1983). Concentrations of NO_3-N and NH_4-N were determined using an Aplkem flow injection analyzer (detection limit 0.05 mg/L). Concentrations of PO_4-P were determined using Dionex I.C. (detection limit 0.01 mg/L). Heavy metal concentrations in water were determined using flame AA, with a replicate performed every 9 samples (detection limit 3.3 μg/L). All results were checked against external standards bracketing the expected concentrations. A subsample of the sediment was analyzed for organic carbon content.

Invertebrate Assemblage Structure Metrics

Metrics describing attributes of the invertebrate assemblages were used to examine longitudinal changes in the structure of assemblages occurring on the leaf packs. This suite included Raw Abundance, Taxa Richness, EPT, Berger-Parker Dominance, Shannon-Weaver Diversity, Total Biomass, %Chironomidae, %Ephemeroptera, %Plecoptera, %Trichoptera, %Scrapers, %Shredders, %Collector-Gatherers, %Filter-Feeders, %Engulfing Predators, and %Piercing Predators. All percentages were calculated on the basis of biomass.

Statistical Analyses

Litter processing parameters, community metrics, and biomass of important shredder taxa were compared using unbalanced two-factor (stream and location) univariate analyses of variance (Neter et al 1996), which accounted for variance due to differences among streams, location with respect to the roadway, and interactions between these factors. Because considerable differences in habitat were evident in the vicinity of the roadway (T.S. Woodcock, *personal observation*), the stations immediately upstream and downstream were treated as a separate group for the purposes of these analyses. Therefore, three groups were included in each stream – upstream stations (1-4), stations nearest the turnpike (5-6), and downstream stations (7-10). Those impacted by industrial inputs (Goosefare Brook 11-13) were excluded from these ANOVAs, since only the effects of the roadway were being examined. Risk of type I error was set at $\alpha=0.05$ for all ANOVAs (25 in total), and a Bonferroni correction was applied, so significance was accepted in each analysis if $p\leq0.002$. Canonical Correspondence Analysis (CCA, Rencher 1995) was used to examine the effects of habitat and sedimentary metal concentrations on the biomass of invertebrate taxa associated with the litter bags.

Principal components analysis (PCA, Rencher 1995) of the physical and chemical variables (flow rate, aqueous nutrient concentrations, sedimentary heavy metal and organic C concentrations, pH, alkalinity, specific conductance, dissolved oxygen, mean substrate particle size, dissolved organic carbon), and of biomass of major shredder taxa, were performed separately for the purpose of data reduction. Annual means of

exchangeable and total sedimentary metal concentrations and water chemistry parameters were used. All variables used in the PCA were standardized prior to analysis. The first six principal components from each analysis were used in a forward stepwise regression (F to enter $\geq$4.0) (Neter et al 1996), to evaluate relationships with each litter processing parameter in each year.

Results

Litter Processing Rates

A total of 294 litter bags were recovered (142 from upstream stations, 134 from downstream stations, and 18 below the industrial inputs in Goosefare Brook). Twenty-four bags were lost due to storm flows. All bags were lost from Stations 9 and 10 in Ward Brook and Station 2 in Branch Brook, four bags from Station 9 in Stevens Brook, and one bag from each of two upstream stations in Cascade Brook. ANOVA showed that litter softening and loss were significantly different among streams. Overall litter loss was greater in Cascade Brook than in other streams ($p<0.0001$, Figure 4.2). Litter softening was different among all streams except Goosefare and Ward Brooks (Cascade > Branch > Goosefare = Ward > Stevens, $p<0.0001$). There was no significant effect of location relative to the turnpike for litter softening or litter softening rate in any stream. The rate of litter loss was significantly faster at downstream stations (-0.0024 degree-day^{-1}) than at upstream stations or those nearest the roadway, which were not different from each other

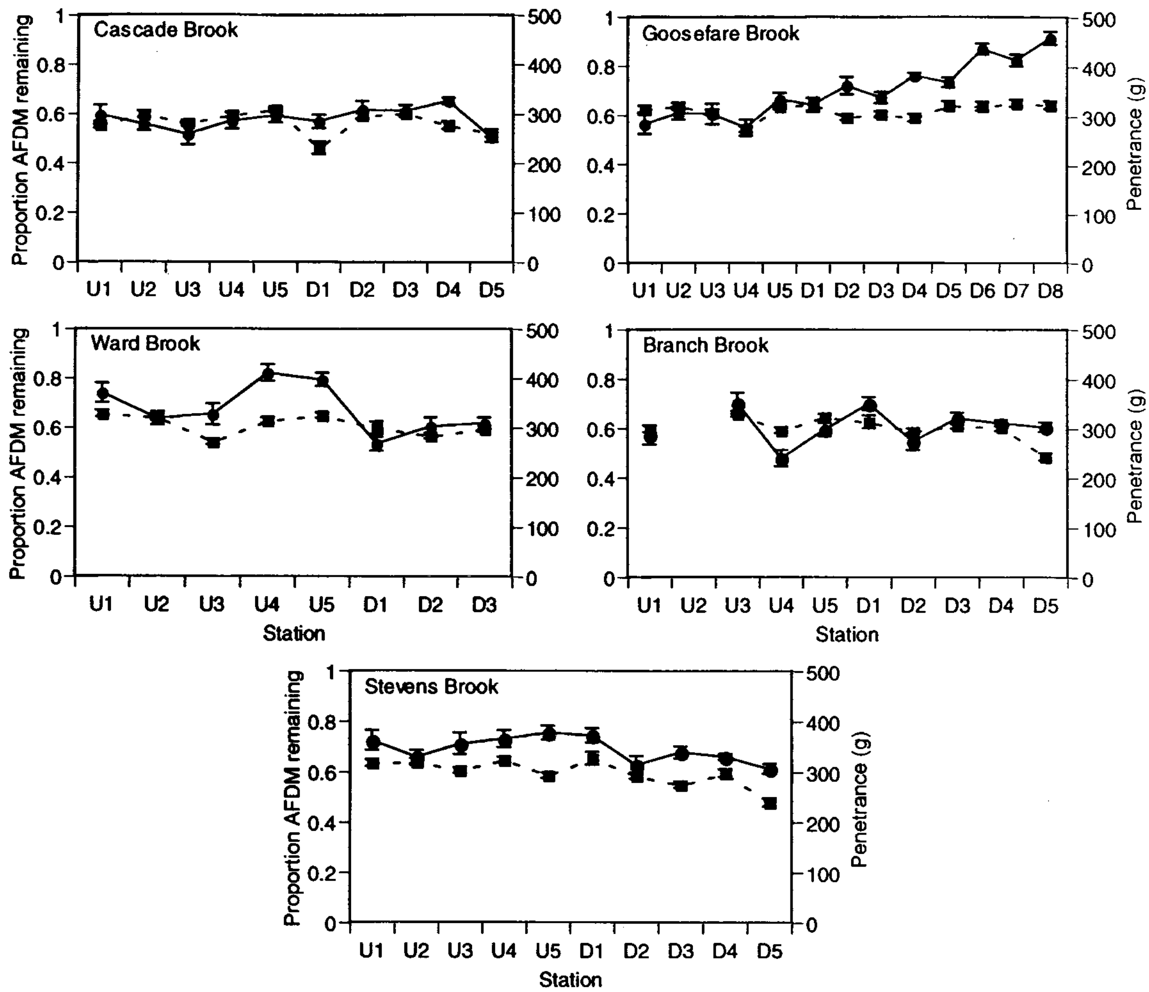

Figure 4.2. Leaf litter softening (solid line) and loss (broken line) in the study streams. Upstream reaches preceded by U, downstream reaches by D. All litter bags at Stations D4 and D5 in Ward Brook and U2 in Branch Brook were lost due to storm flows.

(-0.0022 degree-day^{-1}, $p<0.0001$) (Figure 4.3). Overall softening was lower at the stations downstream of the industrial inputs in Goosefare Brook, but loss was not affected (Figure 4.2).

Invertebrate Assemblage Metrics and Shredder Biomass

All invertebrate assemblage metrics showed a significant difference among streams (Table 4.2). Most also showed an interaction between stream and location with respect to the roadway, indicating that some streams showed a significant effect of location with respect to the roadway while others did not. The proportional biomass of filter feeders was highest near the turnpike, and higher at upstream stations than downstream. In general, biomass, abundance, and richness were lowest in Stevens Brook, while Ward tended to be the most diverse. Overall, the %Trichoptera in the assemblage showed a tendency to decline downstream of the turnpike, while %Plecoptera tended to increase downstream in Ward and Stevens only. Both proportional measures did not show significant locational differences across all streams.

The biomass per litter bag of all important shredder taxa showed a significant difference among streams, except *Amphinemura* (Table 4.2). All except *Amphinemura* and *Tipula* also showed an interaction between stream and location, indicating that some streams showed a significant effect of location with respect to the roadway while others did not. Biomass of *Allocapnia*, *Paracapnia*, *Podmosta*, and *Taeniopteryx* showed a significant effect of location when considered across all study streams. With the

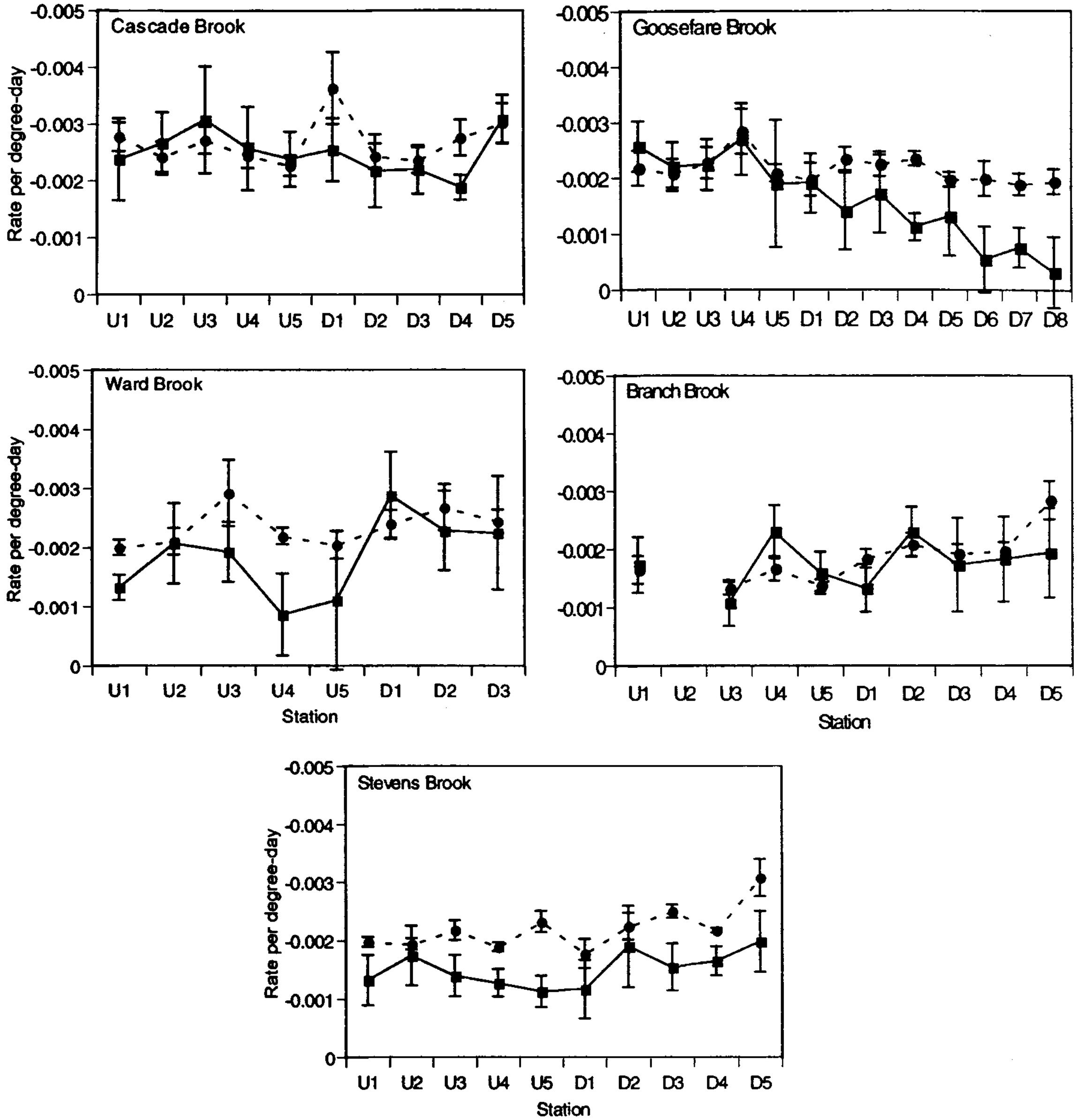

Figure 4.3. Rates of litter softening (solid line) and loss (broken line) in the study streams. Upstream reaches preceded by U, downstream reaches by D. All litter bags at Stations D4 and D5 in Ward Brook and U2 in Branch Brook were lost due to storm flows.

Metric	Stream Effects	Location Effects	Interaction
Assemblage Structure			
Total Abundance	S = B < C = W = G	not significant	C: D < T = U G: D < T < U W: U < D = T S: U = T < D
Taxa Richness	S < G = C = B < W	not significant	G: D < T < U W: T = U < D B: U = D < T S: U < D < T
EPT Index	S < G < C = B < W	not significant	C: T = D < U G: D < T < U W: U = T < D B: U < D < T S: T = U < U = D
Shannon-Weaver Index	S = G = C < B < W	not significant	C: U = T < D W: T < U = D S: D = U < T
Berger-Parker Evenness	W = B < S = G < C	not significant	C: D < T = U G: D < T = U W: U = D < T B: T = D < U S: T < U < D
Total Biomass	S < B = W = G < C	not significant	C: D < U = T G: D < U = T B: U < T = D S: U = T < T = D
% Chironomidae	C < W = B = S < G	not significant	not significant
% Ephemeroptera	W = G = B < B = C < C = S	not significant	not significant
% Plecoptera	G < S < W < B < C	not significant	C: T < D = U W: U = T < T = D S: T < U < D
% Trichoptera	C < S = W = B < G	not significant	C: T < D = U W: T = D < U B: D < T = U S: T = D < U
% shredders	S < G = C = W < C = W = B	not significant	not significant
% collector-gatherers	W = G < B = C < S	not significant	not significant
% collector-filterers	B < S < W = C = G	D < U < T	C: D < U < T G: D = T < T = U W: U < D < T B: D = T < T = U
% scrapers	S < B = C < W = G	not significant	not significant
% predators	C < G = B = W = S	not significant	not significant

Table 4.2. Two-factor ANOVA results for litter processing parameters, invertebrate community metrics, and biomass of important shredder taxa. Only those tests for which a significant difference was found based on location relative to the Maine Turnpike are shown. All proportional measures were calculated as biomass Codes for streams are B=Branch, C=Cascade, G=Goosefare, S=Stevens, W=Ward. Location codes are U=upstream stations (1-4), T=stations near the roadway (5 and 6), D=downstream stations (7-10). The interaction column shows location differences within the indicated stream.

Metric	Stream Effects	Location Effects	Interaction
Shredder Biomass			
Allocapnia	B = W = S = G < C	T < D = U	C: T = D < U G: U = D < T W: T = U < D S: U = T < D
Amphinemura	not significant	not significant	not significant
Lepidostoma	S = C = W < G < B	not significant	G: D < T = U B: U < T = D
Paracapnia	B = G = W = S < C	T = U < D	G: D = T < U W: U = T < D S: D = T < U
Podmosta	G = B = W = C < S	U < D = T	C: D = T < U W: U < D < T
Pycnopsyche	S < B = C = G < W	not significant	G: D < U = T W: T = D < U S: U = T < T =D
Taenionema	S = G = B < B = C = W	not significant	C: U = D < T W: U < D < T
Taeniopteryx	G < S = B = W < C	U < D < T	C: U = D < T W: U < D < T B: U < D = T
Tipula	C < S < G = W = B	not significant	not significant

Table 4.2. continued

exception of *Allocapnia* and *Tipula*, which were prominent in the shredder fauna of all streams, different shredder taxa were important in different streams. Based on biomass in the litter bags, *Paracapnia* and *Taeniopteryx* are important in Cascade Brook, *Lepidostoma* is important in Goosefare and Branch, *Pteronarcys* in Branch, *Podmosta* in Stevens, *Pycnopsyche* in Goosefare, and *Pycnopsyche* and *Taenionema* in Ward. *Allocapnia* showed a significant reduction in the vicinity of the turnpike, although confounded patterns were seen in Goosefare, Ward, and Stevens. *Paracapnia* showed a significant increase downstream of the turnpike, except in Goosefare and Stevens, where the trend was reversed. *Podmosta* and *Taeniopteryx* showed significant increases in biomass near the turnpike and at downstream stations. *Lepidostoma* showed a decline downstream of the turnpike in Goosefare, but increased in Branch. *Pycnopsyche* was highest upstream in Goosefare and Ward, but declined downstream of the turnpike in Stevens.

In the CCA of environmental descriptors (habitat characteristics and water chemistry) and biomass of 182 invertebrate taxa, there is a trend towards high width, depth, flow velocity, pH, nitrate, and small substrate particle size opposed to high sedimentary metals, DOC, ammonia, substrate particle size, alkalinity, and lower pH (Figure 4.4). Phosphate and specific conductance are associated most closely with downstream stations in Goosefare Brook, particularly those receiving industrial inputs (Figure 4.5). In general, the plot of stations with respect to the environmental variables shows less difference between stations upstream and downstream of the turnpike than

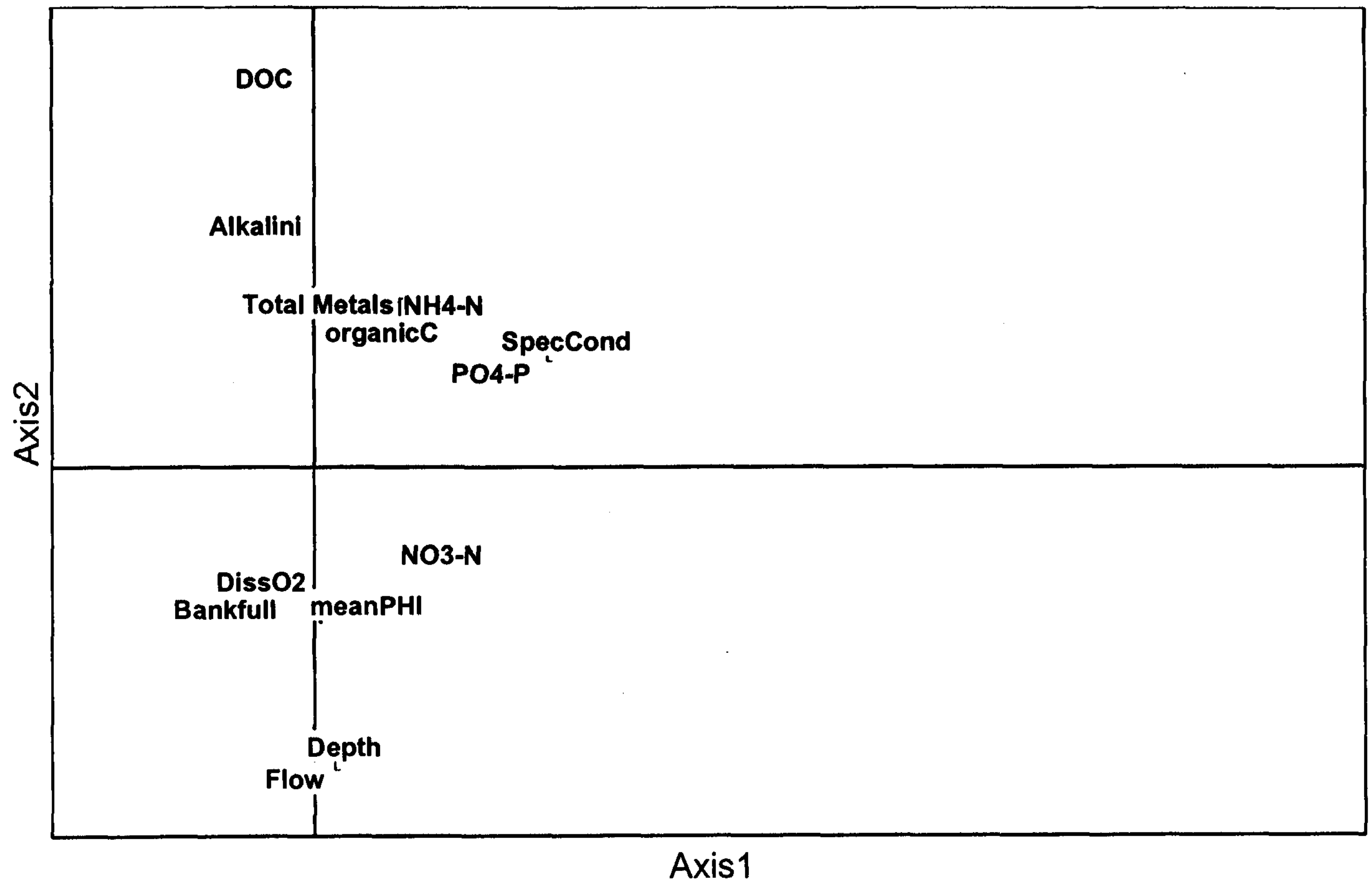

Figure 4.4. Termini of descriptive vectors from the Canonical Correspondence Analysis of litter bag invertebrate biomass and physical and chemical habitat variables. Total metals were highly correlated, and are grouped together into a single vector for clarity.

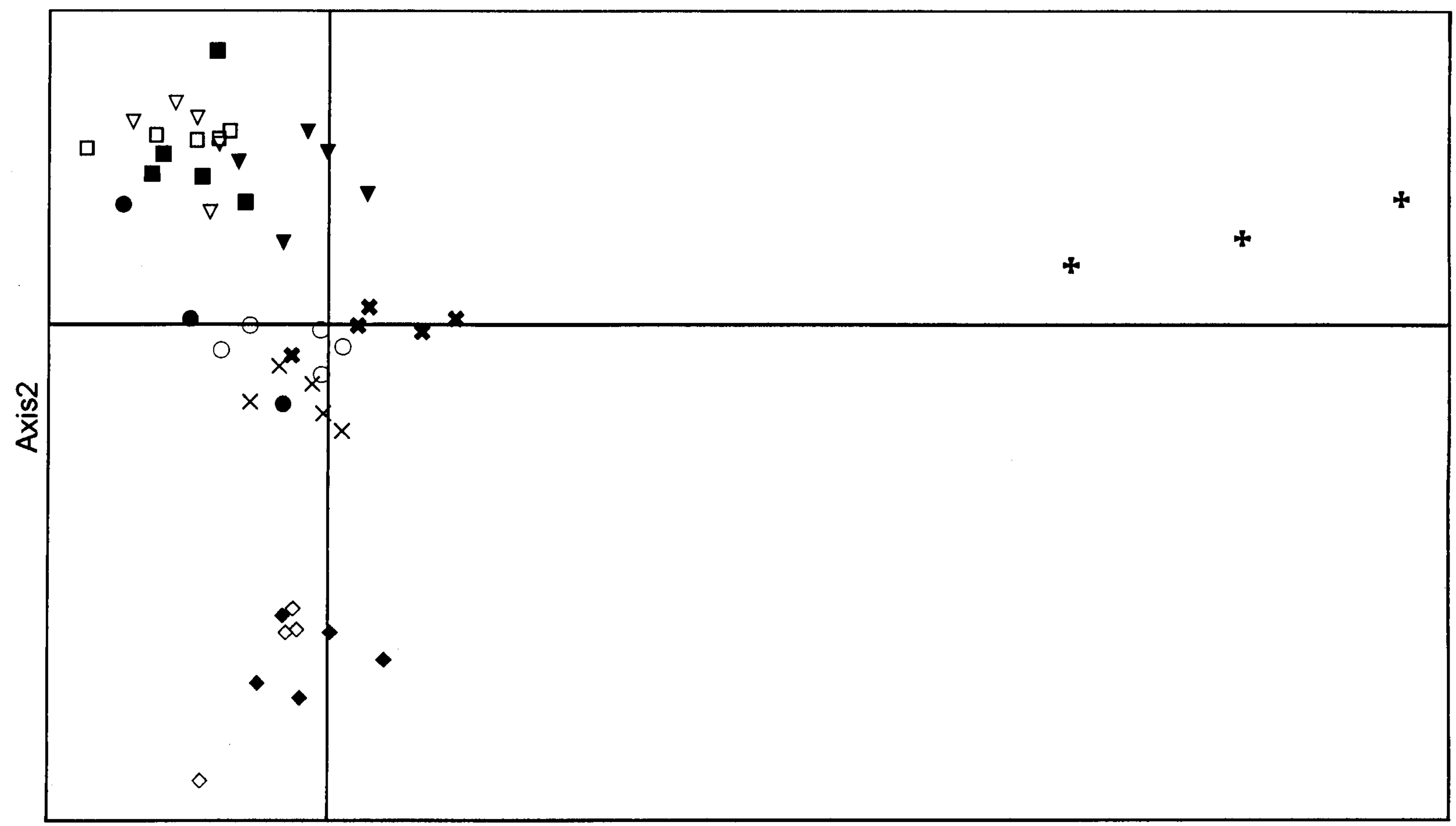

Figure 4.5. Position of sampling stations in the CCA of litter bag invertebrate biomass and physical and chemical habitat variables. Open symbols represent upstream stations, filled symbols represent downstream stations (Cascade-□, Goosefare-×, Goosefare downstream of industrial inputs-✚, Ward-O, Branch-◇, Stevens-▽).

among streams, similar to the analyses of the invertebrate assemblage characteristics. *Hyalella* and *Caecidotea* show a correlation with stations receiving industrial inputs, and *Pteronarcys* and *Lepidostoma* are correlated with Branch Brook (Figure 4.6). Shredders common to all streams, including *Brillia*, *Tipula*, *Leuctra*, *Amphinemura*, and *Pycnopsyche*, are located near the origin. Small stonefly taxa (*Taenionema*, *Podmosta*, *Allocapnia*, *Paracapnia*) generally have highest biomass in Cascade and Stevens Brooks. Although *Allocapnia* was common to all streams, its position on the plot is explained by its higher biomass per litter bag in Cascade Brook.

Habitat and Invertebrate Effects on Litter Processing

The multiple regression of litter processing rates on principal components of both habitat and shredder taxa admitted five components to the model of litter softening (r^2=0.69, Figure 4.7) and three components to the model of litter loss (r^2=0.38, Figure 4.8). The scatter of reaches in individual streams provides further evidence that differences among streams are greater than differences related to the turnpike. While overall effects of habitat and shredder assemblages on processing rates may be indicated by the regression analyses, individual streams do not show differences in rates that are clearly related to a shift along any of the principal components. The range of environmental parameters among streams shows that processing was faster in smaller streams, under conditions of slower flow and higher pH, and with lower levels of pollutant stress. Also, processing rates tended to proceed more quickly with shredder

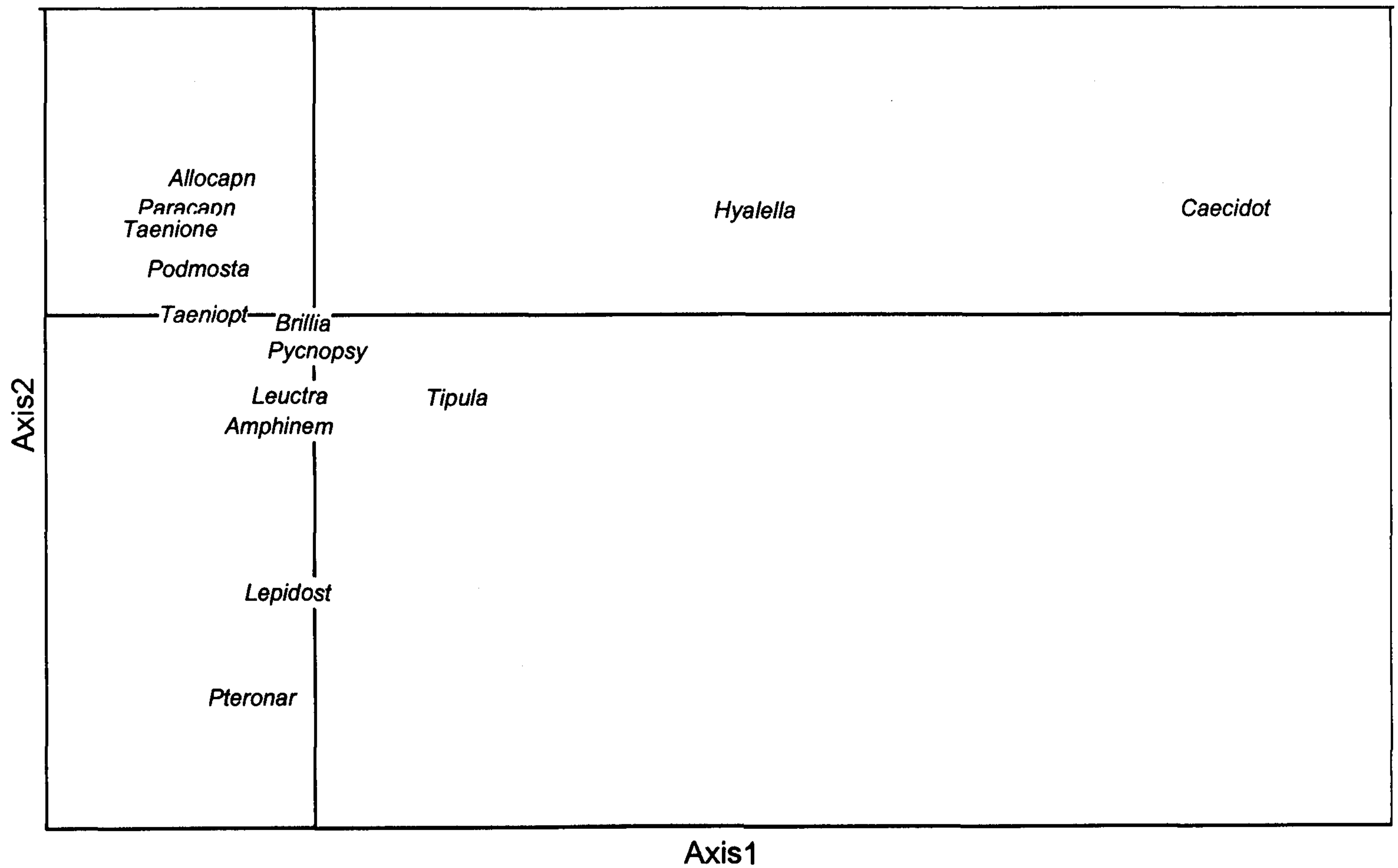

Figure 4.6. Position of important shredder taxa in the Canonical Correspondence Analysis of litter bag invertebrate biomass and physical and chemical habitat variables. Taxa included in this figure are listed in Table 4.3.

