5.0.0. DISCUSSION

5.1.0. Forestry-associated changes to habitat features

5.1.1. Water quality

Temperature

The data demonstrate that effects on a stream's thermal regime brought about by forest harvesting can be reduced by leaving forested strips along streambanks. The PCA ordination of maximum and average temperatures indicates that stream #2, in a recently cut watershed with a wide buffer strip, had a similar thermal regime to those of the three reference streams (Forks, Sweeney, and Upper Vault). Their water temperatures never exceeded 17°C, and the daily range rarely exceeded 4°C. Where no riparian vegetation was left along the cutover streams, high maximum temperatures and large daily fluctuations were recorded. These effects were apparently rather long-lasting: streams in two of the 1970s cutovers reached the highest temperatures, while Cains, the watershed logged in the 1920s, had higher-than-expected maximum temperatures and daily temperature fluctuations. However, Cains may have been subject to other disturbances since logging, for example, agricultural uses, or flooding by beavers.

It is important to note that, even with buffer strips, the temperatures recorded in some streams were higher than expected when compared with the temperatures recorded in

Sweeney, Upper Vault and The Forks. For example, stream #45 had a 30-40-m-wide buffer strip along its sampling reach, and a variable-sized buffer strip (10-30-m-wide) upstream. Nevertheless, higher-than-expected maximum and average temperatures were recorded. Similarly, stream #25 was forested on the north side of the sampling reach, and had a 14-28-m protective strip along the south side. High water temperatures were also recorded on this stream. However, about 250 m above the sampling reach, the buffer strip disappeared, and the stream flowed unshaded through a large clearcut of low relief. Hewlett and Fortson (1982) also observed that deforestation in areas of gentle relief may elevate stream water temperatures, even with large riparian buffers. Sabean (1977), who measured stream temperatures in N.S., found that the re-entry of a stream into a canopied section resulted in a decrease in streamwater temperature, but at a slower rate than the initial increase when first exposed to direct solar radiation. He also observed that temperatures did not always return to their original levels.

Water Chemistry

Concentrations of nitrogen, potassium, and magnesium in streamwater were generally smallest in the reference streams, and greatest in the most recently cutover streams. Stream #45, cut five years before the study, and #7, most recently cut 4 years before, had 6-7 times greater N concentrations than the average of the reference streams. Also, the streams in the oldest clearcuts had slightly larger nutrient concentrations than those in the reference catchments, despite 15-20 years of regeneration. In a study of clearcutting in the Nashwaak watershed of west-central N.B., it was reported that higher than expected exports of K, Ca, Mg, and especially nitrate-N occurred for at least three years post-logging, with nitrate concentrations increasing from background levels of 0.1 mg/L to a maximum of 1.6 mg/L (Krause 1982). In this study, no immediate consequences of clearcutting were measured (i.e. within the first four years of harvesting), however elevated concentrations of dissolved substances in clearcut streams continued well beyond the time of cutting. Furthermore, the concentrations of streamwater N and K recorded in this study were probably smaller than they would have been at any other time of year, partly because nitrate concentrations increase during periods of high discharge, and partly because during the summer, biological activity reduces concentrations of nitrate and potassium in stream water (Johnson *et al.* 1969).

Stream #11 and Dustin Brook had similar water chemistry to that of the reference streams, as seen in the PCA ordination, while Cains fell between the oldest cutover streams and the other park streams. Thus, while Cains appears to be "leaky" compared with the other reference streams, #11 appears to have been well-protected by a buffer strip, while Dustin Brook remains an anomaly.

The longterm losses of nutrients from clearcut watersheds has various implications for site fertility. Losses of nitrate via leaching are accompanied by the loss of cations, including calcium, magnesium, and potassium, which are important as nutrients and in acid-neutralization capacity (Helyar 1976, cited by Patriquin *et al.* 1993).

