THE EFFECTS OF LOGGING ON THE COHO SALMON OF CARNATION CREEK, BRITISH COLUMBIA

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Coho salmon (*Oncorhynchus kisutch*) is perhaps the most ubiquitous of the five species of Pacific salmon found in British Columbia. Although sizable populations of coho can be found in most lakes and larger rivers, the species is usually thought to prefer small streams. Juvenile coho commonly rear in freshwater for one or two years. This life history characteristic and their abundance in small streams potentially make this species sensitive to habitat disturbance of the sort caused by clear-cut logging.

The overall objective of the Carnation Creek study was to document the effects of clear-cut logging on the fish of a small coastal stream and most of the fisheries research effort has focused on coho salmon. The detailed and comprehensive data record at Carnation Creek now extends for 13 complete cohorts.

The objectives of this paper are: 1) to briefly describe the changes that occurred to the coho salmon after logging; 2) to present an interpretation of the mechanisms that are believed to underlie the observed changes; 3) to outline the comprehensive population dynamics model that has been developed for the coho salmon stock; and 4) to present some predictions of the future trends in coho abundance that might occur as the watershed recovers from logging.

METHODS

Two general methods were used to collect the data. First, fish movements in and out of the stream were determined at a fish-counting fence near the mouth of the stream. Adults entering the stream and fry and smolts leaving it were enumerated. Second, population sizes in the stream were estimated at least three times every year through surveys in fixed sections of the stream comprising, in total, about 10% of the total habitat available to coho. There were also more detailed studies of specific aspects of the life history. Important among these were studies of how the juveniles utilized the estuary and the side-channels, feeding studies and fish movements within the stream.

RESULTS AND DISCUSSION

Several of the important aspects of the response of coho salmon to logging can be seen in Fig. 1. The response to the first significant clear-cut logging in the winter of 1976/77 was immediate. Total smolt production from the brood year affected (1976) was almost double that of the years before logging (Fig. 1D). The change in smolt production followed a significant increase in the standing crop of juveniles found in the preceding fall. Standing crop is the product of number X weight. The average weight of individual fingerlings in the fall was strongly correlated with the abundance of fingerlings in the stream over the preceding summer. In years when densities were relatively low (brood years 80 and 81) the fingerlings grew to a relatively large size by the fall (Fig. 1C). The converse was true in brood year 1979. Some effect of logging apparently changed the relationship between fingerling abundance and size. That effect can be clearly seen in the three brood years immediately following logging (1976-1978). In those years fingerlings were about as abundant as

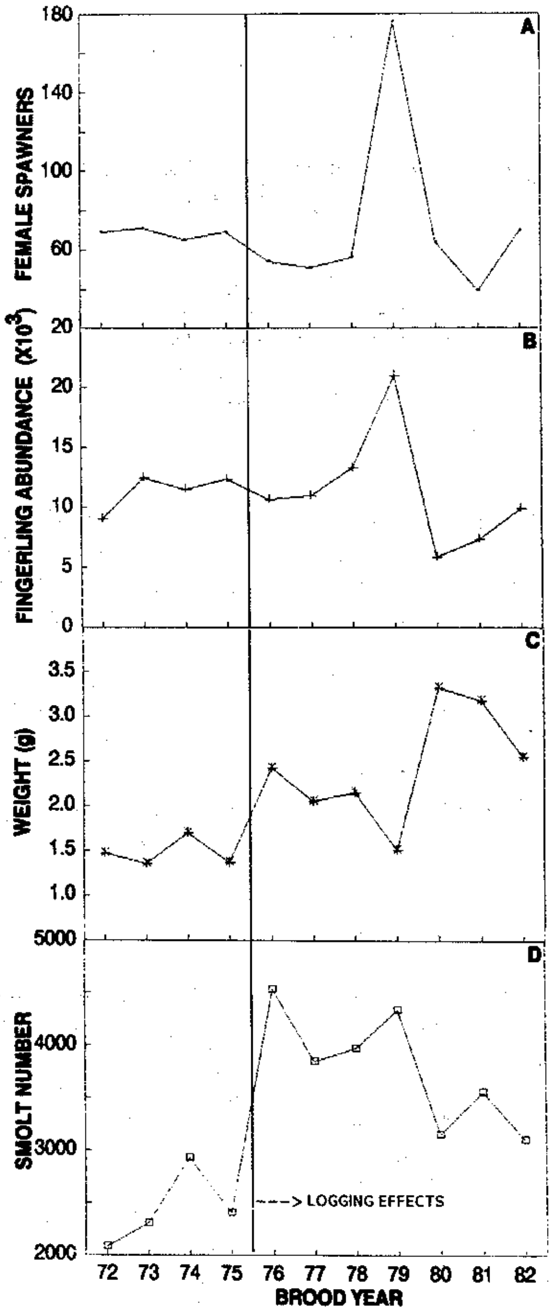


Figure 1. A) Escapement, B) fingerling abundance in the fall of their first year (brood year + 1), C) weight in the fall of their first year (brood year + 1) and D) smolt production (brood year + 2 and brood year + 3). The plots are arranged by brood year. The actual calendar years are for each panel are: A) the brood year shown, B and C) the brood year + 1 and D) brood year + 2 for yearling smolts and brood year + 3 for two-year old smolts (The smolt production is the sum of both age groups). The escapement is only females. The brood years affected by logging are shown.

they had been prior to logging but they were, on average, about 0.8 g heavier. The probable mechanism for the change in the density-size relationship is discussed later.

The increases in smolt numbers (Fig. 1D) did not result from increases in the numbers of female spawners (Fig. 1A), the numbers of fry or the numbers of fingerlings in the system at the end of their first summer (brood year + 1; Fig. 1B). In fact, smolt production is statistically independent of both escapement, (which determines the total number of eggs deposited), and juvenile abundance in the preceding summer. The increase in smolt production resulted from a change in the over-winter survivals of fingerlings (Fig. 2). The increase in over-winter survival of fingerlings appears to have been brought about by the increase in their size in the years after logging (Fig. 1C).

The considerable increases in smolt production were not translated into increased adult escapements. The greater smolt production in the years after logging resulted in only one bumper escapement (1976 brood returning in 1979; Fig. 1A). In the other years of greater smolt production that followed logging, escapements were similar to, or lower than, those observed before logging. Possible reasons for the general failure of increased smolt production to produce increased escapements are discussed later.