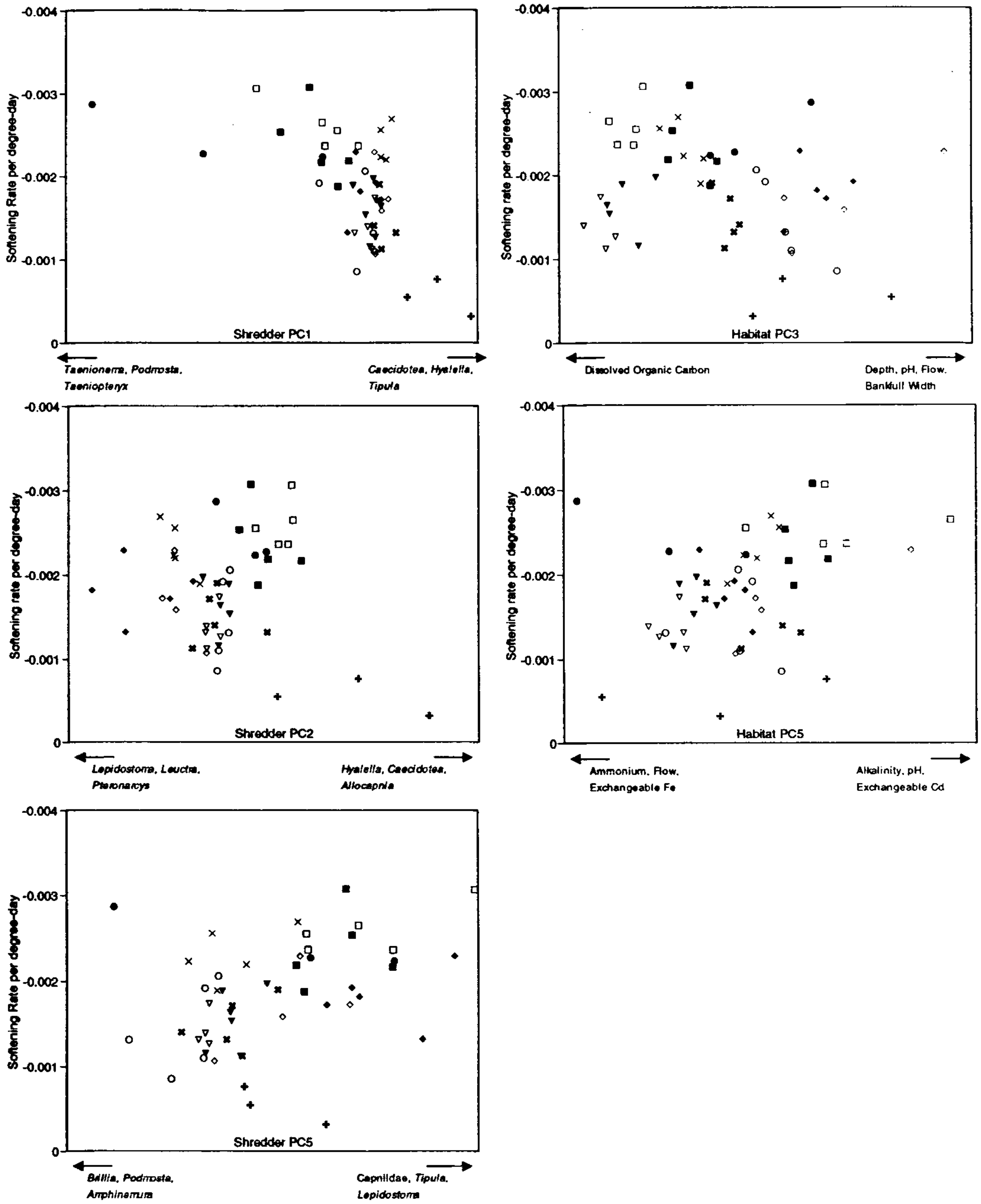

Figure 4.7. Leaf litter softening rate plotted against principal components admitted to the stepwise multiple regression (model r^2=0.69). Open symbols represent upstream stations, filled symbols represent downstream stations (Cascade-□, Goosefare-×, Goosefare downstream of industrial inputs-✚, Ward-O, Branch-◇, Stevens-▽).

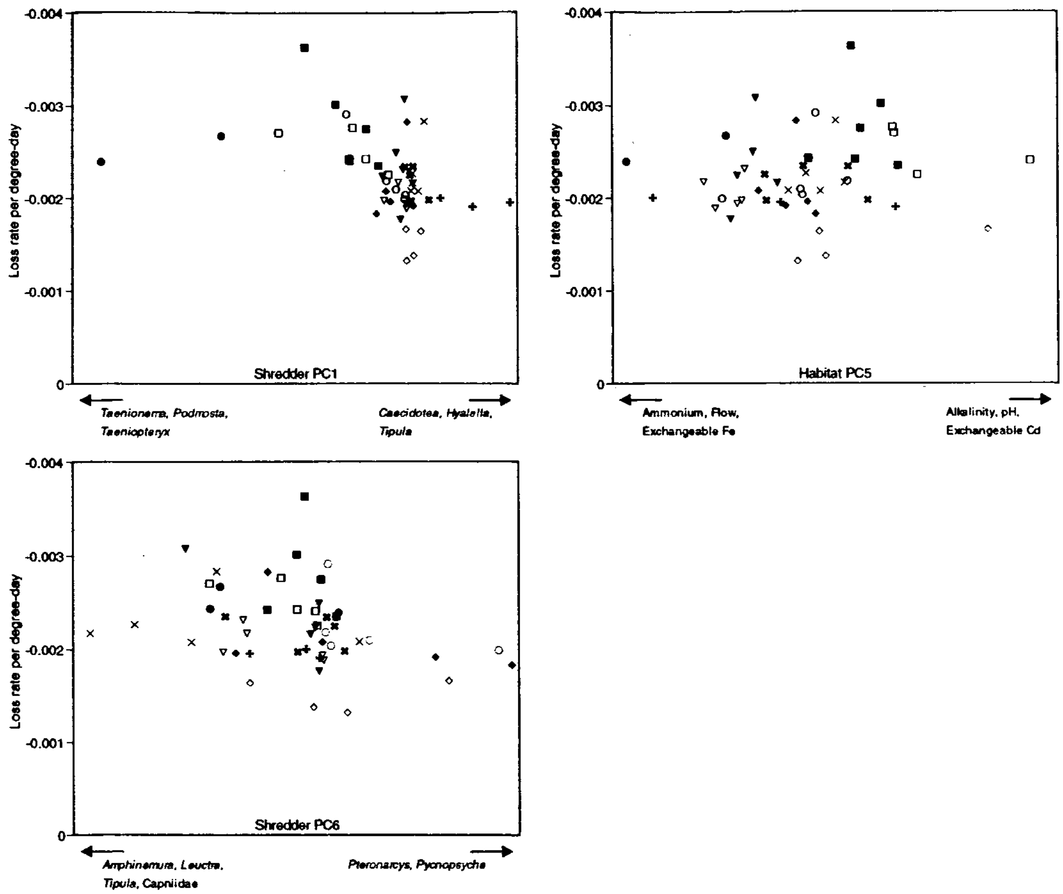

Figure 4.8. Leaf litter loss rate plotted against principal components admitted to the stepwise multiple regression (model r^2=0.38). Open symbols represent upstream stations, filled symbols represent downstream stations (Cascade-□, Goosefare-×, Goosefare downstream of industrial inputs-+, Ward-O, Branch-◇, Stevens-▽).

communities dominated by Plecoptera and Trichoptera than those dominated by *Tipula* and crustaceans, which were found at more impacted stations.

Only Goosefare Brook shows a trend of decreasing softening rate between upstream and downstream stations (Figure 4.3), which, according to the habitat principal components admitted to the model, is most likely related to changes in pH and alkalinity in this stream (Table 4.3). In general, increasing softening was associated with higher DOC and alkalinity, and low softening rates with higher flow, water depth, ammonium, and Fe levels. Although some shredder principal components are related to the softening rate, only Goosefare Brook showed a trend in reduced softening that is clearly associated with the assemblage, with increasing biomass of *Hyalella* and *Caecidotea* that is strongly related to the chemical conditions downstream of the industrial inputs (shredder PC2). The shredders reflect their locations with respect to the environmental variables in the CCA, without necessarily having a strong effect on litter softening.

In the model of loss rate, no single stream shows a clear longitudinal or turnpike-related change in any of the principal components. Decreasing loss rates are most strongly associated with *Caecidotea* and *Hyalella*, which are in turn associated with the industrial inputs at Goosefare Brook. Several taxa are associated with higher loss rates, most of which are Plecoptera. Habitat PC5, which was also significant in the model of softening rate, shows increasing loss associated with higher alkalinity and pH, and lower rates with increasing ammonium, flow velocity, and Fe concentration.

Habitat	**PC3**	c	**PC5**	c				
% variance	**12.1**		**4.8**					
	Dissolved Organic C	-0.44	NH4-N	-0.22				
	Exchangeable Pb	-0.17	Exchangeable Fe	-0.20				
	Exchangeable Cr	-0.10	Flow	-0.19				
	NH_4-N	-0.08	Total Mn	-0.14				
	Exchangeable Cd	-0.07	Total Pb	-0.12				
	Mean ϕ	+0.26	NO_3-N	+0.21				
	Bankfull Width	+0.27	Depth	+0.26				
	Flow	+0.33	Exchangeable Cd	+0.39				
	pH	+0.35	pH	+0.40				
	Depth	+0.43	Alkalinity	+0.53				
Shredder								
Biomass	**PC1**	c	**PC2**	c	**PC5**	c	**PC6**	c
% variance	**16.1**		**12.2**		**8.6**		**7.6**	
	Taenionema	-0.51	*Lepidostoma*	-0.46	*Brillia*	-0.27	*Amphinemura*	-0.51
	Podmosta	-0.48	*Leuctra*	-0.29	*Podmosta*	-0.19	*Leuctra*	-0.41
	Taeniopteryx	-0.44	*Pteronarcys*	-0.23	*Amphinemura*	-0.18	*Tipula*	-0.26
	Paracapnia	-0.32	*Amphinemura*	-0.20	*Taenionema*	-0.15	*Paracapnia*	-0.18
	Allocapnia	-0.24	*Brilla*	-0.05	*Pycnopsyche*	-0.14	*Allocapnia*	-0.04
	Brillia	-0.07	*Podmosta*	-0.05	*Caecidotea*	+0.04	*Brillia*	-0.03
	Pycnopsyche	+0.02	*Taeniopteryx*	-0.04	*Hyalella*	+0.04	*Caecidotea*	-0.02
	Amphinemura	+0.02	*Tipula*	+0.01	*Leuctra*	+0.21	*Podmosta*	0
	Pteronarcys	+0.05	*Pycnopsyche*	+0.02	*Taeniopteryx*	+0.24	*Taenionema*	+0.02
	Leuctra	+0.09	*Taenionema*	+0.04	*Pteronarcys*	+0.31	*Taeniopteryx*	+0.03
	Lepidostoma	+0.10	*Paracapnia*	+0.26	*Lepidostoma*	+0.36	*Hyalella*	+0.05
	Tipula	+0.16	*Allocapnia*	+0.28	*Allocapnia*	+0.36	*Lepidostoma*	+0.09
	Hyalella	+0.20	*Caecidotea*	+0.45	*Tipula*	+0.39	*Pycnopsyche*	+0.30
	Caecidotea	+0.24	*Hyalella*	+0.50	*Paracapnia*	+0.45	*Pteronarcys*	+0.61

Table 4.3. Percent of total variance explained and eigenvector coefficients (c) of the ten most influential variables (habitat analysis) or all variables (shredder biomass analysis) in each principal component. Only components that were significant in the multiple regressions of litter processing rates are included.

Discussion

There is good reason to expect that stream function may be affected by physical and chemical habitat alteration associated with roadways. Several studies have examined the effects of human activities, such as land use and chemical pollution, on the processing of leaf litter in the context of ecosystem function. An insecticide application to a small stream reduced invertebrate biomass and halved the litter processing rate, demonstrating the effect that toxic substances may have on organic matter processing in an unchannelized system (Chung et al 1993). Decreases of similar magnitude were observed by Schultheis et al (1997) in a stream polluted by copper. Nelson (2000) did not find a reduction in processing in a high-altitude stream polluted by Mn and Zn, suggesting that the level of toxic stress was insufficient to impair function and no significant relationship between shredder abundance and litter processing was observed, even though community structure was altered. In a study of 17 streams in central Maine, Huryn et al (2002) found a significant relationship between shredder richness and leaf loss, but a marginally significant relationship with shredder biomass. These findings supported results seen in the laboratory study by Jonsson and Malmqvist (2000), in which the number and types of shredders present were less important than overall shredder richness in determining rates of litter loss.

Few studies have specifically addressed the effects of roads on leaf litter processing. Stout and Coburn (1989) found a decrease in litter processing downstream of a road crossing two years following construction, compared to upstream values. In litter

bags accessible to shredders, processing rates in dowstream riffles were slightly lower than upstream riffles, but downstream pools were higher than those upstream. Shredder abundance decreased downstream of the crossing in both habitats. The reduced shredder abundance and decreased processing rates were attributed to channel alteration and riparian clearing associated with roadway construction. Maltby et al (1995a) found that fungal and shredder assemblages were altered by runoff from a major highway in the U.K., and concluded that runoff did not affect fungal decomposition of leaf litter, but shredder feeding activity was reduced.

Invertebrate Assemblages

The role of leaf litter as an energy source and the documented sensitivity of many leaf shredding taxa (Rosenberg and Resh 1993) make effects on litter processing particularly relevant in the assessment of ecosystem function. Many studies have documented the relationships of community structure to chemical pollution (Clements et al 1988a, 1990, Clements 1994, Kiffney and Clements 1994a, Schultheis et al 1997) and land use (Casper 1994, Huryn et al 2002). These studies typically showing decreased mayfly and stonefly abundance and richness, particularly of shredding taxa, with an increase in collector-gatherers such as chironomids, and an overall reduction in macroinvertebrate abundance and diversity associated with the stress.

Alterations in the structure of litter bag invertebrate assemblages can be seen in both a taxonomic and a functional context, although few clear patterns exist that can be

explicitly related to either physical or chemical habitat changes. All streams show a significant effect of the roadway on metrics describing litter bag invertebrate richness, abundance, and total biomass, although changes may be positive or negative depending on the specific stream. Impacted communities generally show an increased proportion of chironomids and a reduction in that of EPT taxa (i.e. – Clements et al 1990, Clements 1994, Huryn et al 2002). In this study, however, the percentage of Ephemeroptera and Chironomidae showed no relationship to the road in any of the streams. Surprisingly, %Plecoptera downstream of the roadway was consistently equal to or higher than upstream, while %Trichoptera was consistently equal to or greater upstream, relative to downstream stations. However, both taxonomic groups tended to contribute less biomass to the assemblage in the immediate area of the turnpike. This implies that chemical pollution from the roadway was not sufficient to alter community composition. However, physical habitat changes near the turnpike apparently affect the assemblages. Further evidence is provided by the increased proportion of filter-feeders at stations near the turnpike, with generally faster flow and coarser substrate, suggesting that filtering rather than gathering was the more efficient strategy for collecting fine particles at these stations.

Other functional feeding groups showed no significant differences related to the roadway, although all showed differences among streams. Among the fine particle feeders, filterers tended to be more prominent in Goosefare, Cascade, and Ward, while there were more gatherers in the other streams. The second order streams in the study (Cascade, Ward, Branch) tended to have a higher proportion of shredder biomass in the

litter bags than the first-order streams, although the examination of shredder communities at finer taxonomic resolution may shed light on among-stream differences.

In some studies, the maintenance of litter processing rates under stress has been attributed to the crane fly *Tipula* (Sponseller and Benfield 2001, CHAPTER II). The apparent success of *Tipula* under polluted conditions is likely due to inherent tolerance. In this study, *Tipula* biomass was unaffected by the roadway in any stream, although it was lower in Cascade and Stevens Brooks than in the other streams. While *Allocapnia* and *Tipula* are important shredder taxa in all of the study streams in terms of biomass, other taxa were prominent in different streams (*Lepidostoma* in Goosefare and Branch, *Pteronarcys* in Branch, *Pycnopsyche* in Ward, *Podmosta* in Stevens, and taeniopterygids in second-order streams). The examination of shredder assemblages in the context of the habitat template may be informative, in that declining litter processing may be related to characteristics of the shredder assemblages associated with both increasing stream size and pollutant concentrations. The rate of litter processing in different streams was similar despite differences in the shredder taxa present, supporting previous findings that shredder richness is a more important determinant of processing than taxonomic composition of the shredder assemblage (Jonsson and Malmqvist 2000, Huryn et al 2002).

Habitat Alteration

In this study, a decline in both litter loss and litter softening associated with increasing flow velocity was suggested by the multiple regression analyses of habitat PCAs and litter processing (Figures 4.7 and 4.8). In habitat PC3, increased depth and bankfull width were also associated with decreased softening rate, implying slower processing in the larger streams, although such a stream effect was not significant in the ANOVAs of processing rates when stream size is considered. The shredder PCs admitted to the models show a tendency toward slower processing with larger taxa, such as *Tipula*, *Pteronarcys*, *Lepidostoma*, and *Pycnopsyche*, which in turn tended to be associated with larger streams than smaller and more numerous capniid and nemourid stoneflies. Further research is needed into the effects of habitat on physical litter processing (abrasion and fragmentation) and shredder assemblage structure before the effects of channelization, flow velocity and discharge, and stream size on litter processing can be determined.

This apparent "inefficiency" of larger shredders could be an explanation for the lack of relationship between shredder biomass and litter processing rates. Stream size parameters such as discharge and flow velocity are important factors controlling litter processing by determining the available habitat for shredders, and thus which taxa are present. This is in contradiction to the results of previous studies (Gelroth and Marzolf 1978, Sponseller and Benfield 2001), in which faster-flowing habitats were associated with faster litter processing. However, the comparison of low-gradient streams in this study suggests that litter processing is impeded in channelized or fast-flowing habitats,

including streams with greater discharge, by reducing the habitat quality for the shredder taxa that are responsible for the greatest proportion of litter consumption.

The increased flow and coarser substrate in channelized reaches near the roadway may be expected to increase rates of processing by physical abrasion and fragmentation. Sponseller and Benfield (2001) found increased processing rates in streams with larger mean substrate particle size, although this was attributed to higher shredder biomass present in those reaches. Gelroth and Marzolf (1978) found that litter loss proceeded more quickly in riffles than in pools, although more slowly in channelized than in unchannelized habitats. However, studies in Maine streams have not shown a significant relationship between litter processing rate and flow velocity in streams (Huryn et al 2002, CHAPTER II). CHAPTER II showed that while flow was not significantly related to litter processing rates in Goosefare Brook, physical processing may be more important in channelized habitats.

Significant habitat PCs are not as closely correlated to processing rates as the shredder PCs, although it is implicit in the analysis that the shredder assemblages are dependent on the habitat, including anthropogenic factors. Important variables in these PCs, including pH, alkalinity, and DOC concentrations, provide further evidence that litter processing is faster in small, acidic streams (Cascade, Goosefare, Stevens) than the larger streams that are not directly associated with bog areas. These two broad habitat groups, which also differ in discharge, likely control the differences in invertebrate assemblages that are related to differences in processing rates. Increased ammonium concentrations and sedimentary heavy metal concentrations, particularly Fe, are

associated with human activities and also with reductions in softening and loss rates, as indicated by the multiple regression analyses.

Implications for Functional Assessment of Small Streams

The loss of taxa resulting from exposure to stresses results in a simplification of stream communities and food webs, which can in turn lead to changes in key ecosystem attributes, such as organic matter processing, total energy flow and energy pathways, and resistance to additional stresses, which are collectively known as biotic integrity (Fore et al 1996, Wallace et al 1996, Jonsson and Malmqvist 2000). This study suggests that litter processing is not affected by habitat disturbance and pollution associated with the Maine Turnpike, although shifts in the functional and taxonomic composition of invertebrate assemblages associated with leaf litter are evident. This is in agreement with the findings of Nelson (2000) that more traditional structural analyses of communities may be better able to identify stressors than functional measures, because the greater sensitivity of structural measures gives them greater discriminatory power. However, functional measures may be more ecologically relevant in that they reflect in-stream processes, and changes may indicate that community and ecosystem resistance to stress has been exceeded (Hill et al 1997, Huryn et al 2002). Because the inference of function from structural characteristics is often difficult, the direct measurement of function in ecological assessments should receive careful consideration, both in studies of stress

ecology in aquatic ecosystems, and in targeting the most crucial problems in the context of regulation and conservation of surface waters.

Chapter V

HIGHWAY-RELATED PHYSICAL AND CHEMICAL EFFECTS ON THE ECOLOGY OF SMALL STREAMS

Chapter Summary

The effects of habitat and water quality changes related to the Maine Turnpike (Interstate 95) on invertebrate community structure and secondary production, fish community structure and biomass, stored and suspended organic matter, and primary producers were examined in a sample of five small low-gradient streams in southern Maine. The variability in channel and riparian habitat, water and sediment chemistry, stored organic matter, and invertebrate community characteristics among the study streams was greater than the within-stream differences attributable to the roadway. These differences appeared to be related to stream size (discharge), with smaller streams more likely to show biotic effects than larger streams. Total invertebrate production in the study streams was comparable to estimates from other small, low-gradient streams in the coastal plain of the eastern United States (3.5-15.3 gAFDM/m^2/y). Significant differences in habitat parameters, water and sediment chemistry, and biotic communities were evident among streams. Stream structure and function tended to respond to both metal concentrations (exchangeable and total) and several habitat parameters, including pH, substrate particle size, and riparian forest characteristics such as height and percent canopy coverage. This study demonstrates that changes in populations and communities

can occur in response to habitat heterogeneity and stress from a large roadway while ecosystem function is maintained.

Introduction

Exposure to stress results in a simplification of stream communities and food webs, which can in turn lead to changes in key ecosystem attributes, such as organic matter processing, total energy flow and energy pathways, and resistance to additional stresses. Direct measurement of process-level ecosystem attributes, such as primary and secondary productivity, nutrient and organic matter dynamics, and system metabolism, are rarely used in the biological assessment of surface waters, but may improve understanding of ecosystem responses to stress compared to population and community characteristics alone. These parameters are often highly variable within and among systems and require a large investment of time and labour to measure, but are fundamental in the evaluation of stream health because they integrate a broad range of ecosystem characteristics (Wallace et al 1996, Hill et al 1997, Bunn et al 1999, Shieh et al 1999).

Roadways are potentially major sources of stress in both urban and rural landscapes, and the effects of roads on the ecology of surface waters are varied and complex. This stress results from chemical pollution and alteration of habitat conditions in the vicinity of the roadway. Vehicles release petrochemicals, metals, de-icing salts, and a host of other materials (Davis and George 1987, Heliovaara and Vaisanen 1993, Maltby

et al 1995a). Modern roads are designed to drain water as quickly as possible, with little consideration of effects on adjacent receiving water bodies (Mungur et al 1995, Ellis and Hvitved-Jacobsen 1996). Metals characteristic of road runoff include lead, copper, cadmium, zinc, nickel, chromium, manganese, and iron (Davis and George 1987, Maltby et al 1995a). Several studies have shown that the levels of these metals are positively correlated with traffic density (Davis and George 1987, Trombulak and Frissell 2000). Most are deposited on or within 20 meters of the road surface, although those that are emitted in aerosol form, such as lead, may travel further before deposition (Harrison et al 1981, Harrison and Johnston 1985, Lygren et al 1984). Metals and other pollutants are typically found in association with street dust (Shaheen 1975, Grottker 1987), and are carried into streams by drainage waters, where they are deposited in the benthic sediment or transported downstream.

Physical alteration of channel and riparian habitats related to road construction, such as drainage improvement, channelization, and clearing of vegetation, frequently lead to the input of sediment, changes in the flow regime, and alteration of the stream habitat. Channelization and increases in flow associated with road crossing can also remove coarse woody debris, reducing channel complexity and habitat quality for invertebrates (Smock et al 1989) and fish (Angermeier and Karr 1984, Finkenbine et al 2000). Culverts can cause physical impediment to the movement of aquatic invertebrates in the water (Dillon 1988), aerial adult stages (Kjeldsen 1991), and fish (Warren and Pardrew 1998, Kahler and Quinn 1998). Urban land use and associated road networks affect the manner in which precipitation is routed through a catchment into stream channels, and the

dissolved and particulate material transported by drainage waters (Booth and Jackson 1997, Jones et al 2000, Trombulak and Frissell 2000).

The Maine Turnpike is a prominent feature in the landscape of southern Maine, and is a potential source of pollutant runoff to surface waters. Use of the Maine Turnpike began in 1956, and traffic volume has steadily increased since that time, from 3.8 million vehicles in the first year of operation, to 54.7 million vehicles in 2000 (total volume at all exits, *data provided by* the Maine Turnpike Authority). During the study period, mean daily traffic volume ranged between approximately 129 000 vehicles (February 2000) and 181 000 vehicles (August 2000). In a previous study of secondary production in one of the study streams (Goosefare Brook), increases in sedimentary metal concentrations were observed downstream of the roadway, with associated effects on the biota (CHAPTER III).

The objective of this study was to generalize the observations in CHAPTER III to other small streams that cross the Maine Turnpike, and to examine ecosystem-level effects of the roadway in greater detail. This goal was accomplished through an evaluation of the effects of the roadway on a sample of five small streams (1st and 2nd order) that pass beneath it in the coastal plain region of southern Maine. The specific focus was to address the effects of habitat and water quality changes related to roadways on invertebrate community structure and secondary production in small forested streams, in addition to effects on other community components such as primary producers and fish. Secondary production represents an integration of mortality, growth, abundance, reproduction, development time, and standing stock biomass, and is arguably an excellent

measure of the success of a population. Because it provides information that can be used to examine storage and movement of energy between ecosystem components, measurement of production is an appropriate functional approach to bioassessment (Benke 1984, Lugthart and Wallace 1992). The effects of alterations to the physical habitat template and heavy metal pollution by runoff were examined in the context of invertebrate secondary production, fish and invertebrate community structure, stored and suspended organic matter, and primary producers. Processing of leaf litter in these streams has been addressed in CHAPTER IV. This study examines whether the stresses on the streams may cause changes in the community structure, resulting in a shift from pollution-sensitive to pollution-tolerant taxa and a decline in secondary production.

Study Sites

The streams in this study were first- and second-order reaches that cross beneath the Maine Turnpike (Interstate 95) in the coastal plain of southern Maine (Figure 5.1). The streams are generally low gradient and sandy, with large quantities of woody debris. An effort was made to select streams that had similar habitat on either side of the highway. Five 50m study reaches were established in each stream on either side of the highway. The exception is the five downstream reaches in Goosefare Brook (6-10), which were 25m. Three additional 50m stations were added in Goosefare Brook downstream of an industrial discharge that is known to contribute metals to the stream (CHAPTER III), in order to allow examination of the response parameters over a greater

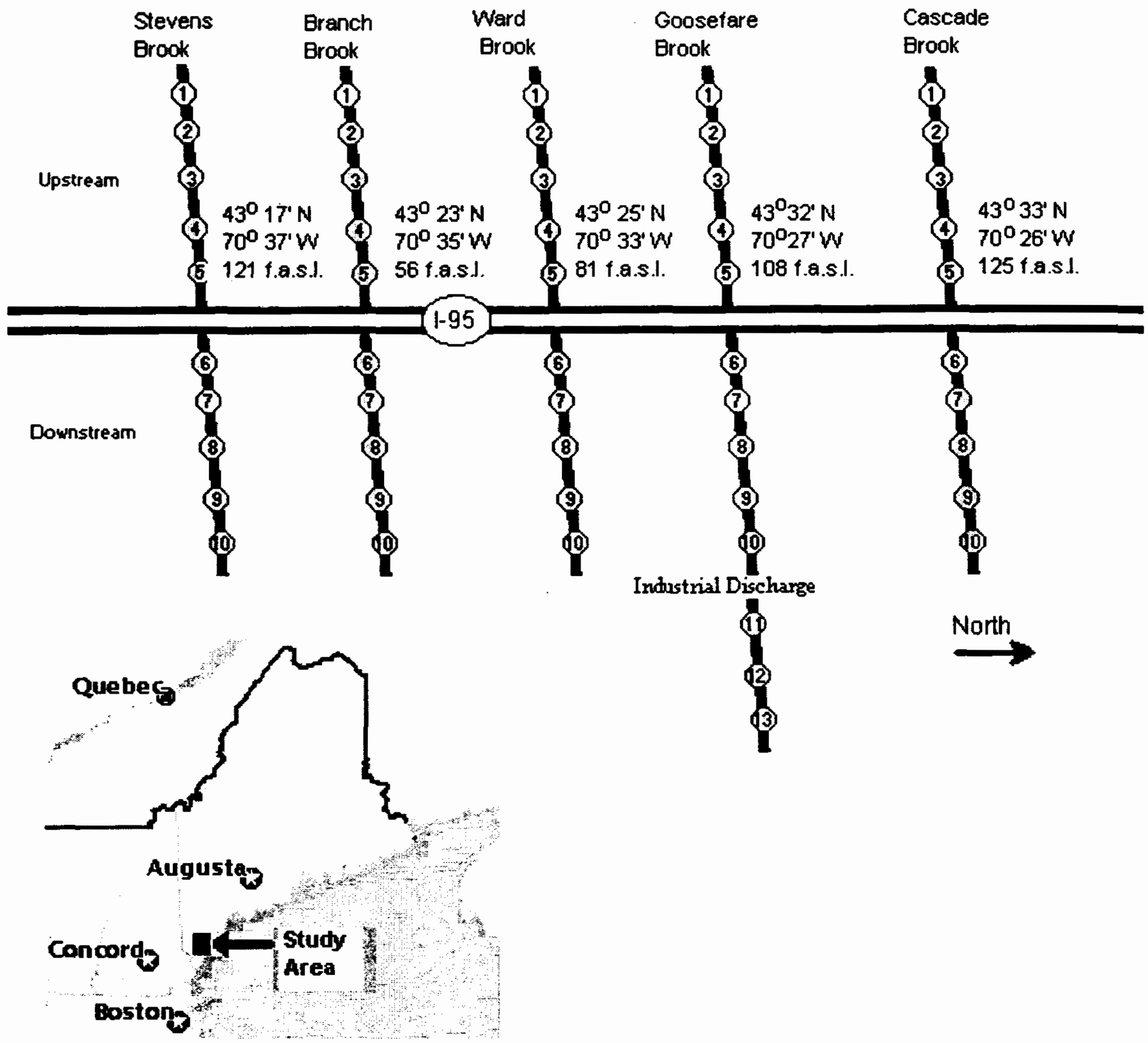

Figure 5.1. Schematic diagram of the study design. Latitude, longitude, and elevation in feet above sea level are given for the point at which the road and stream cross. Inset shows the location of the study sites in Maine. The study area encompasses from Turnpike mile marker 15 (Stevens Brook) to mile marker 36 (Cascade Brook). Study reaches are 50m in length, excepting downstream stations in Goosefare Brook, which are 25m.

range of pollutant levels. The predominant land use in each of the catchments is mixed forest (Table 5.1). Common riparian tree species include oak (*Quercus* spp.), hemlock (*Tsuga canadensis* (L.) Carr.), and red maple (*Acer rubrum* L.), and there is a thick understory of ferns and herbaceous plants. Clearing of vegetation has occurred near the highway to varying degrees, and some of the forest at Ward Brook is in early successional state (*Alnus* spp). Some clearing of the riparian area near the roadway occurred late in the study at Stevens Brook (August 2000), related to a major Turnpike construction project. Three of the five streams (Cascade, Goosefare, and Stevens Brooks) drain bogs.

	Cascade		Goosefare			Ward		Branch		Stevens	
	U	D	U	D	I	U	D	U	D	U	D
Agricultural	**17.9**	**16.6**	**14.4**	**24.7**	**29.3**	**35.2**	**33.5**	**23.0**	**23.0**	**9.2**	**9.4**
Cut Forest	**2.9**	**4.4**	**6.8**	**5.7**	**5.1**	**9.0**	**9.6**	**18.0**	**17.8**	**1.1**	**1.8**
Clear-cut	0.7	1.5	4.9	4.0	3.3	3.8	3.9	0.8	0.8	0.5	1.1
Partial Cut	0.7	1.3	0.3	0.3	0.6	3.8	4.1	14.6	14.4	0.6	0.4
Regenerating	1.5	1.6	1.6	1.4	1.2	1.4	1.6	2.6	2.6	0.0	0.3
Forested	**70.2**	**71.0**	**70.6**	**60.3**	**51.7**	**49.4**	**49.3**	**54.8**	**55.1**	**89.0**	**87.8**
Coniferous	30.6	27.0	1.9	1.6	1.2	1.0	2.3	3.1	3.2	18.0	17.8
Deciduous	4.5	4.4	3.9	3.2	2.6	4.3	4.1	9.2	9.0	16.9	12.0
Mixed	35.1	39.6	64.8	55.5	47.9	44.1	42.9	42.5	42.9	54.1	58.0
Wetland	**8.5**	**7.5**	**1.4**	**1.2**	**0.9**	**5.2**	**5.5**	**2.6**	**2.5**	**0.6**	**0.7**
Urban/Residential	**0.5**	**0.5**	**6.8**	**8.1**	**13.0**	**1.2**	**2.1**	**1.6**	**1.6**	**0.1**	**0.3**

Table 5.1. Percent land use cover in the study catchments. Values are expressed for the catchment upstream of the lowest station in the reach. Major categories of forest are separated into sub-categories.

Methods

Channel and Riparian Habitat

Channel habitat was assessed at transects, located at 5m intervals along each reach. At each transect, bankfull width, flow and depth were measured, and percent coverage of muck, clay, sand, pebble, cobble, and boulder was estimated along each transect at 1m intervals. Particle size was expressed using the modified Wentworth scale (ϕ - Cummins 1962). The percent coverage of debris dam, coarse woody debris (CWD), moss, and macrophyte habitats was also estimated in each interval, and the total area of each habitat type was calculated for each reach. As an indication of the shape and condition of the channel, the upper and lower bank stability index of Weatherred et al (1981 – first 9 metrics) was evaluated at 10m intervals along each reach. Discharge was measured on either side of the roadway in each stream approximately monthly using the velocity-area method of Gore (1996). All flow velocity measurements were taken using a Global flow meter (Global Water Instrumentation, Gold River CA). Temperature was recorded hourly at the stations immediately upstream and downstream of the highway in each stream using Optic StowAway temperature loggers (Onset Computer Corporation, Bourne MA).

