AN EXPERIMENTAL EVALUATION OF THE EFFECT OF DAMS ON DOWNSTREAM INVERTEBRATES

by

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An Experimental Evaluation of the Effect of Dams on Downstream Invertebrates

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ABSTRACT

This study was designed to determine if a 6-week change in temperature would influence the growth and development of the caddisfly Clistoronia magnifica (Banks). I hypothesized that the effect would depend on when, in terms of life cycle stages, the larvae were exposed to a change in temperature and the direction of the change from the natural temperature regime. Control larvae were reared at 13.5C for their entire larval history. Test larvae were reared at either 9.0 or 21.0C for 6 weeks beginning when larvae were in first, third, fourth, or fifth instar.

Larvae exposed to higher than normal field temperatures had a low survival rate and moulted to subsequent instars later in some cases. Small prepupae were found when the increase in temperature occurred during the final (fifth) instar. Larvae exposed to lower than normal temperatures during the first 6 weeks after hatching from eggs had a shorter larval history from first instar to prepupa than larvae reared continuously at 13.5C. Differences are attributed to shifts from the average field temperature and hence the optimum temperature for development in each instar. A stream temperature management plan proposed by the Aluminum Company of Canada (ALCAN) for the Nechako River, north central British Columbia, was used to discuss the implications of these findings.

Short-term changes in temperature of the magnitude suggested by ALCAN could have an impact on the invertebrate community and therefore on resident fish populations in the upper Nechako River. Invertebrates could find the new temperature regime lethal or may be unable to compensate for a temporary impedence or acceleration in normal development and be exposed to adverse environmental conditions. Since invertebrates are the primary food source for many stream dwelling salmonids their species and abundance should be monitored below impoundments where temperature regulation plans are being employed.

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I. INTRODUCTION

The consequences of stream impoundments, or barriers to natural flow, on the downstream environment have not been given adequate consideration in environmental impact assessments. Recent impact assessments for hydro electric projects in British Columbia have acknowledged the potential impacts downstream but have yet to address them adequately (e.g. Table 1.1). In reviewing biophysical impact statements concerning major stream impoundments in western Canada, Geen (1974) found that predictions on the effects of stream regulation on downstream ecology are often speculative. One possible reason for past neglect of downstream impacts is lack of information.

When studies on the downstream environment are included in impact assessments they focus on the direct impacts on fish populations. However, changes in stream morphology, chemistry, temperature, and flow not only affect the fish, but also the community structure and abundance of invertebrates. Studies on stream invertebrates are important since they are the primary food source for stream-dwelling salmonids and their density can limit the production of fish populations (Allen 1969).

Field studies generally show low invertebrate diversity below impoundments (Spence and Hynes 1971; Lehmkuhl 1972; Ward 1974; Armitage 1978; Ward and Stanford 1979b; Perry and Huston

Table 1.1 A summary of recent environmental impact assessments prepared for hydro electric projects in British Columbia and their consideration of downstream impacts. Particular reference is made to temperature modification and stream invertebrates.

Evaluative Criteria	1 Revelstoke Dam (1976)	2 Kootenay Diversion (1978)	3 Stikine-Iskut (1980)
downstream habitat considered in baseline studies and in impact assessments	planned for the area upstream of the proposed dam, however, fisheries and wildlife studies were modified to assess "population losses or gains. . . both upstream and downstream of the project" "project related impacts will be both up and downstream of the project" (e.g. reservoir flooding and operation of the reservoir)	inventories of fish and fish food organisms in the Columbia River, the receiving stream, but not in the Kootenay River downstream of the diversion concerned with decreased flows downstream of the diversion and the reduced dilution capacity for pollutants	fish populations studied in rivers both upstream and downstream of proposed impoundment a brief literature review of available information on the downstream effects of dams on fish populations
explicit reference to downstream water temperature	change predicted due to hypolimnion draw off also summer spillway discharge may increase water temperatures	present temperature of the river below the proposed diversion was studied, however, impacts are not considered quantitatively "water temperature downstream of diversion structure may be slightly higher"	change predicted due to hypolimnetic draw-down

continued.....

Table 1.1 continued.

estimates of impact on downstream fish and invertebrate populations	"productivity" downstream of the proposed dam is considered, however "impacts on fish habitat will occur primarily upstream" "presently available data do not allow more precise predictions of the change in productivity due to altered temperature"	change in thermal regime below the diversion may increase periphyton and influence river benthos, however, primary concern is pollution	literature review primarily concerned with discharge and its affect on benthos chinook salmon population may be adversely affected by a reduction in food, however, no benthic sampling is reported
suggestions for mitigation of these impacts	"study future reservoir behaviour to provide data for optimum reservoir fish populations and minimum downstream impacts" variable powerhouse intakes suggested	— — —	"manipulate water releases to accomodate the needs of fishes", implicitly includes food organisms

1. Environmental Research Consultants 1976.

2. Entech Environmental Consultants Ltd. 1978.

3. McCart Biological Consultants Ltd. 1980.

1983), but show differing effects on biomass. Some researchers have found lower (Armitage 1978; Stanford and Hauer 1978 as cited in Ward and Stanford 1979b) while others have found higher (Ward 1974; Ward and Stanford 1979b; Perry and Huston 1983) invertebrate biomass below impoundments. In some cases these observed differences in diversity and biomass between natural streams and those downstream of an impoundment have been attributed to changes in seasonal temperature patterns caused by impoundment (Lehmkuhl 1972; Ward 1974; Stanford and Hauer 1978 as cited in Ward and Stanford 1979b; Ward and Stanford 1979b).

The temperature regime in regulated rivers downstream from dams (Ward and Stanford 1984) can be modified by impoundment. The extent of modification depends on reservoir characteristics such as the level from which water is drawn, thermal stratification, and retention time; and such operational procedures as the amount of water released (Hubbs 1972).

Reduced stream flows caused by impoundment can result in warmer than normal water temperatures in residual flows in regulated rivers during the summer months because small volumes of water are easily influenced by meteorological conditions (Ward and Stanford 1979). Operating agencies can regulate the downstream temperature to aid salmonids that sometimes find these warm temperatures lethal (IPSFC 1983). If they do, stream temperature is generally regulated for a short time, perhaps one

or two months, during the migration or reproduction period of the fish species.

Temperature is one of the most important factors controlling the structure of the benthic community (Ward and Stanford 1979; Brooker 1981) as it has a strong influence on the distribution, growth, and development of stream invertebrates (Macan 1963; Ward and Stanford 1982). Benthic invertebrates generally lack well-developed temperature compensation mechanisms (Sweeney 1978; Ward and Stanford 1982) therefore, seasonal temperature cycles exert a major influence on their life history. Nonoptimal temperatures may affect their fecundity, egg incubation period, hatching, growth, longevity, and competitive ability (Ward and Stanford 1979).

There is a lack of information on the sensitivity of stream benthos to short-term changes in temperature. Studies have generally looked at invertebrate community structure downstream of impoundments with respect to annual changes in temperature. The effect of short-term changes may be equal to or different from that previously observed because benthic invertebrates may be tolerant of a change in temperature during one stage in their life history, but sensitive to the same change in others (Lehmkuhl 1974). Therefore, these short-term changes in temperature could contribute to the extinction, replacement, or enhancement of some benthic species.

The purpose of this study was:

1. to investigate the magnitude and direction of impact that a temporary change in water temperature has on the growth and development of a caddisfly, Clistoronia magnifica (Banks) when changes in temperature occur during different life stages; and

2. to discuss the implications of managing temperature downstream of impoundments with reference to experimental results.

The concern for temperature management downstream of the Aluminum Company of Canada's (ALCAN) proposed hydroelectric development provided the impetus for this study.