Despite higher-than-expected losses of nitrates from the recently clearcut watersheds, no noticeable pattern in stream water pH was measured over the chronosequence of stands. This is in contrast to several other studies, which have documented either an increase in pH, due to elevated concentrations of Ca^{2+}, Mg^{2+}, K^{+} and Na^{+} (Eshner and Larmoyeux 1963), or a decrease in pH, due to increased rates of nitrification in the surrounding soils (Likens *et al.* 1970). In addition, various studies of conversion of wetlands, moorlands and native-forest to tree plantations have documented the gradual acidification of soils and streamwater through the uptake of base cations by vegetation (Collier *et al.* 1989; Harriman and Morrison 1982; Jenkins *et al.* 1990). The most recently cutover stream, #7, had higher pH (7.3-7.6) and larger Ca concentrations than other streams. This observation could be related to soils or bedrock of #7, or it could indicate that samples from other streams were collected too many years post-harvesting to show any substantial effects. This could have implications for the acidification of the clearcut watershed, as well as for future site fertility.

Sedimentation

Of the 6 streams with the highest rates of sedimentation, four flowed below logging roads (#7, #2, and #45, #40). The first three of these streams were relatively steep and recently cut-over (within 7 years of the study), and discharge on the last, #40, was observed to increase considerably during rainstorms (the culvert had been dislodged above the sampling reach). In Narrow Mountain Brook of the Nashwaak Experimental Watersheds, N.B., sediment loads rarely reached 5 mg/l before road construction, but frequently exceeded this concentration thereafter, reaching 250 mg/l in one branch stream (Krause 1982).

Three other of the study streams were located below logging roads - #41, #21 and #11. Only one of these, #41, had higher than average substrate deposition for the sixteen study streams, and it was located approximately 1 km below a washed out logging road. The road above the sampling reach of #21 was quite old, and was well-vegetated around the stream crossing. The road above the sampling reach of stream #11, however, was still eroding into the stream channel. In Narrows Mountain Brook of the Naskwaak

Experimental Watersheds, it was found that concentrations of suspended sediment were greatly reduced by a riparian strip (Krause 1982). This may have been the case for #21 and for #11, which was protected by a wide buffer strip along one side, and a forest on the other.

Sediment loads are also increased by high stream velocities (Ontario MNR 1988). Stream #25 drained a large, nine-year-old clearcut that was only partially revegetated. The three sediment pots in this stream could have been buried as an indirect result of higher stormflows, which, according to Smith *et al.* (1993) would have increased total boundary shear stress acting on grains in the channel, as well as destabilized debris dams. In turn, this would have led to shifts in debris location and the release and scour of stored sediment. Alternatively, the sediment pots in stream #25 may have been washed away by stormflows. This is unlikely, however, as the sediment pots in both stream #2 and the Forks stayed in position, and the high gradient of both these streams would have resulted in large peakflows.

Sedimentation was negligible for Sweeney, Upper Vault, and the Forks, and slightly higher for Cains. Sediment movements in watersheds of mature forest are minimized by smaller peakflows, stable debris dams, and stable stream banks (Bormann and Likens 1979). Cains may still be recovering from past logging activities or some other occurrence during which riparian vegetation was cut or otherwise disturbed. The resulting scarcity of large trees and snags has reduced the amount of large woody debris entering the stream channel, without which stable debris dams cannot form. Small quantities of sediment were collected in the sediment pots of stream #15 and Dustin Brook, despite flowing through highly disturbed watersheds. This may be due to several factors: first, both streams had large numbers of debris dams (full of sawn timbers), which reduce flow velocities and store sediments; and second, previous log-driving in Dustin Brook would have scoured the streambed of fines, such that there was still a small proportion of fines in the substrates (as indicated by the substrate core analysis).

5.1.2. Stream substrates

The results of the substrate core analysis suggest that clearcutting has had little measurable effect on the composition of stream sediments. This is in keeping with Duncan and Ward (1985), who noted that the composition of stream gravels, and the amount of fine sediments (<2 mm in size), are more closely correlated with the lithology and soils of the drainage basin and the specific climatic, vegetative, topographic, and hydrologic factors present, than with forest management activities.