Riparian habitat was assessed at 10m intervals along each reach, and the height of the canopy and percent canopy cover were estimated. The tree species present and the understory characteristics within 5m of the channel were recorded as presence or absence of grasses, ferns, herbaceous plants, moss, detritus, and young trees. Calculation of tree

species richness and understory complexity was made for each reach. The relative frequency of each tree species to the riparian forest was estimated by summing the number of occurrences of that species in the reach and dividing by the total number of trees enumerated. Catchment land use was quantified using satellite data that are available in the form of a raster image of a vegetation classification for Maine (New England GAP Online Data, Maine Department of Inland Fisheries and Wildlife). Catchment boundaries were digitized from 1:24000 scale topographical maps, and layered onto the land use classification to calculate the proportional cover of land use types in each catchment (Table 5.1).

Benthic Sampling and Invertebrate Production

Four benthic samples were taken from each station at randomly determined points nine times between October 1999 and September 2000. An Ekman dredge ($0.0225m^2$) was used for sand, silt, and clay substrata, while a Surber sampler ($0.09m^2$, mesh size 250μm) was used for cobble/boulder substrata. Samples from each reach were composited, preserved in 10% formalin and returned to the laboratory, where they were rinsed through a 250μm sieve. Invertebrates were removed from the sample and preserved in 95% ethanol, and identified to the lowest practical level, typically genus (Wiederholm 1983, Thorp and Covich 1991, Merritt and Cummins 1996). Chironomids were morphotyped, and a subsample of each group was slide-mounted for generic identification. Body length of invertebrates was measured, and biomass was calculated

using published length-mass relationships (Benke et al 1999). If an equation was not available for a taxon, the most similar taxon possible was substituted. Biomass was estimated as ash-free dry mass (AFDM).

Production was calculated using the size-frequency method (Benke 1984, 1993). Estimates were corrected for the cohort production interval (CPI) of each taxon (Benke 1979), and for unequal sampling intervals (Krueger and Martin 1980). The CPI estimate for each taxon was obtained empirically using length-frequency histograms of data collected in this study, or on the basis of published life history data from the most climatically comparable area available for each taxon. If low population density of a taxon made direct calculation impractical in a given reach, production was estimated by multiplying mean interval biomass by the average annual production divided by mean interval biomass (P/B) of that taxon at all stations where calculations were possible, or by an assumed P/B of 5 (Benke 1984) if no station yielded a sufficient number of specimens.

Water and Sediment Chemistry

A 500 mL grab sample of water was taken on either side of the roadway at each benthic sampling event, and analyzed for nitrate (NO_3-N), ammonium (NH_4-N), phosphate (PO_4-P), dissolved organic carbon (DOC) and alkalinity. Concentrations of NO_3-N and NH_4-N were determined using an Aplkem flow injection analyzer (detection limit 0.05 mg/L). Concentrations of PO_4-P were determined using Dionex I.C. (detection limit 0.01 mg/L). Dissolved oxygen, pH, and specific conductance were measured at the

downstream end of each reach using hand-held probes (Yellow Springs Instrument Company, Yellow Springs OH).

Sediment samples were taken at each station three times during benthic sampling (October 1999, March 2000, September 2000) by pressing a length of 1" PVC pipe into the substrate to a depth of ~2cm, and compositing the collected material to a rinsed, acid-washed amber plastic bottle. Cores were taken at the left, right, and center of channel at the same locations as the benthic samples, for a total of twelve cores per reach in each sample. All samples were stored on ice until their delivery to the Maine State Analytical Laboratory (5722 Deering Hall, University of Maine, Orono ME, 04469-5722) for analysis. A subsample of the sediment was analyzed for organic carbon content. The remaining sediment was analyzed for eight heavy metals (Cd, Cr, Cu, Fe, Mn, Ni, Pb, and Zn) using a two-stage extraction. The first extraction was performed using 1M ammonium acetate at pH 7, and measured aqueous and weakly complexed metals. The remainder of the sample was then digested in nitric acid. The sum of the metal concentration in the two extractions is the total metal concentration for the sample. Details of the extraction methodology are described by Say and Whitton (1983). Heavy metal concentrations in sediments were determined using flame AA, with a replicate performed every 9 samples. All results were checked against external standards bracketing the expected concentrations.

Benthic and Suspended Organic Matter

Organic matter in each benthic sample was separated into categories (wood, leaves, moss, macrophytes, and fine particulate organic matter), dried, and ashed at 550°C for 24 hours to obtain AFDM of organic habitat components. Seston samples were taken by filtering a 1L grab sample of water at the downstream end of each reach at each sampling interval. The pre-weighed glass-fibre filters (0.7μm pore size) were stored on ice until returning to the laboratory, dried, and burned to obtain AFDM and the mass of inorganic suspended material. Wood only includes that recovered in benthic samples, and do not include large logs and branches stored in the channel and debris dams.

Primary Producers

Relative abundance of periphyton was estimated using chlorophyll *a* from samples of native substrata four times (November 1999, March, May, August 2000). In streams with cobble substrate (Cascade and Stevens), two cobble-sized substrate particles were collected from the upstream end of each study reach, while a core of known surface area was taken to ~1cm depth in streams with sandy substrate. Samples were placed in acid-washed amber plastic bottles and transported to the laboratory on ice in light-tight coolers. In the laboratory, samples were vacuum-filtered through glass-fibre filters (0.7μm pore size) to remove as much water as possible, and substrate and filter discs were extracted for 24 hours in 90% ethanol. Chlorophyll *a* and phaeophytin were measured spectrophotometrically using the methodology of Nusch (1980). The surface area sampled was calculated using the size of the corer for soft

substrates, or by calculating the cobble surface area. Surface area was calculated by drying each cobble and tightly wrapping it in aluminum foil, which was then weighed and divided by the known mass of the foil per square meter. The colonizable surface area for periphyton was taken as half of this measurement. Analysis of benthic photosynthetic pigments was performed on the sum of chlorophyll *a* and phaeophytin, because it was not possible to process the samples quickly enough to avoid apparent degradation of chlorophyll *a* in the samples.

Fish

To assess fish populations, blocking seines were placed at each end of the reach, and two passes were made with a backpack electroshocker. Body length and live weight of all captured fish were measured at streamside. Fish were identified to species according to Page and Burr (1991). The physical condition of each fish was expressed using the following index (Clements and Rees 1997),

$$\text{Condition} = \{[\text{Weight (g)}] / [\text{Length (mm)}]^3\} \times 10^5$$

Statistical Analyses

The total area of each substrate type in each reach and mean channel characteristics were used in the analysis of reach-scale parameters, while patch-scale parameters were calculated as the mean habitat characteristics from the location of the four randomly located benthic samples from each interval, as determined from the 5m habitat transects. The channel and riparian habitat characteristics, annual means of

sediment and water chemistry variables, annual means of suspended and stored organic matter and photosynthetic pigments, fish community characteristics, and annual secondary production of invertebrates are referred to as annual measures. Interval values of suspended and stored organic matter, invertebrate biomass, photosynthetic pigments, and habitat characteristics from sampling locations are referred to as repeated measures.

Parameters expected to influence sedimentary metal concentrations (iron, manganese, organic carbon content, particle size - Combest 1991) were related to sedimentary metal concentrations using forward stepwise regressions (F to enter $\geq$4.0). These regressions were performed on measurements pooled from all stations to relate each metal variable to sediment characteristics (Neter et al 1996). Transformation of the data was not required, because residuals from a univariate regression of each parameter revealed no serious deviations from normality or constant variance. The Multi-Response Permutation Procedure (MRPP – Slauson et al 1994) was used to examine differences in sedimentary metal concentrations between upstream and downstream reaches in each stream. This nonparametric multivariate procedure compares the average distances between members of a group with a Monte Carlo distribution constructed of a random permutation of members of all groups within multivariate space, and determines the probability that the observed distribution of groups is a random occurrence. These analyses were conducted separately for exchangeable and total metals, with 24 response variables each (8 metals x 3 sampling dates).

Highway effects on water chemistry (specific conductance, NO_3-N, NH_4-N, PO_4-P, alkalinity, DOC), in-stream resources, total invertebrate biomass, total community

production and P/B, proportional functional feeding group production, total invertebrate richness, fish body length and condition, and fish density and biomass per square meter of channel were compared using unbalanced two-factor (stream and location) univariate analyses of variance in the case of annual measures, or three-factor ANOVA including sampling date in the case of repeated measures (Neter et al 1996). Because considerable differences in habitat were evident in the vicinity of the highway (T.S. Woodcock, *personal observation*), the stations immediately upstream and downstream were treated as a separate group for the purposes of these analyses. Thus, three groups were included in each stream; upstream stations (1-4), stations nearest the roadway (5-6), and downstream stations (7-10). Those impacted by industrial inputs (Goosefare Brook 11-13) were excluded from the ANOVAs, since only the effects of the highway were being examined. This procedure accounted for variance due to differences among streams, location with respect to the roadway, and interactions between these factors. In the analysis of repeated measures, including sample invertebrate biomass and sample richness, the addition of the time interval to the model allowed comparison of temporal changes within reaches. Proportional measures were arcsine-transformed prior to analysis, and other variables were ln(x+1) transformed when necessary. (Neter et al 1996).

To examine the influence of physical and chemical habitat factors on the biota simultaneously, multivariate procedures were performed. Mean biomass per sampling interval was examined using Canonical Correspondence Analysis (CCA – Rencher 1995), using the mean characteristics of the patch-scale habitat from the randomly

determined sampling locations in the environmental matrix. The habitat characteristics used included stored organic matter, seston, pH, and specific conductance from the sampling interval, and channel characteristics from each sampling location (from the habitat assessment of each reach). Invertebrate production (mgAFDM/m^2/y) and fish biomass (g/m^2) by taxon were also compared using MRPP separately for each stream (Slauson et al 1994).

Results

Habitat Characteristics

The channel form index of Weatherred et al (1981) is a semi-quantitative method of assessing habitat changes, with higher values of the index indicating 'poorer' channel condition. Differences were evident among streams, with Cascade and Branch having higher values than the others ($F_{4,35}$=4.19, p=0.007), but overall most reaches were similar and stresses such as erosion or bank slumping were not evident. The index was marginally higher in reaches near the roadway when pooled across all streams (p=0.07), implying some negative effect of the road on channel condition.

The plot of explanatory vectors from the habitat patch characteristics used in the CCA of invertebrate biomass (Figure 5.2) showed a separation of coarse and fine substrate particles in habitat, with higher stored organic matter and seston associated with

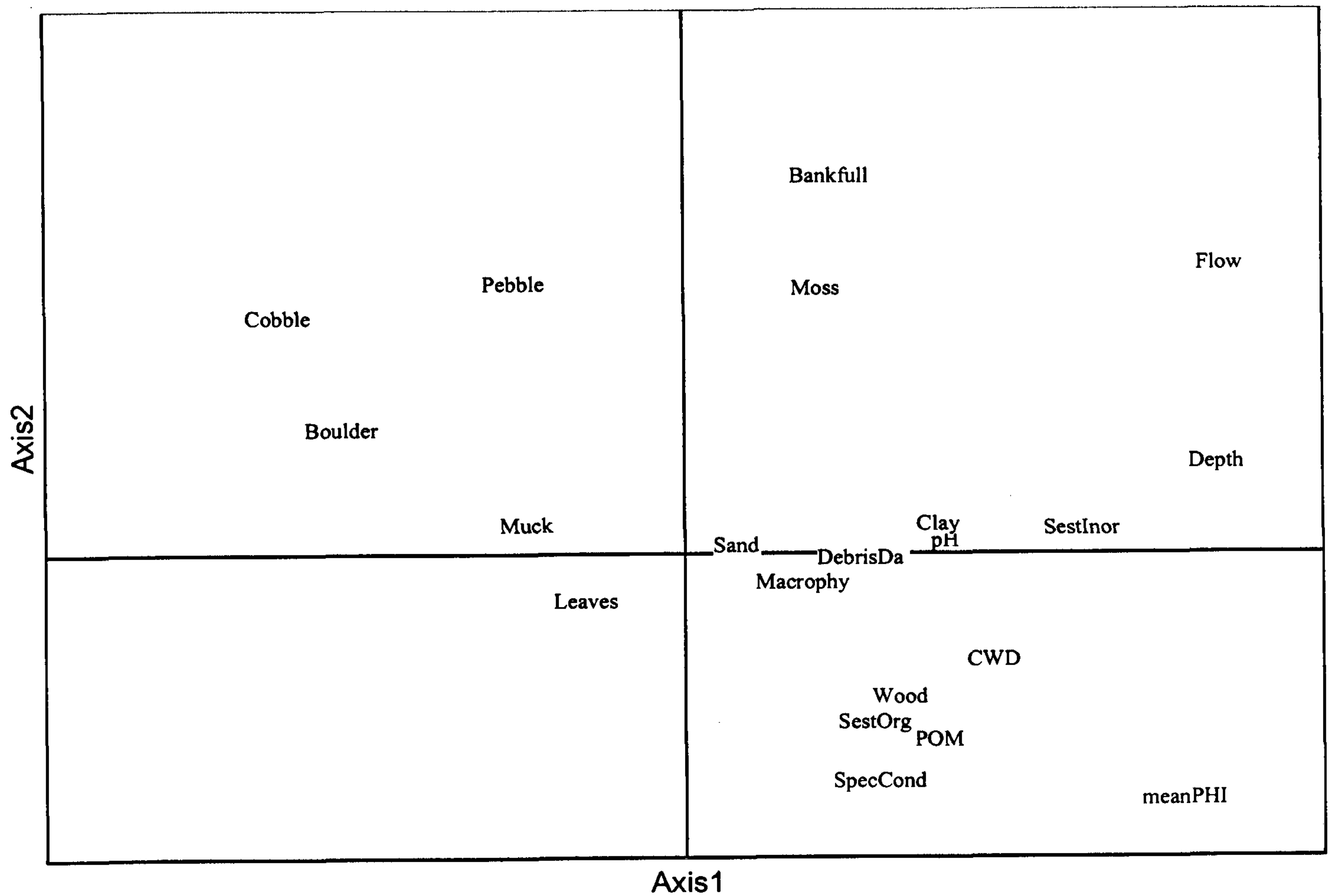

Figure 5.2. Orientation of habitat parameters from the CCA of interval biomass. Explanatory vectors stretch from the origin to the code for that parameter (actual vectors are not included in order to minimize obscuring of data points).

finer substrate (sand and clay). Leaves were not associated with particle size or stored wood, probably due to high temporal variability, but this vector was oriented opposite to flow velocity, width, and depth, suggesting higher leaf retention in smaller streams and areas with slower flow velocity. However, the plot of the individual samples (Figure 5.3) shows a separation of habitat patches among all streams except Cascade and Stevens, indicating the ability of the environmental parameters to discriminate among streams. Cascade and Stevens grouped together because they have coarser substrata than the other streams. There was little difference between samples taken upstream and downstream of the highway in each stream except Branch, in which two downstream stations tended to have higher flow and depth than those upstream. The homogeneity of habitat at stations within streams improves comparability of chemical and biotic measurements between upstream and downstream reaches.

Sediment and Water Chemistry

Mean annual specific conductance was significantly higher downstream of the roadway than upstream ($F_{2,280}$=45.2, p<0.0001) (Figure 5.4). Differences among streams were also evident (Goosefare= Cascade> Ward= Stevens> Branch). The variability and apparent magnitude of the roadway influence was greater for small streams (Cascade, Goosefare, Stevens) than large (Ward, Branch). NO_3-N, alkalinity, and DOC showed differences among streams, but not with respect to location (Table 5.2). PO_4-P was

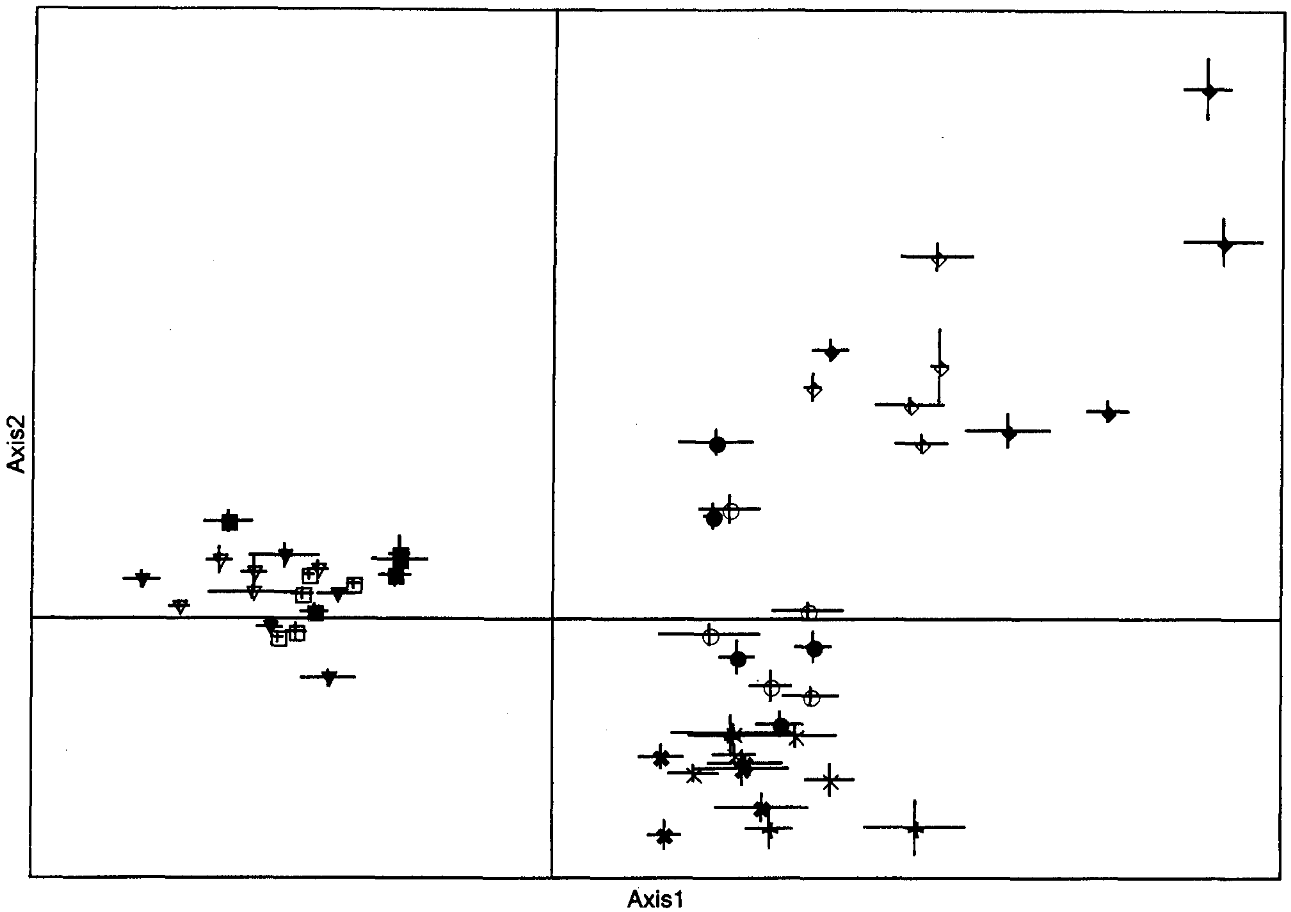

Figure 5.3. Position of sampling stations from the CCA of interval biomass, as determined by environmental parameters. Open symbols represent upstream stations, filled symbols represent downstream stations (Cascade-□, Goosefare-X, Goosefare downstream of industrial inputs-✚, Ward-O, Branch-◇, Stevens-▽). Error bars show ±1S.E. of mean axis values for all samples from that study reach.

Parameter	units	Cascade		Goosefare			Ward		Branch		Stevens	
		U	D	U	D	I	U	D	U	D	U	D
Habitat												
Bankfull Width	m	3.86	5.67	2.25	2.05	2.67	5.69	5.86	7.28	6.64	3.24	3.32
Depth	cm	8.4	9.8	12.3	11.3	15.9	21.8	13.4	24.7	19.7	2.5	4.2
Flow	cm/s	8.7	3.6	4.0	4.2	3.2	3.8	8.2	22.5	26.1	1.0	1.0
Particle Size	mean ϕ	-1.42	-2.17	2.82	2.35	0.68	4.77	2.90	1.01	-0.06	-2.57	-1.07
Min temperature	°C	0.0	0.0	0.0*	0.0	0.0*	0.0	0.0	2.3	0.0	0.6	0.1
Max temperature	°C	20.5	21.5	19.9*	19.9	19.9*	22.0	22.6	18.7	16.5	19.4	19.9
Degree-days	°C	2696	2779	2742*	2742	2742*	2986	2978	3036	2420	2863	2832
Water												
pH	-	6.29	6.41	5.84	6.07	6.34	6.79	6.46	6.46	6.50	4.61	5.49
Dissolved O_2	ppm	9.74	10.32	9.00	9.05	9.54	10.91	10.28	10.30	10.55	9.89	9.65
NO_3-N	ppm	0.11	0.09	0.29	0.27	-	0.04	0.05	0.13	0.13	0.01	0.02
NH_4-N	ppm	0.02	0.03	0.03	0.04	-	0.01	0.05	0.01	0.02	0.02	0.03
PO_4-P	ppm	0.003	ND	ND	0.011	-	ND	ND	0.003	ND	ND	ND
Alkalinity	mgCaCO3/L	47.5	49.1	18.0	21.7	-	18.1	19.5	15.0	16.1	1.9	9.2
DOC	ppm	22.3	21.5	13.0	11.8	-	7.3	7.3	3.0	3.4	18.5	15.7

Table 5.2. Physical and chemical habitat descriptors. *assumed value, due to temperature equipment malfunction. Water samples were not taken in Goosefare downstream of the industrial inputs. ND indicates levels were not detectable.

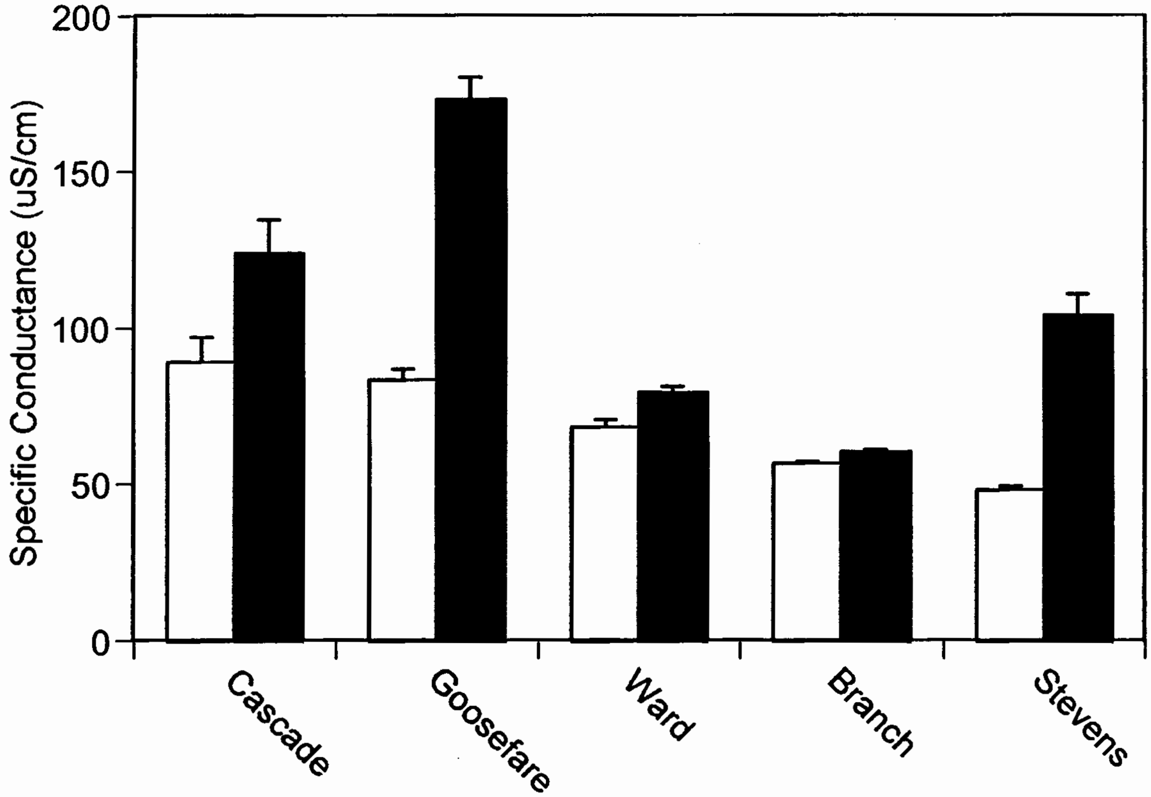

Figure 5.4. Annual mean of specific conductance upstream (open bars) and downstream (closed bars) of the Maine Turnpike, 1999-2000. Error bars are +1S.E.

usually not detectable, while NH_4-N showed no significant differences in concentration among or within streams.

The MRPP analyses of exchangeable and total sedimentary metals showed significant road-related changes in Ward ($p=0.041$) and Stevens ($p=0.004$) for exchangeable metals, and in Goosefare ($p=0.015$) for total metals. Inspection of the data indicates that specific differences included higher total metal levels downstream in Goosefare Brook, and higher exchangeable metal levels upstream in Ward and Stevens. Multiple regression analysis showed little influence of sediment attributes on exchangeable metal concentrations (Table 5.3). The exception is Zn, which showed evidence of sorption to Fe, Mn, and organic carbon in the sediment. Cu showed a weak relationship to Fe and Mn content, and Pb showed a weak relationship to organic carbon

	Total Fe	Total Mn	Organic C	Mean ϕ	r^2
Exchangeable					
Cd	-	-	-	-	-
Cr	-	-	-	-	-
Cu	0.0003	0.044	-	-	0.10
Ni	-	-	-	-	-
Pb	-	-	0.042	-	0.03
Zn	<0.0001	<0.0001	0.0001	-	0.43
Total					
Cd	0.0012	0.021	-	-	0.40
Cr	<0.0001	<0.0001	0.01	0.018	0.95
Cu	<0.0001	0.0028	-	-	0.96
Ni	<0.0001	0.043	-	0.0016	0.85
Pb	<0.0001	0.0019	0.0006	-	0.70
Zn	<0.0001	<0.0001	-	0.0021	0.93

Table 5.3. Variables admitted into univariate multiple regressions of metal concentrations on sediment characteristics. Numbers given are p-values of the sediment characteristic if admitted to the model, while r^2 is given for the entire model.

content. Total metals showed a stronger relationship to sediment characteristics. Fe and Mn content showed the greatest control, organic C was correlated with total Cr and Pb, and particle size affected Cr, Ni, and Zn.

In-Stream Organic Matter

There was a significant difference in stored wood among streams ($F_{4,280}$=19.3, p<0.0001) (Goosefare> Stevens> Ward= Branch> Cascade). Wood remained fairly constant over the year (~220gAFDM/m^2) when all streams were pooled (Figure 5.5), although a drop to approximately 30gAFDM/m^2 occurred in May, possibly related to increased spring discharge (Figure 5.6). The stream*location interaction term was significant ($F_{8,280}$=4.41, p<0.0001). There was higher storage downstream of the roadway than upstream in Goosefare Brook. Stevens Brook showed a similar pattern, although wood storage near the roadway was significantly higher than at other locations. The other streams did not show locational differences when examined individually. Goosefare and Stevens may have behaved differently because the spring discharge peak in these first-order streams is not as great (Figure 5.6, upper panel) as it is in the second-order streams (Figure 5.6, lower panel).

Stored FPOM was correlated with stored wood (r^2=0.61), and showed a relatively constant level of 140gAFDM/m^2, with a significant decrease to 40gAFDM/m^2 in May ($F_{7,280}$=8.10, p<0.0001 - Figure 5.7). Both the stream*location ($F_{8,280}$=2.83, p=0.005) and

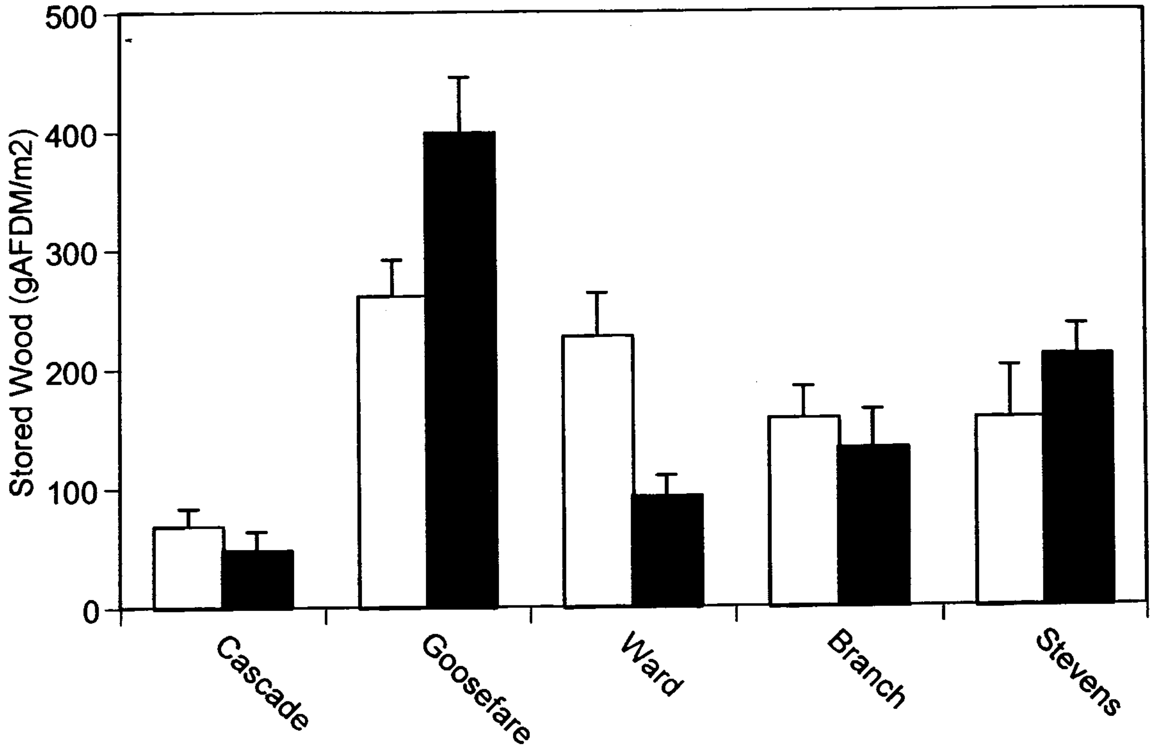

Figure 5.5. Annual mean of stored wood recovered in benthic samples upstream (open bars) and downstream (closed bars) of the Maine Turnpike, 1999-2000. Error bars are +1S.E.

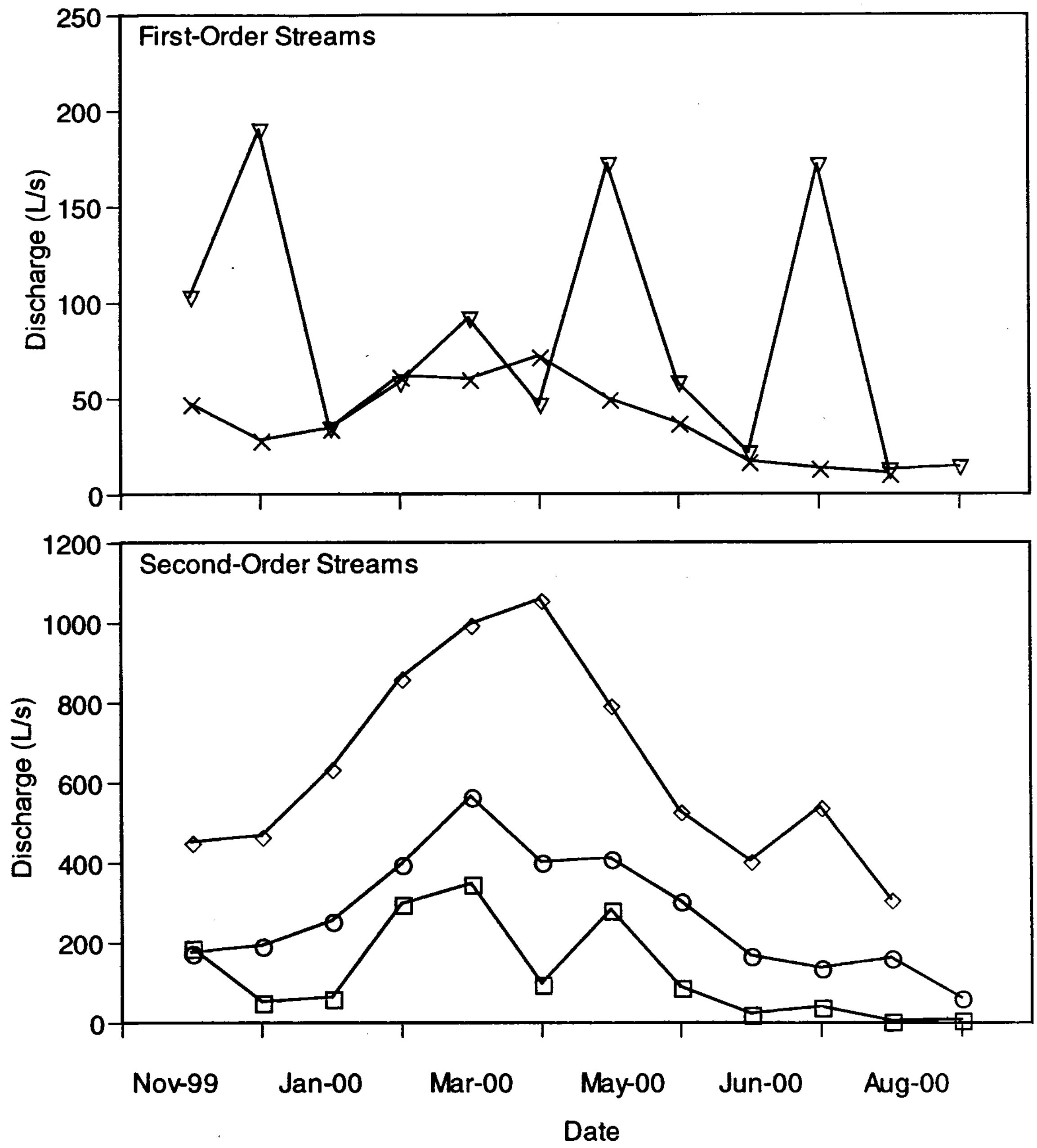

Figure 5.6. Hydrographs, 1999-2000. (Cascade-□, Goosefare-×, Ward-O, Branch-◇, Stevens-∇).