The government of British Columbia granted ALCAN a conditional water licence in December 1949 to store and divert waters from portions of the Nechako and Nanika River watersheds. Impoundment of the Nechako River, completed in 1957, generates electricity at Kemano which is then transmitted to Kitimat for aluminum smelting (Figure 1.1). ALCAN was not compelled to provide facilities for flow or temperature regulation in the Nechako River as requested by the Department of Fisheries and Oceans (DFO) (Canada 1984) and the International Pacific Salmon

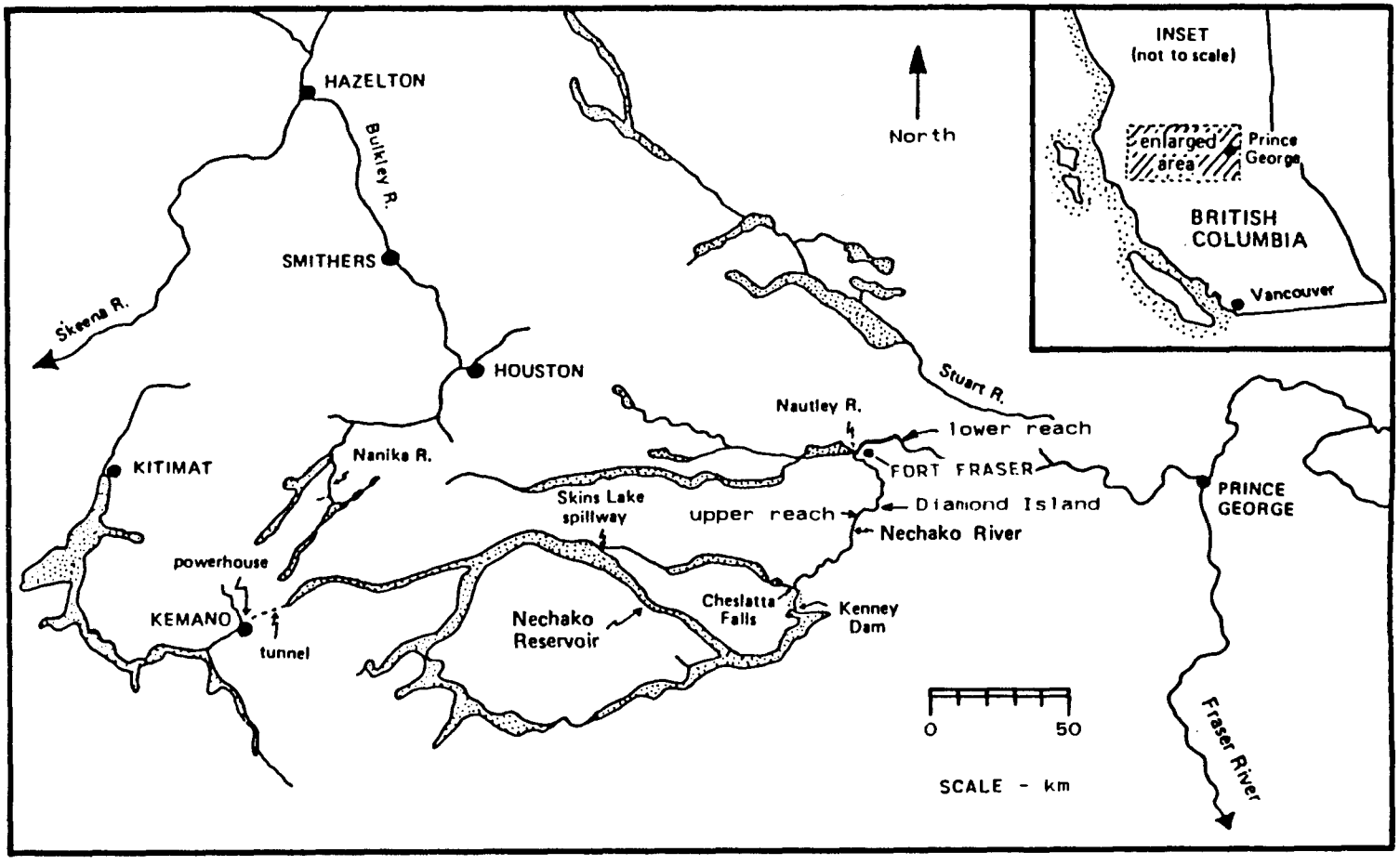

Figure 1.1 Map of Nechako River Area

(adapted from Russell et al. 1983. Figure 1.)

Fisheries Commission (IPSFC 1983).

In 1978 ALCAN began investigating the possiblity of increasing its energy generating capacity by diverting more water from the Nechako River and supplementing the diversion by adding water from Nanika Lake. With the completion of this phase, reduced downstream flows could create high summer water temperatures in the lower Nechako River between Fort Fraser and Prince George (Figure 1.1) and endanger spawning Stuart and Nautley River sockeye salmon (IPSFC 1983). In an attempt to mitigate this potential impact ALCAN has proposed a temperature management plan.

ALCAN proposes to keep the water temperature in the lower Nechako River within the limits acceptable for migrating sockeye salmon by mixing cold water released at Kenney Dam with warmer surface water released at Chestlatta Falls. This plan involves the discharge of water, varying from 31 to 170 cms, at the Nechako-Cheslatta confluence for a 6-week period during July and August. Increased cooling flows of 10C would be provided when predicted temperatures in the lower Nechako River would otherwise rise above 19C (IPSFC 1983). It may be difficult to attain desired temperatures in the lower Nechako through reservoir release strategies because of the distance between the source of regulation and the management area, the lower Nechako River, (between 65 and 140km) (see Larson 1984, 1985). However,

assuming this management strategy is effective, temperatures in the lower Nechako River would generally remain below 20C, the maximum average pre-diversion (1952) temperature for July and August (Envirocon 1981). However, this plan would reduce temperatures in the upper portion of the Nechako River between July and August by as much as 8C (Figure 1.2).

Some chinook salmon use the upper Nechako River for spawning and rearing. An estimated 35% of the chinook salmon fry migrate downstream past Diamond Island (Figure 1.1) by mid July, but an unquantified portion of the chinook salmon population remain in the upper Nechako River during their first year (Russell et al. 1983; Canada 1984). In addition small resident populations of Rainbow trout and Dolly Varden char are concentrated in the upper portion of the Nechako River (Envirocon 1981). A decrease in temperature during July and August may directly affect these fish through changes in growth rates or indirectly affect them by influencing the availability of food organisms. Changes in invertebrate species and density as a result of the proposed temperature managment plan could affect the quality and quantity of food available to resident fish in the upper Nechako River.