The increases in smolt production observed after logging were the eventual result of small increases in stream temperatures in the late winter and early spring. During the months of February and March the stream was approximately 15% warmer than it had been before logging. Increased stream temperatures during this period (and during the rest of the year as well) were probably due to the removal of the forest canopy over the lower 3 km of the stream. The stream would have warmed immediately after the removal of the canopy and so this particular effect of logging was apparent in the very first winter of logging. Increased stream temperatures either accelerated the development of incubating eggs or brought forward the emergence of fry after they hatched with the result that, in the years after logging, coho fry emerged from one to six weeks earlier than they had before logging. Earlier emergence increased the length of the growing season with the result that, for any particular level of abundance, the fingerlings were larger by the fall of the years after logging (Fig. 1C). Thus, even in the year of high fingerling abundance (brood year 1979; Fig. 1), when the average fall weight was comparable to the average observed before logging, the fry in that year were approximately 1 g heavier than they would have been at comparable densities in the years before logging.

Over-winter survival in Carnation Creek is size-dependent for 0+ coho (fingerlings entering their first winter; Fig. 3). The larger fingerlings found after logging had high over-winter survivals and smolt production nearly doubled as a result. There were also increases in the sizes of smolts (Fig. 6).

The increased over-winter survival of fingerlings and the increased size of fingerlings has led to a dramatic change in the age composition of the smolts (Fig. 4A). Prior to logging significant numbers of fingerlings remained in the stream after their first winter and smolted as 2+ smolts the following spring (Fig. 4B). After logging a much smaller proportion of fingerlings remained in the stream (Fig. 4A). Before logging the numbers of 1+ and 2+ smolts were roughly equal while after logging most smolts were of the 1+ group (Fig. 4B). The observed shift in age composition is an indication of the increase in stream productivity that resulted immediately after logging. The consequences of this change in age composition are uncertain. In theory at least, the Carnation Creek stock has become more susceptible to oscillations in numbers. The large number of yearling fish in the stream might have served to stabilize smolt production in years of recruitment failures. (Such failures might result from a poor escapement or poor egg-to-fry survival.) However, smolt production (1+ or total) is insensitive to numbers of fry over a very broad range. In other words, smolt production is strongly buffered against changes in recruitment even without the buffering capacity provided by the yearling fish.

Coho spend about 18 months in the ocean before returning to their natal streams. The causes of mortality over this period can be ascribed either to fishing or to the catch-all of "natural" sources. The coho smolts leaving Carnation Creek were never marked or tagged so it was not possible to determine in any direct way the numbers of fish caught by the sport and commercial fisheries. Consequently, no direct estimates of smolt-to-adult survivals or the proportion of the observed mortality that was due to "natural" causes could be made. In order to "link-up" smolt production with the observed returns of adult fish, it was necessary to extrapolate, from other coho stocks, relationships which explain variation in

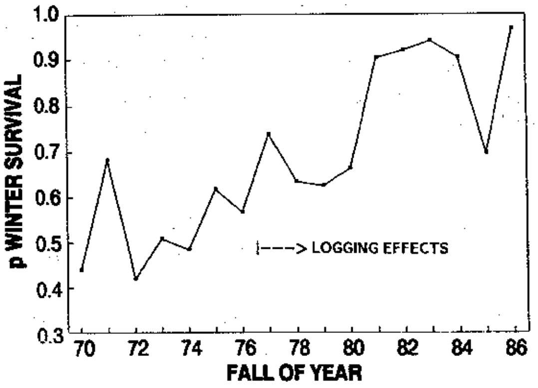


Figure 2. Proportions of fingerlings that survived the first winter in the stream. The numbers of fish in the fall going into the winter were estimated by in-stream census in late September. The numbers surviving the winter are the sum of 1+ smolts and residual yearlings present during the spring in-stream census. The years affected by logging are indicated.

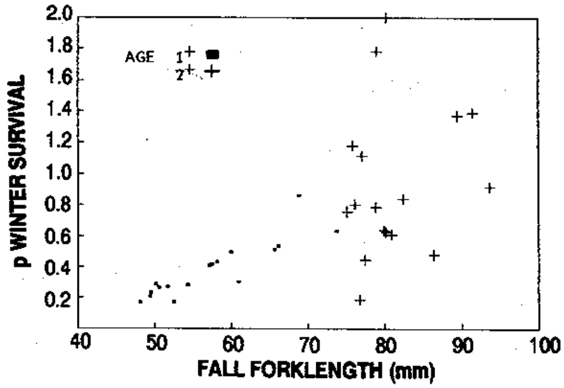


Figure 3. Proportions of fish surviving the winter as a function of fork length in the preceding fall. Both age groups are indicated.

smolt-to-adult survival.

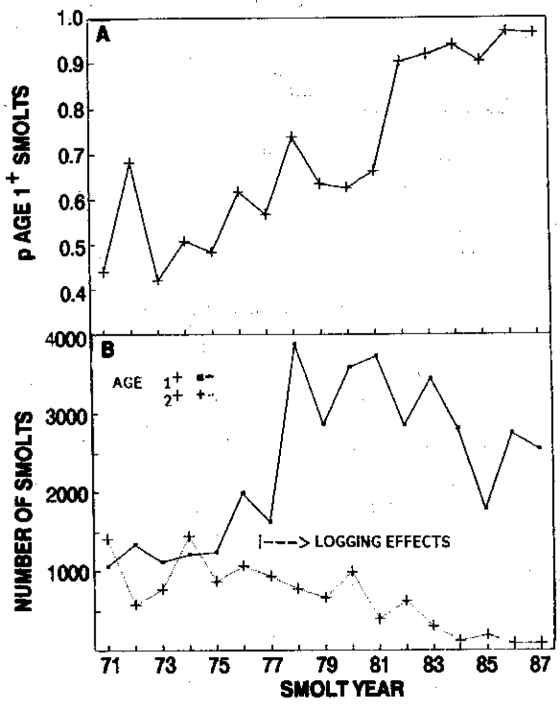


Figure 4. A) The proportion of smolts that were age 1+ by year of migration. B) The observed numbers of yearling (1+) and two-year old (2+) smolts by year of migration. Note that for any particular cohort, the two-year old smolts migrate one year after the yearlings. The change in the age composition of smolts resulted from the dramatic increase in the numbers of the younger age group (1+) rather than an abrupt decline in the numbers of older smolts.