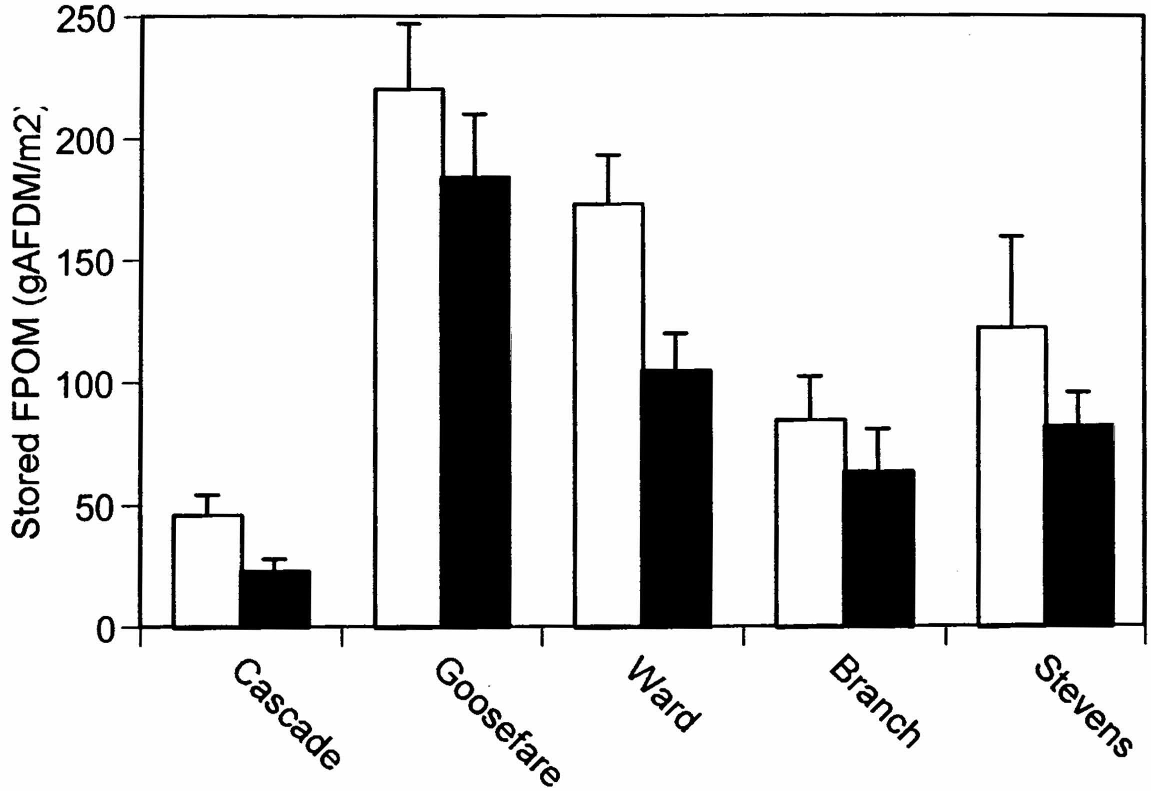

Figure 5.7. Annual mean of stored FPOM (>250μm) upstream (open bars) and downstream (closed bars) of the Maine Turnpike, 1999-2000. Error bars are +1S.E.

stream*date ($F_{28,280}$=1.87, p=0.006) interaction terms were significant in the analysis. FPOM in Stevens Brook was significantly higher near the roadway than at the upstream or downstream stations. There were significant differences among streams in the quantity of stored leaves, with Goosefare and Stevens Brooks significantly higher than the other streams ($F_{4,280}$=9.78, p<0.0001) (Figure 5.8). The stream*location ($F_{8,280}$=3.54, p=0.0006) interaction term was significant. Ward had significantly more stored leaves at upstream reaches ($F_{2,63}$=3.25, p=0.045). Stevens Brook had more leaves at stations near the roadway than in other reaches, and more at downstream stations than upstream ($F_{2,63}$=3.81, p=0.027). The stream*date interaction term was also significant ($F_{28,280}$=2.68, p<0.0001). Mean leaf storage at all stations showed a peak of approximately 70gAFDM/m^2 in November and declined through April until a steady level of approximately 10gAFDM/m^2 was reached.

Organic and inorganic suspended material showed significant differences among streams and sampling dates (Figure 5.9). Organic seston was consistently higher in Goosefare Brook than the other streams ($F_{4,280}$=5.01, p=0.0007), although a significant interaction with date occurred in April ($F_{28,280}$=2.98, p<0.0001), when Ward and Stevens both carried more organic seston than Goosefare. The highest levels of organic seston were present in spring, and were likely related to transport of material into the stream with runoff water (Figure 5.6). Levels were also higher in autumn than in summer. All streams except Cascade showed this annual pattern.

Inorganic seston was higher downstream of the highway, driven by differences in Stevens and Ward (Figure 5.9). Inorganic suspended material may be an indication of

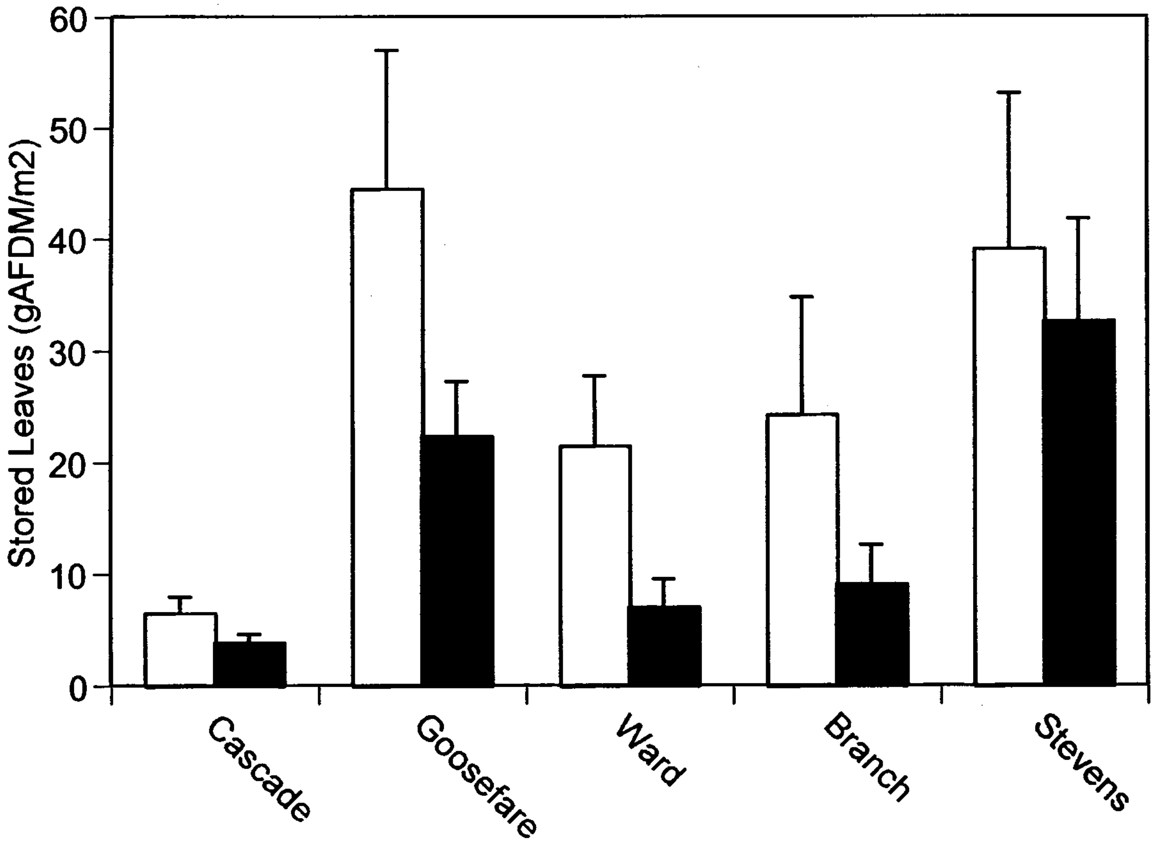

Figure 5.8. Annual mean of stored leaves upstream (open bars) and downstream (closed bars) of the Maine Turnpike, 1999-2000. Error bars are +1S.E.

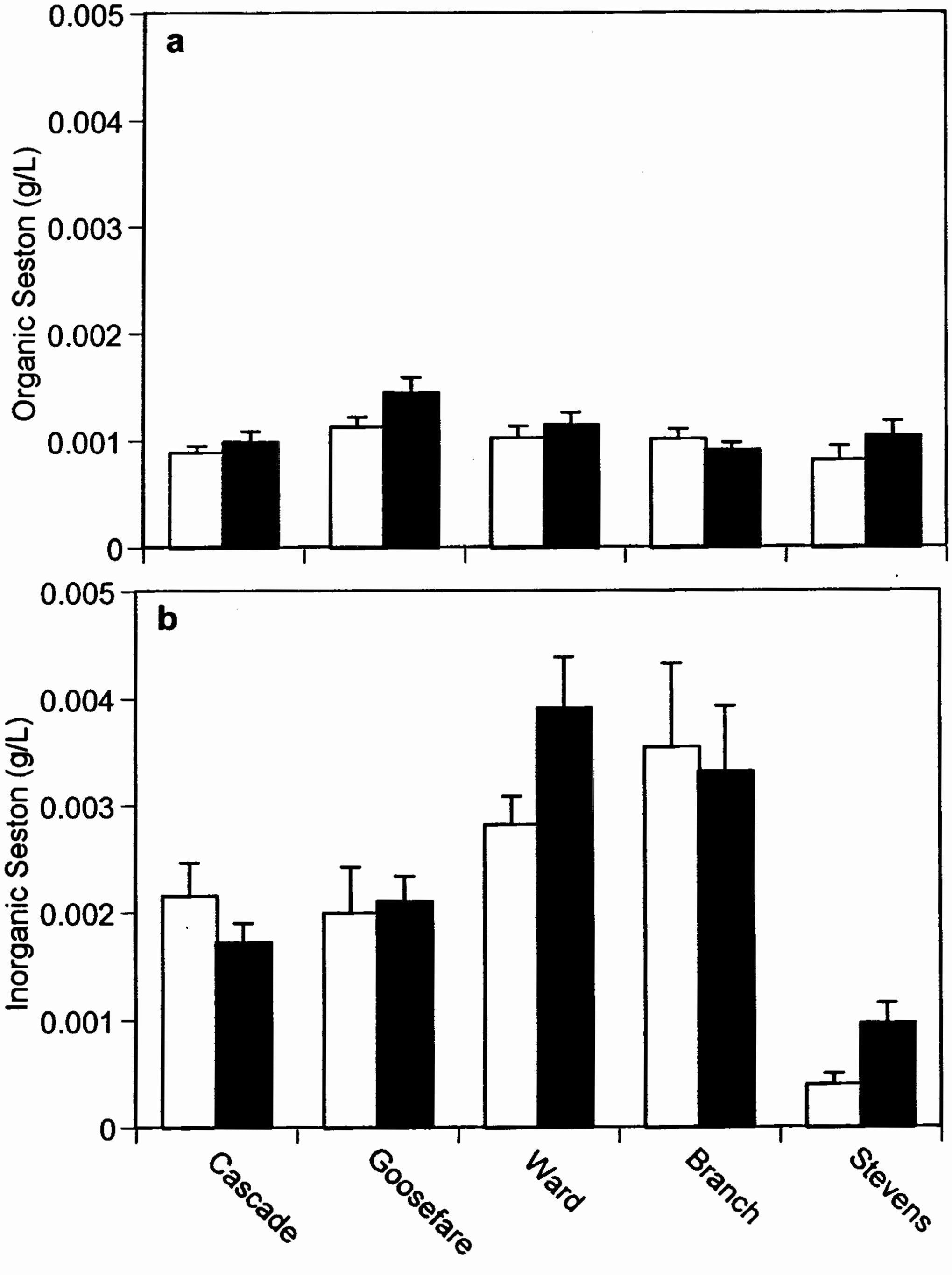

Figure 5.9. Annual mean of (a) organic and (b) inorganic seston upstream (open bars) and downstream (closed bars) of the Maine Turnpike, 1999-2000. Error bars are +1S.E.

sediment inputs from the highway, and significantly higher levels were recorded near the roadway and at downstream stations ($F_{2,280}$=4.22, p<0.02). Significant differences also existed among streams ($F_{4,280}$=56.4, p<0.0001) (Branch= Ward> Goosefare= Cascade> Stevens). Overall levels were fairly constant during the year, although March, April, and June levels were significantly higher than the apparent 'baseline' ($F_{7,280}$=72.0, p<0.0001). Both the stream*location ($F_{8,280}$=4.34, p<0.0001) and stream*date ($F_{28,280}$=14.1, p<0.0001) interaction terms were significant, and individual examination of the streams showed that this annual pattern existed in all streams except Stevens, possibly due to the commencement of construction activities in the late summer. Stevens, Ward, and Branch showed significant increases in inorganic seston associated with the roadway, particularly in the spring. Goosefare had higher levels upstream of the roadway in March only.

Moss and macrophytes were not a large portion of the organic matter pool. Small quantities of moss occurred in most reaches, although the mean quantity was less than 1gAFDM/m^2 in all reaches except upstream of the roadway in Stevens (3.0gAFDM/m^2) and downstream of the roadway in Branch (37.7gAFDM/m^2, mostly at Stations 6 and 7). Macrophyte beds occurred in Ward Brook, especially in downstream reaches where habitat was approximately 7% macrophytes (annual mean biomass of 2.8gAFDM/m^2). There was also one small macrophyte bed in Goosefare Brook at Station 10. Photosynthetic pigment levels (chlorophyll + phaeophytin) were fairly constant at ~35mg/m^2. The stream*location interaction was marginally significant ($F_{8,140}$=1.90, p=0.065). When streams were analyzed separately, only Branch Brook had significantly higher levels downstream of the roadway, due to the large quantities of moss at Stations 6

and 7 ($F_{4,140}$=3.96, p=0.0045 - Figure 5.10). Also, a significant decrease in the annual mean was observed downstream of the roadway in Cascade and Stevens.

Invertebrates

Mean invertebrate richness (#taxa collected per sample at each station over the year) showed no significant differences with respect to the roadway, although there were differences among streams ($F_{4,35}$=35.7, p<0.0001) (Cascade= Ward> Stevens> Goosefare= Branch - Figure 5.11). Total invertebrate biomass also showed significant differences among streams ($F_{4,35}$=4.04, p=0.008) (Stevens> Goosefare= Cascade= Ward> Branch), but the only locational difference was in Goosefare, where there was a decrease downstream of the highway (Figure 5.12).

Both total invertebrate secondary production ($F_{4,35}$=5.64, p=0.0012) (Stevens >Goosefare= Cascade= Ward> Branch) and P/B ($F_{4,35}$=5.92, p=0.0009) (Stevens> Cascade> Branch= Goosefare= Ward) showed significant differences among streams. A significant decrease in production downstream of the highway was observed only in Goosefare Brook (Figure 5.13). An examination of the ten most productive taxa in the upstream reaches of each stream (Figure 5.14) showed that many were also among the most productive downstream (six in Goosefare, Ward, and Branch, eight in Stevens, nine in Cascade). Some of the top ten producers at downstream stations were likely less important upstream due to changes in habitat. For instance, *Promoresia* and *Isoperla*

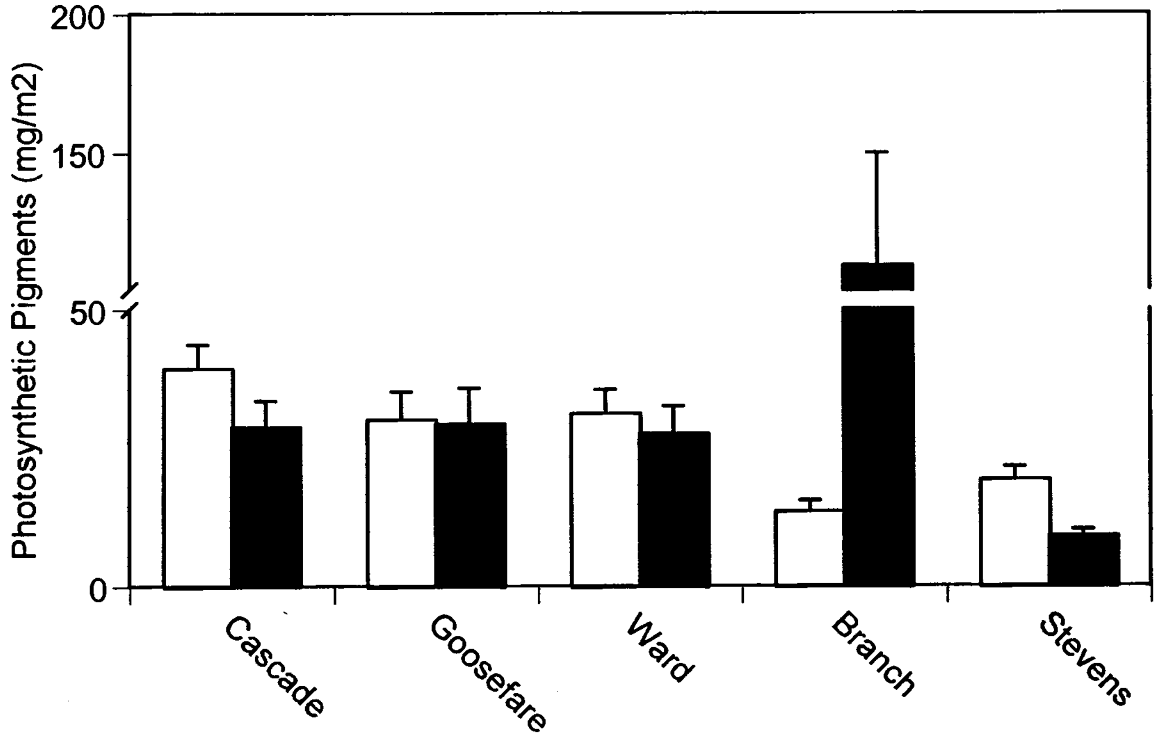

Figure 5.10. Annual mean of photosynthetic pigments upstream (open bars) and downstream (closed bars) of the Maine Turnpike, 1999-2000. Error bars are +1S.E.

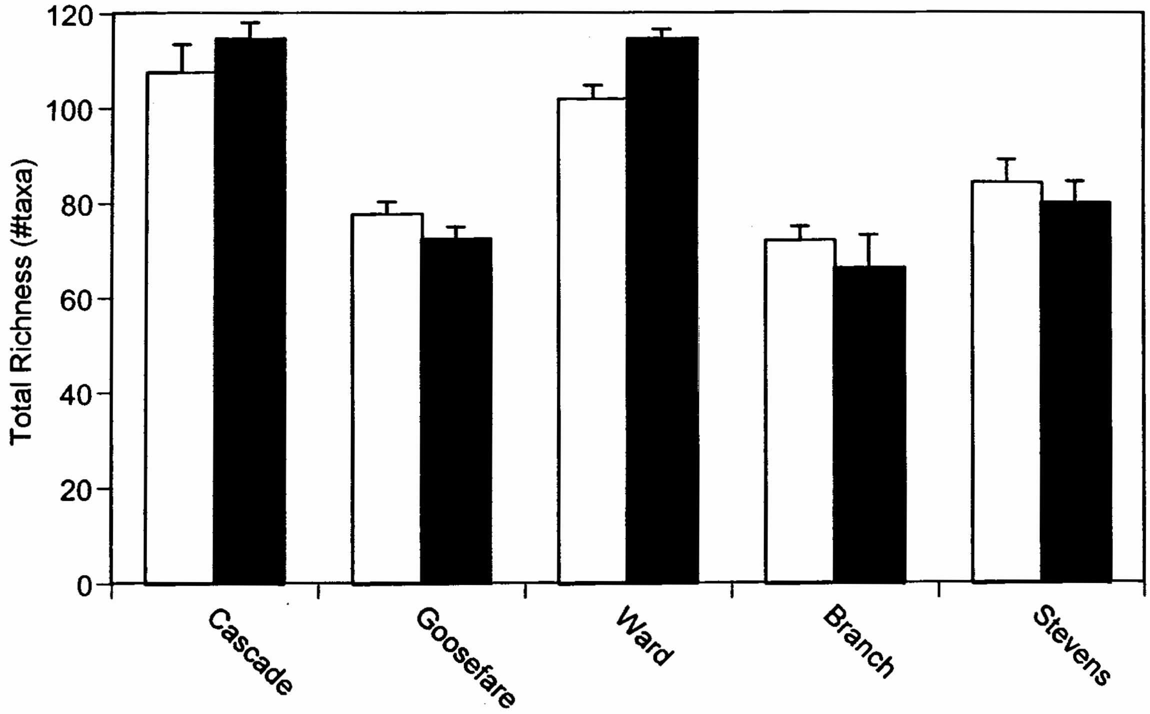

Figure 5.11. Total macroinvertebrate richness upstream (open bars) and downstream (closed bars) of the Maine Turnpike, 1999-2000. Error bars are +1S.E.

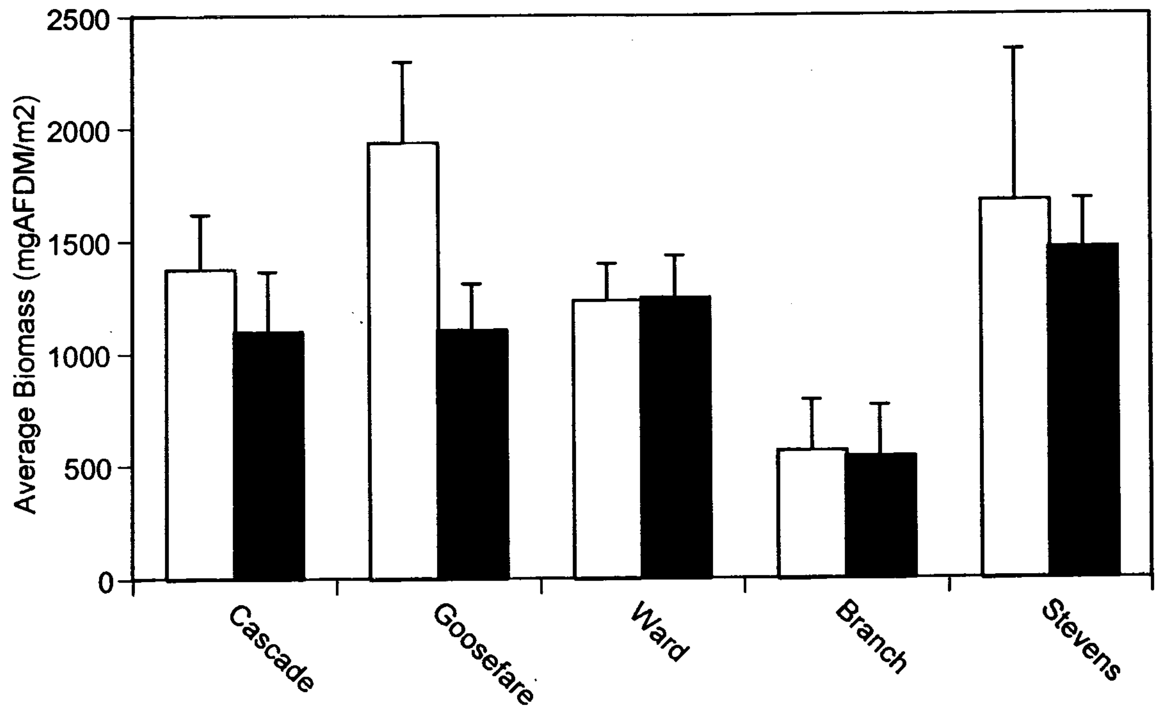

Figure 5.12. Mean macroinvertebrate standing stock biomass upstream (open bars) and downstream (closed bars) of the Maine Turnpike, 1999-2000. Error bars are +1S.E.

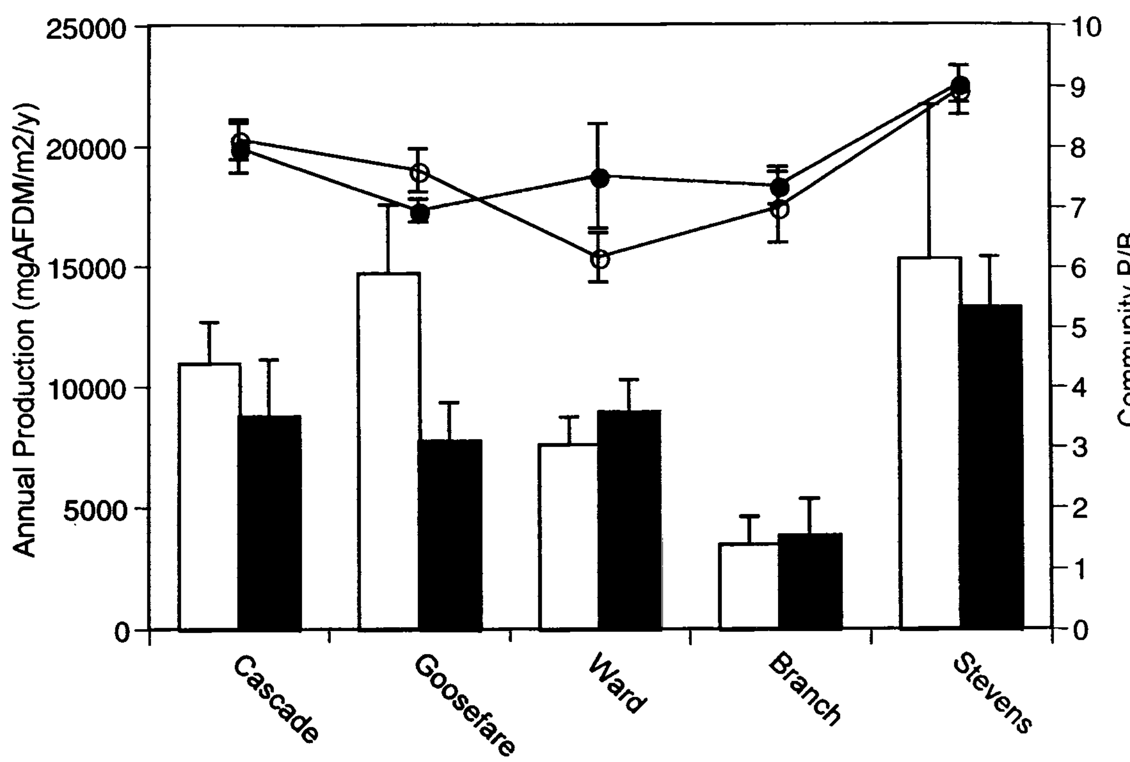

Figure 5.13. Mean annual macroinvertebrate secondary production (bars) and whole-community P/B (lines) upstream (open symbols) and downstream (closed symbols) of the Maine Turnpike, 1999-2000. Error bars are $\pm$1S.E.

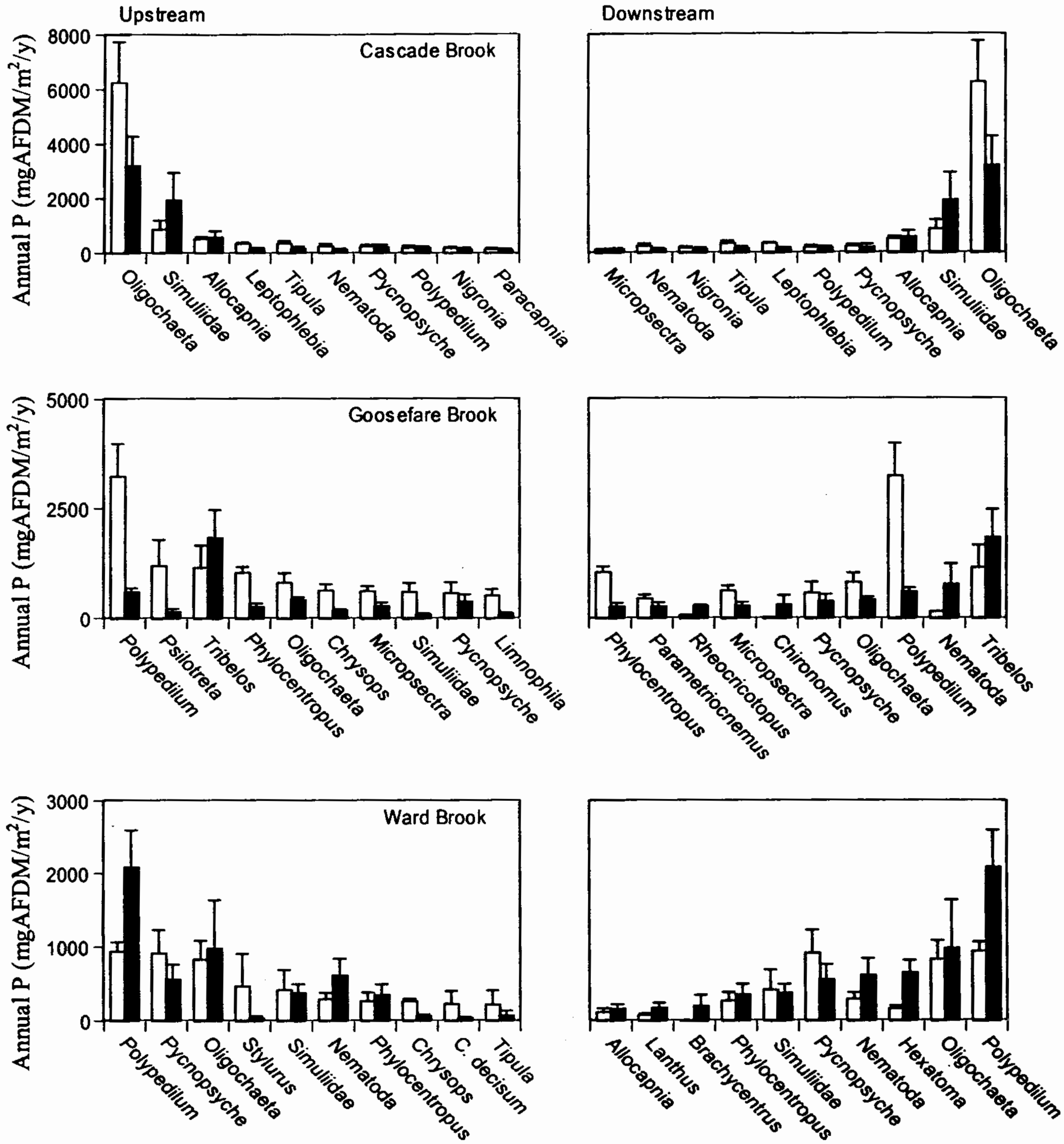

Figure 5.14. Mean annual production of the ten most productive taxa at stations upstream (open bars) and downstream (closed bars) of the Maine Turnpike, 1999-2000. Error bars are ±1S.E.