To illustrate the need for evaluation of secondary impacts of the proposed regime the effects of a short-term change in temperature on the growth and development of a benthic

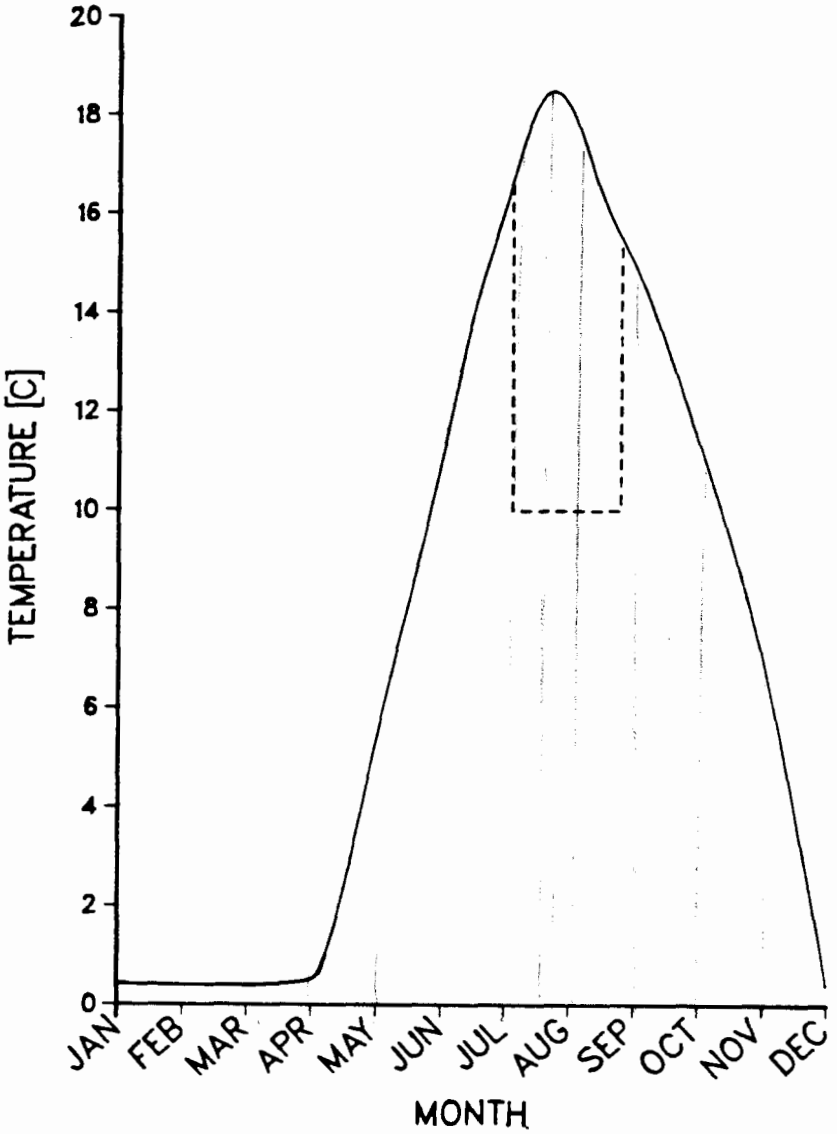

Figure 1.2 The average temperature regime for the upper Nechako River (——) and the probable temperature regime after the implementation of the Aluminum Company of Canada's proposed temperature management plan (- - - -).
(adapted from Envirocon, 1981. Vol 5. Figure 2).

invertebrate were investigated as a possible index of the effects on invertebrates generally. This paper discusses the implications of temperature management downstream of impoundments with respect to the experimental results presented in this report.

II. MATERIALS AND PROCEDURE

A laboratory experiment was designed to investigate the effect of a 6-week change in water temperature on the growth and development of a benthic invertebrate.

The Test Species and Its Life History

When taxa are partitioned on the basis of feeding habits shredders and collectors are found to dominate most forested headwater streams (Anderson and Cummins 1979). Limnephilinae, a subfamily of Limnephilidae, one of the largest and most widely distributed families of Trichoptera (Wiggins 1974), has representatives in all types of lentic (lake) and lotic (stream) systems (Wiggins 1977). Lotic limnephilid shredders are common in upstream areas of western montane regions (Wiggins and Mackay 1978).

The limnephilid Clistoronia magnifica (Banks), a lentic species, was chosen for this experiment because its taxonomy and feeding habits are similar to those of many lotic montane species (Anderson and Cummins 1979). In addition, it is common in the lower mainland (Winterbourn 1971) and can be reared easily (Anderson 1978).

Clistoronia magnifica is common in mountainous regions of

Oregon, Washington, and British Columbia (Anderson 1978). Larvae construct a portable case of sand, wood, plant material, and silk secretions shortly after hatching and continue to add to this case or modify it during each instar.

In a study in Marion Lake, British Columbia, Winterbourn (1971) found C. magnifica egg masses attached to the undersurfaces of lily pads (Nuphar polysepalum), on leaves of pond weed (Potamogeton natans), and on submerged logs during August and September. Larvae remained in the submerged marginal vegetation during the first several instars before moving down to the sediment and dispersing. Fifth instar larvae overwintered in and on the sediment at the lake margin. Larvae developed rapidly in late summer and early fall and reached the fifth and final instar in less than 10 weeks. Pupation occurred from April to mid-June when water temperatures increased. Adults emerged from May to June, matured over the summer and reproduced from August to September.

Experimental Procedure

Clistoronia magnifica egg masses were collected from Loon Lake in the University of British Columbia Research Forest during late August, 1984. The egg masses were kept in the laboratory in shallow enamel trays containing aerated, dechlorinated water at approximately 15C until hatching

occurred. Once larvae had constructed their cases from the leaf material present, individuals were placed in labelled plexiglass cylinders (4.3cm diameter, 2.2cm height) with 475um Nitex screen bottoms. The units were raised slightly above the tray bottom to allow waste material to pass through and to facilitate the exchange of water between the plexiglass unit and the enamel tray. A small amount of gravel, on average 2mm in diameter, was placed in the bottom of each plexiglass unit to provide substrate and material for larval case construction. Rearing larvae in individual units eliminated competition for food and cannibalism. In addition, the development of individual larvae throughout their life history could be followed.

Twenty-five units were placed in each of 12 enamel trays (35x20x6cm); four controls and eight test trays, filled with aerated dechlorinated water. Larvae in the four control trays were reared at 13.5(±1.5)C which is near the optimum temperature found by Anderson (1978) for laboratory cultures. On the basis of life history I identified four potentially critical development stages were identified with respect to temperature. They were: first, third, fourth, and fifth instar. Two trays were needed for each of these instars. Larvae in one tray were reared at 9.0(±0.5)C, while larvae in the other were reared at 21.0(±0.5)C, for 6 weeks when 75% of the individuals in that tray were at the desired development stage.

The higher temperature, 21.0C, is slightly below the upper lethal limit for trichopterans (Gaufin and Hern, 1971) but within the range investigated by Anderson (1978). The lower temperature, 9.0C, was chosen because it represents an anticipated 5C reduction in temperature below a hypolimnetic reservoir drain. Results from this study could be compared with those of Grafius (1977) and Anderson (1978) who reared C. magnifica at temperatures of 10, 15, or 20C throughout their life history. A 6-week period was selected because it represents the duration of an artifically controlled temperature management scheme, such as that proposed by ALCAN, for streams containing spawning salmon (eg. IPSFC 1983 and Canada 1984). Before and after the 6-week period, trays were held at control conditions, 13.5(±1.5)C. Larvae were reared for 43 weeks, after which time it was assumed that those not already pupating would not do so.

Larvae were fed alder leaves (Alnus rubra) that were picked in late summer and air dried. Dried leaves were conditioned in the laboratory at 13.5(±1.5)C in aerated dechlorinated water. Wheat grains were added to each plexiglass chamber as a dietary supplement to ensure normal growth (Anderson 1976, 1978). The food was changed once or twice a week to reduce the amount of decaying leaf material and to ensure an excess of food. Trays were cleaned and the water was changed twice weekly. The photoperiod was 16 hours light, 8

hours dark.

Instar duration and prepupal weight were used as indicators of larval growth, development, and viability. The development of individual larvae was recorded weekly. Growth was expressed as the time required to complete various instars. Larvae were sacrificed after they sealed their case. Prepupae, defined as the stage between when the pupal case is fastened to the substrate and the ends sealed and the time when the insect changes from larva to pupa, were dried for 24 hours at 55C and weighed to the nearest 0.1mg on a digital balance.

Statistical Analysis

All statistical tests were conducted using the Michigan Interactive Data Analysis System (MIDAS) computer program (Anon. 1976). Significance was accepted at the 95% level ($p<0.05$).