Two of the presumably many factors which can affect the survival of smolts are smolt size and the time of migration. Generally larger smolts that migrate late in the spring survive better than smaller smolts that migrate early in the spring (Bilton et al. 1982). Logging and to a lesser extent, climatic variation, affected the size of smolts and the timing of their entry into the ocean. Small increases in spring water temperatures brought forward the seaward migration of coho smolts by from 7 to 14 days (Fig. 5). Smolts, particularly yearling smolts, were generally larger after the beginning of logging (Fig. 6). Over the ranges of smolt weight and migration time observed, variation in smolt survival is determined more by variation in migration timing than in weight. Smolt-to-adult survival is predicted to have decreased from 15% before logging to 10% in the years after logging. This predicted decline in survival was caused by earlier migration and assumes a constant ocean environment. I would like to emphasize that such a decline in smolt-to-adult survival was not directly measured, nor could it be measured, for Carnation Creek coho. The stated decline in survival was calculated from the relationships generated by the time and size-at-release experiments of Bilton et al.

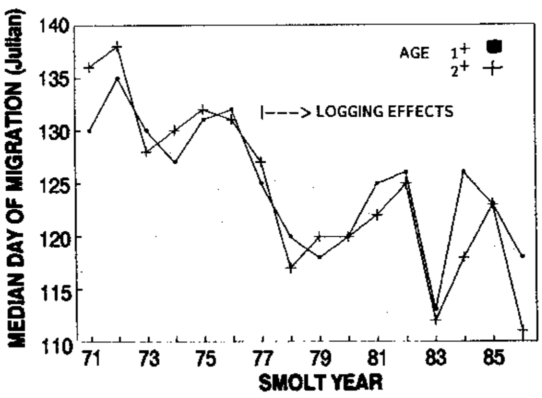


Figure 5. Median Julian day of migration of yearling and two-year coho smolts from Carnation Creek by year of migration.

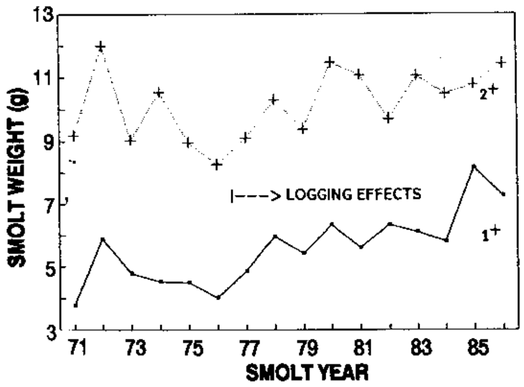


Figure 6. Mean weights of yearling and two-year old coho smolts by year of migration. The years affected by logging are indicated.

(1982) for coho released from the Rosewall hatchery. Similar declines in survival with early release have been observed at other hatcheries (pers. comm. B. Morley, Pacific Biol. Sta., Nanaimo, B.C.). The only study on the effects of migration timing for wild coho of which I am aware was done at Porcupine Creek, Alaska (Thedinga and Koski 1984). There, smolts migrating 1-2 weeks before or after the peak migration had 50% the survival of smolts migrating during the peak period. The reasons for such a strong dependence of survival on migration timing are unknown.

The increased mortality of smolts that may have resulted from earlier entry into the ocean would have partially reduced the impacts of increased smolt production on the magnitudes of subsequent adult returns but those impacts do not fully explain the discrepancies between observed smolt numbers and adult returns to the stream (compare Fig. 7A and Fig. 7D). It is probable that there were changes in "natural" mortality and/or fishing mortality over the course of the study. Fortunately it has been possible to estimate mortality due to the fishery and natural causes using data gathered from coded-wire tagged releases of coho from the nearby Robertson Creek hatchery. The application of natural and fishing mortality rates from Robertson Creek necessitate the important but untestable assumption that coho from the Robertson Creek hatchery behave similarly in the ocean to coho from Carnation Creek. The assumption that hatchery stocks can be used as indicators of wild stocks has been widely made but is only now being critically examined through field experimentation (pers. comm. C. Walters, U.B.C., Vancouver, B.C.). Although fishing mortality has been variable (Fig. 7C), there has been no systematic change that would explain the discrepancy between potential and observed returns to Carnation Creek. Furthermore the very large return from smolt year 1978 (brood years 1975 & 1976, return year 1979, Fig. 7D) cannot be explained by a decrease in the fishing mortality. However, there has been a substantial and systematic decline in smolt-to-adult survivals of the Robertson Creek coho (Fig. 7B). Similar declines in smolt survival have been observed for sockeye salmon smolts originating in Barkley Sound (pers. comm. K. Hyatt, Pacific Biol. Sta., Nanaimo, B.C.). Furthermore, the variability in smolt-adult-survival is significantly correlated with sea surface temperatures and salinities in Barkley Sound around the time of smolt migration, suggesting that the variability in smolt-to-adult survivals in some way results from variability in ocean "conditions". It is reasonable to assume that the marine survival of Carnation Creek smolts also declined.

Escapements to Carnation Creek were predicted from smolt numbers as follows: 1. the observed smolt numbers for each year (Fig. 7A) were multiplied by the survival rates calculated from the time and size- at-release relationships discussed above to give expected adult numbers before all fisheries and assuming constant ocean conditions. (Although not shown in the figure, the two age classes of smolts were kept separate throughout all of these calculations); 2. the expected adult numbers from 1. were multiplied by a standardized survival calculated from the observed smolt-to-adult survivals for the Robertson Creek hatchery coho (Fig. 7B). Those