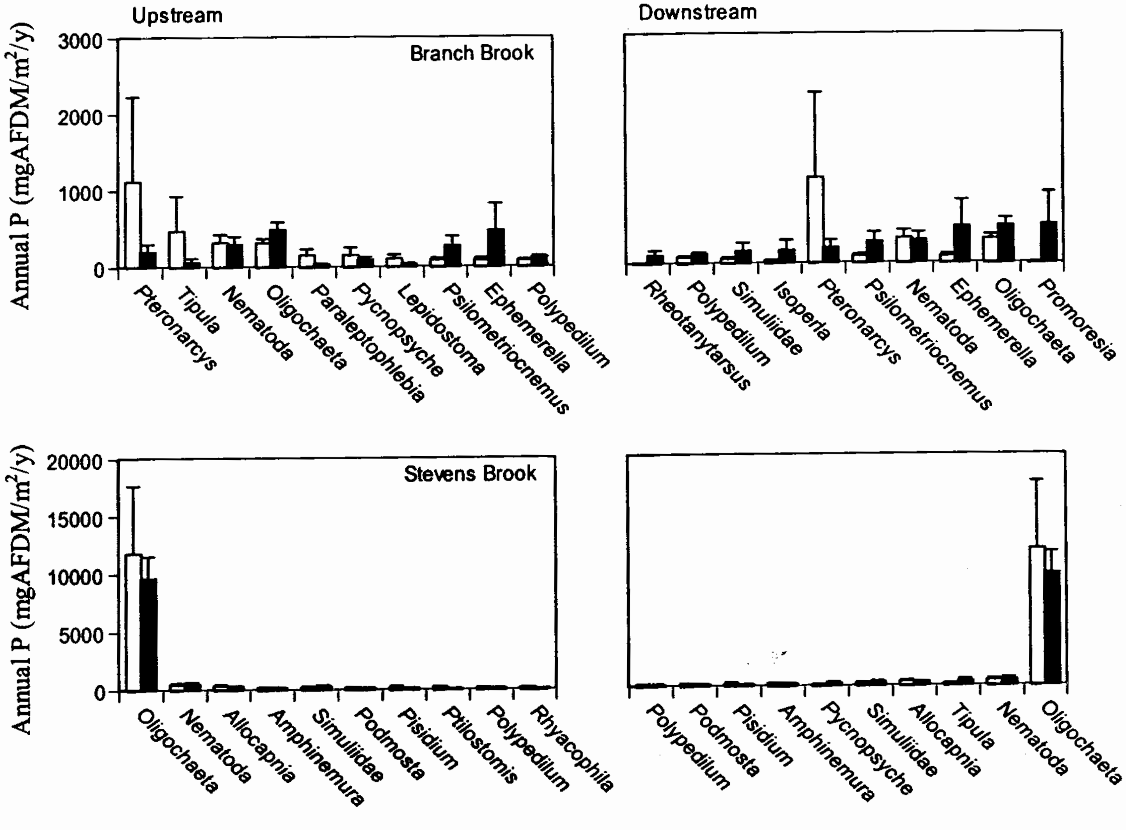

Figure 5.14. continued

downstream in Branch and *Brachycentrus* downstream in Ward were mainly associated with moss and macrophytes, respectively, habitats that were much less extensive at upstream stations. Some streams showed an upstream-downstream replacement by taxa with a similar ecological role, for example the replacement of *Stylurus* (upstream) by *Lanthus* (downstream) in Ward Brook.

The proportional production of each functional feeding group differed among streams, but not within streams upstream and downstream of the roadway (Figure 5.15). Production was dominated by collector-gatherers (50-75% of community production), and was significantly greater in Stevens than other streams ($F_{4,35}$=8.85, p<0.0001). Predators contributed more production in Goosefare and Ward than in the other streams ($F_{4,35}$=14.2, p<0.0001), while filterers contributed more in Goosefare, Cascade, and Ward than in Stevens and Branch ($F_{4,35}$=6.77, p=0.0004). Scrapers contributed the least production overall, significantly less in Stevens than the other streams ($F_{4,35}$=6.51, p=0.0005). The proportional production of shredding taxa was ~17% in all streams, although in upstream reaches in Branch was almost 40%, largely due to high values for *Pteronarcys*.

Comparisons of pollution tolerance among taxa were made using the North Carolina Biotic Index (NCBI - Lenat 1993), in which taxa are assigned scores between 0 (most sensitive) and 10 (most tolerant). For the purposes of this study, these scores were assigned to four groups (0-2.5, 2.6-5.0, 5.1-7.5, and 7.6-10.0). Where different values were identified for several species within a genus the mean of all given values was used. Taxa which had calculable levels of production but for which scores were unavailable

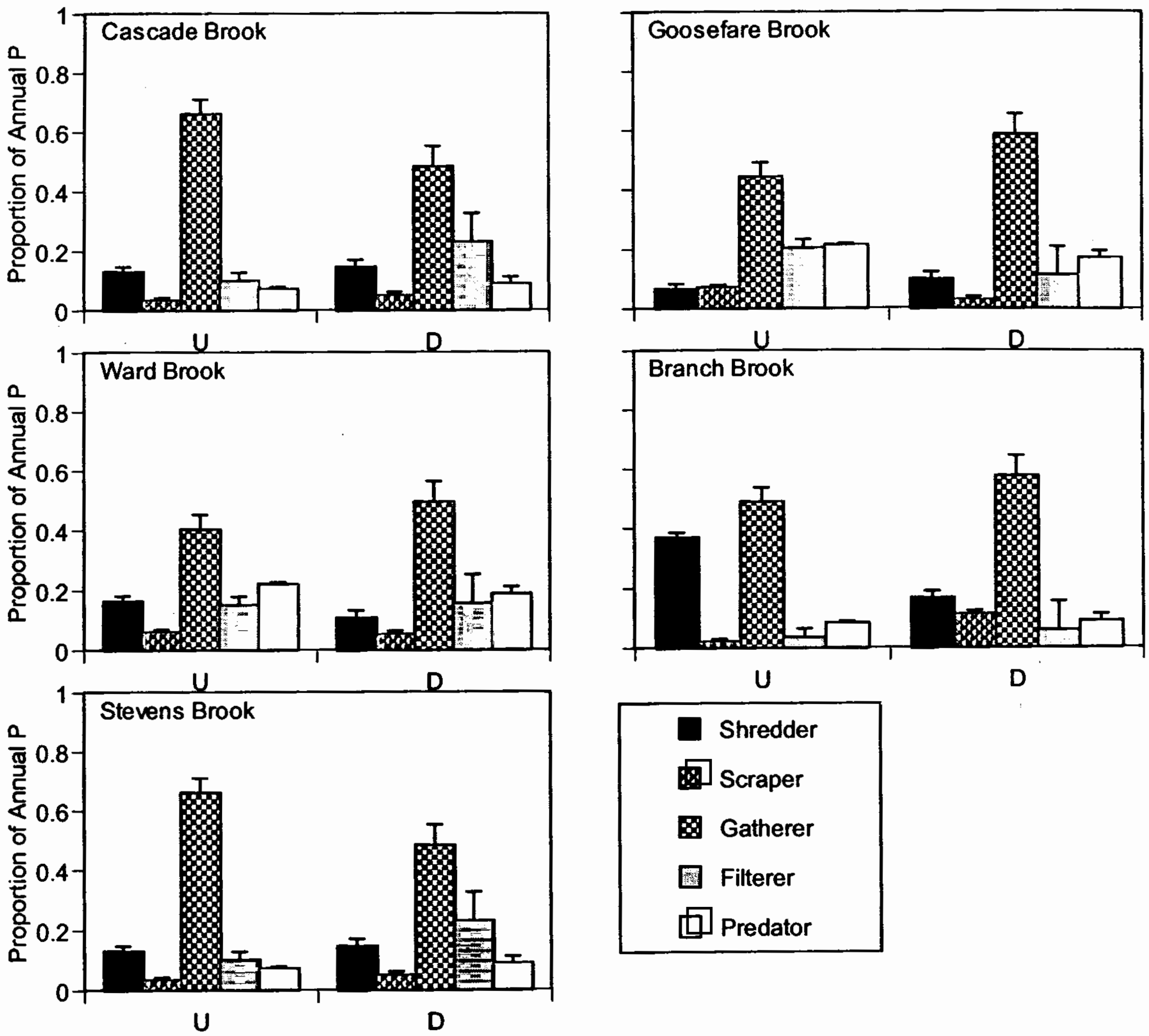

Figure 5.15. Proportional secondary production of functional feeding groups upstream (U) and downstream (D) of the Maine Turnpike, 1999-2000. Error bars are +1S.E.

were arbitrarily assigned to Group 2, in order that those production comparisons would be included in this examination. The CCA of invertebrate biomass explained only 15.5% of the variance in the data set on the first two axes, and investigation of further axes did not serve to clarify the analysis. The plots of biomass of individual taxa in the CCA (Figure 5.16) showed the majority of taxa form a group stretching between the coarse substrate of Cascade and Stevens Brook to the finer particles and higher levels of stored and suspended organic matter in Goosefare. A third group of taxa is evident, which is composed of less tolerant taxa, that was associated with large channel size and found only in Branch Brook. There is no a discernable pattern in functional feeding groups, suggesting that the level of stress is not great enough to alter functional group distribution.

The MRPP analyses of invertebrate secondary production by taxon showed significant changes for Goosefare ($p=0.003$) and Ward ($p=0.043$), indicating that a change in the structure of the community occurred that was related to the roadway. When production of individual taxa above and below the roadway in each stream were compared, the distribution of production showed variation that could be explained by the tolerance of the taxon and significant differences in habitat and sediment chemistry within the streams (Figures 5.17-5.21). Taxa that deviated considerably from the line of equality on each of these plots can be said to have a bias toward higher production on one side of the roadway (Table 5.4 and Figure 5.22). Taxa in NCBI Groups 1 and 2 in

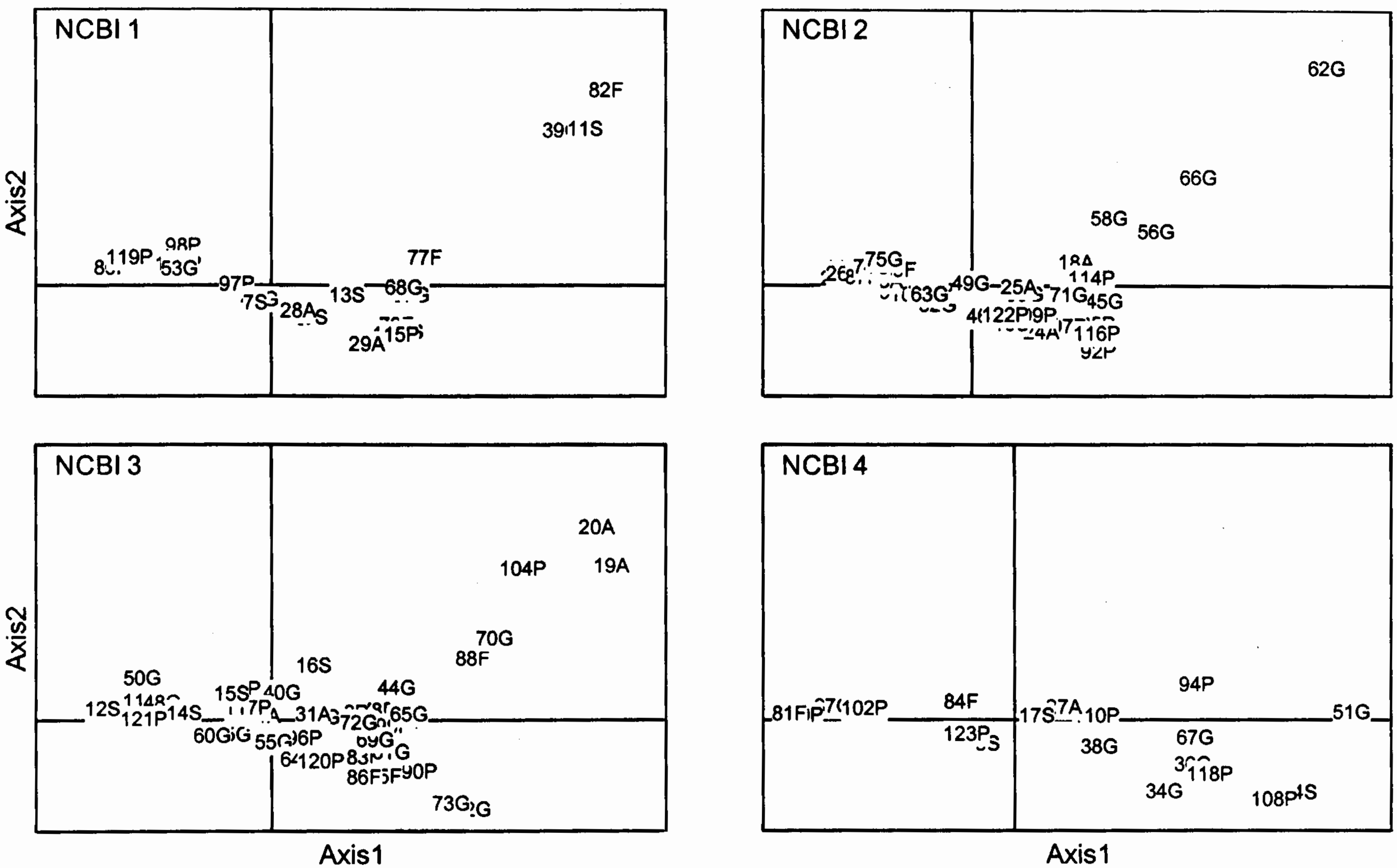

Figure 5.16. CCA plots of biomass by taxon, as explained by habitat parameters. Taxa are grouped by NCBI score, and codes are listed in the Appendix.

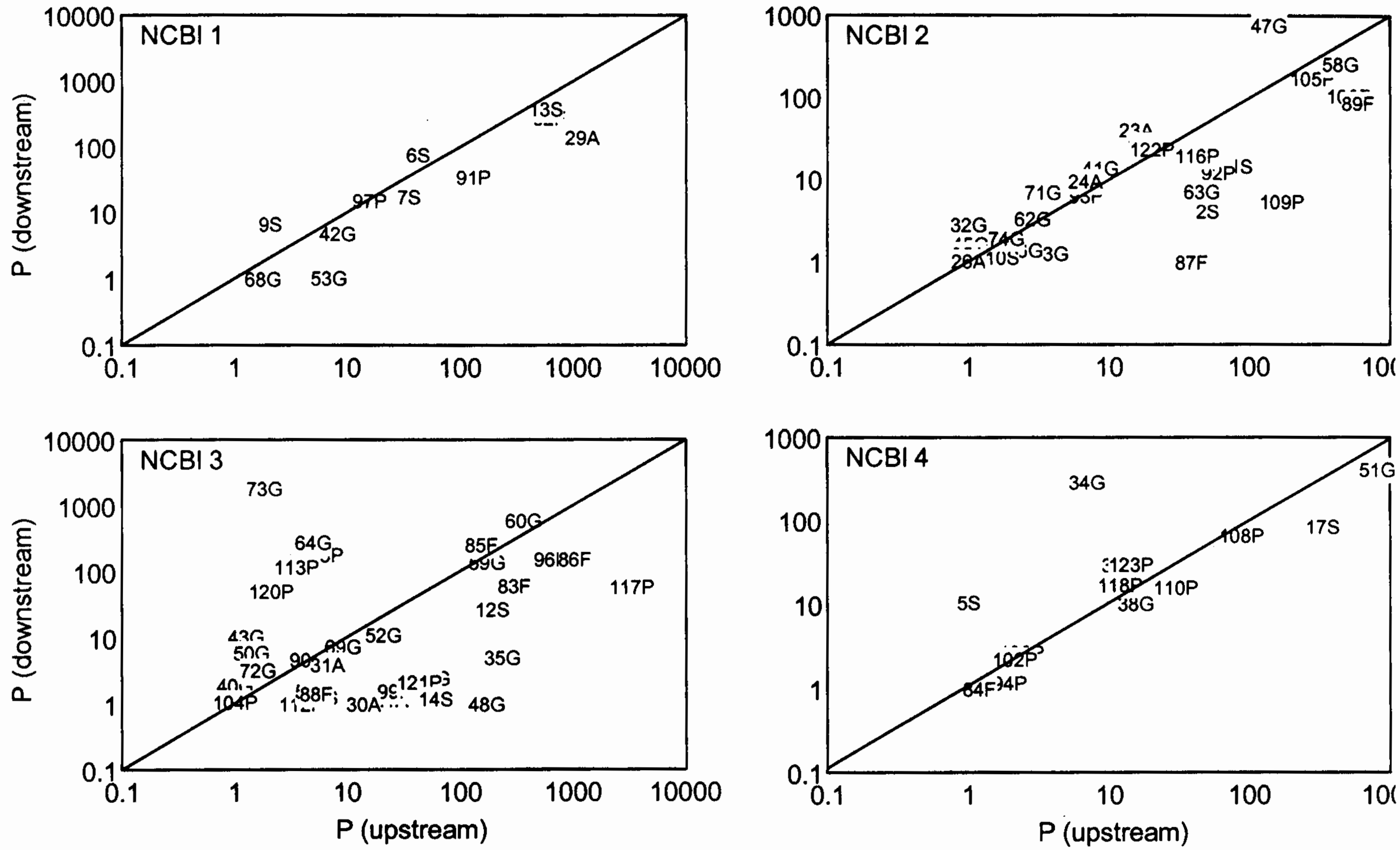

Figure 5.17. Comparison of upstream (X-axis) and downstream (Y-axis) annual production of taxa in Goosefare Brook. Taxa are grouped by NCBI score, and codes are listed in the Appendix. Values are expressed as mgAFDM/m^2/y.

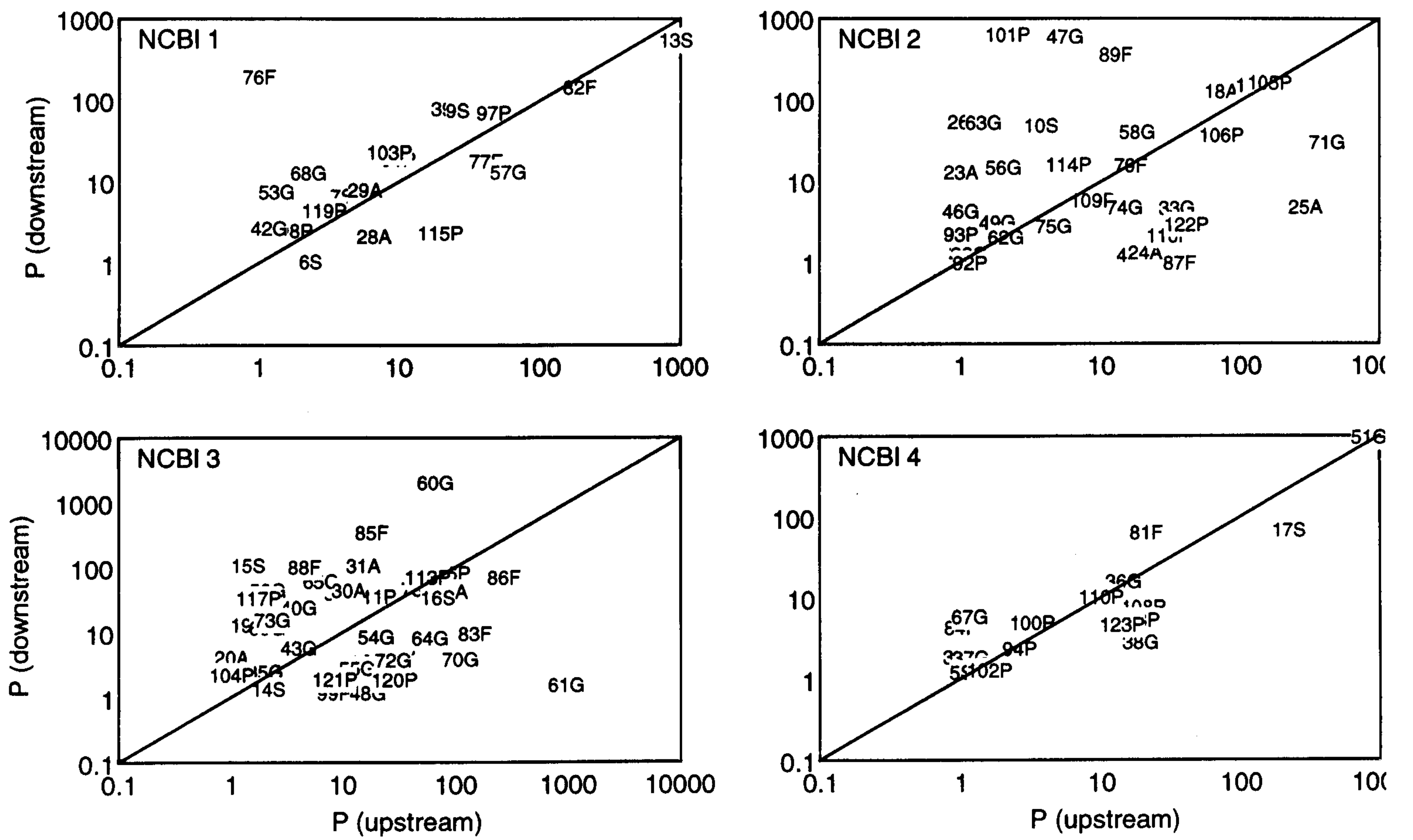

Figure 5.18. Comparison of upstream (X-axis) and downstream (Y-axis) annual production of taxa in Ward Brook. Taxa are grouped by NCBI score, and codes are listed in the Appendix. Values are expressed as mgAFDM/m^2/y.

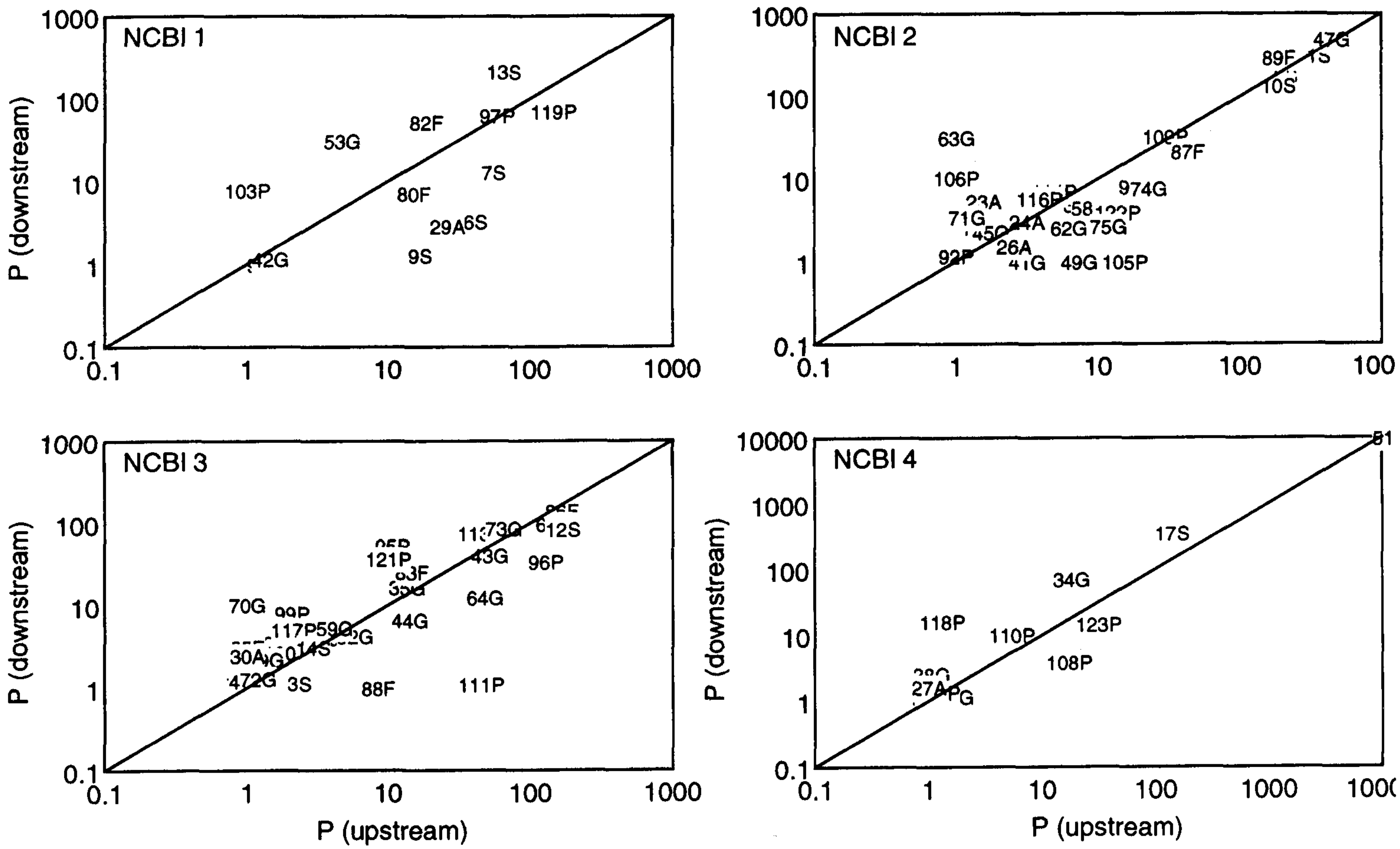

Figure 5.19. Comparison of upstream (X-axis) and downstream (Y-axis) annual production of taxa in Stevens Brook. Taxa are grouped by NCBI score, and codes are listed in the Appendix. Values are expressed as mgAFDM/m^2/y.

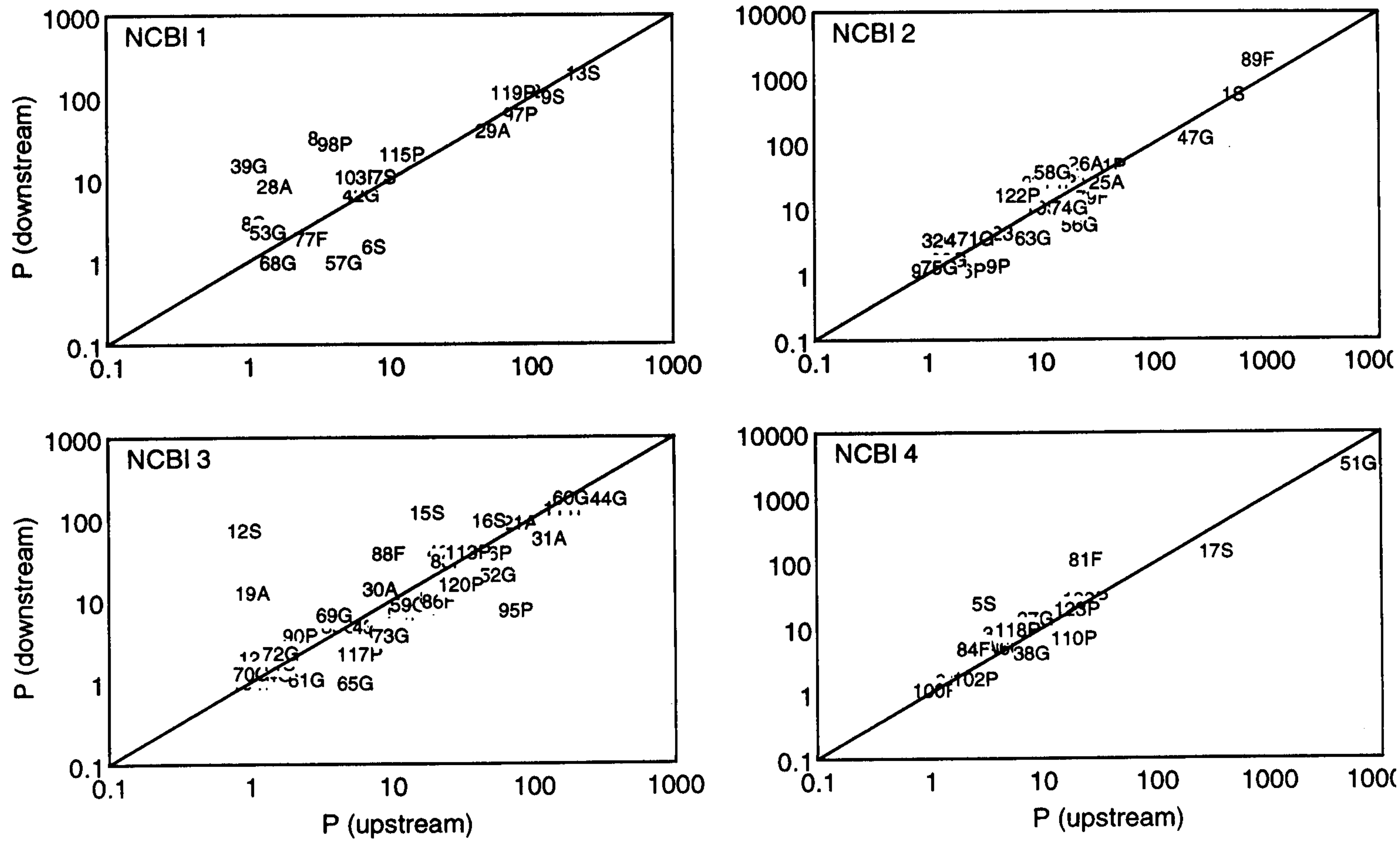

Figure 5.20. Comparison of upstream (X-axis) and downstream (Y-axis) annual production of taxa in Cascade Brook. Taxa are grouped by NCBI score, and codes are listed in the Appendix. Values are expressed as $mgAFDM/m^2/y$.

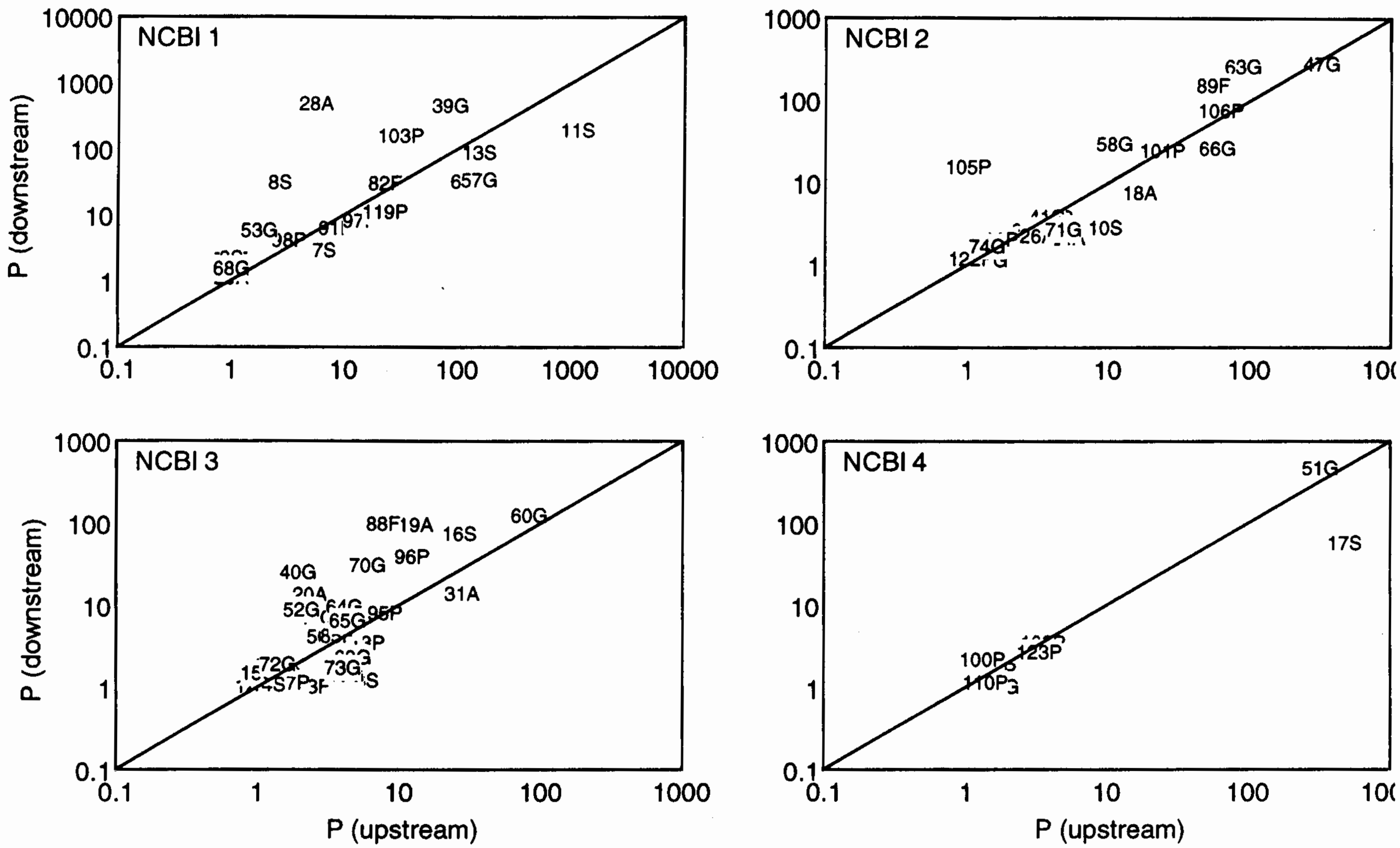

Figure 5.21. Comparison of upstream (X-axis) and downstream (Y-axis) annual production of taxa in Branch Brook. Taxa are grouped by NCBI score, and codes are listed in the Appendix. Values are expressed as mgAFDM/m^2/y.