On the other hand, it should be noted that the surface substrate estimates showed significant differences in surface fines and coarse gravels between the four reference and the 12 cutover streams. These results agree with Cederholm *et al.* (1981, as cited in Duncan and Ward 1985), who showed that the percentage of sediment <0.85 mm in spawning gravels increased in proportion to basin area affected by timber harvesting and roads. Similarly, Adams (1980, as cited in Duncan and Ward 1985) found that watershed hydrology, especially magnitude of peak flows, was of particular importance in determining the composition of streambed gravels. Though water yields were not measured in this study, it is well accepted that peakflows increase with clearcutting of most or all of a watershed (Hetherington 1986).

The proportions of surface fines and embeddedness were greatest for #21, #45, #41, and #15. The first three of these streams flowed under logging roads, and #15 appears to have been used as a skidder trail. Eaglin and Hubert (1993) measured the amount of surface fines and embeddedness in 28 stream reaches affected by clearcutting and logging roads in Wyoming, and found positive correlations with the extent to which roads crossed watercourses within a drainage, and with the proportion of the drainage that was logged. However, streams #2, #40, #7 and #11 also flowed below roads, but did not have high proportions of surface fines.

5.1.3. Channel features

Streambank cutting reduced shading and the long-term input of large woody debris (LWD) into the stream channel. We did not quantify LWD in stream channels, but we can infer the future situation from the nature of the riparian vegetation. The lack of snags and large trees along Cains, McGee, #15 and Haley, and stumps in the riparian zones of #11, #40, Dustin and parts of #7 suggest that these streams will experience long-term large woody debris impoverishment. The consequences of this are: a reduction in channel complexity and number and volume of pools, thereby decreasing current heterogeneity and increasing stream power and erosiveness; a decrease in the amount of cover for stream biota; and a diminished capacity to retain, store, and process organic and inorganic matter (Trotter 1990; Hicks *et al.* 1991; Ehrman and Lamberti 1992). Large woody debris in streams draining clearcuts is further reduced by rapid breakdown and by the destabilization and erosion of natural debris dams (Golladay *et al.* 1989). A study done in Alaska showed that LWD in stream channels would be reduced by 70% ninety years after streambank logging of an old-growth forest, and recovery to pre-cutting amounts would take more than 250 years (Murphy and Koski 1989).

Streambank logging and selective removal of large trees in the riparian area results in decreased pool depth and hydraulic variability, and increases the frequency of riffles and runs (Welch *et al.* 1977; Murgatroyd and Ternan

1983; Sedell *et al.* 1988; Trotter 1990). Small pieces of debris entering streams in the postcutting phase tend to be flushed from the watershed, and scour the stream bottom of sediment and debris. Sedell *et al.* (1988) maintain that natural accumulations of large woody debris (on the west coast) have been observed to deflect current laterally, causing lateral migration of the channel, and producing midchannel bars, secondary channels and braided reaches. In this study, pre-logging channel data is unavailable. However, the paucity of large trees and snags along several streams indicates that the morphology of these streams will have been affected by a lack of LWD.

Stream width and depth are also affected by other factors, such as sediment and water input (Sullivan *et al.* 1987), mechanical disturbance, and successional vegetation. Alders that colonize disturbed riparian areas have shallow root systems, giving them little resistance to undercutting (Sedell *et al* 1988). Dustin Brook, for example, was bordered by alders, and was also the widest stream measured. Disturbance of stream banks by machinery may also widen stream channels, as was the case with the trail crossing below the sampling reach of Sweeney Brook, which reached 8.1 m in width at an unbridged crossing.