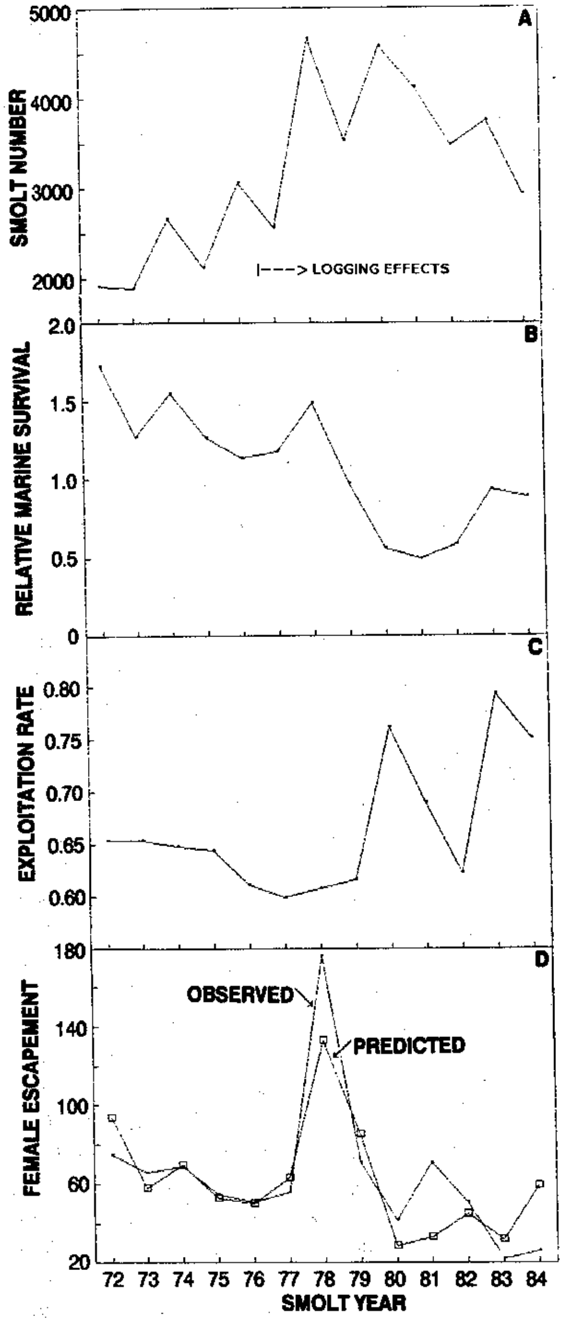


Figure 7. A) Smolt production, B) relative marine survival, C) fishery exploitation rates and D) escapements arranged by smolt year. Note that the smolt production is the sum of both age groups and that escapements are for females only. Relative marine survivals and fishery exploitation rates were calculated from coded-wire tagged releases of coho from the nearby Robertson Creek hatchery.

survivals include all fish captured in the commercial and sport fisheries. The estimate produced here is for total number of adults that were present immediately prior to the fishery; and 3. the number of adults estimated in 2. were multiplied by one minus the fishery exploitation rate observed for the Robertson Creek coho (Fig. 7C). The number produced is the expected escapement to Carnation Creek. This sequence of calculations makes reasonable predictions of observed escapements (Fig. 7D).

Since logging affected both the weight of smolts and the timing of the smolt migration, changes in the numbers of adults caused by changes in either of these smolt parameters are properly considered effects of logging. Changes in smolt-to-adult survival that were due to changing ocean conditions or to changes in fishing mortality are clearly not effects of logging. Therefore, the net effect of logging on the coho stock must be estimated using the numbers of adults predicted by step 1 above. The net effect of logging is expressed in terms of percentage change in the numbers of adult females relative to the average number presumed to have been present before logging (Table 1). On average, in the years following logging, the total number of adult female coho increased by an average of 9% over the number present prior to logging (Table 1).

Generalizations about Coho Population Ecology

In developing the explanation for the observed changes in coho abundance after logging, that were presented above, several generalizations about the population ecology of coho of Carnation Creek have become apparent.

First, smolt production in Carnation Creek is limited (or controlled) more by physical factors than by biological ones. For the Carnation Creek coho stock there are three important production bottlenecks in freshwater: egg mortality, fry mortality immediately after emergence and mortality of fingerlings over their first winter in the stream. All three processes seem to be controlled by physical processes rather than biological interactions, and, for the most part, mortality rates are density Independent. In this regard, Carnation Creek is probably typical of small streams of low productivity, in regions of cool temperatures and dynamic flow regimes. In streams

Table 1. Estimates of total adult female returns prior to the fishery, averaged over the before and after logging periods. The smolt years before logging "<LOG" were 1971-1976, those after ">LOG" were 1977-1984. The effects of logging and climate are shown as both absolute numbers of females and as percentages of the pre-logging estimated returns. Logging effects are calculated by using the estimated returns with and without logging. Climatic effects are calculated by using the estimated returns without logging for the before and after logging periods.

Smolt age	Period	Estimated returns		Effects of	
		with logging	without logging	logging	climate
1+	<LOG	99	99	-	-
	>LOG	159	130	+29/+29.3%	+31/+31.3%
2+	<LOG	84	84	-	-
	>LOG	30	43	-13/-15.5%	-41/-48.8%
total	<LOG	183	183	-	-
	>LOG	189	173	+16/ +8.7%	-10/ -5.5%

of higher productivity with, perhaps, warmer temperatures and more benign flow regimes, density-dependent, biological controls probably predominate. Carnation Creek can be thought of as representative of one end of the physical-biological control continuum envisaged by Allen (1969).

Egg mortality is determined largely by gravel quality and by peak scour events (Holtby and Healey 1986; Scrivener and Brownlee 1982). Gravel quality was adversely affected by the logging practices used in Carnation Creek and there have been significant increases in egg mortality. Over the range of spawner densities that have been observed, there is no evidence that any biological factors (e.g. numbers or size of spawners) affected egg mortality. In other streams where spawner densities are higher and flow regimes are more benign, total egg mortality is affected by spawner densities and the survival of eggs in individual redds is strongly influenced by parental size (van den Berghe and Gross 1984).

Mortality of fry soon after emergence is determined by flow conditions around the time of emergence and some, as yet poorly understood habitat limitation. Except when total fry emergence is greater than 45,000 (which has been the case in only one year), a constant proportion (.54) of emergent fry leaves the stream. Some of the fry that are displaced downstream take up residence in the estuary but there is no evidence that these fry make a disproportionate contribution to adult returns. The number of fry which took up residence in the stream was not affected by the number of fry that emerged and competition among the fry for territories within the stream does not appear to have been an important factor determining resident fry numbers, except when emergence was very large (>15,000 fry/km).

The single most important factor limiting coho production from Carnation Creek is mortality of fingerlings during their first winter in the stream. A large decrease in this mortality (Fig. 2) in the years immediately after logging was responsible for virtually all of the increases in smolt production that were observed. Over-winter mortality of juvenile coho is strongly related to the size at which the fish enter the winter. In the years immediately after logging coho fingerlings were up to 60% larger going into the winter than they had been prior to logging (Fig. 1C) and mortalities during those winters fell correspondingly (Fig. 2).