The parametric analysis of variance (ANOVA) and the nonparametric Median Test were used to compare results. ANOVA and Scheffe's Multiple Range Test for determining differences between treatments were performed when the assumptions of equal variances and normality were satisfied. Equality of variance was tested using Box's improvement of Bartlett's method (Anon. 1976). Normality was assessed graphically through histogram plots of residuals. If sample variances were not equal or the

distribution of residuals showed no central tendency, the Median Test was used. In this test differences between treatments were determined by comparing the percentage of values in a given treatment that were greater than, less than, or equal to the median.

III. EXPERIMENTAL RESULTS

Results from the Median Test and ANOVA, when applicable, showed that there was no significant difference in the duration of the various instars or the prepupal weights between larvae reared in the four control trays (Table 3.1). Data on the number of larvae in a particular development stage over time, the number of deaths before pupation, and the number of individuals not pupating after 43 weeks also showed no difference between larvae reared in the control trays. I therefore pooled the control data. All comparisons were made between test trays and the pooled controls. For reference purposes treatment trays were labelled according to the instar in which the temperature regime was changed (1, 3, 4, or 5) and the direction of this change (I being 21.0C, D being 9.0C).

Survival Rate

The survival of experimental larvae is shown in Table 3.2. Low mortality was observed when third and fourth instar larvae were reared at 9.0C for 6 weeks. All surviving larvae reared at this temperature during some part of their life history successfully pupated. In contrast, poor survival was observed when third, fourth, or fifth instar larvae were reared at 21.0C for a 6-week period (Table 3.2). Figure 3.1 shows that the majority of deaths occurred during or subsequent to the instar

Table 3.1 Summary of statistical comparisons between four control[1] trays in which *Clistoronia magnifica* were reared. Differences considered significant if $p<0.05$.

Variable Measured	Median of all 4 controls	Median Test (p value) between trays	Mean of all 4 controls	Standard Deviation	ANOVA (p value) between trays
1st instar duration	3 weeks	0.1157	2.5 weeks	0.56	N.A.[2]
2nd instar duration	3 weeks	0.9786	2.5 weeks	0.59	N.A.
3rd instar duration	5 weeks	0.0687	5.9 weeks	2.5	0.3670
4th instar duration	11 weeks	0.6338	11.1 weeks	2.9	0.8101
5th instar duration	10 weeks	0.4144	10.2 weeks	3.4	N.A.
duration of larval stage	33 weeks	0.4008	31.9 weeks	4.7	0.9818
prepupal dry weight	34.7 mg	0.9919	35.3 mg	5.6	0.7776

1. The temperature for the entire larval history was 13.5(±1.5C)

2. Not Applicable. The use of the ANOVA test for this variable is not appropriate because the assumptions of equal variance and normality are not satisfied.

Table 3.2 Percentage of *Clistoronia magnifica* larvae successfully pupating when reared at several temperature regimes.

Treatment[1]	Number of Larvae[2]	Total Number of Deaths	Number Not Pupating in 43 weeks	% Pupating
control[3]	98	16	4	80
1 - D	25	4	0	84
1 - I	25	4	2	76
3 - D	25	1	0	96
3 - I	24	7	2	63
4 - D	25	1	0	96
4 - I	23	7	1	65
5 - D	25	4	0	84
5 - I	23	11	2	43

1. Control larvae were reared at 13.5(±1.5)C for their entire larval history. Others reared at 9.0(±0.5)C, "D", or 21.0(±0.5)C, "I", for 6 weeks during different development stages (1, 3, 4, or 5 instar).

2. All treatments started with 25 larvae. Some larvae went missing during the course of the experiment.

3. Combination of four controls.

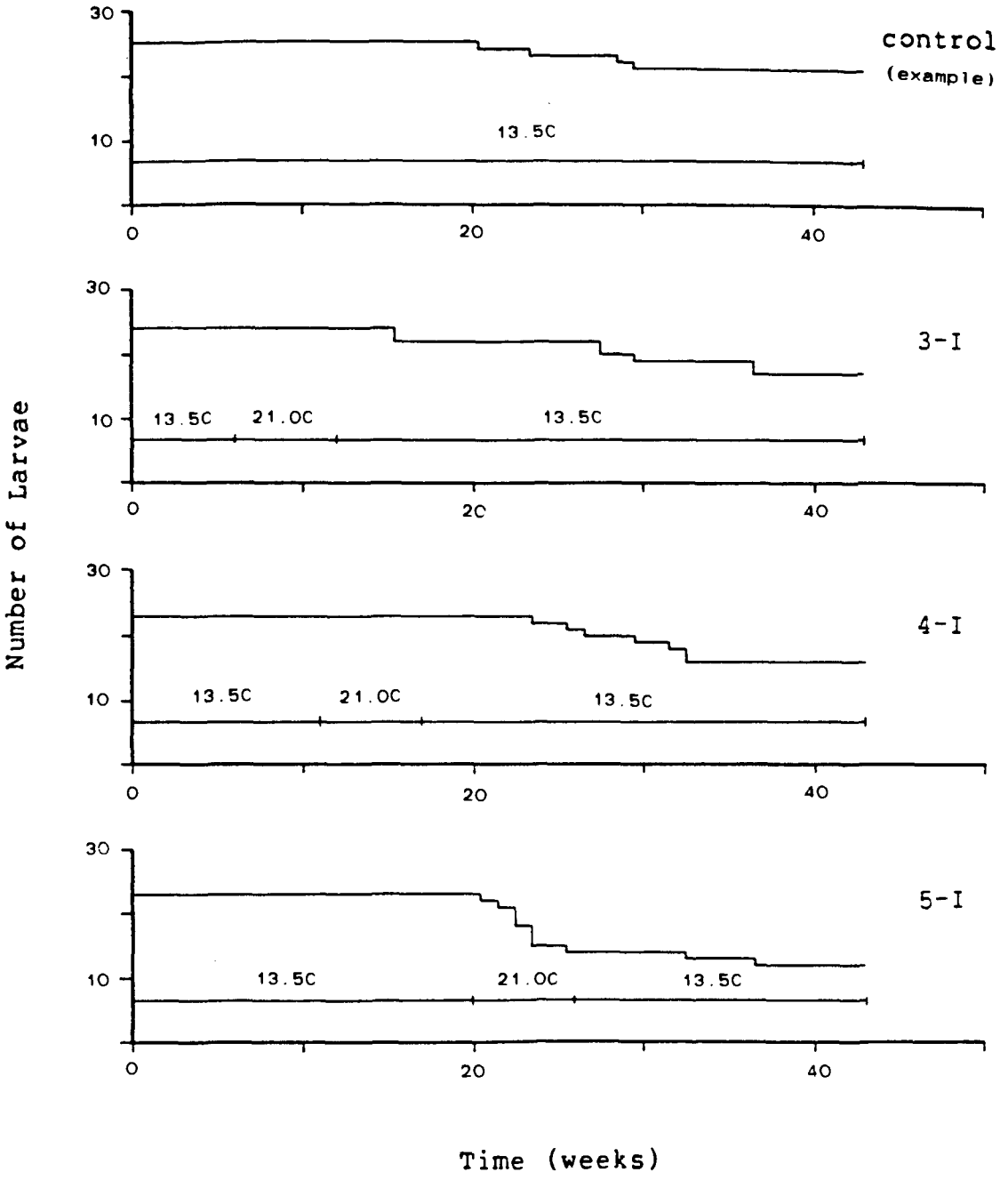

Figure 3.1 Survival of Clistoronia magnifica larvae reared at various temperature regimes. Control larvae were reared at 13.5C. Larvae in other treatments were reared at 21.0C for 6 weeks during a portion of their life history beginning at third, fourth, or fifth instar. The temperature regime for each treatment is shown.

in which larvae were reared at 21.0C. No trend in mortality of larvae reared at 9.0C was observed.