Taxon	NCBI group	Code	Cascade	Goosefare	Ward	Branch	Stevens
Brachycentrus	1	76F	-	-	D	-	-
Diplectrona	1	80F	D	-	-	-	-
Ephemerella	1	39G	D	-	D	D	-
Haploperla	1	98P	D	-	-	-	-
Isoperla	1	103P	-	-	-	D	D
Lepidostoma	1	6S	U	-	U	-	U
Leuctra	1	7S	-	-	-	-	U
Micrasema	1	8S	D	-	-	D	-
Micropsectra	1	82F	-	-	-	-	D
Paracapnia	1	9S	-	-	-	-	U
Parachaetocladius	1	53G	-	U	D	-	D
Paraleptophlebia	1	57G	U	-	-	-	-
Paranyctiophylax	1	115P	-	-	U	-	-
Promoresia	1	28A	D	-	U	D	-
Psilotreta	1	29A	-	U	-	-	U
Pteronarcys	1	11S	-	-	-	U	-
Pycnopsyche	1	13S	-	-	-	-	D
Serratella	1	68G	-	-	D	-	-
Allocapnia	2	1S	-	U	-	-	-
Amphinemura	2	2S	-	U	-	-	-
Brundiniella	2	92P	-	U	-	-	-
Chaetocladius	2	33G	-	-	U	-	-
Eurylophella	2	41G	-	-	-	-	U
Hexatoma	2	101P	-	-	D	-	-
Lanthus	2	105P	-	-	-	D	U
Limnophila	2	106P	-	-	-	-	D
Limnophyes	2	45G	-	-	U	-	-
Lype	2	23A	-	-	D	-	D
Molanna	2	24A	-	-	U	-	-
Molophilus	2	109P	-	U	-	-	-
Mystacides	2	46G	-	-	D	-	-
Nematoda	2	47G	-	D	D	-	-
Neophylax	2	25A	-	-	U	-	-
Ochrotrichia	2	49G	-	-	-	-	U
Optioservus	2	26A	-	-	D	-	-
Paralauterborniella	2	56G	-	-	D	-	-
Pilaria	2	116P	-	-	U	-	-
Podmosta	2	10S	-	-	D	-	-
Polycentropus	2	87F	-	U	U	-	-
Psilometriocnemus	2	63G	-	U	D	-	D
Simuliidae	2	89F	-	U	D	-	-
Stilocladius	2	71G	-	-	U	-	-
Trissopelopia	2	122P	-	-	U	-	U
Tvetenia	2	74G	-	-	-	-	U
Zalutschia	2	75G	-	-	-	-	U

Table 5.4. Summary of taxa showing evidence of roadway effects on secondary production. U indicates higher production upstream of the highway in that stream, D indicates higher production downstream, - indicates no effect.

Taxon	NCBI group	Code	Cascade	Goosefare	Ward	Branch	Stevens
Ablabesmyia	3	90P	-	-	U	-	-
Baetis	3	19A	-	-	D	D	-
Brillia	3	3S	-	U	U	U	-
Centroptilum	3	20A	-	-	-	D	-
Chrysops	3	95P	U	D	-	-	D
Cordulegaster	3	96P	-	-	-	D	U
Corynoneura	3	35G	-	U	-	-	-
Dubiraphia	3	21A	-	U	-	-	-
Eukiefferiella	3	40G	-	-	D	D	-
H. stagnalis	3	99P	-	U	U	-	D
Heterotrissocladius	3	43G	-	D	-	-	-
Leptophlebia	3	44G	-	-	-	D	-
Microtendipes	3	83F	-	-	U	-	-
Nigronia	3	111P	-	-	-	-	U
Nilothauma	3	48G	-	U	U	-	-
Orthocladius/ Cricotopus	3	52G	-	-	D	D	-
Palpomyia	3	113P	-	D	-	-	-
Paracladopelma	3	54G	-	U	-	-	-
Parakiefferiella	3	55G	-	-	U	-	-
Paratendipes	3	59G	-	-	D	-	-
Phylocentropus	3	85F	-	-	D	-	-
Polypedilum	3	60G	-	-	D	-	-
Potthastia	3	61G	-	-	U	-	-
Probezzia	3	117P	-	U	D	-	-
Ptilostomis	3	12S	D	U	-	-	-
Rheocricotopus	3	64G	-	D	U	-	U
Rheosmittia	3	65G	U	U	D	-	-
Rheotanytarsus	3	88F	D	U	D	D	U
Sialis	3	120P	-	D	U	-	-
Sphaeromias	3	121P	-	U	U	-	D
Stempellinella	3	69G	-	-	D	-	-
Stenelmis	3	30A	-	-	D	-	-
Stenonema	3	31A	-	-	D	-	-
Stictochironomus	3	70G	-	-	U	D	D
Symposiocladius	3	14S	-	U	-	-	-
Taenionema	3	15S	D	-	D	-	-
Taeniopteryx	3	16S	-	-	-	D	-
Thienemanniella	3	72G	-	-	U	-	-
Tribelos	3	73G	-	D	D	-	-
Chironomus	4	34G	-	D	-	-	-
Diplocladius	4	38G	-	-	U	-	-
Hyalella	4	5S	D	D	-	-	-
Hydropsyche	4	81F	D	-	D	-	-
Paratanytarsus	4	84F	-	-	D	-	-
Procladius	4	118P	-	-	U	-	D
Saetheria	4	67G	-	-	D	-	-
Tipula	4	17S	-	U	U	U	-
Zavrelimyia	4	123P	-	-	U	-	-

Table 5.4. continued.

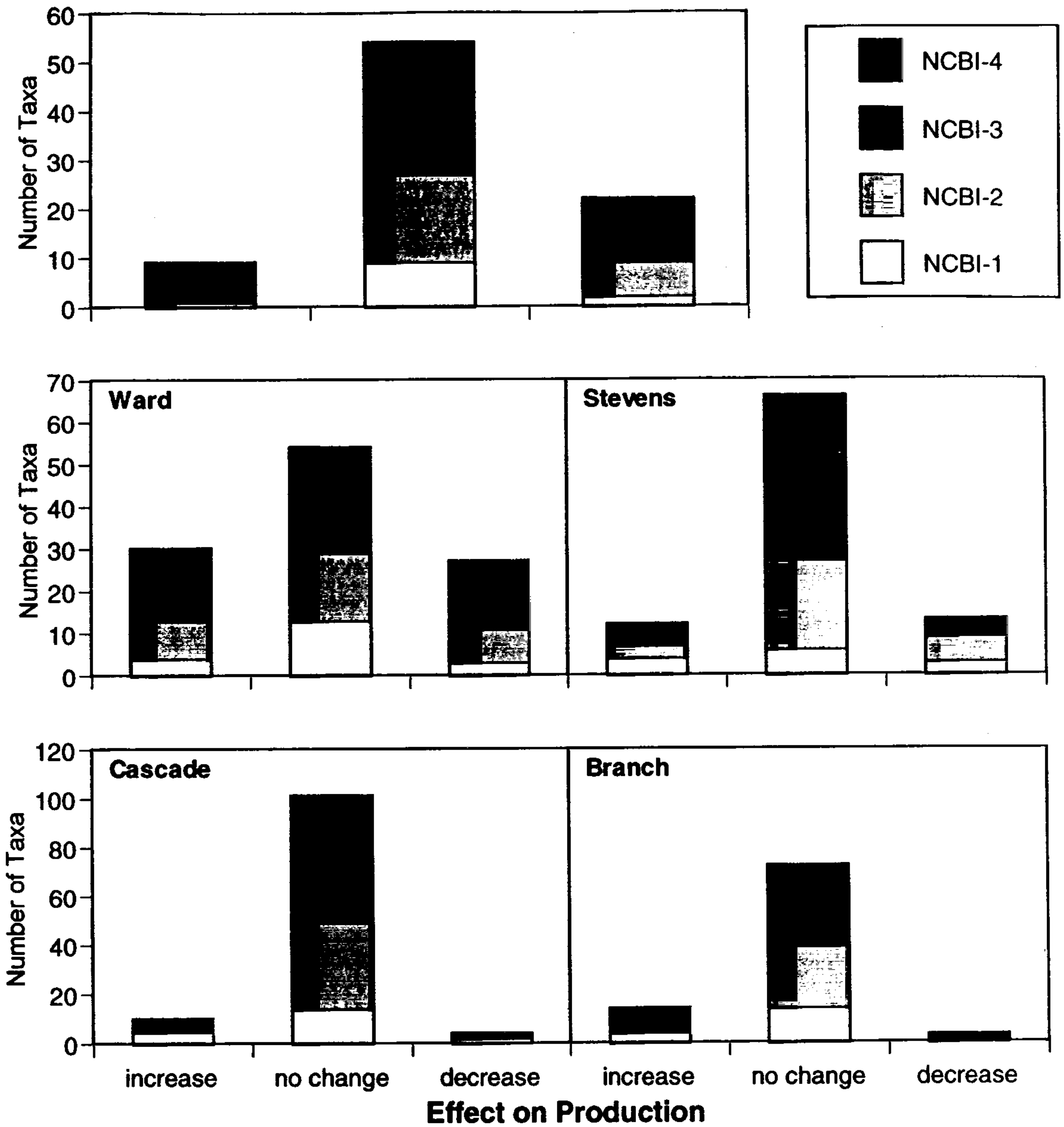

Figure 5.22. Number of invertebrate taxa showing change in annual production associated with the Maine Turnpike. Taxa are grouped by NCBI score (Lenat 1993).

Goosefare Brook showed an upstream bias, while bias in NCBI Groups 3 and 4 were less strongly related to the location of the roadway (Figure 5.17). The significantly higher exchangeable metals upstream in Ward was related to a downstream bias in NCBI Group 1 (Figure 5.18). Different taxa in Groups 2 and 3 were biased , but not in a consistent direction, while Group 4 showed weak bias only. Stevens Brook was similar to Ward, except that Group 1 showed the same pattern as Groups 2 and 3 (Figure 5.19). Bias is weaker in Cascade (Figure 5.20) and Branch (Figure 5.21), neither of which had significant differences in metal concentrations as determined by MRPP. However, some taxa in these streams do show changes related to the turnpike, particularly towards downstream stations in Branch. These differences may be more closely related to habitat, at least in Branch which was the most heterogenous of all streams (Figure 5.3), because they do not show as clear a pattern related to tolerance as those streams with significant differences in metal concentrations.

Fish

Ten fish species were captured in the streams. Five of the species (*Alosa pseudoharengus*, *Esox niger*, *Lepomis gibbosus*, *Luxilis cornutus*, and *Rhinicthys atratulus*) were found only in a single stream, and are included only in analyses of total fish biomass. Ammocoetes of the sea lamprey (*Petromyzon marinus*) were found in both Ward and Branch Brooks, but were uncommon and contributed little biomass to the fish community. The remaining species (*Anguilla rostrata*, *Catostomus commersoni*,

Couesius plumbeus, and *Salvelinus fontinalis*) were found in multiple streams. All species except *A. rostrata* showed a significant difference among streams in fish biomass per square meter, but no effects of the roadway were evident (Figure 5.23). Total fish biomass per square meter showed no differences among streams or location with respect to the roadway.

S. fontinalis showed a significant influence of the roadway on mean density in Branch and Goosefare, and mean length in Goosefare (Figure 5.23). However, density downstream in Branch was greater than upstream, and the pattern was opposite in Goosefare. Length of *S. fontinalis* was significantly greater upstream in Goosefare, but greater downstream in Stevens. *A. pseudoharengus*, which was present only in Ward Brook and abundant at downstream stations, was apparently unable to move through the culvert to upstream reaches. *A. rostrata* (n=106) was the only species to show a locational difference in the fish condition metric, with fish downstream of the roadway having lower values than those upstream ($F_{1,96}$=4.65, p=0.034). *C. plumbeus* (n=224) showed higher values in Ward Brook than in the other streams in which it occurred (Goosefare and Branch) ($F_{5,218}$=6.93, p<0.0001). The MRPP analyses of fish community biomass showed no significant difference in any of the streams, although Stevens was marginally affected by the roadway (p=0.06), likely due to the increased biomass of *S. fontinalis* at downstream stations.

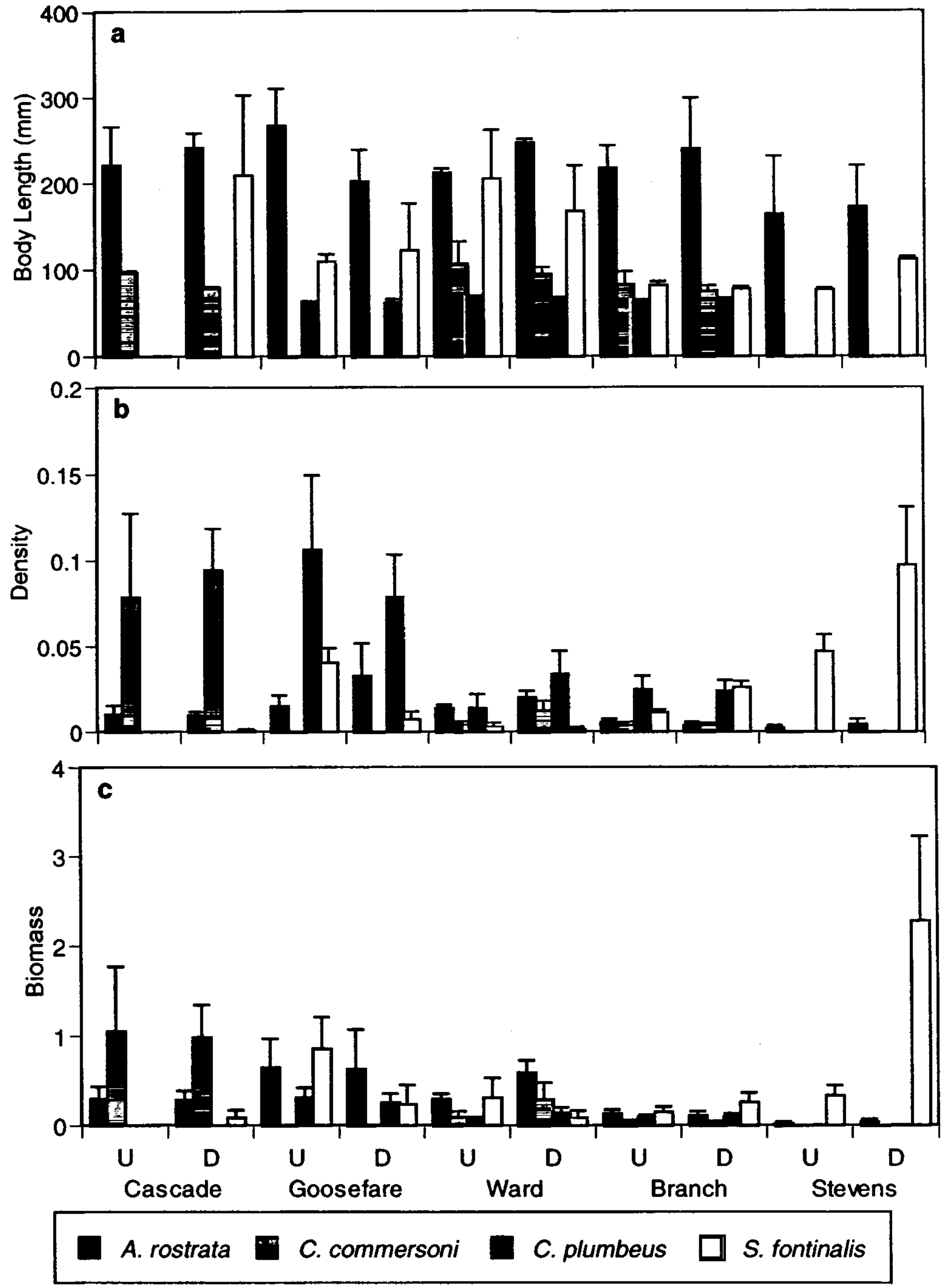

Figure 5.23. Mean body length (a), density (b), and biomass per square meter (c) of fish species upstream (U) and downstream (D) of the Maine Turnpike. Error bars are +1S.E. Density is expressed as individuals/m^2, biomass as g wet mass/m^2.

Discussion

The addition of paved surfaces to a catchment causes physical impacts on both the hydrology and the types of materials entering a stream (Arnold and Gibbons 1996, Booth and Jackson 1997, Jones et al 2000). The release of contaminants is proportional to the quantity of traffic, and may arise directly from vehicles, from wear on the road surface, or from materials such as de-icing salt (Hewitt and Rashed 1990, Maltby et al 1995a, Trombulak and Frissell 2000). These chemicals may be deposited onto the road surface, deposited in the immediate vicinity of the road, or disperse into the atmosphere. Deposited pollutants (pathways 1 and 2) are dissolved or re-suspended by runoff and discharged into surface waters (Hewitt and Rashed 1990). Most pollutants are associated with particulate matter, which may be incorporated into stream sediments. Thus, the concentration of the pollutant in the sediments may be much greater than that in the water, rendering the benthic community particularly vulnerable to toxic effects. Degradation of the channel and riparian area can cause additional stress to stream organisms and alteration of ecological function. The alteration of riparian vegetation can change the composition of allochthonous energy inputs, light and temperature regimes, and patterns of sediment and nutrient input (Bunn et al 1999).

Habitat and Land Use

The spatial and temporal scale of measurement is important in determining biotic responses to habitat, although interpretation of the scale of those responses is often

difficult. Land use quantification showed that all of the catchments in this study were dominated by forested land (Table 5.1), and the chosen streams could be said to represent the population of streams that cross beneath the Maine Turnpike in the southern part of the state. However, sampling of riparian and channel habitats at the scale of the habitat patch demonstrates that there were considerable differences among the streams. The ordination of samples shows that habitat within streams was comparable upstream and downstream of the roadway (Figure 5.3). Therefore, while the streams were not necessarily comparable to each other, biotic characteristics upstream and downstream of the roadway were not seriously confounded by habitat differences within streams. Stevens and Cascade stations group together, Goosefare and Ward stations group together, and Branch stations tend to be separate. This pattern of within-stream habitat patches and habitat similarities among streams was also observed in a CCA of litter decomposition and litter bag invertebrate assemblages in the same reaches (CHAPTER IV).

Most chemical and biotic parameters were related to habitat differences, suggesting a stream-specific response to the stress. For example, upon casual observation Stevens and Cascade Brooks have considerable differences in habitat, including riparian forest characteristics, channel dimensions, and discharge patterns (Figure 5.6). Nevertheless, these streams were similar in a number of characteristics, such as pH and substrate particle size, which were important explanatory variables in separating them from the others (Figures 5.2 and 5.3). These factors may also play important roles in structuring the biotic community. For example, invertebrate production at all stations in

Stevens and Cascade was dominated by oligochaetes, which had a considerably lesser role in the other streams (see Appendix B). These streams were also the only two to have a significant decrease in primary producers downstream of the roadway (Figure 5.10). A shift in Stevens Brook to smaller substrate particle size that supported less moss growth could be the explanation, while in Cascade Brook greater canopy cover was evident in the downstream reaches.

Invertebrate Communities

Estimates of whole-community production in lotic systems are typically 5-10 $g/m^2/y$, and values greater than 100 $g/m^2/y$ or less than 3 $g/m^2/y$ are rare (Huryn and Wallace 2000). Few whole-community production estimates are available for low-gradient coastal plain streams in the United States. Such streams can be very productive, particularly in the southeast (Benke et al 1984, Benke 1998). Several estimates are also available for low-gradient sandy streams in Virginia. Smock et al (1985) found habitat-weighted production values up to 4.1 $g/m^2/y$ in a second-order stream, and Kedzierski and Smock (2001) estimated 41 $g/m^2/y$ in an unlogged reach of a low-gradient stream. These estimates show that the productivity of these systems vary over an order of magnitude, and the streams in this study have comparable levels of production despite latitudinal differences (3.5-15.3 $gAFDM/m^2/y$). A previous study of Goosefare Brook (1998-1999) showed production as high as 26.4 $gAFDM/m^2/y$ at the reference station,

although mean estimates in the reaches immediately upstream and downstream of the roadway were considerably lower (6.2 – 9.3 gAFDM/m^2/y, CHAPTER III).

Reduced production in response to chronic stress can occur at the population level due to a lower standing stock, or at the individual level due to reduced growth rate, although such changes may cancel at the community level (Carlisle 2000, Huryn and Wallace 2000). In this study, only Goosefare and Ward Brooks showed a decrease in whole-community production related to the roadway. When community structure was accounted for by MRPP, however, Ward and Goosefare showed a significant change in production downstream. These streams also showed a multivariate change in exchangeable (Ward) or total (Goosefare) metal concentrations when analysed with MRPP. However, Stevens also showed a significant difference in the exchangeable metals MRPP, without an accompanying difference in invertebrate production. Ward and Stevens also tended to have higher metal concentrations at upstream stations, suggesting that runoff from the roadway was not the cause.

Higher metal concentrations showed a tendency to alter the community by changing the production of individual taxa, particularly decreasing that of sensitive taxa, and in the case of Goosefare Brook reducing whole-community production. Goosefare had higher total metal concentrations downstream of the roadway, and most taxa that showed a difference between upstream and downstream stations had higher production upstream. Some taxa in NCBI Groups 3 and 4 showed higher production associated with downstream stations (Figure 5.17), particularly the midges *Chironomus* and *Tribelos*, which had production one to three orders of magnitude higher downstream than

upstream. The taxa in the most tolerant group showed no upstream bias, except for a small difference in *Tipula*. Ward Brook had significantly higher exchangeable metal concentrations at upstream stations, which was reflected in the downstream bias of many taxa, particularly those in the least tolerant group (Figure 5.18). However, the most biased taxon in NCBI Group 1 (*Brachycentrus*), was associated strictly with the macrophyte beds at downstream stations, a habitat that was much less extensive upstream. NCBI Groups 2 and 3 showed a wide variation, with most taxa showing bias in one direction or the other. NCBI Group 4 showed differences in some taxa, but these were weak. Stevens Brook also had significantly higher exchangeable metal concentrations upstream of the roadway. All NCBI groups had taxa that showed a biased production upstream or downstream, although in Group 4 those differences were weak (Figure 5.19).

Cascade and Branch Brooks did not show a significant effect of the roadway on sedimentary metal concentrations, although Branch did have a greater difference in upstream and downstream habitat and greater overall heterogeneity than the other streams (Figure 5.3). Most taxa in Cascade Brook have similar production upstream and downstream of the roadway, although several taxa in the least tolerant group show some bias (Figure 5.20). All of these taxa are of low relative importance to the whole community, producing less than 10 mgAFDM/m^2/y each. Some of the more tolerant taxa in NCBI Groups 3 and 4 also showed a difference, such as *Taenionema*, *Hydropsyche* (downstream bias) and *Chrysops* (upstream bias), but these taxa also contributed relatively little to the community (less than 100mgAFDM/m^2/y each). Most taxa that

showed a difference in Branch Brook are in NCBI Groups 1 and 3, which is further evidence that the differences are related to habitat rather than the roadway (Figure 5.21). The pollution tolerance of the taxa was apparently not related to differences in production, as it was in streams that had a difference in metals between upstream and downstream reaches.

Fish

Negative effects on fish community structure have been related to agricultural and urban land use due to riparian degradation (Wichert and Rapport 1998), channelization, sedimentation (Scott and Hall 1997, Fitzgerald et al 1998), and impervious surface coverage (Reash and Berra 1987, Wang et al 2000). In this study the effects of the roadway on the fish community was minimal, although some individual taxa showed a response in some streams in size, density (*S. fontinalis*), and condition (*A. rostrata*). However, the observed effect of the roadway was not always negative with regards to condition and abundance. It is possible that the mobility of fish makes it difficult to resolve differences in these population characteristics, or allows the fish to avoid the stress by preferentially using habitat patches with low levels of toxins, and avoiding those where toxins accumulate. These areas of low sedimentary pollutant retention would likely result in lower pollutant body burdens in the prey of the fish.

Primary Producers

Primary producers did not contribute greatly to the organic matter pool when compared with allochthonous resources, which is expected in small forested streams with heavy shade and large leaf litter inputs (Vannote et al 1980). Macrophytes were uncommon, and thus likely played a small role in organic matter dynamics. Moss occurred only on hard substrate in faster-flowing water, particularly near the roadway where channelization promoted these habitat characteristics. However, the moss habitat supported considerable production of some taxa, such as *Promoresia* in Branch Brook Stations 6 and 7, that were much less abundant or absent in areas without moss. Stations 1, 2, and 3 in Stevens Brook also had considerable moss growth.

Changes in algal community structure (Foster 1982, Deniseger et al 1986, Barranguet et al 2000) and reduced photosynthetic activity (Barranguet et al 2000, Hill et al 2000) have been recorded in response to heavy metal pollution. A significant decrease in chlorophyll a downstream of the roadway did occur in Cascade and Stevens, and an increase in Branch, although differences in Stevens and Branch were readily attributable to the locations of heavy moss growth. Furthermore, in systems with high iron inputs, hydroxide precipitates can blanket the streambed, reducing benthic habitat and inhibiting periphyton growth (McKnight and Feder 1984, Wellnitz and Sheldon 1995, Niyogi et al 1999). This effect is observed at the stations downstream of the industrial inputs in Goosefare Brook, but Fe concentrations elsewhere were not sufficient except in the small groundwater seeps common in the area, where Fe precipitation was evident (T.S. Woodcock, *personal observation*).

Synthesis and Conclusions

In general, the response of stream macroinvertebrate community structure to pollutants is determined by sensitivity of its members, their recolonization ability, and longitudinal variation in environmental conditions such as particle size and sediment organic matter content (Clements 1994). Loading with many chemical or physical impacts tends to result in general declines in richness and abundance. Many studies have documented the relationships of community structure to chemical pollution (Clements et al 1988a, 1990, Clements 1994, Kiffney and Clements 1994a) and land use (Casper 1994), typically observing decreased mayfly and stonefly abundance and richness, an increase in collector-gatherers such as chironomids, and an overall reduction in macroinvertebrate abundance and diversity associated with the stress. This study does not show such generalized effects in the five streams that were examined, because the magnitude of stress from the roadway is apparently insufficient to alter such broad structural or functional characteristics, although effects on individual taxa may occur.

In this study, roadway effects on habitat characteristics were assessed at three spatial scales (catchment, reach, and patch) and two temporal scales (single or annual measures and repeated sampling). The similarity of the habitats and the apparently small biological effects provides evidence for the low stress level that the roadway has on stream function. A significant difference in metal concentrations, whether or not it was attributable to the roadway, was associated with differences in production of individual

taxa, and a decline in production was often more pronounced for pollution-sensitive taxa. In comparison, streams that did not have a difference in metal concentrations showed more constant rates of production among taxa upstream and downstream of the roadway (Table 5.4 and Figure 5.22).

This study of ecosystem level effects of a particular stress has demonstrated that changes in the production of individual taxa can occur without affecting the functioning of the system. The Maine Turnpike does not have a serious effect on the functioning of the streams that it crosses, particularly in reaches that are greater than 50m from the roadway itself. The physical and chemical alterations caused by the highway are not sufficient to consistently alter the biota, stored and suspended food resources, or water and habitat quality as related to the functioning of the streams, as measured by whole-community production. The variability among the study streams is greater than the effects of the highway, although smaller streams appear more likely to show negative effects than larger ones, perhaps because the surface area of the roadway is proportionally greater in smaller catchments. The effects of the industrial inputs in Goosefare Brook have been demonstrated previously to be much more serious than effects of the roadway (CHAPTERS II and III).

The larger spatial and temporal scales used in this study illustrate the difficulty in inferring functional changes from traditional assessment methods that rely on instantaneous measurements of water and habitat quality or invertebrate assemblages. The integration of direct functional measurements over larger spatial and temporal scales is necessary to quantify these effects. However, the interpretation of confounded effects

on communities and their habitats does present difficulties in assessment of stream condition. The demonstrated effectiveness of such catchment-scale indicators as impervious surface coverage (Arnold and Gibbons 1996, Morse et al *unpublished data*), and the construction of predictive models of stress (Tsihrintzis and Hamid 1997, 1998) and biotic integrity is leading to a more holistic approach to stream assessment. Traditional structural measures tend to have greater discriminatory power to identify stressors than functional measures, and have a valuable role in identification and monitoring of problems (Nelson 2000). However, functional changes in stream processes suggest that system resistance to stress has been exceeded, and the direct measurement of these processes is necessary in order to address these issues. Improved understanding of the relationships between community structure and ecosystem function will ultimately lead to improvements in the understanding and mitigation of anthropogenic stresses on streams.

Chapter VI

Synthesis and Conclusion

Introduction

Roadways are a major feature in both urban and rural landscapes, and their construction and use are associated with a number of physical and chemical stresses, including alteration of habitat and non-point source pollution. Both biotic and abiotic components of stream systems may be impacted by physical habitat changes, such as channelization, removal of riparian vegetation, and sediment inputs, or by toxic effects from heavy metals, hydrocarbons, and other materials deposited by traffic and carried into streams by runoff water. Physical alterations often result in a reduction of channel complexity and habitat quality for stream biota, and culverts at road crossing may impede the movement of aquatic organisms. The effects of chemical pollutants on stream-dwelling organisms depends on such factors as sediment and water chemistry, bioavailability, uptake and elimination processes, and tolerance mechanisms. These interacting effects on individuals may result in effects on the success of populations, community structure, and ultimately on ecosystem function.

In the analysis of aquatic ecosystems, functional variables are typically inferred from other measurements, such as water chemistry, suspended solids, and community structural metrics. The goal of the studies presented in this thesis is the examination of changes in process-level indicators by directly measuring both structural and functional

characteristics. The approach was to examine relationships between the habitat template and pollutant loads (heavy metals) and ecosystem-level variables such as macroinvertebrate secondary production, stored benthic organic matter, and leaf litter processing. These parameters were first studied in Goosefare Brook, a stream with a history of severe degradation of the benthic community and a number of current potential sources of stress, including habitat channelization, runoff from residential roadways and the Maine Turnpike (Interstate 95), and runoff from industrial property. This approach was expanded in the following year to include five streams, with the goal of assessing the effects of a single stressor, the Maine Turnpike.

Water and Sediment Chemistry

The largest increases in sedimentary metal concentrations in Goosefare Brook were associated with runoff from industrial property, although there is also evidence of roadway inputs (CHAPTER III). However, the analysis of sedimentary metal concentrations in CHAPTER V revealed little evidence of increased metal storage related to the roadway. Total sedimentary concentrations of metals were closely correlated with concentrations of Fe and Mn in the sediment in both studies, while organic matter content and particle size were only related to some of the metal species. The exchangeable fraction, which represented metals with greater bioavailability, was not closely correlated with these predictors. However, the significant increase in specific conductance associated with the roadway does indicate an elevation in ion concentration downstream

of the roadway, some of which may represent bioavailable aqueous metals. Thus, while the roadway may cause an increase in ion concentration in the water column, sedimentary metal concentrations were not significantly affected by the Turnpike.

Habitat

CHAPTER III indicated that flow velocity and particle size differed between channelized and unchannelized stations in Goosefare Brook, and were positively related to each other (r^2=0.88). These physical habitat parameters were related to habitat type rather than position along the gradient of metal pollution. Stored particulate organic matter, wood, and leaves showed a decreasing trend along the gradient, although higher levels were evident in unchannelized habitats. Channelized habitats had significantly less wood than unchannelized habitats, suggesting a lower retentiveness for other types of organic matter. Benthic organic matter storage also showed a linear decline over the gradient, suggesting a relationship to chemical rather than habitat factors. There was not a significant change in any of the organic matter pools related to the Turnpike alone (CHAPTER V), indicating that habitat parameters that were not significantly affected by the roadway controlled the accumulation and retention of organic matter. Both stored and transported organic matter varied with stream, date, and habitat, but were not clearly influenced by the roadway. Inorganic transported material, however, did show a significant increase in the annual mean downstream from the roadway, and may represent street dust entering the channel.

Leaf Litter Processing

In forested headwater streams, terrestrial detritus in the form of leaf litter supports the majority of consumer production, and is processed by invertebrates that directly consume leaf tissue (shredders) into fine particulate organic matter. This material is arguably an important energy source to other organisms in the community, and to communities downstream as transported particulate and dissolved organic matter (Anderson and Sedell 1979, Vannote et al 1980, Cummins et al 1989). Litter processing thus represents potentially one of the most important functions in the study streams, and stress from human activities may affect it by altering the habitat or impairing biological activity. Both microbial and macroinvertebrate assemblages may be affected by physical and chemical changes in habitat.