Winter mortality was also related to the physical integrity of the stream channel. The structural complexity of the stream appears to be an important requirement for high winter survivals. In fact, an increased appreciation of the importance of large organic debris (Tschaplinski and Hartman 1983), side-channel winter habitat (Bustard and Narver 1975) and off-channel sloughs in the over-winter survival of coho has been one of the important contributions of the Carnation Creek study. The importance of over-winter mortality in limiting coho production is becoming more generally recognized (eg. Heifetz et al. 1986).

The logging practices used in Carnation Creek severely damaged the stability of the stream banks in about 40% of the stream utilized by anadromous fishes (Hartman et al. 1987). The removal of large organic debris from the stream channel appears to have been particularly damaging. As a direct result of streamside disturbance there have been significant declines in the amount of summer and winter rearing habitat over at least half of the stream length. These changes have apparently resulted in harsher winter conditions in the stream and increased mortality during the winter. Winter mortality is not related to fish densities during the winter, however, suggesting that the fish are not competing between themselves for prime habitat.

Until recently there has been little evidence to suggest that summer conditions affect smolt production from Carnation Creek. Smolt output was not correlated with any measured summer condition, and in particular, there was no evidence that smolt output varied with minimum summer discharge or with available rearing area at summer low flow. Although summer stream temperatures increased considerably after logging there was no evidence that those higher temperatures adversely affected the juvenile salmon. However, in the aftermath of a major debris torrent in the upper section of the anadromous zone in the winter of 1984, extensive de-watering during the summer has now been observed and rearing populations in the upper sections have fallen. If habitat damage extends further down the stream, which appears likely, then it is highly probable that severe de-watering will affect as much as 40% of the stream. During dry summers this will almost certainly affect smolt production.

The second general principle to emerge from the study is that the initial logging impacts on the coho were effected by changes in the timing of important life-history events. Most of the initial impacts of logging can be understood by first examining the effects that logging had on the temperature regime of Carnation Creek and then by examining the effects that those temperature changes had on the timing of two events, fry emergence and smolt migration. The timing of both fry emergence and smolt migration was disrupted by small changes in stream temperature during the late winter and spring. Earlier fry emergence was largely responsible for the increases in smolt production observed immediately after logging. Earlier smolt migration was partially responsible for the failure of increased adult returns to be realized from that increased smolt production. Significantly, the effects that these temperature perturbations had on the abundance of coho were in opposite "directions" and the net effect on the stock was small.

Third, logging impacts on the coho salmon can be roughly divided into two general types: those related to stream temperatures and those related to channel integrity. Both increased stream temperatures and decreased channel integrity resulted directly from streamside logging. In many respects the natures of these general impacts are quite different (Table 2). Thermal impacts were immediate, were relatively easy to measure, for the most part are easy to understand, and had a modest and positive benefit in that smolt production and adult abundance were enhanced. Furthermore the future time course of the thermal effect can be readily anticipated: the thermal effects are expected to gradually wane as the streamside revegetates. On the other hand, physical effects have been slow to develop, develop in response to chance events such as large storms and debris torrents, are difficult to quantify (but, perhaps, are also readily understood) and are uniformly destructive to fish production. Physical effects are not only difficult to quantify but they are exceedingly difficult to anticipate quantitatively. Subjectively, it seems reasonable to expect that the physical integrity of the stream banks and channel will continue to decline for many years, but exactly how and to what extent cannot be predicted. Anticipating the effects of future change in the stream on the productive capacity of the stream is even more difficult.

Fourth, variability in the survival of smolts in their first few months in the ocean was an important source of the year-to-year variation in coho abundance. Even though adult returns to Carnation Creek were predicted to increase by an average of 9% after logging, escapements actually fell (Fig. 7D; with the exception of the return in 1979 from smolts produced in 1978). This apparent decrease in ocean survival was also observed for coho released from the nearby Robertson Creek hatchery where survival by 1983 was one-third of that observed in 1973 (Fig. 7B). The decline in smolt survival is not due to any change in the fishery exploitation rate but is correlated with the warming of sea surface temperatures off the coast of Vancouver Island.

Modeling the Effects of Logging on the Coho Salmon

The wealth of biological and physical data collected in

Table 2. A summary of the characteristics of the two basic types of logging perturbations that coho responded to in Carnation Creek.

Type	Thermal	Physical
Period of effect (years after logging)	0-?30	5-?100
Major effect	increased stream temperatures	channel instability bank erosion loss of large organic debris loss of winter and summer habitat
Biological effects	changes in timing of critical life history events	increased mortality
Net effect on coho	average 9% increase in adult	negative and increasing, but magnitude unknown
Quantification of effects	yes, easily accomplished	partially, difficult to quantify and difficult to relate physical changes to fish production
Future effects	fairly easy to anticipate stream will cool as bank revegetates	very difficult to anticipate extent and severity of future physical degradation and restabilization
Applicable elsewhere?	limited: absence of effects of higher summer temperatures only to other cool coastal streams; impacts on timing of life history events not detected in other studies	historically yes, but modern logging practices preclude damage to stream bank or channel

Carnation Creek has enabled me to develop a model of the entire life-cycle of coho salmon. The model is comprised of approximately 30 relationships between physical and biological factors (the independent variables) and the survival and growth of coho at most life stages (the dependent variables). Growth in the ocean was not modeled. The individual relationships are linked together so that the output of any one step of the model serves (where appropriate) as the input to the next. Starting with the number of females and their size in the first generation and with time series of physical variables (e.g. temperatures, flows, etc.) and independent biological variables (e.g. fishing pressures) the model predicts escapements for the duration of the time series provided. The relationships of particular importance to this discussion are detailed in Table 3.

I have used the simplest form of the model for this summary in that I follow the progeny of the original spawners for many generations. The real situation is somewhat more complex since there are two smolt age groups and a large percentage of the male smolts (25%) mature precociously. Consequently, the progeny of each brood return to spawn over three years and not one, as I have assumed. Furthermore, the adults return after 18 months in the ocean during which time the progeny of three earlier broods have spawned. The results of using a more realistic but computationally more complex model are similar to those produced by the simple model however.