Larval Development

The length of time larvae spend in each instar and the time at which larvae moult to the next instar are two key aspects of development. The former reflects the viability of larvae and the length of time larvae of a particular size are theoretically available to fish as food. The latter reflects the time at which larvae of a particular size are available as food and the possibility of nonsynchrony between development stage and environmental conditions. The experimental temperature regimes had affected both aspects of development of C. magnifica larvae.

The cumulative average instar duration of larvae in each treatment is illustrated in Figure 3.2 and shows that larvae reared at 9.0C for 6 weeks (D) appear to have a shorter larval history than control larvae or larvae reared at 21.0C for 6 weeks (I). Because this difference in larval history can be attributed to differences in the duration of the individual instars the remainder of this section presents the observed behaviour during each instar.

A 6-week change in temperature during first, second, and

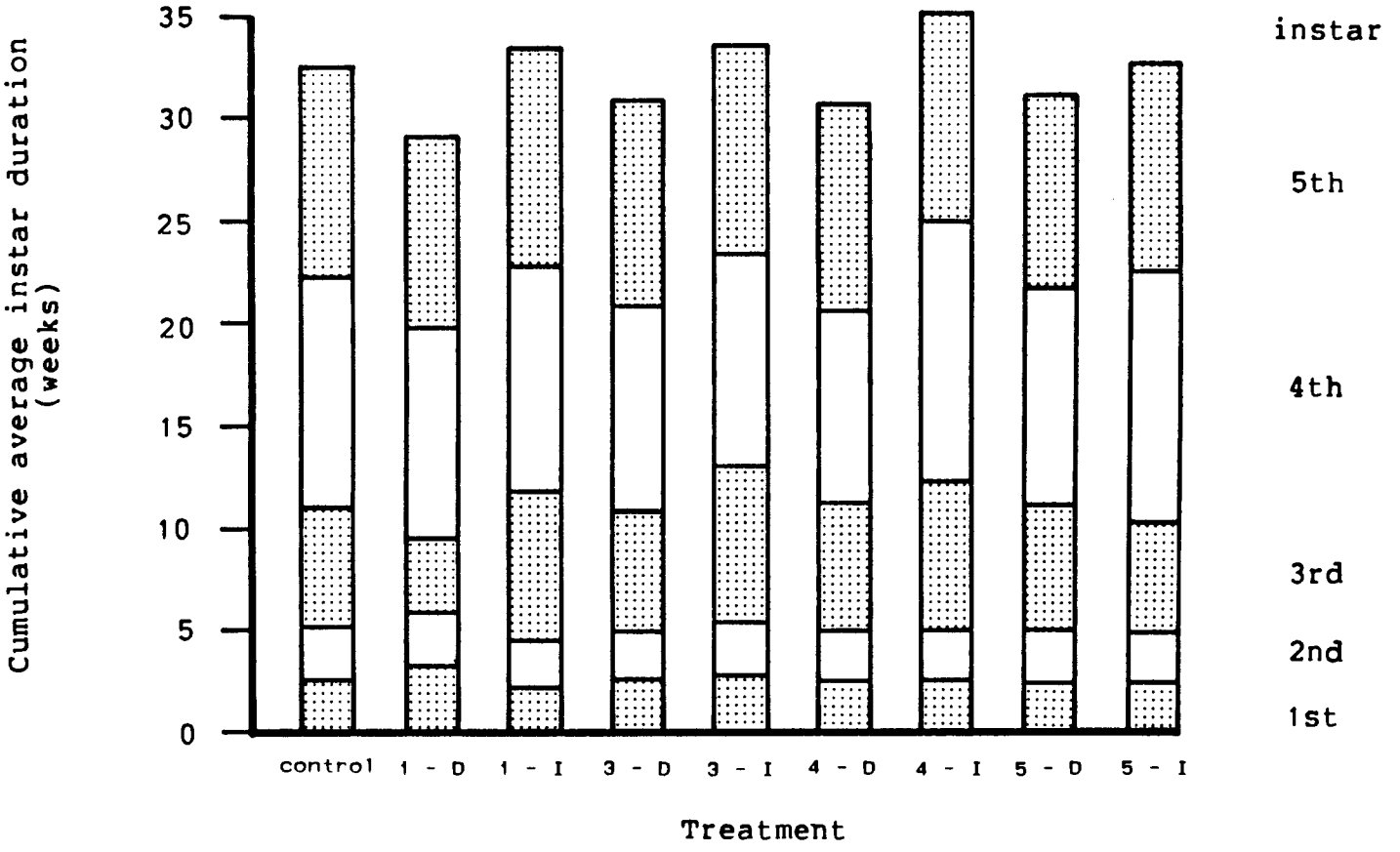

Figure 3.2 Summary of the length of time Clistoronia magnifica larvae spent in each instar when reared at 13.5C for their entire larval history (control) or at 9.0C (D) or 21.0C (I) for 6 weeks during a portion of their life history beginning in 1, 3, 4, or 5 instar. When larvae were not at the test temperatures they were reared at 13.5C. (See Appendix I for data on mean instar duration and the standard deviation.)

the beginning of third instar influenced the development rate of larvae. Larvae spent longer in first instar when reared at 9.0C (1-D) than when reared at 21.0 or 13.5C and larvae reared at 21.0C spent less time in first instar than those at 13.5C (Median Test, $p<0.001$). (See also Appendix I where further information on larval development is presented.) However, no difference in duration of the second instar was observed (Median Test, $p=0.175$).

Trends in third instar duration differ from those observed in first instar. Larvae spent less time in third instar when reared at 9.0C during first, second, and the beginning of third instar (1-D) than larvae reared at 21.0 or 13.5C during the same development stage (Figure 3.2). The number of weeks C. magnifica larvae reared at 21.0C (1-I) spent in third instar was greater than larvae at 9.0C and 13.5C (Figure 3.2) as none of these larvae moulted from third to fourth instar in less than 5 weeks and 63% of them took between 6 and 13 weeks to moult (Appendix I). The trend towards rapid development of larvae reared at 9.0C during early instars (1-D) continued during fourth and fifth instar (Figure 3.2) and these larvae had a significantly shorter overall larval history than control larvae and larvae reared at 21.0C sometime during their life history (ANOVA, $p=0.044$). All larvae in 1-D pupated by week 37, but control larvae required up to 41 weeks to pupate.

Differences in development were also observed when larvae were reared at the test temperatures for 6 weeks beginning when they were in third instar. Third instar larvae reared at 21.0C (3-I) remained in this development stage longer than larvae reared at 13.5C (Figure 3.2). Only a few of them moulted to fourth instar at the same time as controls. As a result they moulted to fifth instar 4 weeks later and to prepupa 6 weeks later than control larvae.

The average duration of third instar for larvae reared at 9.0C during this instar (3-D) was not different from larvae reared at 13.5C. However, this temperature regime did influence the length of time larvae spent in fourth instar (Fiure 3.2) with 67% of the larvae remaining as fourth instars for less than the median amount of time (Appendix I).

Temperatures of 9.0C and 21.0C for 6 weeks during the beginning of fourth instar respectively decreased and increased the duration of that instar (Figure 3.2 and Appendix I). Fourth instar larvae reared at 21.0C for 6 weeks (4-I) moulted to fifth instar approximately 4 weeks later than larvae at 13.5C, with the final larva in 4-I taking 8 weeks longer.

Neither the duration nor the timing of the fifth instar was affected when larvae were reared at 9.0C and 21.0C for 6 weeks during the beginning of that instar (ANOVA, p=0.898), however,

fifth instar larvae in 4-I began pupating 6 weeks after larvae in controls.