5.1.4. Riparian Vegetation

The density of snags and shrub-sized species in riparian areas provided an indication of disturbance history, as well as an indication of future ecosystem health. The absence of large trees and snags in a riparian forest indicates some form of disturbance: streambank or selective logging in the riparian zone, agricultural use, disease, windthrow, or flooding. The streamside forests of Cains and Dustin had small densities of large trees and snags, substantiating evidence of past disturbance. The high densities of shrubs along these and other study streams without wide buffer strips (McGee, #15, #7, Haley) showed that shrub-sized species, particularly *Alnus rugosa*, predominated in disturbed areas where snag density was small. This shift from mostly long-lived, large-sized canopy trees to small-stemmed, low-canopy, fast-growing shrub species can have a significant influence on the stream environment. The ecological functions of aquatic macro-invertebrates in headwater streams are strongly dependent on the type of energy inputs available (Stout *et al.* 1993). Initially, clearcutting riparian forests reduces the volume of leaf litter reaching streams. Rapid regrowth of early successional herbs, shrubs and trees allows for the recovery of inputs, but of a different quality. For example, leaves from many early successional forest trees are processed relatively rapidly and inefficiently, while those from mature forests are processed slowly or at moderate rates (Stout *et al.* 1993). Where coniferous plantations replace mixed-forests, the stream would receive fewer litterfall inputs, with a smaller seasonal peak in the fall (Webster and Patten 1979). Following perturbations such as clearcutting, complete recovery of the stream ecosystem is limited by the recovery rate of allochthonous inputs.

5.1.5. Overall patterns in habitat data

One important finding in the principal components analysis of a reduced set of physico-chemical factors was that the three reference streams, Sweeney, Forks, and Upper Vault, were closely associated with respect to the measured environmental variables. Cains differed from the other reference streams in its associations with chloride, sodium, moss cover, canopy cover, snag density, maximum August temperature, tree diversity, and cobble. According to the analysis, Cains was more like the older cutover streams than the other reference streams, and appeared to be recovering from some previous disturbance(s). Biotic regulation of major nutrient losses, sedimentation, and bedload movement had been restored in the Cains watershed, but more time will pass before large woody debris input, moss cover, canopy cover, riparian tree diversity, and channel and current heterogeneity reach pre-disturbance levels.

In retrospect, Cains was not a good choice as a reference stream; however, it was not known initially that Cains had been cut in the 1920s, or that it could have been an old pasture, or the site of a beaver dam. Similarly, the history of logdrives and cutting in the Dustin Brook catchment was not known before selection of this stream. It appears that these past perturbations may have confounded some of the results of this study, such that both streams behaved more like streams draining older 1970s clearcuts than the more recently cutover or older, reference streams. On the other hand, inclusion of these watersheds in this study has produced some potentially interesting insights into the longer-term effects of logging.

Another important finding in the principal components analysis was the clumping of the five most recently cutover streams and the three reference streams according to factors 2 and 3. This would imply that recently cutover streams were fairly well protected by buffer strips. Nevertheless, they differed with respect to nutrients, sedimentation and bedrock. Of these five streams, #11 appears to be most closely associated with the three park streams, possibly because only 65% of #11's watershed was cut, and one side of the sampling reach was left forested. We know from other studies that the impacts of clearcutting, such as increased discharge and sedimentation, increase with the proportion of the watershed that is logged and the extent to which roads cross watercourses (Eshner and Larmoyeux 1963; Rich and Gottfried 1976; Growns and Davis 1991; Eaglin and Hubert 1993).

5.2.0. Implications for fish habitat

Brook trout (*Salvelinus fontinalis*) are common throughout the freshwaters of Fundy National Park and the surrounding area (Woodley 1985). Brook trout abundance was not measured in this study, but according to Raleigh (1982) and Carlson *et al.* (1990), it is possible to utilize the measured physical and chemical variables to make inferences about the suitability of streams as trout habitat (Raleigh 1982; Carlson *et al.* 1990). Trout were observed in Cains, McGee, #41, #40, #21, #45, #25, and Haley. Large, impassable debris dams of logging slash may have prevented the movement of brook trout into the sampling reaches of #7, #15, and Dustin Brook. Most trout were observed in pools, deep runs, or below undercut banks.