The time series of physical and biological variables can be used to simulate the number of adults (or numbers at any other life stage) that were actually

Table 3. The important relationships from the coho life history model developed for Carnation Creek. "Modifiers" are the independent variables that were significantly correlated with the observed rate in the "Modeled Relationship". The "Effect on Recruitment" column shows the effect that changing the independent variable (in the direction shown to the left of the arrow) had on recruitment (the number of adults), e.g. "+ –>–" indicates that increasing the independent variable had the effect of decreasing recruitment. The final two columns indicate whether logging or climate determine the level of each independent variable. "FW spring temperature" is the stream temperature during the months February through April. "Habitat quality" is a qualitative measure of stream stability and of the amount of large organic debris present.

COHO MODEL

Modifier	Modeled Relationship	Effect on Recruitment	Affected by	
			logging	climate
gravel quality	egg→fry survival	+ ⇒ +	●	
peak discharge	egg→fry survival	+ ⇒ -	●	
FW spring temperature	fry emergence timing	+ ⇒ +	●	●
	smolt migration timing	+ ⇒ -	●	●
habitat "quality"	winter survival	+ ⇒ +	●	
ocean surface temperature	smolt→adult survival	+ ⇒ -		●
ocean surface salinity	smolt→adult survival	+ ⇒ +		●

observed at Carnation Creek, or they can be set to explore the effects of hypothesized trends in stream conditions after logging.

I used the model in three ways. First, by holding all independent variables constant I examined the relationships between adult production and spawner numbers, i.e. the stock-recruitment relationships. Stock-recruitment relationships are used extensively in the management of fisheries to estimate such stock parameters as required spawner escapements, maximum sustained yields, permissible harvest rates, and relative stock productivities. By holding all of the independent variables constant at pre- or post-logging values the effects of logging on the stock-recruitment relationship can be calculated. Second, by holding all but one of the independent variables constant, I have examined how fish numbers vary over a range of values for that one independent variable. By doing this I could estimate what the effects of specific logging effects were, independent of all other effects. For example, by holding all of the independent variables constant except gravel quality, I could estimate what impacts logging had on the stock that were operating through changes to gravel quality alone. Third, by assuming various time series for recovery after logging (principally forest regrowth and channel restabilization) I have simulated possible futures for the Carnation Creek coho stock.

Stock-Recruitment Relationships

I have calculated the stock-recruitment relationships under four sets of stream conditions: 1) average values of all physical variables before logging, 2) average values three years after logging was completed (the peak of the temperature perturbations but before any physical degradation of the stream was observed), 3) hypothetical conditions 11 years after logging (temperature effects are beginning to wane, gravel quality is seriously degraded and destabilization of the stream channel is accelerating and 4) hypothetical conditions 30 years after logging (the temperatures and the gravel quality have returned to the pre-logging state, but the stream channel remains unstable). I emphasize that scenarios 3 and 4 are possible futures only. The form of the stock-recruitment relationship predicted by the model is of the classical Ricker type (Ricker 1975) with a broad peak of production at intermediate escapements and declining production at higher escapements (Fig. 8). The stock was most productive immediately after logging and is predicted to be least productive 30 years after logging (Table 4: productivity is gauged by the R/S or recruits/spawner ratio. R/S values of 3-4 are typical of coastal coho stocks). Before logging, maximum surplus production was attained with between 50 and 60 female spawners (about 18 to 20 females per kilometer of stream or slightly below the average before logging); and 3) the exploitation rate at maximum sustainable yield varies from 61%, 30 years after logging when the stock is predicted to be least productive to 75%, 3 years after logging when the stock was most productive. Currently the average exploitation rate is approximately 65%. Under the stream conditions that might be present 30 years after logging the Carnation Creek stock would be somewhat over-exploited. However, under stream conditions like those observed before logging and thus far after logging the stock would remain healthy provided that all of the other production parameters remained near average. In fact, marine survivals independent of any logging effects have not remained constant but have declined by as much as 60% since the mid-seventies (Fig. 7B). This decline in ocean survival is partially responsible for the absence of large increases in adult returns following the increased smolt productions observed after logging. As a result the Carnation Creek stock and probably most others in the Barkley Sound area were seriously over-fished in the early eighties.

Simulations of Single Factor Effects

In the second set of simulations I varied, singly, gravel quality, peak winter discharge, stream temperatures, ocean survival (smolt survival independent of logging effects) and channel stability. Each of these variables, (for temperatures a set of 5 variables), was varied over the observed range of the past 15 years. All other independent variables in the model were held constant. The results (Fig. 9) are measures of the sensitivity of coho production to variation in each of the variables. The variables in descending order of importance were: ocean survival > stream temperature = channel stability > peak winter flows = gravel quality. The sensitivity of coho production to these variables, when production is measured by adult returns follows the reverse chronological order in which the variables affect survival.

The model can also be used to estimate the effects of logging independent of climatic factors by using the time series of stream temperatures predicted in the

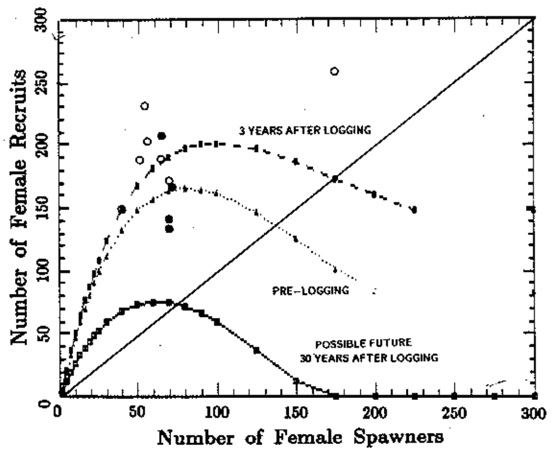
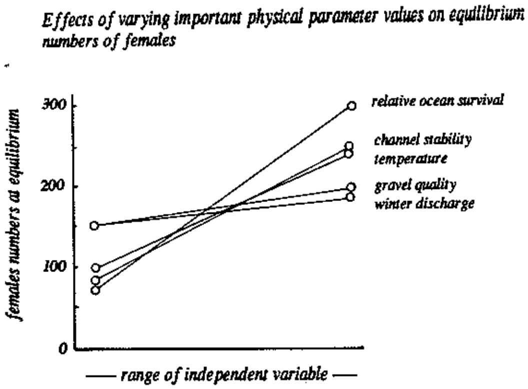