Prepupal Weight

Prepupal weights ranged from 16.2 to 50.2mg, the average being 35.3(±5.3)mg. A summary of mean prepupal weight for each of the treatments is presented in Table 3.3. Prepupae of larvae reared at 21.0C for 6 weeks during fifth instar weighed less than prepupae from the controls and all other treatments (ANOVA, $p<0.001$). Prepupae of larvae reared at 21.0C during fourth instar also had a significantly lower average weight than those of larvae reared at 9.0 or 21.0C during first, second, and the beginning of third instar; at 9.0C during third or fifth instar; or at 21.0C during fifth instar (Scheffe, $p<0.05$), but not lower than prepupae of larvae reared continuously at 13.5C.

In summary, mortality was low for larvae exposed to 9.0C during the third or fourth instar and high for larvae exposed to 21.0C during the first 6 weeks of either third, fourth, or fifth instar. Moulting was delayed when larvae were exposed to 21.0C during the first 6 weeks of either third or fourth instar, however, these delays did not significantly affect prepupal weight. Small prepupae were observed when larvae were exposed to 21.0C for the first 6 weeks of fifth instar while exposure to 9.0C during the first 6 weeks after the eggs hatched resulted in a shorter larval history.

Table 3.3 Summary of mean prepupal weights[1] of *Clistoronia magnifica* larvae reared at several temperature regimes.

Treatment[2]	Number of Pupae	Mean Prepupal Weight (mg)	Standard Deviation
control[3]	80	35.3	5.6
1 - D	21	36.1	4.3
1 - I	19	36.1	4.5
3 - D	23	36.7	4.7
3 - I	15	34.0	3.1
4 - D	24	35.7	4.5
4 - I	14	32.5	5.1
5 - D	19	37.5	5.4
5 - I	9	27.9	5.4

ANOVA $p<0.001$

1. Prepupae were killed after they sealed their larval case. Prepupae were dried at 55C for 24 hours and weighed.

2. Controls reared at 13.5(±1.5)C for their entire larval history. Others were reared at 9.0(±0.5)C, "D", or 21.0(±0.5)C, "I", for 6 weeks during different development stages (1, 3, 4, or 5 instar).

3. Combination of four controls.

IV. DISCUSSION

Since the growth rate of benthic invertebrates may not be affected equally by temperature in each instar (Macan 1963), a short-term change in the temperature regime of a stream could change species composition. Stream temperature management plans, like those proposed by ALCAN, may influence the life history of benthic organisms and potentially contribute to their local extinction, replacement, or enhancement. The hypothesis being tested is that both the magnitude and direction of the effect of a short-term change in temperature will depend on the direction of change from the natural temperature regime and the life stage at which a particular organism is exposed to the change.

The results from my experiment indicate that the development of Clistoronia magnifica is affected by a 6-week exposure to temperatures of 9.0 or 21.0C during different life stages when larvae are otherwise reared at 13.5C. Temperatures of 9.0 and 21.0C during different development stages can affect survival, timing of moult to subsequent instars, prepupal weight, and larval lifetime.

When reared either continuously at 13.5C or at the altered temperature regimes, larvae took between 29 and 34 weeks to develop from first instar to prepupa. This is longer than the

development time at 15.5C of 17.5 weeks found by Anderson (1978) but slightly less than he observed for larvae reared continuously at 10C. The observed difference in development times could be a result of one or more of the following factors: rearing temperature, genetic differences, or food quality.

Van Frankenhuyzen (1985), using C. magnifica larvae collected from a lake near the source of larvae used in this study, reared larvae from first instar to prepupa in an average of 20 weeks at approximately 10-13C. This probably eliminates both rearing temperature and genetic differences as possible causes for the difference in development time. Another factor relating to the difference in development times is food quality.

Temperature and food quality and quantity interact to affect larval growth rate (Anderson and Cummins 1979). Food quantity could not have influenced the growth rate of C. magnifica in this study since leaf material and wheat grains were supplied in excess of consumption. However, temperature can directly influence the rate at which leaves are invaded by microbial organisms in both the laboratory (Anderson and Sedell 1979) and the field (Short and Ward 1980), warm temperatures enhancing microbial activity. For this study all leaves were soaked in dechlorinated water at 13.5C with leaves in the individual rearing units being replaced twice a week. This frequent replacement of food material likely eliminated

disparate food quality between treatments at the various temperatures. The longer larval history observed in this study is probably a result of the method used to induce microbial colonization of the leaves.

Both Anderson (1978) and Van Frankenhuyzen (1985) conditioned their alder leaves with an inoculum of homogenized decaying leaf material containing aquatic hyphomycete fungi. In this experiment, decaying alder leaves were soaked in dechlorinated water without the addition of the inoculum. This likely resulted in less microbial colonization by fungi and less utilization by C. magnifica .

Microbial conditioning of leaves, especially by fungi, tends to improve their nutritional value to shredders (Kaushik et al. 1971; Anderson and Sedell 1979; Findlay et al. 1984) and increase their palatability (Barlocher and Kendrick 1975). Even though alder leaves conditioned without the inoculum are palatable (Anderson and Grafius 1975) and larvae can adjust their consumption rate to maintain their growth rate (Anderson and Cummins 1979), larvae in this study developed more slowy than expected. Low concentrations of fungi probably limited the nutritional quality of food available and larvae were satiated before consuming enough leaf material to achieve the development rates observed by Anderson (1978) and Van Frankenhuyzen (1985). However, larvae were able to reach a prepupal weight similar to

that observed by Anderson and Cummins (1979) because development was delayed.

Grafius (1977) and Anderson (1978) reared C. magnifica larvae from first instar to prepupa at continuous temperatures of 10, 15 (control), and 20C. My results are similar to trends observed in their studies. At lower temperatures early instar larvae developed more slowly. In addition, they generally experienced lower mortality, and tended to have larger prepupae, although the difference in prepupal weights in my study was not significant. When larvae were reared at 10C for their entire larval history, Grafius (1977) and Anderson (1978) both observed slower development in all instars. In contrast, in my study larvae reared at 9.0C during fourth instar developed more rapidly than larvae continually reared at 13.5C.

Early instar larvae developed more rapidly at higher temperatures. Larvae generally experienced higher mortality when reared at 20C (Grafius 1977; Anderson 1978) or 21.0C (this study) during any of the instars studied and gave rise to smaller prepupae when reared at 20C for their entire larval history (Grafius 1977; Anderson 1978) or reared at 21.0C during the fifth instar.

Grafius (1977) observed smaller prepupae at 20C than at 15C. In my study only larvae reared at 21.0C during fifth

instar had lower prepupal weights. This same temperature during first, third, or fourth instar did not significantly influence prepupae size. Therefore, temperature during the fifth instar may be critical in determining both survival and adult fecundity since the latter is directly related to adult and therefore pupal size (Sweeney and Vannote 1978; Ward and Stanford 1982).

The differences observed in response between early and late instars to both experimental temperature regimes can be explained by the relationship between natural temperature regime and life history. Early instars are present during late summer when temperatures are generally high, consequently slower development at 9.0C is observed. Because overwintering fifth instar larvae are acclimated to cooler temperatures, a temperature of 21.0C during later instars causes high mortality and low prepupae weights. Shifts from the normal field temperature and hence the optimum tend to temporarily enhance or impede larvae development depending on the direction of deviation and larval development stage.

To explain how movement from optimal to non-optimal thermal conditions effects adult body size and thus fecundity in invertebrates Vannote and Sweeney (1980) suggest that the rate and duration of larval growth and the specific time in larval development that adult structures begin maturing and the rate of this maturation process are temperature dependent. Although

their theory is derived for different species active during different times of the year, it may be used to explain the impact of nonoptimal thermal conditions on particular development stages of one species if development at each stage is optimal under different thermal conditions.