Optimal brook trout habitat is characterised by clear, cold spring-fed water, silt-free rocky substrates, a 1:1 pool to riffle ratio, areas of slow deep water, well-vegetated streambanks, abundant instream cover, and stable water flow, temperature regimes, and streambanks (Raleigh 1982). According to Raleigh (1982), warm water temperatures are the single most important factor limiting the distribution and production of brook trout. The temperatures recorded on #15, #25, and McGee reached lethal levels for brook trout fry and adults (>23°C), while the large fluctuations and maximum temperatures observed in #41, #40, and #10 were sufficient to cause physiological stress (van Groenewoud 1977; Lynch *et al.* 1984). Nevertheless, brook trout were observed in four of these six streams: #41, #40, #25 and McGee. This is probably because (1) the maximum temperatures recorded were short-lived, and thus tolerable, and (2) refuge could be sought in cooler places. It is possible that higher-than-average temperatures recorded on cutover watersheds, in combination with nutrient enrichment, may have increased primary productivity, thereby increasing insect and trout production (Englert *et al.* 1982).

The dissolved oxygen concentrations measured in September, 1993, would not cause immediate injury or mortality to most stream organisms, but long-term exposure to the lowest observed O_2 concentrations (7.7 and 8.2 mg/l) would have been harmful to brook trout. Optimum oxygen concentrations for brook trout are > 7 mg/l at temperatures < 15°C, and > 9 mg/l at temperatures > 15°C (Raleigh 1982). The swimming performance and growth rates of salmonids are adversely affected as O_2 falls below these optimum concentrations. There were hot days in July and August when O_2 concentrations would have been considerably lower than those measured in September. Furthermore, the summer of 1993 was abnormally cool and wet, which suggests that dissolved oxygen concentrations were lower than those typically recorded.

Large woody debris plays an important role in creating and maintaining water depth and cover, both of which are essential components of good salmonid habitat. Instream logs produce a diversity of hydraulic gradients; create large, deep pools with ample cover and low velocity, enabling fish to hold their position against the current; and provide cover in the form of overhanging vegetation, submerged logs, stumps, roots, water depth, and undercut banks (Sedell *et al.* 1988; Hicks *et al.* 1991). Removal of LWD decreases the number and size of pools, and is often linked to a decrease in abundance of salmonids (Sedell *et al.* 1988). The absence of buffer strips along all or part of #15, McGee, #25, and #7, and of snags and large trees along Cains and Dustin indicates that these streams will have little natural input of LWD for decades to come.

Trout habitat quality is related to annual flow regime. Clearcutting of a watershed increases discharge during the plant growing season, which can result in greater baseflows during the critical summer low-flow period. Alternatively, the higher peak flows may destabilize spawning gravels, and enhance scouring, erosion and sedimentation (Reiser and Bjornn 1979; Englert *et al.* 1982). Higher rates of sedimentation and higher proportions of surface bedrock were measured in the more recently cutover streams. Brook trout are sensitive to both suspended and deposited enhance sediments. High turbidities may cause direct injury by coating gills - impairing water circulation and respiration, as well as indirect injury, by reducing visibility, thereby impairing the trout's ability to locate food (Raleigh 1982). Silt can also smother and suffocate eggs and alevins buried in stream gravels, and reduce the productivity of invertebrates (Cordone and Kelley 1961). Spawning fish tend to avoid silty areas, unless upwelling ground water is present (Meehan and Bjornn 1991). Elevated rates of sedimentation were observed in some cutover streams. It is possible that all the cutover streams had elevated sediment loads at one time or another, but have recovered since the time of cutting.

5.3.0. Effects of forestry activities on invertebrate taxa

Oligochaeta

The majority of oligochaetes are adapted to living in sediments ranging from sand to mud (Brinkhurst and Gelder 1991). In this study, we found the greatest numbers of oligochaetes in the rockballs of stream #21, #45, #2, and Haley. The latter 3 had high to medium rates of sedimentation and bedload movement, while #21 had a high percentage of streambed fines. From Figure 40b we see that, in this study, oligochaetes were closely associated with sedimentation, as well as with the more recently cutover streams. The greater abundance of oligochaetes colonizing rockballs in the more recently cutover streams agrees with the research of Cordone and Kelly (1961), who found that a change in the type of invertebrate species occurs with deposition of sediment, such that sediment-loving, burrowing organisms become more prevalent.