Leaf pack invertebrate assemblages and processing rates were examined along a gradient of heavy metal pollution and habitat alteration in Goosefare Brook in 1997 and 1998 (CHAPTER II). There was no significant difference in softening rate between stations in 1997, and only the most polluted station showed a decrease in 1998. Litter loss rates showed decreases associated with metal stress in both years. Both softening and loss rates were slower in 1997, likely due to colder water temperatures. Changes in a suite of metrics showed that structure of invertebrate assemblages changed in response to stress, and shredder biomass decreased in response to both pollution and channelization. Shredder biomass at all stations was dominated by *Tipula*, although the biomass of other

shredder taxa showed a progression along the gradient of stress. Litter processing rates were more closely related to water and sediment quality variables (metals, nutrients, alkalinity, specific conductance) than to characteristics of the invertebrate assemblages. It is important to note, however, that biomass of shredder taxa in litter bags was not closely related to shredder production at the same stations (CHAPTER III).

The effects of the Maine Turnpike (Interstate 95) on leaf litter processing were examined in five first- and second-order coastal plain streams (CHAPTER V). Invertebrate assemblages and red maple leaf softening and loss rates were compared at 53 stations upstream and downstream of the turnpike. Litter softening rate was not affected by the roadway, and litter loss rate was significantly faster at downstream stations than at upstream stations or those nearest the roadway, which were not different from each other. Litter softening and loss rates were more strongly related to physical and chemical habitat variables than to shredder assemblage characteristics, and habitat variation among streams was greater than within streams. Among-stream differences were observed in most community structural metrics and biomass of important shredder taxa, but effects of the roadway were rarely consistent among streams. This study suggests that while the presence of the Maine Turnpike may influence stream habitats, the effects of roadway drainage are insufficient to overcome within-stream variability in litter processing and leaf pack invertebrate assemblage structure.

Macroinvertebrate Production

The response of a population to physical and chemical habitat characteristics may be quantified using such parameters as mortality, growth, abundance, reproduction, development time, and standing stock biomass. Because it represents an integration of these attributes, it has been argued that secondary production is a definitive measure of the success of a population (Benke 1984, Lugthart and Wallace 1992). Secondary production is the rate of formation of heterotrophic biomass, calculated as a product of population biomass and individual growth rate (Benke et al 1988, Benke 1993). Measurement of production allows evaluation of growth and biomass turnover rates, improving understanding of the interaction of populations with each other and the environment, through such processes as feeding and habitat use (Grubaugh et al 1997, Clements 1997). Studies of process-level parameters have tended to focus on relatively undisturbed systems, and have rarely been used in the ecological assessment of polluted systems.

In the study of production along the pollution gradient in Goosefare Brook (CHAPTER III), metal concentrations were negatively correlated with the interval macroinvertebrate biomass pooled across all stations and sampling events, indicating a toxic effect of metals on the biomass portion of the production calculation. The decline in biomass was not linear along the gradient, demonstrating that pollution-tolerant taxa increased in relative importance as the level of stress increased. Whole-community production showed a linear decline related to the gradient, although both structure and function of the community shifted in response to habitat channelization. Production

decreased along the pollution gradient for most taxa, although fewer taxa showed changes in response to habitat. Biomass turnover rates (P/B), which are an estimator of growth, were less affected by the stresses than production. Changes in functional structure of the community were evident at stations with channelized habitat, but overall production declined in a linear pattern that mirrored the increase in metals. Populations of taxa with documented pollution tolerance were more likely to maintain or increase production and P/B.

The study of the effects of the Maine Turnpike alone on invertebrate community structure and secondary production (CHAPTER V) indicated a limited effect of metal concentrations on invertebrate community structure and function. The variability in channel and riparian habitat, water and sediment chemistry, stored organic matter, and invertebrate community characteristics among the study streams was greater than the within-stream differences attributable to the roadway. Significant differences in habitat parameters, water and sediment chemistry, and biotic communities were evident among streams. Stream structure and function tended to respond to both metal concentrations (exchangeable and total) and several habitat parameters, including pH, substrate particle size, and riparian forest characteristics such as height and percent canopy coverage.

Ecosystem Function

Human activities may affect both components of production through lethal and sublethal effects, or reduction of food and suitable habitat due to channelization. These

effects range from the shifts in the pathways of energy flow observed at stations exposed to moderate physical or chemical stress, to the loss of most taxa and a major decrease in production under severe stress. However, the shifting prominence of different taxa along a continuum of stress shows that while simple metrics may be able to detect impairment, the nature of the change in a functional context is not so easily measured. Consideration of the interaction of habitat, food resources, and chemical contaminants rather than simple metrics alone is needed to further understanding of the effects of stress on stream function. These studies have demonstrated that changes in populations and communities can occur in response to local habitat heterogeneity and stress from a large roadway, while ecosystem function is maintained.

The studies of Goosefare Brook (CHAPTERS II and III) compared the effectiveness of two methods of functional assessment in evaluating stress. The significant changes in both leaf litter processing and secondary production associated with the pollution gradient in Goosefare Brook illustrate that these parameters are useful in detecting stress. In light of these studies, the apparently minimal effects of the Maine Turnpike on streams in general can be made with confidence. Conversely, the larger decrease in production associated with low levels of urbanization in 1998-1999 (CHAPTER III) indicates that significant functional changes can occur that are not detected by the single-occasion sampling protocols on which most current bioassessment is based.

The larger spatial and temporal scales used in this study illustrate the inadequacy of information from traditional assessment methods that rely on instantaneous

measurements of water and habitat quality or invertebrate assemblages in evaluating stream functional integrity. The integration of direct functional measurements over larger spatial and temporal scales is necessary to quantify these effects. However, the interpretation of confounded effects on communities and their habitats does present difficulties in assessment of stream condition. Functional changes in stream processes suggest that system resistance to stress has been exceeded, and the direct measurement of these processes is necessary in order to address these broader and potentially more serious issues affecting stream integrity. The development of methods that include functional characteristics in ecological assessments deserves further investigation, and improved understanding of the relationships between community structure and ecosystem function will ultimately lead to improvements in the understanding and mitigation of anthropogenic stresses on streams.

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APPENDIX A. Invertebrate secondary production data from Goosefare Brook, 1998-1999.

Table A.1. Summary of production values for organisms in Goosefare Brook, 1998-1999. Production values are given in mg AFDM/m^2/y, and are followed by the bootstrapped estimate of the ±95% confidence interval of the mean in parentheses. Results presented only for organisms where production was calculated using the bootstrap size-frequency method, except all are included in feeding group and overall totals. Superscript a indicates that an assumed mean P/B was used for that taxon.

Taxon	Secondary Production								
	Station								
	1	2	3	4	5	6	7	8	9
Shredders									
Allocapnia	410 (273)	159 (86)	13[a]	24 (10)	8[a]	14[a]	56 (21)	22 (17)	11 (5)
Amphinemura	198 (113)	33 (20)	47 (36)	76 (35)	0.4[a]	15 (20)	30 (15)	1[a]	0.2[a]
Brillia	39 (38)	11 (7)	3[a]	0.7[a]	1[a]	0.3[a]	7 (4)	3 (2)	3 (3)
Caecidotea	-	-	-	-	-	122 (69)	150 (57)	35 (26)	-
Hyalella	16[a]	0.3[a]	-	0.9[a]	-	12 (8)	9 (4)	0.5[a]	0.3[a]
Lepidostoma	88 (73)	242 (382)	23 (21)	56 (41)	23[a]	1[a]	3 (1)	-	-
Leuctra	610 (346)	135 (49)	26 (13)	98 (31)	9 (6)	14 (10)	91 (21)	17 (7)	3 (2)
Paracapnia	87 (48)	144 (74)	-	17 (9)	1[a]	-	14 (8)	0.3[a]	0.2[a]
Psilotreta	3795 (1478)	718[a]	397 (286)	43 (32)	525 (506)	1[a]	12[a]	-	0.5[a]
Pycnopsyche	5771 (1809)	577 (431)	533[a]	81 (71)	379[a]	17[a]	15[a]	-	21[a]
Symposiocladius	2[a]	11 (8)	0.1[a]	0.05[a]	2[a]	-	0.2[a]	-	0.2[a]
ALL SHREDDERS	11781 (2350)	4691 (592)	1298 (291)	497 (104)	987 (506)	206 (73)	608 (67)	170 (32)	45 (7)
Scrapers									
Acerpenna	-	-	-	-	-	-	-	-	4 (2)
Molanna	157 (133)	31[a]	4[a]	-	5[a]	2[a]	0.2[a]	-	-
Neophylax	-	5[a]	-	10 (8)	-	0.2[a]	-	-	-
Optioservus	-	.03[a]	-	2 (2)	-	-	-	-	0.06[a]
Stenonema	3[a]	43[a]	21 (16)	60 (28)	-	-	0.04[a]	-	4[a]
ALL SCRAPERS	161 (133)	82 (0)	25 (16)	82 (29)	6 (0)	3 (0)	2 (0)	0 (0)	10 (3)
Gatherers									
Antocha	-	4[a]	0.1[a]	123 (22)	8[a]	-	3 (2)	-	0.6[a]
Corynoneura	19 (12)	7 (5)	14 (12)	5 (3)	2[a]	3[a]	1 (1)	0.4[a]	0.7[a]
Cryptochironomus	-	0.6[a]	2[a]	0.2[a]	14 (9)	11 (7)	-	-	1[a]

Table A.1. continued

	1	2	3	4	5	6	7	8	9
Gatherers, cont'd									
Diplocladius	0.8[a]	11 (12)	2 (3)	13 (8)	17 (13)	41 (27)	62 (35)	24 (13)	20 (8)
Eukiefferiella	2[a]	6[a]	0.5[a]	14 (13)	-	21[a]	40 (22)	3[a]	3 (2)
Eurylophella	81 (81)	23 (19)	10 (8)	48 (15)	11[a]	2[a]	8 (4)	-	0.04[a]
Heleniella	12 (13)	2 (1)	25 (30)	0.8[a]	3 (3)	0.3[a]	4 (2)	0.8[a]	4 (1)
Heterotrissocladius	33 (22)	13 (11)	1[a]	-	3 (3)	1[a]	0.1[a]	0.8[a]	0.7[a]
Leptophlebia	198 (253)	227 (111)	40 (21)	79 (37)	106 (107)	63 (36)	8 (5)	7 (7)	23 (12)
Limnophyes	8 (7)	0.9[a]	0.6[a]	0.09[a]	0.2[a]	-	1[a]	0.1[a]	0.2[a]
Lype	118 (102)	24 (24)	20 (13)	9 (12)	4[a]	3[a]	1[a]	1[a]	-
Nematoda	80 (45)	20 (15)	2[a]	25 (16)	7 (8)	8[a]	12 (7)	4 (2)	3[a]
Oligochaeta	662 (226)	369 (206)	87 (34)	214 (60)	110 (50)	407 (202)	66 (14)	164 (62)	310 (97)
Orthocladius/ Cricotopus	0.6[a]	5 (3)	1[a]	50 (23)	6 (4)	30 (24)	130 (47)	6 (4)	33 (19)
Parachaetocladius	73 (72)	4[a]	0.8[a]	0.3[a]	2[a]	-	-	3[a]	-
Paracladopelma	13 (6)	1 (1)	2 (1)	-	4 (3)	-	-	-	0.05[a]
Paralauterborniella	0.9 (0.6)	0.2[a]	0.4[a]	0.4[a]	0.7[a]	0.9[a]	-	-	0.03[a]
Parametriocnemus	285 (118)	65 (37)	601 (329)	294 (203)	442 (157)	113 (49)	253 (42)	68 (32)	87 (28)
Paratendipes	28 (22)	6 (5)	6[a]	2[a]	12 (8)	66 (97)	0.2[a]	0.5[a]	-
Polypedilum	3179 (980)	251 (90)	1460(1293)	337 (188)	868 (346)	121 (100)	54 (22)	15 (9)	183 (102)
Psectrocladius	-	0.8[a]	-	1[a]	0.6[a]	12 (13)	3 (2)	-	0.07[a]
Psilometriocnemus	110 (131)	33 (28)	34 (27)	17 (11)	126 (144)	8 (6)	5 (3)	2 (1)	1 (2)
Rheocricotopus	27 (19)	4 (5)	30 (21)	133 (56)	19 (13)	156 (71)	72 (32)	14 (9)	62 (48)
Rheosmittia	1.9[a]	0.4[a]	16 (16)	0.1[a]	5 (4)	0.01[a]	0.05[a]	0.1[a]	-
Stilocladius	0.09[a]	-	0.01[a]	0.3[a]	0.3[a]	4 (2)	-	0.3[a]	0.4[a]
Thienemanniella	19 (8)	6 (4)	5 (5)	14 (3)	1 (1)	2 (2)	1 (1)	0.2[a]	0.1[a]
Tribelos	59[a]	94 (100)	7[a]	30[a]	643 (642)	130 (159)	1[a]	0.6[a]	-
Tvetenia	95 (61)	134 (87)	15 (11)	75 (52)	4 (3)	6 (5)	45 (16)	3 (3)	2 (1)
ALL GATHERERS	5282 (1071)	1359 (294)	2403(1334)	1498 (303)	2439 (792)	1258 (299)	820 (93)	345 (73)	745 (147)
Filterers									
Cladotanytarsus	148 (148)	6 (3)	11 (6)	1 (1)	2 (1)	0.7[a]	0.02[a]	-	-
Diplectrona	557 (480)	97[a]	-	-	-	-	-	-	-
Hydropsyche	-	576 (554)	9[a]	231 (168)	-	-	88[a]	3[a]	157 (78)
Micropsectra	629 (257)	240 (209)	416 (231)	65 (22)	334 (129)	67 (22)	29 (9)	5 (4)	17 (6)
Microtendipes	2[a]	17 (13)	49 (28)	5[a]	48 (41)	19 (8)	2[a]	-	0.8[a]

Table A.1. continued

	1	2	3	4	5	6	7	8	9
Filterers, cont'd									
Phylocentropus	2228 (1314)	93 (78)	64[a]	25[a]	7[a]	-	-	-	-
Pisidium	171 (85)	4 (4)	67 (39)	9 (3)	43 (16)	109 (91)	4 (2)	0.7[a]	0.5[a]
Rheotanytarsus	24[a]	3 (3)	20 (18)	10 (8)	4 (3)	2 (3)	4 (4)	0.06[a]	5 (3)
Simuliidae	186 (100)	1482(1039)	572 (421)	1347 (867)	18[a]	225 (303)	2759(1125)	437 (165)	16 (10)
ALL FILTERERS	3961 (1438)	2531(1203)	1209 (486)	1697 (879)	459 (135)	426 (325)	2892(1125)	447 (165)	239 (79)
Engulfers									
Brundiniella	62 (36)	10 (6)	64 (29)	5 (2)	71 (25)	3 (2)	3[a]	-	0.6[a]
Cordulegaster	665 (490)	1251[a]	3105[a]	1240[a]	1128[a]	2779[a]	1137[a]	-	57[a]
Dicranota	63 (33)	64 (36)	31 (17)	36 (21)	30 (18)	14[a]	41 (21)	4 (2)	0.7[a]
Diura	-	155 (137)	-	-	-	-	-	-	-
Lanthus	2208(2463)	-	586 (387)	82 (59)	362[a]	74[a]	46[a]	-	-
Limnophila	666 (359)	10[a]	214 (104)	53 (28)	353 (147)	4[a]	2[a]	-	3[a]
Meropelopia/ Conchapelopia	152 (63)	42 (19)	26 (12)	30 (7)	49 (24)	24 (10)	30 (13)	18 (8)	57 (23)
Ormosia	-	76 (48)	-	-	-	-	-	-	-
Palpomyia	408 (275)	155 (106)	49 (29)	109 (56)	22 (13)	35 (22)	48 (19)	20 (14)	81 (12)
Probezzia	105 (66)	20 (21)	43 (48)	5[a]	57 (29)	14[a]	-	0.4[a]	0.07[a]
Procladius	36[a]	5[a]	5[a]	2[a]	11[a]	63 (44)	-	-	0.01[a]
Sialis	12[a]	12[a]	4[a]	31 (25)	9[a]	35 (23)	5[a]	12 (5)	12 (7)
Zavrelimyia	15[a]	11 (7)	4[a]	5[a]	5[a]	3[a]	1[a]	0.7[a]	12 (11)
ALL ENGULFERS	4683 (2541)	2005 (183)	4162 (402)	1622 (95)	2243 (156)	3353 (54)	1463 (27)	55 (17)	227 (28)
Piercers									
Atherix	36[a]	98 (65)	102 (106)	259 (106)	11[a]	-	7[a]	-	-
Chelifera	1[a]	1 (1)	2 (1)	2 (1)	0.3[a]	0.8 (0.5)	3 (1)	0.5 (0.3)	3 (1)
Chrysops	475 (187)	16[a]	20[a]	30 (15)	54 (29)	142 (105)	4[a]	4[a]	10[a]
Hemerodromia	-	-	1[a]	0.5[a]	1[a]	0.1[a]	2 (1)	-	0.2[a]
ALL PIERCERS	513 (187)	116 (65)	221 (106)	312 (107)	67 (29)	157 (105)	20 (1)	4 (1)	16 (1)
GRAND TOTAL	26380 (3884)	10784 (1404)	9318 (1545)	5707 (963)	6201 (964)	5402 (471)	5806(1133)	1021 (184)	1282 (168)

Table A.2. Rates of biomass turnover, expressed as P/B ratio, for organisms in Goosefare Brook, 1998-1999. Results presented only for organisms where production was calculated using the bootstrap size-frequency method. The mean cohort production interval and the source used is included. Superscript a indicates that an assumed mean P/B was used for that taxon.

CCA code	Taxon	Annual Biomass Turnover (P/B) Station 1	2	3	4	5	6	7	8	9	CPI (d)	CPI Reference
	Shredders											
1S	*Allocapnia*	8.63	9.65	13.07[a]	13.60	13.07[a]	13.07[a]	17.61	15.02	13.93	213	This study
2S	*Amphinemura*	5.44	6.35	9.39	7.22	6.96[a]	7.39	5.96	6.96[a]	6.96[a]	288	This study
3S	*Brillia*	5.27	6.75	6.89[a]	6.89[a]	6.89[a]	6.89[a]	9.33	7.09	6.01	244	This study
4S	*Caecidotea*	-	-	-	-	-	6.20	4.87	5.39	-	365	This study
5S	*Hyalella*	4.13[a]	4.13[a]	-	4.13[a]	-	5.21	3.04	4.13[a]	4.13[a]	350	This study
6S	*Lepidostoma*	8.63	5.18	10.57	9.76	8.08[a]	8.08[a]	6.24	-	-	259	This study
7S	*Leuctra*	3.24	3.69	4.71	3.70	2.94	3.69	3.07	3.22	4.36	608	This study
8S	*Paracapnia*	8.02	7.50	-	7.84	9.30[a]	-	13.85	9.30[a]	9.30[a]	229	This study
9S	*Psilotreta*	5.03	5.42[a]	4.97	6.22	5.47	5.42[a]	5.42[a]	-	5.42[a]	335	Huryn and Wallace (1988)
10S	*Pycnopsyche*	8.02	7.33	7.63[a]	7.53	7.63[a]	7.63[a]	7.63[a]	-	7.63[a]	274	This study
11S	*Symposiocladius*	7.72[a]	7.72	7.72[a]	7.72[a]	7.72[a]	-	7.72[a]	7.72[a]	7.72[a]	183	This study
	Scrapers											
12A	*Acerpenna*	-	-	-	-	-	-	3.77[a]	-	3.77	365	This study
13A	*Molanna*	5.41	5.41[a]	5.41[a]	-	5.41[a]	5.41[a]	5.41[a]	-	-	365	This study
14A	*Neophylax*	-	7.77[a]	-	7.77	-	7.77[a]	-	-	-	288	This study
15A	*Optioservus*	-	2.66[a]	-	2.66	-	-	-	-	2.66[a]	365	Huryn and Wallace (1987)
16A	*Stenonema*	4.23[a]	4.23[a]	4.05	4.41	-	-	4.23[a]	-	4.23[a]	365	This study
	Gatherers											
17G	*Antocha*	-	12.27[a]	12.27[a]	11.67	12.27[a]	-	12.86	-	12.27[a]	175	Fuller and Hynes (1987)
18G	*Corynoneura*	16.64	15.67	18.49	16.93	16.48[a]	16.48[a]	14.67	16.48[a]	16.48[a]	106	Lindegaard and Mortensen (1988)
19G	*Cryptochironomus*	-	11.15[a]	11.15[a]	11.15[a]	10.04	12.25	-	-	11.15[a]	183	This study
20G	*Diplocladius*	7.00[a]	10.03	5.05	7.11	8.31	7.00	6.48	5.49	6.51	336	This study
21G	*Eukiefferiella*	17.13[a]	17.13[a]	17.13[a]	16.48	-	17.13[a]	19.36	17.13[a]	15.56	120	Berg and Hellenthal (1992)
22G	*Eurylophella*	4.27	3.33	2.72	3.20	3.59[a]	3.59[a]	4.41	-	3.59[a]	621	This study
23G	*Heleniella*	5.53	4.43	3.98	5.15[a]	5.87	5.15[a]	5.75	5.15[a]	5.33	318	This study
24G	*Heterotrissocladius*	5.96	6.61	6.21[a]	-	6.07	6.21[a]	6.21[a]	6.21[a]	6.21[a]	303	This study

Table A.2. continued

		1	2	3	4	5	6	7	8	9	CPI (d)	CPI Reference
	Gatherers, cont'd											
25G	*Leptophlebia*	5.97	10.37	7.05	7.25	5.81	7.52	6.26	8.36	5.97	321	This study
26G	*Limnophyes*	6.74	6.74[a]	6.74[a]	6.74[a]	6.74[a]	-	6.74[a]	6.74[a]	6.74[a]	212	This study
27G	*Lype*	5.15	6.75	4.71	4.50	5.28[a]	5.28[a]	5.28[a]	5.28[a]	-	332	Huryn and Wallace (1988)
28G	Nematoda	19.72	11.05	11.81[a]	10.12	10.18	11.81[a]	8.74	11.03	11.81[a]	183	Smock et al (1985)
29G	Oligochaeta	17.83	20.53	18.07	22.16	19.13	17.22	12.28	27.15	29.78	183	Smock et al (1985)
30G	*Orthocladius/ Cricotopus*	13.40[a]	12.34	13.40[a]	16.06	12.73	15.47	10.89	11.62	14.42	150	This study
31G	*Parachaetocladius*	4.76	4.76[a]	4.76[a]	4.76[a]	4.76[a]	-	4.76[a]	4.76[a]	-	350	Barton et al (1987)
32G	*Paracladopelma*	9.16	3.45	9.80	-	7.34	7.44[a]	-	-	7.44[a]	288	This study
34G	*Paralauterborniella*	3.89	3.89[a]	3.89[a]	3.89[a]	3.89[a]	3.89[a]	3.89[a]	3.89[a]	3.89[a]	336	This study
35G	*Parametriocnemus*	32.83	18.90	28.03	19.67	22.89	17.61	22.29	29.20	26.25	91	Berg and Hellenthal (1991)
36G	*Paratendipes*	9.04	7.23	7.52[a]	7.52[a]	8.25	5.57	7.52[a]	7.52[a]	-	259	This study
37G	*Polypedilum*	36.07	32.49	47.18	41.68	38.03	35.03	32.31	30.15	44.29	59	Berg and Hellenthal (1991)
38G	*Psectrocladius*	-	7.03[a]	-	7.03[a]	7.03[a]	7.33	6.73	-	7.03[a]	365	This study
33G	*Psilometriocnemus*	11.20	12.19	12.19	12.65	16.69	12.43	10.04	11.94	16.52	106	This study
39G	*Rheocricotopus*	11.28	5.95	14.17	12.23	14.58	14.97	10.68	10.39	14.08	168	This study
40G	*Rheosmittia*	5.46[a]	5.46[a]	6.87	5.46[a]	4.05	5.46[a]	5.46[a]	5.46[a]	-	241	This study
41G	*Stilocladius*	7.88[a]	-	7.88[a]	7.88[a]	7.88[a]	7.88	-	7.88[a]	7.88[a]	183	This study
42G	*Thienemanniella*	17.18	11.28	11.27	8.78	14.39	12.72	13.41	12.72[a]	12.72[a]	120	Lindegaard and Mortensen (1988)
43G	*Tribelos*	7.72[a]	8.00	7.72[a]	7.72[a]	6.44	8.71	7.72[a]	7.72[a]	-	274	This study
44G	*Tvetenia*	8.71	10.99	5.76	8.69	6.53	4.33	6.87	7.48	6.89	288	This study
	Filterers											
45F	*Cladotanytarsus*	16.14	11.94	12.32	7.30	14.58	12.46[a]	12.46[a]	-	-	139	Berg and Hellenthal (1992)
46F	*Diplectrona*	5.08	5.08[a]	-	-	-	-	-	-	5.08[a]	332	Huryn and Wallace (1988)
47F	*Hydropsyche*	-	4.12	5.69[a]	5.26	-	-	5.69[a]	5.69[a]	7.69	365	This study
48F	*Micropsectra*	12.29	10.55	12.09	13.52	13.73	9.88	10.40	10.93	14.27	197	Lindegaard and Mortensen (1988)
49F	*Microtendipes*	5.77[a]	6.06	5.84	5.77[a]	6.34	4.81	5.77[a]	-	5.77[a]	336	This study
50F	*Phylocentropus*	6.57	6.30	6.44[a]	6.44[a]	6.44[a]	-	-	-	-	365	This study
51F	*Pisidium*	3.64	3.80	3.26	4.13	3.63	5.71	4.50	4.10[a]	4.10[a]	259	This study
52F	*Rheotanytarsus*	11.67[a]	9.78	8.15	13.37	14.05	12.07	10.94	11.67[a]	13.34	168	Berg and Hellenthal (1992)
53F	Simuliidae	7.67	8.63	6.83	7.18	7.80[a]	7.66	7.31	8.60	8.56	365	This study

Table A.2. continued

		1	2	3	4	5	6	7	8	9	CPI (d)	CPI Reference
	Engulfers											
54E	*Brundiniella*	5.35	5.89	6.04	4.57	6.07	4.07	5.33[a]	-	5.33[a]	336	This study
55E	*Cordulegaster*	5.40	5.40[a]	5.40[a]	5.40[a]	5.40[a]	5.40[a]	5.40[a]	-	5.40[a]	1140	Lugthart and Wallace (1992)
56E	*Dicranota*	2.59	3.61	4.49	3.93	2.31	3.23[a]	2.83	2.86	3.23[a]	712	This study
57E	*Diura*	-	9.99	-	-	-	-	-	-	-	230	This study
58E	*Lanthus*	3.15	-	2.47	2.67	2.76[a]	2.76[a]	2.76[a]	-	-	668	Huryn and Wallace (1987)
59E	*Limnophila*	10.13	9.79[a]	8.60	12.11	8.36	9.79[a]	9.79[a]	-	9.79[a]	197	This study
60E	*Meropelopia/ Conchapelopia*	5.04	6.21	6.96	6.20	5.18	5.66	5.68	5.16	5.84	365	Lindegaard and Mortensen (1988)
61E	*Ormosia*	-	5.07	-	-	-	-	-	-	-	365	This study
62E	*Palpomyia*	11.32	9.68	8.03	12.60	7.24	9.69	9.76	12.00	10.05	183	Smock et al (1985)
63E	*Probezzia*	4.68	3.94	4.37	4.34[a]	4.36	4.34[a]	-	4.34[a]	4.34[a]	365	This study
64E	*Procladius*	23.31[a]	23.31[a]	23.31[a]	23.31[a]	23.31[a]	23.31	-	-	-	70	Smock et al (1985)
65E	*Sialis*	2.16[a]	2.16[a]	2.16[a]	2.52	2.16[a]	2.18	2.16[a]	1.83	2.09	730	This study
66E	*Zavrelimyia*	11.43[a]	11.27	11.43[a]	11.43[a]	11.43[a]	11.43[a]	11.43[a]	11.43[a]	11.59	183	This study
	Piercers											
67P	*Atherix*	5.74[a]	4.81	6.52	5.88	5.74[a]	-	5.74[a]	-	-	365	Lauzon and Harper (1993)
68P	*Chelifera*	3.19[a]	3.24	3.02	2.46	3.19[a]	3.15	3.33	3.09	4.08	365	This study
69P	*Chrysops*	5.23	4.92[a]	4.92[a]	4.73	4.31	5.42	4.92[a]	4.92[a]	4.92[a]	365	This study
70P	*Hemerodromia*	-	-	3.72[a]	3.72[a]	3.72[a]	3.72[a]	3.72	-	3.72[a]	365	This study

APPENDIX B. Invertebrate secondary production data from Maine Turnpike study, 1999-2000.

Table B.1. Summary of locational means of secondary production, P/B value, and cohort production interval for stream invertebrates in southern Maine. Only those taxa for which at least one calculated production value was available are included. US denotes the mean of all study reaches upstream of the roadway, DS denotes downstream reaches, and IN denotes reaches exposed to industrial inputs (Goosefare Brook only). Production is expressed as mgAFDM/m^2/y, annual P/B values are shown in parentheses. CPI is given in days. Taxon codes in parentheses are applicable to plots of invertebrate taxa.