Early instar C. magnifica larvae present during late August and September experience warm temperatures in the field (Winterbourn 1971). Colder than optimal conditions may reduce the rate of energy assimilation per mg individual (Grafius 1977, Table 16) but allocate energy to growth and maintenance in the normal way. Maturation to the next instar proceeds slower than anticipated. Conversely, increased rates of energy assimilation per mg individual (Grafius 1977) at warmer than optimal temperatures hastens maturation to the next instar. For late instar larvae experiencing warmer than usual temperatures, the energy assimilation rate per individual increases, but less energy is available for growth because of a disproportionate increase in maintenance metabolism (e.g. higher respiration rate for late instar larvae at warm temperatures observed by Grafius 1977 (Figure 24) and for other trichopterans Collardeau 1961; Collardeau-Roux 1964; Roux 1979). Larvae advance more rapidly towards pupation, adult tissue maturation begins sooner and proceeds more rapidly thereby limiting the time available for larval growth. This agrees with my finding of small prepupae when fifth instar larvae were reared at 21.0C.

Respiration and assimilation rates of C. magnifica larvae at the experimental temperature regimes need to be measured if this theoretical model is to be confirmed.

Grafius (1977) suggests that larvae in the field continue to grow during winter until spring when an increase in water temperature or a change in day length stimulates pupation. In this study the temperature was increased from 13.5C to 21.0C during fifth instar while the photoperiod remained constant. Fifth instar larvae under these thermal conditions did not begin pupating until the temperature was increased to 21.0C at week 20. This observation agrees with Grafius' contention that an increase in temperature during fifth instar stimulates pupation. However, if the temperature remained at 13.5C larvae would probably have pupated about 2 weeks later with control larvae. I agree with Grafius that changes in temperature during fifth instar influence the onset of pupation, although an increase in temperature from 13.5C is not a necessary criterion.

In this study I have considered the effects of temporary changes in temperature on the development of C. magnifica larvae. Several researchers have studied the relationship between life history and temperature for several other aquatic invertebrate species. The results of their laboratory studies have shown that temperature can effect hatching period, larval development, emergence period, adult body size, and fecundity.

Changes in any of these parameters could result in the local extinction, replacement, or enhancement of some species.

Elliot (1972) found that as temperature increased the period of time between oviposition and the start of hatching and the length of hatching period for the mayfly Baetis rhodani increased. Diel changes in temperature have been shown to accelerate the development rate of eggs of the mayfly Ecdyonurus picteti (Humpesch 1978) and the eggs and larvae of the mayfly Isonychia bicolor (Sweeney 1978). In addition, larval development through to pupal and adult stages can increase with increasing temperature for Simulium (blackfly) larvae (Becker 1973).

Changes in the time required for eggs to hatch and the rate of larval development are important as they can affect the natural relationship between environmental conditions, such as stream temperature and flow, and larval development stage. Larvae may be exposed to suboptimal environmental conditions if significant changes in development patterns occur. In addition, temperatures causing high growth rates may be suboptimal for growth efficiency, emergence success, and adult longevity (Heiman and Knight 1975).

Rupprecht (1975) found that Sericostoma (Trichoptera) larvae and larvae of three lotic dragonfly species pupated and

emerged more rapidly in warm lab water than in colder stream water. He also observed an increase in abnormal breathing behaviour with increasing temperature. Abnormal undulations during breathing may cause invertebrates to become more noticeable to predators. Nebeker (1971) observed premature emergence of fully developed larvae of several species of stoneflies, mayflies, caddisflies, and midges when larvae were exposed to constant warm water temperatures during winter months. The timing and duration of emergence periods are important because the air temperature may be lethal to adults and resources may be more fully exploited when periods of emergence are longer or staggered.

Small adults and reduced fecundity in the mayfly Centroptilum rufostrigatum result when temperature is either warmed or cooled with respect to the thermal conditions optimal for larval development (Vannote and Sweeney 1980). Reduced fecundity could result in a decrease in population size.

Under harsh environmental conditions abiotic factors, such as water temperature, control the structure of the invertebrate community (Peckarsky 1983). Changes in the relationship between abiotic conditions and larval development stage may result in the enhancement, replacement, or extinction of some invertebrate species. Hatching period, larval development rate, emergence period, and adult body size are all influenced by temperature.

Survival, timing of moult to subsequent instars, prepupal weight, and duration of the larval stage are affected by short-term (6-week), sublethal changes in temperature. Therefore regulating temperature to meet management objectives downstream of impoundments may have an impact on invertebrate and hence fish populations in the reaches immediately below the impoundment.

In general, stream regulation may increase the total biomass of benthic invertebrates (Stanford and Ward 1979) but the species composition switches from high quality foodstuffs to smaller, less available burrowing species (Benda and Proffitt 1974; Ward and Stanford 1980; Perry and Huston 1983). Results from my study indicate that short-term changes in temperature may do the same thing. Invertebrates that are unable to compensate for a temporary shift in normal development may be exposed to suboptimal environmental conditions. Nonoptimal temperatures may also increase mortality during some development stages. Less desirable burrowing species may replace those species unable to adapt to temporary changes in temperature. Any study investigating changes in the temperature regime in streams supporting fish populations should investigate the effect on their food, particularly, mayflies, stoneflies, and caddisflies.

ALCAN's temperature management plan for the Nechako River

attempts to reduce potentially harmful downstream temperatures for spawning or migrating sockeye salmon. Results from this study indicate that the impact this plan has on caddisflies immediately below the Nechako-Cheslatta confluence will depend on the development stage of larvae exposed to the altered temperature regime.

It is estimated that invertebrates would experience as much as an 8C reduction in temperature during July and August (Figure 1.2). This study shows that a 4.5C reduction in temperature can shorten the larval history and affect the timing of moults of C. magnifica larvae. However, neither significantly influences prepupal weight with the time between moults having no affect on the timing of pupation. Temporarily decreasing the temperature by 4.5C during the first, second, and beginning of third instar for an organism that normally experiences warmer temperatures during those instars, significantly decreases the length of the larval history. This may disrupt the relationship between larvae and environmental conditions. Short-term decreases in temperature of similar magnitude during third, fourth, or fifth instar for larvae normally experiencing cold temperatures during these instars, do not have a significant effect on the variables measured in this study. However, the effect of similar changes in temperature on other invertebrate species may be different and a decrease of 8C may significantly affect timing of moults and larval growth in C. magnifica and other larvae.

Further ramifications of ALCAN's temperature management plan include changing the time of the normal maximum summer temperature (Figure 1.2). If temperature is regulated during the entire 6-week period or a portion of it, the time at which the maximum temperature occurs may change. This may be signficant as delayed summer maxima may lead to species elimination by causing premature adult emergence of some benthic species possibly exposing them to lethal air temperatures, or widen the time lag between emergence of males and females (Ward and Stanford 1979). Conversely, thermal modifications of this nature could delay adult emergence and organisms may be unable to complete their life cycle (Ross and Merritt 1978; Prat 1981). Impact predictions for the temperature management plan will probably be affected if changes in invertebrate species or abundance occur in the upper Nechako River.

Using a computer simulation model, Knight (1985) predicted that enhanced summer growth of juvenile chinook salmon in the upper Nechako River could occur if ALCAN s temperature management plan was adopted. In arriving at this preliminary conclusion, Knight assumed that feeding levels, and hence invertebrate abundance, would not be affected by further development of hydroelectric resources and plans for temperature management. Results from my study suggest that the benthic invertebrate species composition could be affected by the proposed temperature management plan, although the degree of

impact will depend on the relative change in absolute temperature and temperature pattern. Changes in benthic community structure could affect the quality and/or quantity of food available to juvenile chinook salmon which would invalidate the assumptions and conclusions made by Knight (1985).