Chironomidae

Chironomids are the largest family of aquatic insects, often occurring in high densities and diversity, and accounting for at least 50% of the total macroinvertebrate species diversity in streams (Coffman and Ferrington 1984). Their life cycles and feeding habits vary widely (Hilsenhoff 1991): most chironomids are herbivores or detritivores, grazing on fine particles on and in the substratum, or filtering food from the water column. Chironomids have been found in a great range of conditions, including extremes of temperature, dissolved oxygen, pH, salinity, velocity, depth, and productivity. They also have short generation times and rapid colonization rates, enabling them to cope with fluctuating environments, and to build up large populations opportunistically (Newbold *et al.* 1980).

Because numerous studies have shown increases in chironomid abundance with disturbance, it might be expected that chironomids would constitute a relatively large proportion of the post-disturbance stream fauna. Sprules (1947, cited in Hynes 1970) found that the deposition of sandy silt reduced the total numbers of emerging insects, but increased the proportion of emerging chironomids. In

British Columbia, Culp and Davies (1982) observed that elevated inputs of alder detritus in the post-logging phase increased the biomass and density of Chironomidae and the mayfly *Baetis*. Similarly, both Newbold *et al.* (1980), and Noel *et al.* (1986) reported higher densities of total fauna, in particular Chironomidae and *Baetis*, in streams running through cutovers.

In this study chironomids numerically dominated most samples, but many more individuals were found in streams draining reference and older clearcuts than in streams draining more recent cuts. This may have partially been a consequence of the mesh size used to rinse invertebrates in the laboratory: tiny individuals of the subfamily Chironominae, known to tolerate warmer waters and low oxygen concentrations, could have slipped through the 300 µm mesh. Alternatively, habitat heterogeneity in the streams draining recent clearcuts could have been reduced by the deposition of fines and by scouring action, such that chironomids had fewer refuges and were more susceptible to predation (Wilzbach *et al.* 1986). Many plecopteran species, for example, are predatory, and plecoptera were more abundant in the rockballs placed in recently cutover streams. Walde and Davies (1984) showed that plecopteran predators can reduce total prey biomass, mean prey size, and the density of invertebrate populations. Alternatively, as colonists of wood, chironomids may have been affected by the quantity of woody debris in stream channels (Golloday and Webster 1988). Woody debris was not, however, quantified in this study.

Plecoptera

Plecoptera, or stoneflies, are associated with clean, cool running waters (Harper and Stewart 1984). They lack extensive gills and are generally intolerant of low dissolved oxygen concentrations. Most species are univoltine or semivoltine, and are thus unable to respond quickly to disturbance. Plecoptera are usually shredders or predators, feeding on leaf detritus or smaller insects.

In this study, Plecoptera displayed a smaller abundance in the rockballs in older stands. This might suggest that plecopteran species found in rockballs in this study are associated with conditions typical of disturbed habitats, such as bedrock, sedimentation, N and Mg concentrations, surface fines, and high maximum summer temperatures, than with conditions typical of the reference streams, such as high moss cover, Cl, and snag density. Wilzbach *et al.* (1986) found that high habitat complexity increased prey refuges, and in turn, decreased predator abundance. This would suggest that the higher number of Plecoptera in the streams in recent cutovers may reflect greater hunting success, which is a consequence of lower habitat complexity (such as high rates of sedimentation). It is unlikely that the smaller number of Plecoptera in the reference streams was a consequence of litter inputs, because the vegetation along reference streams was similar to the vegetation along the more recently cutover streams, as indicated by the principal components analysis of vegetation data.

Nymphomyiidae

Palaeodipteron walkeri is the only species of the rather primitive and rare Nymphomyiidae family found in the study region (Borror *et al.* 1989). The larvae feed on diatoms and algae in pebble and moss habitats of small, cold, rapidly flowing streams (Back and Wood 1979; Teskey 1984; Hilsenhoff 1991). Large numbers of *P. walkeri* are found as far north as the middle subarctic zone of Quebec, where average annual air temperatures are -3.7°C (Back and Wood 1979). In this study, no Nymphomyiidae were collected in rockballs in the seven most recently cutover streams, while a few were collected from each of the reference streams. The canonical correspondence analysis suggests a strong association between Nymphomyiidae and the reference streams; as well as a positive association between Nymphomyiidae and moss cover, snag density, stream width, and chloride concentrations; and a negative association with bedrock, sedimentation, surface fines, Mg and N concentrations, and high temperatures. *P. walkeri* did not occur in streams with measurable amounts of sedimentation. However, the greatest number of individuals was found in

#15, which was slow-moving and reached some of the highest temperatures recorded.