Figure 8. Stock recruitment curves for the Carnation Creek coho stock. The curves were calculated using the coho model by varying the numbers of spawners and calculating the eventual returns while holding all independent variables constant. The results of this simulation with three sets of assumptions are shown: i) all independent variables were set to average conditions observed before logging; ii) all independent variables were set to average conditions three years after logging, i.e. maximum coho productivity; and iii) all independent variables were set to hypothetical conditions 30 years after logging, i.e. minimum coho productivity. The closed circles are the actual observed values before logging and the open circles are the actual observed values after logging. Note that the stock-recruitment curves were not fitted to the observed values but are the predicted relationships generated by the coho model described in the text. The diagonal line is the replacement line.

absence of logging (described elsewhere in this volume), and by setting other physical variables to the average values observed before logging. On average, logging produced a 9% increase in adult numbers (Table1). Had logging not occurred, the model estimates that adult numbers would have declined by about 5.5% due to natural variation in stream temperatures. (Both of these estimated changes in adult numbers assume constant ocean survival of smolts and are calculated prior to all fisheries.)



relative ocean survival	*03 - 18*
relative channel stability	*unstable - stable*
temperature	*150 - 400 CTU (spring)*
Fredle index	*2 - 38*
peak winter discharge	*60 5 m3/sec*

Figure 9. Model sensitivity to variation in the independent variables. The curves were calculated using the coho model by setting all independent variables to the conditions observed before logging. The five independent variables shown were then varied singly over the range shown and the number of females at equilibrium was calculated. (This number is found where the stock recruitment curve crosses the replacement line.) Note that the ranges of the independent variables have been depicted as going from severe (in terms of their effects on recruitment) on the left to benign on the right so that in some the values of the variables are reversed (e.g. peak flows).

Of particular interest in these result is the equivalence of temperature effects and effects of logging on the integrity of the stream channel (Fig. 9). Remembering my general characterizations of these two general logging impacts (Table 2) it is fairly easy to anticipate the model projections of future time series of coho abundance after logging (discussed in the next section).

Speculations on the Future

Lastly, I simulated a possible future time series of smolt and adult abundance (Fig. 10). In this simulation logging occurred in the 75th year. The model predicts nine years of heightened production immediately after logging due to the predominance of temperature effects. This short period is followed by 30 years or so of declining abundance as the temperature effects wane with revegetation and the physical effects begin to predominate. Full recovery

Table 4. Stock-recruitment parameters for the Carnation Creek coho stock under four sets of assumptions. All values were calculated at the point of maximum sustainable harvest. The actual harvest can be calculated from the exploitation rate and the spawner density. R/S or recruits per spawner is a measure of stock productivity. Productivity is highest immediately after logging when the beneficial thermal effects are greatest and there have been few deleterious physical effects. Conversely, productivity is lowest 30 years after logging when stream temperatures have returned to pre-logging levels and physical effects are greatest. This modeling assumes that ocean conditions are constant.

Time	Females/km	Adults/km	R/S	%exploitation
pre-logging averages	17.8	40.6	3.01	66.7
3 yr. post-logging	26.7	60.9	4.00	75.0
11 yr. post-logging	24.2	55.2	2.78	64.0
30 yr. post-logging	12.2	27.8	2.54	60.7

does not take place for almost 100 years after logging. This result is purely speculative of course, since the rates of channel destabilization and restabilization, gravel quality and stream temperatures are hypothetical. Nevertheless the stability of the channel was not assumed to get any worse than it already is, just 5 years after the completion of logging. The temperature effect does appear to be lessening and it is reasonable to expect that the canopy will close over the stream 15-20 years from now as the model assumed. It is probable that large organic debris will continue to disappear from the system for at least the next 50 years (Grette 1985) and recovery may be further delayed by renewed logging activity in the upper watershed.

When the simulations are run deterministically, that is to say without environmental uncertainty, the projected time series of smolt production and adult (female) abundance appear disarmingly simple and the predicted abundances, even during the worst years are not cause for concern (Fig. 10). However, when realistic levels of environmental uncertainty are added, including natural levels of variability in ocean conditions, smolt production and escapements become very erratic (Fig. 11). At various times female escapements fall below 20 fish. (Note that an escapement almost this low has already been seen after logging!). Predicted reductions to fewer than 20 female spawners of stock occurred anytime from 20 to 100 years after logging. Severe depressions in adult numbers were most frequent when logging damage to the stream channel and ocean survivals were at their worst simultaneously, and there was a succession of severe winters.

Several reviewers of this paper have been particularly critical of this particular section of the paper, and especially its apparent pessimism. Although the model is being extended far into the future in what is clearly a speculative exercise, I have carefully avoided making arbitrary decisions about the future condition of the stream. In particular, conditions in the stream channel were not assumed to get any worse than has already been observed. Furthermore, the expected time course of recovery is based on my understanding of the latest research results concerning the importance of large debris and its dynamics in logged-over streams (Bisson et al. 1987; Grette 1985) and the dynamics of canopy closure. The predictions of occasional dips in female escapements to 20 do not appear unrealistic in light of returns in recent years. To assert, as some reviewers have that recovery times will be very rapid is, in my opinion, to fly in the face of increasing evidence that historical logging practices severely disrupted the normal dynamics of large organic debris in small streams (Bisson et al. 1987). However, only time, or further research into the current status of streams logged decades ago, will help resolve the question of the future state of Carnation Creek.

CONCLUSIONS

The coho salmon in Carnation Creek responded to two different kinds of habitat perturbations produced by logging (Table 2). Thermal effects were immediate and operated through changes in the timing of critical life history events. The thermal perturbation has had a modest beneficial effect on coho production. The large effects that the thermal perturbations had on