Taxon	Cascade Brook		Goosefare Brook			Ward Brook		Branch Brook		Stevens Brook		CPI	CPI reference
	US	DS	US	DS	IN	US	DS	US	DS	US	DS		
Shredders													
Allocapnia	503.0	570.4	85.6	13.9	5.4	108.6	157.9	3.7	2.9	356.2	312.7	213	This study
(1S)	(10.0)	(11.7)	(8.5)	(8.2)	(4.0)	(9.0)	(16.4)	(5.6)	(5.6)	(8.7)	(9.5)		
Amphinemura	30.3	30.3	48.9	3.2	-	-	0.4	1.5	1.7	206.6	176.4	288	This study
(2S)	(9.2)	(10.1)	(6.5)	(6.6)			(8.0)	(8.0)	(8.0)	(7.3)	(8.0)		
Brillia	0.5	0.7	5.5	0.3	12.1	13.6	2.6	4.9	0.3	1.3	0.1	244	Chapter III
(3S)	(7.7)	(7.7)	(8.5)	(8.5)	(8.5)	(6.9)	(6.9)	(7.7)	(7.7)	(7.7)	(7.7)		
Caecidotea	-	-	-	-	429.8	-	-	-	-	-	-	365	This study
(4S)					(4.4)								
Hyalella	1.9	23.4	-	9.6	16.1	-	0.2	-	-	-	-	350	Chapter III
(5S)	(4.7)	(6.0)		(4.7)	(4.7)		(4.7)						
Lepidostoma	6.6	0.6	41.3	75.3	0.4	1.3	0.06	106.8	32.6	39.8	2.3	223	This study
(6S)	(8.2)	(8.2)	(8.4)	(8.7)	(8.4)	(8.2)	(8.2)	(6.7)	(8.4)	(8.3)	(9.0)		
Leuctra	8.0	10.1	34.1	16.5	2.8	2.9	5.9	5.6	2.0	54.0	12.1	608	Chapter III
(7S)	(3.0)	(3.4)	(3.0)	(3.0)	(3.5)	(3.3)	(3.3)	(2.8)	(2.9)	(3.2)	(3.9)		
Micrasema	0.07	2.0	-	-	-	-	-	1.7	31.3	-	-	243	This study
(8S)	(7.5)	(7.5)						(7.5)	(7.5)				
Paracapnia	140.7	102.3	1.1	5.8	-	24.6	76.6	-	1.3	15.8	0.3	243	This study
(9S)	(8.1)	(8.8)	(8.1)	(8.1)		(7.8)	(9.2)		(8.1)	(8.2)	(7.5)		
Podmosta	9.2	9.6	0.7	0.2	-	35.1	48.8	8.5	2.0	183.9	135.9	152	This study
(10S)	(10.7)	(11.9)	(10.9)	(10.9)		(8.6)	(13.2)	(10.9)	(10.9)	(12.2)	(11.1)		
Pteronarcys	-	-	-	-	-	-	-	1114.0	196.7	-	-	-	*Assumed P/B=5
(11S)								(5.0)*	(5.0)*				
Ptilostomis	-	10.8	4.0	26.0	-	-	-	-	-	164.7	83.2	183	Roeding and Smock
(12S)		(7.5)	(7.5)	(7.5)						(7.5)	(7.5)		(1989)

Table B.1. continued

Taxon	Cascade Brook		Goosefare Brook			Ward Brook		Branch Brook		Stevens Brook		CPI	CPI reference
	US	DS	US	DS	IN	US	DS	US	DS	US	DS		
Shredders, cont'd													
Pycnopsyche	229.4	197.5	560.7	379.9	168.5	913.7	555.8	150.3	90.5	63.8	215.6	274	This study
(13S)	(6.8)	(7.3)	(6.6)	(5.2)	(6.0)	(6.2)	(6.3)	(6.0)	(6.0)	(4.8)	(4.8)		
Symposiocladius	0.5	0.8	0.6	0.2	0.6	0.4	0.4	0.2	0.2	1.9	2.1	183	Chapter III
(14S)	(5.9)	(5.9)	(5.9)	(5.9)	(5.9)	(5.9)	(5.9)	(5.9)	(5.9)	(7.3)	(5.3)		
Taenionema	16.5	119.1	-	-	-	67.6	109.4	-	0.5	-	-	137	This study
(15S)	(12.4)	(12.1)				(14.1)	(14.5)		(13.0)				
Taeniopteryx	46.6	94.6	-	-	-	26.7	34.0	25.1	75.9	-	-	304	This study
(16S)	(8.2)	(8.0)				(4.8)	(4.8)	(8.8)	(8.8)				
Tipula	333.1	147.3	326.2	83.2	486.8	217.1	68.4	467.6	58.1	135.0	352.6	310	Huryn and Wallace
(17S)	(6.2)	(7.6)	(5.9)	(5.9)	(5.9)	(5.9)	(5.9)	(5.9)	(5.9)	(5.9)	(5.9)		(1987)
Σ Shredders	**1333.3**	**1322.2**	**1186.0**	**705.4**	**1125.9**	**1417.1**	**1071.3**	**1946.1**	**516.2**	**1256.9**	**1334.9**		
Scrapers													
Acerpenna	10.0	7.9	-	-	-	70.2	133.3	15.5	6.8	-	-	183	This study
(18A)	(7.4)	(7.4)				(8.8)	(8.8)	(8.3)	(8.3)				
Baetis	0.02	11.8	-	-	0.7	0.4	12.4	11.8	97.2	-	-	183	This study
(19A)	(8.3)	(8.3)			(9.3)	(9.4)	(9.4)	(10.2)	(10.2)				
Dubiraphia	78.2	88.8	-	0.2	0.6	166.2	66.7	-	-	-	0.2	365	This study
(21A)	(5.0)	(5.3)		(5.0)	(5.0)	(9.6)	(9.7)				(5.0)		
Ectopria	8.7	24.3	-	-	-	-	-	-	-	-	-	365	This study
(22A)	(4.5)	(4.2)											
Lype	4.2	3.4	14.3	39.8	13.5	19.3	12.2	2.3	1.8	0.6	4.4	332	Huryn and Wallace
(23A)	(6.3)	(6.3)	(5.6)	(6.4)	(4.0)	(6.9)	(6.9)	(6.3)	(6.3)	(6.3)	(6.3)		(1988)
Molanna	0.68	0.16	5.7	8.6	-	7.6	0.35	-	-	2.1	2.1	365	Chapter III
(24A)	(5.4)	(5.4)	(5.4)	(5.4)		(5.4)	(5.4)			(5.4)	(5.4)		
Neophylax	36.6	24.9	-	0.3	-	0.8	4.0	0.3	-	3.6	7.4	288	Chapter III
(25A)	(7.4)	(5.8)		(7.2)		(7.2)	(7.2)	(7.2)		(7.2)	(7.2)		
Optioservus	23.7	48.8	-	0.04	0.06	4.8	54.3	2.1	1.4	1.5	0.6	365	Huryn and Wallace
(26A)	(4.4)	(4.7)		(4.4)	(4.4)	(5.0)	(4.8)	(4.1)	(4.1)	(4.1)	(4.1)		(1987)
Palmacorixa	1.7	4.2	-	-	-	-	-	-	-	-	0.7	120	This study
(27A)	(16.2)	(16.2)									(16.2)		
Promoresia	0.5	7.6	-	-	-	5.6	1.2	4.5	502.9	-	-	365	This study
(28A)	(4.8)	(4.9)				(5.7)	(5.7)	(6.7)	(6.6)				

Table B.1. continued

Taxon	Cascade Brook US	Cascade Brook DS	Goosefare Brook US	Goosefare Brook DS	Goosefare Brook IN	Ward Brook US	Ward Brook DS	Branch Brook US	Branch Brook DS	Stevens Brook US	Stevens Brook DS	CPI	CPI reference
Scrapers, cont'd													
Psilotreta	51.8	39.1	1177.0	139.4	-	4.7	7.1	-	0.1	24.9	1.9	335	Huryn and Wallace
(29A)	(4.4)	(4.4)	(5.9)	(7.3)		(4.8)	(4.8)		(5.1)	(5.2)	(5.2)		(1988)
Stenelmis	7.1	13.0	5.6	-	-	14.1	44.3	-	-	-	-	365	Smock et al (1985)
(30A)	(4.4)	(5.1)	(4.9)			(4.5)	(5.7)						
Stenonema	126.8	56.4	58.6	3.0	-	107.2	107.6	26.3	13.4	-	-	365	This study
(31A)	(5.6)	(5.9)	(4.2)	(4.4)		(5.0)	(6.3)	(3.3)	(3.3)				
Σ Scrapers	**382.3**	**381.2**	**1261.5**	**191.3**	**16.4**	**451.6**	**496.6**	**66.0**	**771.9**	**33.0**	**33.6**		
Gatherers													
Antocha	2.4	0.28	-	1.9	-	0.15	0.28	-	-	-	-	175	Fuller and Hynes
(32G)	(12.3)	(12.3)		(12.3)		(12.3)	(12.3)						(1987)
Chaetocladius	1.2	0.4	2.8	0.3	-	33.2	3.8	-	0.01	11.2	6.6	365	This study
(33G)	(4.2)	(4.2)	(4.2)	(4.3)		(4.2)	(4.3)		(4.2)	(8.2)	(7.0)		
Chironomus	3.2	13.6	5.9	29.3	292.5	-	0.9	-	-	17.0	69.8	303	This study
(34G)	(6.3)	(12.2)	(6.2)	(6.7)	(5.7)		(6.3)			(6.0)	(5.1)		
Corynoneura	3.2	4.0	23.1	4.1	0.3	1.0	1.5	0.2	0.9	12.5	15.7	106	Lindegaard and
(35G)	(15.3)	(15.3)	(14.4)	(14.4)	(14.4)	(14.4)	(14.4)	(14.4)	(14.4)	(14.6)	(13.0)		Mortensen (1988)
Cryptochironomus	3.7	5.5	10.8	28.4	7.3	13.1	15.1	0.3	0.3	0.1	0.9	304	This study
(36G)	(8.5)	(9.5)	(11.4)	(11.8)	(7.3)	(6.7)	(6.8)	(8.7)	(8.7)	(8.7)	(8.7)		
Dicrotendipes	7.5	13.1	-	-	-	0.2	0.9	-	-	0.7	0.2	243	This study
(37G)	(5.8)	(7.7)				(7.0)	(7.0)			(7.0)	(7.0)		
Diplocladius	6.7	3.2	14.3	9.3	6.5	26.2	1.9	0.8	0.06	0.06	1.6	336	Chapter III
(38G)	(5.9)	(6.0)	(5.2)	(4.5)	(4.9)	(8.0)	(5.4)	(5.4)	(5.4)	(5.4)	(5.4)		
Ephemerella	-	14.3	-	-	-	21.4	80.4	82.8	472.4	-	-	320	This study
(39G)		(5.6)				(4.9)	(4.7)	(6.7)	(6.9)				
Eukiefferiella	22.6	38.4	0.3	0.9	0.2	3.0	23.8	0.9	25.1	3.2	3.1	120	Berg and Hellenthal
(40G)	(11.5)	(13.9)	(12.4)	(12.4)	(12.4)	(9.4)	(13.6)	(13.9)	(14.7)	(11.8)	(12.2)		(1992)
Eurylophella	28.4	34.4	7.6	13.0	-	1.1	1.0	2.7	3.0	2.2	-	621	Chapter III
(41G)	(3.4)	(4.6)	(3.2)	(3.2)		(3.6)	(3.6)	(3.6)	(3.6)	(3.8)			
Heleniella	5.2	5.7	7.2	3.9	2.6	0.2	1.7	-	-	0.5	0.2	243	This study
(42G)	(5.9)	(6.3)	(5.8)	(5.8)	(5.8)	(6.0)	(6.0)			(6.0)	(6.0)		
Heterotrissocladius	6.0	3.9	25.1	9.4	12.3	7.2	4.9	3.2	0.5	50.7	39.6	303	This study
(43G)	(5.9)	(6.9)	(5.8)	(5.4)	(6.1)	(8.1)	(8.1)	(6.5)	(6.5)	(6.1)	(4.7)		

Table B.1. continued

Taxon	Cascade Brook US	Cascade Brook DS	Goosefare Brook US	Goosefare Brook DS	Goosefare Brook IN	Ward Brook US	Ward Brook DS	Branch Brook US	Branch Brook DS	Stevens Brook US	Stevens Brook DS	CPI	CPI reference
Gatherers, cont'd													
Leptophlebia	338.9	173.4	296.7	143.3	5.3	145.8	12.9	1.6	6.3	13.1	5.6	321	Chapter III
(44G)	(7.6)	(7.2)	(6.7)	(5.0)	(6.2)	(5.3)	(6.2)	(6.4)	(6.4)	(5.7)	(5.9)		
Limnophyes	0.3	0.5	0.03	0.7	-	-	0.3	-	0.1	0.7	1.3	212	Chapter III
(45G)	(9.5)	(9.5)	(9.5)	(9.5)			(9.5)		(9.5)	(9.5)	(9.5)		
Mystacides	1.1	2.4	-	-	-	-	-	-	-	-	-	336	This study
(46G)	(5.2)	(5.2)											
Nematoda	232.0	124.2	135.1	763.7	95.1	288.6	612.3	317.2	292.7	439.2	492.3	183	Smock et al (1985)
(47G)	(9.7)	(10.8)	(12.1)	(12.1)	(12.1)	(12.9)	(12.6)	(11.8)	(11.3)	(13.1)	(12.7)		
Nilothauma	0.5	0.9	0.4	-	-	1.1	0.2	-	-	-	0.2	243	This study
(48G)	(4.3)	(4.3)	(4.3)			(4.3)	(4.3)				(4.3)		
Ochrotrichia	0.2	0.07	-	-	-	0.07	2.2	-	-	6.3	-	304	This study
(49G)	(6.2)	(6.2)				(6.2)	(6.2)			(6.2)			
Odontomesa	-	-	2.9	4.9	0.07	-	-	2.0	3.3	-	-	365	This study
(50G)			(4.6)	(4.6)	(4.6)			(4.3)	(4.7)				
Oligochaeta	6246.0	3194.0	801.6	412.2	1250.0	826.8	978.3	314.6	483.8	11766.0	9629.0	183	Smock et al (1985)
(51G)	(10.0)	(11.8)	(18.7)	(17.5)	(14.1)	(11.8)	(16.6)	(11.6)	(13.0)	(10.8)	(10.7)		
Orthocladius/	54.1	19.7	2.5	10.1	6.7	54.8	44.4	1.0	8.1	4.8	3.3	152	Chapter III
Cricotopus (52G)	(15.1)	(14.9)	(12.4)	(12.6)	(11.3)	(13.7)	(11.9)	(8.9)	(11.0)	(12.2)	(12.4)		
Parachaetocladius	0.4	1.4	5.9	0.04	57.2	0.3	6.7	0.8	5.0	3.7	30.4	365	This study
(53G)	(4.5)	(4.5)	(5.8)	(5.8)	(5.8)	(3.8)	(3.8)	(3.4)	(3.4)	(4.9)	(5.2)		
Paracladopelma	0.4	0.3	4.0	0.6	0.8	12.3	7.8	3.1	4.5	-	1.4	288	This study
(54G)	(6.1)	(6.1)	(6.1)	(6.1)	(6.1)	(7.6)	(7.4)	(6.1)	(6.1)		(4.6)		
Parakiefferiella	19.1	7.3	-	-	-	8.7	1.9	-	0.08	0.2	1.3	213	This study
(55G)	(7.0)	(7.0)				(9.2)	(9.5)		(8.0)	(8.0)	(8.0)		
Paralauterborniella	0.5	-	1.5	0.4	0.2	16.8	14.2	0.4	0.2	-	-	336	Chapter III
(56G)	(4.7)		(4.7)	(4.7)	(4.7)	(4.1)	(5.0)	(4.7)	(4.7)				
Paraleptophlebia	24.4	4.8	-	-	-	57.7	12.6	150.4	34.3	-	-	243	This study
(57G)	(7.7)	(7.4)				(7.0)	(7.0)	(6.5)	(6.6)				
Parametriocnemus	11.6	36.2	437.5	262.4	68.5	28.9	40.9	9.9	29.7	7.6	3.5	91	Berg and Hellenthal
(58G)	(21.2)	(22.2)	(20.8)	(21.9)	(30.0)	(15.6)	(17.9)	(21.0)	(21.0)	(21.1)	(21.1)		(1991)
Paratendipes	11.9	8.1	152.1	137.9	35.6	17.2	40.5	0.5	0.5	3.1	4.4	259	Chapter III
(59G)	(7.7)	(7.6)	(11.0)	(10.0)	(7.9)	(8.3)	(7.4)	(8.5)	(8.5)	(9.0)	(8.3)		
Polypedilum	182.9	179.9	3223.0	590.2	175.7	934.5	2082.0	80.1	126.8	144.0	97.0	59	Berg and Hellenthal
(60G)	(35.1)	(35.8)	(34.9)	(37.2)	(39.4)	(33.3)	(35.6)	(26.0)	(29.4)	(35.7)	(29.7)		(1991)

Table B.1. continued

Taxon	Cascade Brook		Goosefare Brook			Ward Brook		Branch Brook		Stevens Brook		CPI	CPI reference
	US	DS	US	DS	IN	US	DS	US	DS	US	DS		
Gatherers, cont'd													
Potthastia	1.4	0.1	-	-	-	0.74	0.58	-	-	-	-	365	Chapter III
(61G)	(5.2)	(5.2)				(5.2)	(5.2)						
Psectrocladius	0.51	0.70	1.9	2.4	0.1	0.45	1.1	-	0.15	5.2	1.6	365	Chapter III
(62G)	(7.0)	(7.0)	(7.0)	(7.0)	(7.0)	(7.0)	(7.0)		(7.0)	(7.0)	(7.0)		
Psilometriocnemus	7.5	2.7	44.3	6.3	3.5	11.6	53.3	87.3	269.6	-	30.9	183	This study
(63G)	(7.4)	(7.4)	(7.2)	(7.1)	(7.2)	(6.6)	(6.4)	(6.0)	(6.6)		(5.4)		
Rheocricotopus	8.1	3.3	54.3	273.9	7.3	5.3	7.5	4.2	8.9	46.5	11.6	168	Chapter III
(64G)	(13.2)	(13.2)	(11.8)	(10.6)	(11.7)	(8.9)	(7.4)	(12.2)	(9.4)	(8.0)	(6.8)		
Rheosmittia	4.4	-	4.3	1.5	0.5	3.5	61.3	3.3	5.7	-	-	241	Chapter III
(65G)	(5.6)		(4.8)	(4.9)	(4.9)	(5.8)	(7.5)	(5.4)	(5.9)				
Robackia	-	-	-	-	-	-	-	57.2	26.2	-	-	365	This study
(66G)								(4.8)	(4.4)				
Saetheria	-	-	-	-	-	0.2	5.0	-	-	-	-	304	This study
(67G)						(6.4)	(6.4)						
Serratella	0.58	-	-	-	-	1.2	12.1	-	0.59	-	-	365	This study
(68G)	(6.0)					(6.0)	(6.0)		(6.0)				
Stempellinella	2.8	5.8	12.8	6.4	1.9	10.2	11.0	3.7	1.4	0.3	1.2	183	This study
(69G)	(9.1)	(9.0)	(5.9)	(6.5)	(6.2)	(7.7)	(7.3)	(6.3)	(6.9)	(7.5)	(7.5)		
Stictochironomus	-	0.3	-	-	-	1.1	3.0	4.9	30.9	-	9.3	304	This study
(70G)		(6.0)				(6.0)	(6.0)	(6.0)	(6.1)		(6.0)		
Stilocladius	1.6	2.6	2.4	6.0	0.9	39.0	30.8	3.8	1.8	0.2	3.1	183	Chapter III
(71G)	(6.9)	(6.9)	(6.3)	(6.3)	(6.3)	(9.8)	(9.5)	(7.6)	(7.6)	(8.4)	(10.4)		
Thienemanniella	0.6	1.3	0.8	2.2	0.2	1.3	2.8	0.4	1.0	0.2	0.3	120	Lindegaard and Mortensen (1988)
(72G)	(11.9)	(11.9)	(11.9)	(11.9)	(11.9)	(11.9)	(11.9)	(11.9)	(11.9)	(11.9)	(11.9)		
Tribelos	8.6	2.8	1135.0	1818.0	984.1	26.0	15.1	3.0	0.8	63.3	86.4	274	This study
(73G)	(5.9)	(6.7)	(8.0)	(7.0)	(7.2)	(8.2)	(5.8)	(7.1)	(7.1)	(7.3)	(8.0)		
Tvetenia	16.7	9.6	0.9	1.0	0.5	3.6	3.9	0.4	0.8	21.6	6.9	365	This study
(74G)	(4.5)	(5.9)	(4.4)	(4.4)	(4.4)	(3.9)	(4.2)	(4.4)	(4.4)	(3.5)	(4.3)		
Zalutschia	0.3	0.3	-	-	-	2.3	1.9	-	-	10.7	1.7	183	This study
(75G)	(10.2)	(10.2)				(10.2)	(10.2)			(10.2)	(10.2)		
Σ Gatherers	**7345.4**	**3966.1**	**6457.0**	**4830.2**	**2786.2**	**2877.5**	**4258.2**	**1151.3**	**1860.0**	**12728.0**	**10626.3**		

Table B.1. continued

Taxon	Cascade Brook		Goosefare Brook			Ward Brook		Branch Brook		Stevens Brook		CPI	CPI reference
	US	DS	US	DS	IN	US	DS	US	DS	US	DS		
Filterers													
Brachycentrus	-	-	-	-	-	-	197.8	-	-	-	-	152	This study
(76F)							(12.9)						
Ceratopsyche	1.7	1.0	-	-	-	39.9	17.4	-	1.2	-	-	365	This study
(77F)	(3.9)	(3.9)				(5.8)	(4.1)		(3.9)				
Cheumatopsyche	2.8	9.7	-	-	-	66.0	72.0	-	0.2	-	-	336	Peterson and Martin-
(78F)	(4.5)	(8.1)				(8.5)	(9.5)		(5.2)				Robichaud (1986)
Cladotanytarsus	27.4	14.1	0.9	-	-	27.6	28.8	-	0.07	-	-	139	Berg and Hellenthal
(79F)	(10.8)	(11.4)	(12.4)			(16.6)	(26.7)		(12.4)				(1992)
Diplectrona	2.4	31.9	-	-	-	-	-	-	-	14.3	6.2	332	Huryn and Wallace
(80F)	(5.1)	(5.1)								(5.1)	(5.1)		(1988)
Hydropsyche	22.8	110.6	-	-	-	19.7	34.2	-	-	-	-	365	Chapter III
(81F)	(6.0)	(6.0)				(7.0)	(6.4)						
Micropsectra	107.6	120.8	609.3	275.7	43.8	189.7	147.6	21.8	30.5	17.7	51.6	197	Lindegaard and
(82F)	(10.3)	(10.7)	(8.7)	(11.8)	(12.2)	(14.1)	(11.3)	(10.8)	(10.7)	(9.6)	(9.0)		Mortensen (1988)
Microtendipes	23.5	29.9	167.1	59.6	8.8	17.6	8.9	1.5	0.06	13.8	24.7	336	This study
(83F)	(6.0)	(6.9)	(6.2)	(4.3)	(5.2)	(4.6)	(4.8)	(5.4)	(5.4)	(6.1)	(5.0)		
Paratanytarsus	1.4	3.9	0.2	-	-	-	3.4	-	-	-	-	335	This study
(84F)	(4.7)	(4.8)	(4.7)				(4.7)						
Phylocentropus	19.4	10.1	1026.0	252.8	251.4	264.5	352.4	2.7	3.4	-	2.1	336	This study
(85F)	(5.3)	(5.3)	(5.3)	(5.1)	(5.3)	(4.6)	(4.6)	(5.1)	(5.1)		(5.1)		
Pisidium	20.2	9.0	357.2	151.9	29.4	64.4	70.7	3.2	5.6	164.7	140.6	259	Chapter III
(86F)	(7.1)	(5.5)	(7.0)	(7.0)	(5.5)	(7.4)	(7.3)	(5.5)	(5.5)	(7.5)	(7.4)		
Polycentropus	0.5	0.4	37.5	-	-	1.1	-	-	-	41.6	20.9	365	This study
(87F)	(4.8)	(4.8)	(4.8)			(4.8)				(4.8)	(4.8)		
Rheotanytarsus	8.4	14.9	1.1	0.4	0.2	27.3	102.2	6.7	100.6	7.5	-	168	Berg and Hellenthal
(88F)	(13.8)	(15.1)	(12.1)	(12.1)	(12.1)	(10.6)	(10.7)	(9.4)	(13.2)	(12.1)			(1992)
Simuliidae	848.6	1921.0	591.6	87.7	37.2	414.3	370.5	53.7	158.3	187.6	295.4	365	Chapter III
(89F)	(5.5)	(6.4)	(6.1)	(5.4)	(5.3)	(5.4)	(4.7)	(4.7)	(5.6)	(5.8)	(4.9)		
Σ Filterers	**1102.6**	**2330.1**	**2791.2**	**828.2**	**370.8**	**1146.5**	**1460.9**	**89.5**	**299.9**	**451.3**	**604.7**		
Predators													
Ablabesmyia	1.2	2.8	3.4	3.7	26.2	29.5	3.7	-	-	0.7	2.6	80	Smock et al (1985)
(90P)	(20.1)	(20.1)	(20.1)	(20.1)	(20.1)	(22.3)	(19.3)			(20.1)	(20.1)		
Atherix	6.1	11.9	127.8	33.7	-	8.8	18.4	7.3	5.6	-	-	365	Lauzon and Harper
(91P)	(4.8)	(4.7)	(5.5)	(5.5)		(4.2)	(4.2)	(4.8)	(4.8)				(1993)

Table B.1. continued

Taxon	Cascade Brook US	Cascade Brook DS	Goosefare Brook US	Goosefare Brook DS	Goosefare Brook IN	Ward Brook US	Ward Brook DS	Branch Brook US	Branch Brook DS	Stevens Brook US	Stevens Brook DS	CPI	CPI reference
Predators, cont'd													
Brundiniella	0.01	0.2	58.3	11.4	3.2	0.2	-	1.0	1.1	-	0.2	336	Chapter III
(92P)	(4.6)	(4.6)	(4.6)	(5.1)	(4.9)	(4.6)		(6.1)	(4.3)		(4.6)		
Ceratopogon	4.7	3.5	5.8	5.4	-	-	1.3	-	-	17.4	7.2	304	This study
(93P)	(6.4)	(6.4)	(6.4)	(6.4)			(6.4)			(6.5)	(6.4)		
Chelifera	0.55	0.61	0.94	0.18	0.09	1.6	1.4	0.70	0.70	-	0.12	365	Chapter III
(94P)	(3.2)	(3.2)	(3.2)	(3.2)	(3.2)	(3.2)	(3.2)	(3.2)	(3.2)		(3.2)		
Chrysops	72.4	6.6	623.4	178.4	33.2	260.6	63.8	6.9	7.4	9.6	52.5	365	Chapter III
(95P)	(5.4)	(5.1)	(5.5)	(6.7)	(6.2)	(4.8)	(4.4)	(5.0)	(5.0)	(3.7)	(3.8)		
Cordulegaster	50.9	37.4	230.2	153.3	8.4	92.5	82.1	11.1	39.1	125.8	32.9	1140	Lughthart and Wallace
(96P)	(1.8)	(1.8)	(1.9)	(1.9)	(1.9)	(1.8)	(1.8)	(1.8)	(1.8)	(1.2)	(1.7)		(1992)
Dicranota	81.8	62.1	14.7	14.3	12.3	45.2	71.7	15.2	7.4	56.9	62.5	712	Chapter III
(97P)	(7.2)	(5.4)	(2.7)	(2.5)	(2.4)	(7.2)	(8.0)	(6.7)	(5.6)	(6.7)	(5.4)		
Haploperla	27.1	5.2	-	-	-	0.8	1.6	2.2	3.3	0.3	-	243	This study
(98P)	(7.3)	(5.9)				(7.1)	(7.1)	(7.1)	(7.1)	(7.1)			
Helobdella	11.2	6.1	-	0.6	-	-	0.2	-	-	1.1	7.1	365	This study
stagnalis (99P)	(4.0)	(4.5)		(4.4)			(4.4)			(4.4)	(4.4)		
Hemerodromia	0.08	0.2	1.4	1.7	1.8	2.2	4.0	0.3	1.3	0.2	0.4	365	Chapter III
(100P)	(3.7)	(3.7)	(3.7)	(3.7)	(3.7)	(3.7)	(3.8)	(3.7)	(3.7)	(3.7)	(3.7)		
Hexatoma	45.2	45.7	0.2	-	-	158.6	644.0	22.8	24.4	0.5	1.6	365	This study
(101P)	(5.9)	(5.4)	(4.5)			(5.5)	(5.7)	(4.6)	(5.1)	(4.5)	(4.5)		
Hydroporus	1.4	0.7	1.1	1.2	-	0.6	0.3	-	-	15.4	3.9	365	This study
(102P)	(4.3)	(4.3)	(4.3)	(4.3)		(4.3)	(4.3)			(4.6)	(3.9)		
Isoperla	4.7	10.0	-	-	-	7.4	22.7	29.8	161.6	-	6.9	365	This study
(103P)	(4.2)	(4.2)				(4.7)	(4.3)	(5.6)	(6.9)		(4.9)		
Labrundinia	0.03	0.02	2.9	-	-	1.2	1.3	-	-	0.01	0.2	167	This study
(104P)	(7.3)	(7.3)	(7.3)			(7.3)	(7.3)			(7.3)	(7.3)		
Lanthus	1.3	0.07	275.3	174.5	-	70.6	169.8	-	15.0	14.3	-	668	Huryn and Wallace
(105P)	(2.34)	(2.34)	(2.3)	(2.3)		(2.3)	(2.3)		(2.3)	(2.3)			(1987)
Limnophila	1.0	0.4	504.6	106.6	100.6	16.2	37.9	60.5	77.4	-	18.5	197	Chapter III
(106P)	(6.2)	(6.2)	(8.9)	(8.1)	(8.9)	(5.2)	(5.3)	(4.7)	(5.5)		(10.4)		
Macropelopia	-	-	23.5	20.1	1.6	-	-	-	-	-	-	365	Lindegaard and
(107P)			(4.8)	(4.8)	(4.8)								Mortensen (1988)
Meropelopia/	22.1	26.8	85.5	65.2	9.0	18.5	6.8	2.5	2.6	16.1	2.9	365	This study
Conchapelopia	(4.4)	(5.1)	(5.1)	(4.5)	(5.7)	(4.8)	(4.7)	(5.0)	(4.8)	(4.5)	(4.7)		
(108P)													

Table B.1. continued

Taxon	Cascade Brook		Goosefare Brook			Ward Brook		Branch Brook		Stevens Brook		CPI	CPI reference
	US	DS	US	DS	IN	US	DS	US	DS	US	DS		
Predators, cont'd													
Molophilus	2.3	0.4	166.8	4.5	-	-	5.0	4.1	1.2	28.1	32.1	243	This study
(109P)	(7.8)	(7.8)	(7.9)	(7.8)			(7.7)	(7.8)	(7.8)	(9.0)	(7.7)		
Natarsia	17.2	6.1	28.3	14.9	23.8	8.8	9.4	0.4	1.2	4.3	9.1	365	This study
(110P)	(5.3)	(5.0)	(4.5)	(4.8)	(5.7)	(5.9)	(5.6)	(5.5)	(5.5)	(5.5)	(6.3)		
Nigronia	167.9	131.8	-	-	-	15.5	35.4	-	-	43.6	0.1	730	This study
(111P)	(3.0)	(2.9)				(3.0)	(3.0)			(3.2)	(3.2)		
Ormosia	-	-	19.8	-	-	-	-	-	-	-	-	365	Chapter III
(112P)			(5.1)										
Palpomyia	32.9	38.6	168.6	116.7	25.3	18.6	75.3	4.4	2.6	42.9	74.8	183	Chapter III
(113P)	(9.0)	(7.6)	(8.2)	(9.9)	(9.8)	(8.7)	(9.4)	(9.3)	(9.3)	(11.0)	(10.8)		
Paradelphomyia	11.9	32.6	18.0	26.4	14.8	1.0	15.5	-	-	3.8	6.2	365	This study
(114P)	(4.4)	(5.6)	(4.4)	(4.4)	(4.4)	(4.4)	(4.4)			(4.4)	(4.4)		
Paranyctiophylax	10.9	19.9	-	-	-	18.4	1.4	-	-	-	-	183	This study
(115P)	(9.3)	(9.3)				(9.3)	(9.3)						
Pilaria	1.0	0.2	40.7	19.0	14.0	2.7	1.2	-	-	2.8	4.9	304	This study
(116P)	(6.2)	(6.2)	(6.4)	(6.1)	(6.2)	(6.2)	(6.2)			(6.2)	(6.2)		
Probezzia	4.8	1.3	186.4	57.2	6.0	57.5	33.2	0.6	0.2	1.1	4.1	365	Chapter III
(117P)	(4.8)	(4.8)	(4.2)	(4.2)	(4.2)	(5.0)	(4.4)	(4.4)	(4.4)	(3.9)	(3.9)		
Procladius	4.8	8.6	10.8	16.1	6.4	16.7	4.4	-	-	0.3	15.1	183	This study
(118P)	(12.0)	(11.1)	(13.1)	(10.6)	(11.8)	(8.2)	(7.1)			(7.0)	(7.3)		
Rhyacophila	72.6	115.5	-	-	0.2	1.9	3.5	21.6	10.6	143.2	70.0	336	This study
(119P)	(5.2)	(5.9)			(5.5)	(5.5)	(5.5)	(5.5)	(5.5)	(5.3)	(6.0)		
Sialis	29.0	37.1	41.7	49.5	17.1	7.3	0.9	-	0.07	0.9	1.7	730	Chapter III
(120P)	(3.1)	(2.9)	(2.1)	(2.8)	(2.4)	(2.7)	(2.7)		(2.7)	(2.7)	(2.7)		
Sphaeromias	0.2	1.0	8.1	1.1	-	1.1	0.9	-	-	8.9	36.0	183	This study
(121P)	(9.1)	(9.1)	(9.1)	(9.1)		(9.1)	(9.1)			(8.1)	(9.4)		
Trissopelopia	5.2	15.3	18.9	22.9	13.9	13.4	2.0	0.06	0.2	12.5	3.0	274	This study
(122P)	(6.0)	(7.2)	(7.8)	(7.9)	(8.4)	(7.1)	(7.1)	(7.0)	(7.0)	(6.7)	(6.5)		
Zavrelimyia	18.4	18.8	13.1	28.9	4.8	12.8	3.7	2.3	1.8	29.8	13.8	183	Chapter III
(123P)	(10.4)	(9.6)	(10.5)	(12.4)	(9.5)	(10.8)	(10.9)	(10.4)	(10.4)	(10.3)	(9.5)		
Σ Predators	**774.6**	**745.9**	**2981.1**	**1177.2**	**488.5**	**1672.3**	**1644.0**	**198.8**	**375.9**	**800.1**	**684.4**		
GRAND TOTAL	**10938.2**	**8747.5**	**14683.6**	**7743.2**	**4788.8**	**7568.4**	**8932.5**	**3454.1**	**3825.0**	**15274.9**	**13293.8**		
	(8.1)	**(8.0)**	**(7.6)**	**(6.9)**	**(7.4)**	**(6.1)**	**(7.5)**	**(7.0)**	**(7.3)**	**(8.9)**	**(9.0)**		

BIOGRAPHY OF THE AUTHOR

Thomas Woodcock was born in North York, Ontario, Canada on June 22, 1972. He was raised in Toronto and Brantford, Ontario and graduated from North Park Collegiate and Vocational School in Brantford in 1990. He attended the Ontario Agriculture College, University of Guelph and graduated in 1994 with a Bachelor of Science in Agriculture degree, with a major in Environmental Biology. After working for three years at several jobs relating to invertebrate ecology, he entered the Ecology and Environmental Sciences graduate program at the University of Maine in September 1997. Thomas is a candidate for the Doctor of Philosophy degree in Ecology and Environmental Sciences in August, 2002.