Thus, the small, delicate Nymphomyiidae may not be as sensitive to warm waters as the literature suggests. These insects may, however, be quite sensitive to some habitat changes associated with clearcutting. Further study may demonstrate that they could be used as an indicator of ecological integrity of streams.

Elmidae

Elmidae ("riffle beetles") usually live in oxygen-rich waters, and are typical inhabitants of the swifter portions of streams (White *et al.* 1984; Hilsenhoff 1991). Elmidae are semi-voltine, and feed on algae, decaying wood and detritus. In this study, Elmidae most abundantly colonized rockballs in older cuts, and least abundantly in recent cutovers and reference streams. The older cutover streams differed from the other streams with respect to chloride, sodium, moss cover, canopy cover, snag density and maximum August temperature. It is possible that the lower canopy closure and higher temperatures measured in these streams resulted in higher primary productivity, allowing a greater abundance of algae-eating Elmidae (Gurtz and Wallace 1984). Alternatively, Elmids in headwater streams are most commonly found clinging to moss on rocks, and with an abundance of moss in streams draining recent clearcuts as well as reference stands in this study, these insects are unlikely colonizers of gravel-filled rockballs (D. Giberson, pers. comm. 1995).

Simuliidae

Simuliidae are found in swift currents, adhering to solid surfaces, straining diatoms and other microscopic food particles from the water (Peterson 1984). Many species have short generation times, are highly opportunistic, and rapidly colonize disturbed areas. As filter-feeders, blackflies are moderately tolerant of sedimentation, particularly when the sediment has a large proportion of organics. Too much sediment, however, can have a smothering effect on blackflies (D. Giberson, pers. comm. 1995). In this study, streams with the largest proportions of surface fines and the highest rates of sedimentation did not have a smaller abundance of simuliids. In Czechoslovakia, simuliid larvae developed more rapidly in areas where streams received direct sunlight (Olejnicek 1986). This was thought to be a response to higher temperatures and the more rapid development of microorganisms suitable as food for simuliid larvae. In this study, however, no evidence of greater simuliid densities was found in the warmer, exposed reaches of the study streams. It is possible that rockballs were unsuitable for sampling blackflies, due to their contagious distribution of these insects.

5.3.1. Overall trends

There were fairly distinct differences between the invertebrate communities colonizing rockballs in the reference and older cutover streams, and those of the more recently cutover streams. Stream #11 and Dustin Brook were, however, exceptions. Stream #11 was most recently clearcut in 1986, and Dustin Brook in 1983. The invertebrate communities of both streams were more like the reference and older cutover streams than the more recently cutover streams. For #11, two partial cuts over several years may have resulted in a less-severe disturbance than would have occurred with a faster clearcutting of the watershed. Alternatively, both Dustin Brook and stream #11 had relatively high concentrations of organic carbon in streambed substrates. The larger-than-average amounts of detritus in these streams may have offset some effects of clearcutting.

This distinction between the reference and older cuts, and the more recent cuts was apparent in the results of the principal components analysis, in which the sites were arranged on the basis of physical and chemical variables alone. These two groupings differed with respect to surface bedrock, sedimentation, nitrogen, magnesium, and stand age. It would appear that these variables play a significant role in distinguishing the invertebrate communities. However, according to the canonical correspondence analysis, *only one* *variable* - stand age, had a significant influence over the invertebrate communities in this study. Thus *none* of the measured physical or chemical variables were able to explain the patterns in invertebrate abundance over the chrono-sequence of cutover and reference streams.