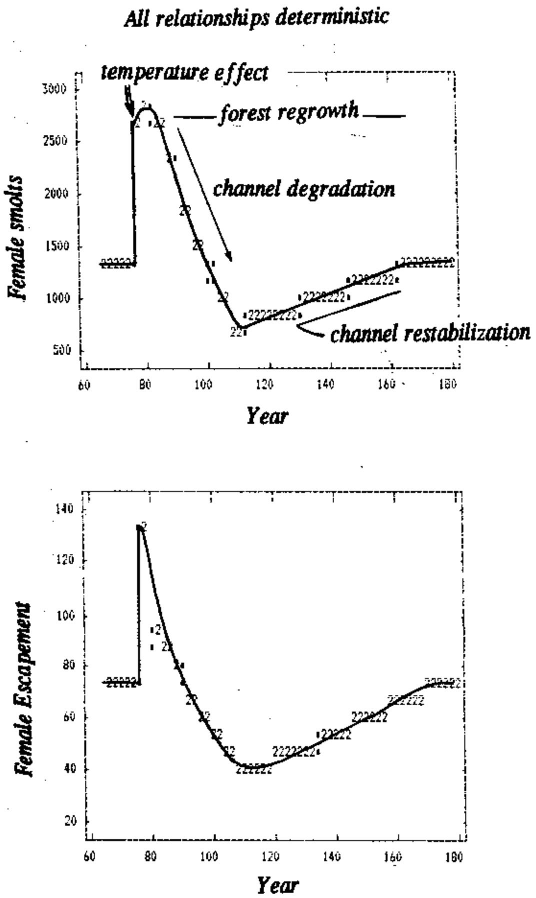


Figure 10. Hypothetical time series for the Carnation Creek coho stock in the aftermath of logging. All of the relationships are deterministic which means that there is no uncertainty in the model's predictions. The major events following logging in year 75 are shown. The model assumes that 40% clear-cutting occurred in year 75 and that there was no further stream disturbance.

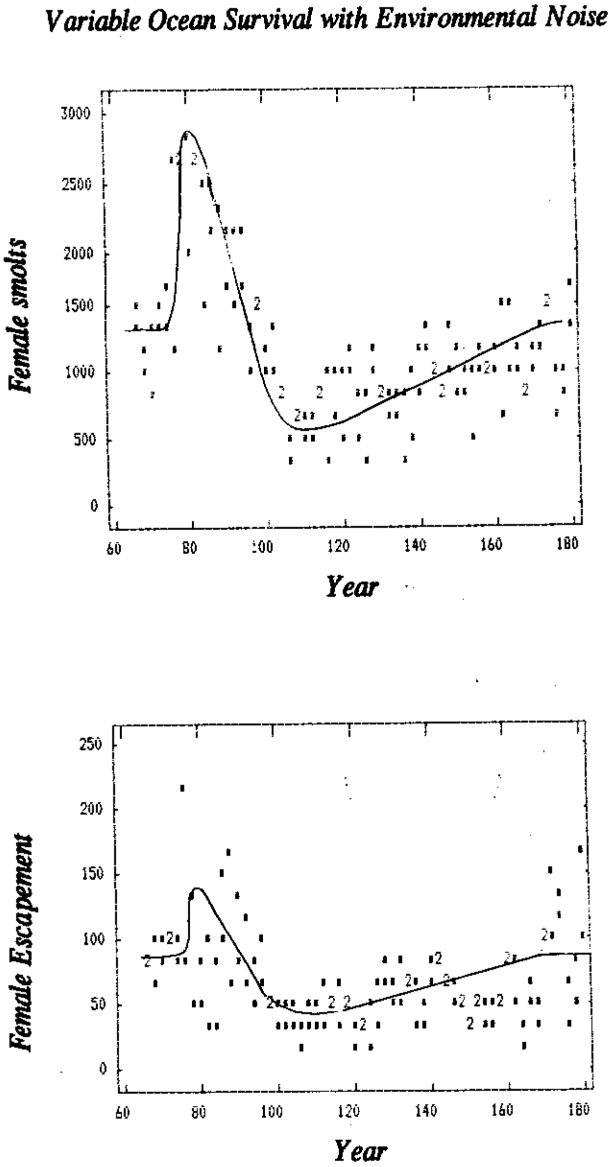


Figure 11. Hypothetical time series for the Carnation Creek coho stock in the aftermath of logging. This is the same simulation as shown in Fig. 10 except that realistic levels of environmental variation have been introduced. On several occasions predicted escapements fall below 20 females.

the coho are interesting in several respects. First, the thermal effects were indirect; in other words the temperature changes themselves did not change survival or growth rates. Instead, the temperature changes affected the timing of fry emergence and smolt migration. Second, the temperature perturbations were separated in time from their effects. In the case of early fry emergence, the effects on survival of elevated temperatures during February and March were not realized until the following winter. Third, the temperature effects came at an unexpected time of the year, late winter and early spring. Concern over the effects of logging on stream temperatures has typically focused on summer temperature elevations. In cool coastal streams such as Carnation Creek, temperature elevations during the summer probably increase temperatures into the preferred range of coho. Fourth, the temperature changes observed in early spring affected two different life stages of coho in "opposite" directions. The idea that habitat perturbations can affect different life stages simultaneously but differently is not novel, but was well demonstrated in Carnation Creek.

The coho have also been affected by physical changes to the stream caused by logging. In contrast with the thermal effects of logging, the physical effects were much slower to appear, are accelerating and have been entirely negative. Like the thermal effects, the physical effects stem largely from logging activity adjacent to and in the stream. The loss of stream habitat that has occurred affects juvenile coho throughout the time that they are in the stream. Loss of winter habitat has affected the fish sooner but de-watering of summer habitat now appears to be occurring as well. Loss of winter habitat has already significantly reduced the benefits of warmer stream temperatures on coho smolt production. However, the full extent of the effects of stream degradation will be seen only when the streamside revegetates and the temperature effects moderate. The future effects of summer habitat loss are uncertain.

The Carnation Creek study has certainly provided a wealth of information about coho salmon in a small coastal stream. Perhaps the most important information to come out of the Carnation Creek coho studies, and certainly the most widely cited, concerns the role of side-channels in over-winter survival. The early side-channel studies can now be seen as a specific indication of the more general importance of the wintertime to juvenile coho. To date, all of the important effects of logging have affected winter survivals, either directly in the case of physical effects or indirectly in the case of temperature effects.

A more philosophical conclusion, but an equally important one, is that the proper evaluation of the impact of a habitat perturbation on an animal population must include the entire life cycle. There are at least three components to this generality. First, it is apparent from the results that I have presented above, that looking at abundance of any two life stages can lead to diametrically opposed conclusions. Consider, for instance what conclusions are possible if adult returns were the only abundance estimate collected and then consider what conclusions would have been drawn from the smolt numbers alone. Second, it is also apparent that impacts on one life stage propagate through time. For instance, temperature increases in early spring led to earlier fry emergence, then to larger fingerling size, increased over-winter survival and so on. Finally, the time scale of any impact study must be based on the time scale of the processes involved. Five years for the study of post-logging impacts was an enormous span for research, yet it was barely adequate to give even an indication of the physical changes that are yet to come in the stream.

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