However, under the current situation Knight's assumption is justified. Recent field and laboratory studies on the relationship between temperature and benthic invertebrates do not adequately determine the effect of altered thermal regimes and do not consider short-term changes in temperature.

Field studies comparing invertebrate development, composition, and abundance between unregulated and regulated streams (Scullion et al. 1982; Perry and Huston 1983; Nyman et al. 1985), regions in the same stream up- and down-stream of impoundments (Spence and Hynes 1971; Langford 1975; Young et al. 1976; Dumont 1985), pre- and post-impoundment conditions in the same stream (Hilsenhoff 1971; Armitage 1978; Perry and Huston 1983), distance downstream from the impoundment (Ward 1974) include confounding factors such as water chemistry, flow rates, and organic content and physical differences between sites. The presence of these additional factors does not allow researchers to accurately determine the direct effect of downstream changes in temperature on benthic invertebrates.

Most laboratory studies focus on thermal tolerance to either constant temperature regimes (Becker 1973; Heiman and Knight 1975; Rupprecht 1975) or heated waters (Nebeker and Lemke 1968; Gaufin and Hern 1971). Neither of these types of laboratory experiments can indicate the impact that temperature management plans, such as the one proposed by ALCAN, would have on the benthic community. The tolerance of organisms to heated waters may be of questionable ecological significance since organisms are often weakened or eliminated by temperatures below laboratory determined lethal levels (Heiman and Knight 1975) and results from experiments in which organisms are reared at constant temperatures do not indicate the effect of short-term changes in temperature.

Laboratory studies in which larvae in a particular development stage are temporarily exposed to adverse temperatures do not monitor larval development after larvae are returned to "natural" temperatures (e.g. Elliot 1972 and Humpesch 1978). Changes in larval development brought about by these changes in temperature may affect the future ability of larvae to develop normally.

In this study short-term changes in temperature affected the growth and development of Clistoronia magnifica larvae. Larvae exposed to higher than normal temperatures had a low survival rate, moulted to subsequent instars later in some

instances, and had small prepupae when the temperature was increased during the fifth instar. Larvae exposed to lower temperatures during the first, second and beginning of third instar had a shorter larval history. Similar studies on other invertebrate species are required if generalizations are to be made.

Constant daily temperatures are often associated with regulated streams and with temperature management plans, however, the importance of diel temperature patterns to invertebrates remains virtually uninvestigated (Ward 1976). The impact of short-term temperature changes and the importance of diel temperature fluctuations require further study. Armitage (1984) observed that there are many reviews and general monitoring studies on stream regulation and benthic invertebrates but that there is a relative lack of investigations into causal relationships and of testable hypotheses that could be used to develop predictive models. It is hoped that this study will be one of many investigations into the thermal requirements of stream macroinvertebrates and a step towards developing predictive models.

APPENDIX I

Summary of Clistoronia magnifica larval instar durations when larvae were reared at several temperature regimes.[1]

This table shows the mean duration of each instar and the distribution of instar durations around the median duration of all treatments. Only those treatments in which larvae are being or have previously been reared at the experimental temperature regimes are included in the summary for a particular instar but all treatments were included in the statistical analysis. Also included for each instar is the mean instar duration (in weeks) and the range over all treatments.
*Note that since there was very little difference between median and mean durations, the mean duration for each treatment is presented so that the standar deviation may also be included.

First Instar Duration:

grand median - 2 weeks
grand mean (st. dev.) - 2.5 (±0.6)
range - 2-6

Treatment	Number of Larvae	Mean Duration (weeks)	Standard Deviation
control[2]	99	2.5	0.6
1 - D	24	3.3	1.0
1 - I	24	2.1	0.3
3 - D	25	2.5	0.5
3 - I	25	2.7	0.5
4 - D	25	2.4	0.5
4 - I	24	2.5	0.6
5 - D	25	2.3	0.5
5 - I	25	2.4	0.6

Median Test $p<0.001$

Treatment	% less than the median	% equal to the median	% greater than the median
control	0	49	51
1 - D	0	8	92
1 - I	0	88	12

Second Instar Duration:

grand median - 2 weeks
grand mean (st. dev.) - 2.5 (±0.6)
range - 1-5

Treatment	Number of Larvae	Mean Duration (weeks)	Standard Deviation
control	99	2.6	0.6
1 - D	24	2.6	0.6
1 - I	24	2.3	0.7
3 - D	25	2.3	0.5
3 - I	25	2.6	0.7
4 - D	25	2.4	0.6
4 - I	23	2.4	0.7
5 - D	25	2.7	0.7
5 - I	25	2.4	0.8

Median Test p=0.175

Treatment	% less than the median	% equal to the median	% greater than the median
control	0	48	52
1 - D	0	46	54
1 - I	8	58	33

Third Instar Duration:

grand median - 5 weeks
grand mean (st. dev.) - 6.2 (±3.0)
range - 2-15

Treatment	Number of Larvae	Mean Duration (weeks)	Standard Deviation
control	99	5.9	2.5
1 - D	24	3.6	1.0
1 - I	24	7.3	2.5
3 - D	25	6.0	1.8
3 - I	25	7.7	3.7
4 - D	24	6.3	2.7
4 - I	23	7.3	3.9
5 - D	25	6.1	3.3
5 - I	23	5.4	1.9

Median Test p<0.001

Treatment	% less than the median	% equal to the median	% greater than the median
control	34	18	47
1 - D	83	13	4
1 - I	0	37	63
3 - D	16	20	64
3 - I	12	24	64

Fourth Instar Duration:

grand median - 11 weeks
grand mean (st. dev.) - 10.9 (±2.9)
range - 5-23

Treatment	Number of Larvae	Mean Duration (weeks)	Standard Deviation
control	96	11.2	2.9
1 - D	23	10.3	2.3
1 - I	23	10.9	2.5
3 - D	24	9.9	2.7
3 - I	21	10.3	2.8
4 - D	24	9.4	2.0
4 - I	20	12.7	3.2
5 - D	25	10.5	2.3
5 - I	23	12.2	4.5

Median Test p=0.014

Treatment	% less than the median	% equal to the median	% greater than the median
control	43	20	38
1 - I	65	13	22
1 - I	52	4	43
3 - D	67	13	21
3 - I	41	27	32
4 - D	71	13	17
4 - I	25	10	65

Fifth Instar Duration:

grand median - 10 weeks
grand mean (st. dev.) - 10.1 (±3.0)
range - 3-20

Treatment	Number of Larvae	Mean Duration (weeks)	Standard Deviation
control	80	10.2	3.4
1 - D	21	9.3	3.2
1 - I	19	10.8	3.1
3 - D	23	10.1	2.9
3 - I	15	10.2	1.9
4 - D	24	10.2	2.4
4 - I	14	10.1	2.8
5 - D	21	9.5	2.5
5 - I	10	10.3	3.5

Median Test p=0.965
ANOVA p=0.898

Treatment	% less than the median	% equal to the median	% greater than the median
control	43	16	41
1 - D	48	29	24
1 - I	42	5	53
3 - D	30	22	48
3 - I	47	13	40
4 - D	42	13	46
4 - I	50	21	29
5 - D	48	24	29
5 - I	50	0	50

1. Control larvae were reared at 13.5 (±1.5)C for their entire larval history. Others were reared at 9.0 (±0.5)C, "D", or 21.0 (±0.5)C, "I", for 6 weeks during different development stages (1,3,4, or 5 instar).

2. Combination of four controls.

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