A common dispute among stream ecologists is whether streams are physically- or biologically-controlled environments. Some would argue that abiotic factors such as temperature, water chemistry, substrate, and current velocity are of far greater importance to the stream community than biotic factors, such as food availability, competition, and predation (Hart 1983). In this study we did not record biological characteristics such as algal standing crop, large woody debris, detritus collected in rockballs, abundance of brook trout and predatory insects, or competition amongst aquatic invertebrates, nor did we measure current velocity or discharge. Perhaps one or more of these unmeasured factors had a strong influence on the invertebrate assemblages found in this study. Among the variables that were measured, however, stand age was paramount in explaining the variation in the invertebrate data.

5.4.0. Problems with methodology

The device used in this study to sample invertebrates undoubtedly had a strong influence on the results. Minshall and Minshall (1977, cited in Silsbee and Larson 1983) found significantly larger numbers of organisms colonizing trays of introduced substrate than in natural stream substrate, as well as large differences in species composition between introduced and natural substrate. While the samples collected in their study may not have accurately described the local fauna of the streams, they found that the differences between streams were consistent between sampling methods, and probably represented real differences in the benthic communities. Coleman and Hynes (1970) found many times more animals in fully colonized samplers extending 30 cm into the streambed, than in Surber samples collected at the substrate surface. This would further suggest that the invertebrate assemblages sampled in this study do not accurately represent the complete invertebrate community of the study streams, although they do provide a repeatable, standardized indicator of colonization under differing environmental conditions and a constant substrate.

Other problems with the invertebrate sampling procedure include: sampling of riffle habitats only, sampling for one year only, and the use of 300 µm mesh, such that smaller-sized organisms would have escaped.

5.5.0. Conclusions

5.5.1. Effects of clearcutting and road-building on stream

ecosystems in the Fundy area

Biotic regulation of nutrient exports appeared to recover with time since cutting, with the smallest concentrations of dissolved substances recorded, in general, in the reference streams, and the greatest concentrations in the streams draining the most recent clearcuts. Stream #45, draining a five-year-old clearcut, and #7, most recently 30% cut 4 years before, had 6-7 times greater N concentrations than the average of the references. Therefore, elevated concentrations of dissolved substances in streams draining clearcuts continued for at least five years after cutting.

Continued maintenance of logging roads, road washouts, and peakflow events complicated monitoring of the recovery of sediment exports with time since clearcutting. Some of the lowest rates of sedimentation were recorded in the references Sweeney, Upper Vault, and the Forks, as well as in Dustin, draining a 1983 clearcut, and stream #15, draining a 1979 clearcut. However, one of the highest rates of sedimentation was measured in the sampling reach of stream #40, draining a 1973 clearcut, but located directly below a washed out logging road.

The thermal regimes of streams draining recent clearcuts were more like the thermal regimes of the reference streams than those of streams draining 1970s clearcuts. This is because legislation introduced in the early 1980s required that streams be protected from clearcutting by buffer strips. Before this, buffer strips were rarely left along streams, with the consequence that, in 1993, streams like #40, #15 and McGee still had higher maximum temperatures and greater diurnal fluctuations than the streams clearcut in the 1980s. Streams draining partially cutover watersheds, or with wide buffer strips along their length, had similar thermal regimes to the reference watersheds (especially stream #2).

The presence of buffer strips along streams draining recent clearcuts also ensured the rapid recovery of allochthonous inputs of biomass. Principal components analysis demonstrated that the vegetation along the three reference streams, Forks, Sweeney and Upper Vault, was most similar to the vegetation along the streams draining more recent clearcuts with relatively wide buffer strips (#45, #25, #11, #21, #2). These 8 streams were characterised by low shrub densities, high in-stream moss cover, and higher-than-average tree and snag densities. By contrast, vegetation along streams cutover in the 1970s and early 1980s, including stream #7 (cut in 1982, 1986 and 1989) and the reference, Cains (watershed cut in the 1920s and potentially disturbed since then), indicated that these streams will experience long-term impoverishment of large-dimension woody debris. Shrub density was high, and the most common shrub-sized species was *Alnus rugosa* or, occasionally, *Abies balsamea*.