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ROBERT E. BILBY AND PETER A. BISSON

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Emigration and Production of Hatchery Coho Salmon (*Oncorhynchus kisutch*) Stocked in Streams Draining an Old-growth and a Clear-cut Watershed

Robert E. Bilby

Weyerhaeuser Co., Western Forestry Research Center, Centralia, WA 98531, USA

Peter A. Bisson

Weyerhaeuser Co., Technology Center, Tacoma, WA 98477, USA

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Downstream movement of coho salmon fry (*Oncorhynchus kisutch*) stocked in old-growth and clear-cut watersheds occurred in three phases: (1) a brief period of heavy emigration immediately after stocking, (2) relatively little movement throughout most of the summer, and (3) intermittent heavy emigration during early autumn freshets. Coho emigrated whenever a streamflow change $\geq 3\% \cdot d^{-1}$ occurred, but movement nearly ceased at flows above a certain level. Temperature changes were less important than discharge in triggering movement. When high densities were stocked, emigrant fry were smaller than residents. When low densities were stocked, emigration after the initial pulse of downstream movement was generally lower and there were no size differences between emigrants and residents. Production in the clear-cut was greater than in the old-growth watershed. Proportionately fewer fish emigrated from the old-growth stream, but when population densities were high, mortality in the old-growth exceeded the clear-cut. Greater emigration from the clear-cut site was possibly related to a scarcity of pools. Although the old-growth stream possessed better rearing habitat, less food may have been available, as suggested by gross photosynthesis rates 50% lower than in the clear-cut stream. Coho production therefore appeared to be most strongly influenced by trophic conditions, while volitional residency was most strongly influenced by habitat quality.

Les déplacements vers l'aval d'alevins de saumon (*Oncorhynchus kisutch*) ensemencés dans des bassins versants à peuplement mûr ou faisant l'objet d'une coupe rase se sont effectués en trois phases : 1) une brève période d'émigration marquée immédiatement après l'ensemencement, 2) relativement peu de déplacements pendant presque tout le reste de l'été et 3) une émigration marquée intermittente pendant les crues du début de l'automne. Les cohos ont émigré quand le débit variait de $\geq 3\ \% \cdot j^{-1}$ mais les déplacements ont presque cessé à des débits supérieurs à un certain volume. Les variations de la température étaient moins importantes que le débit dans le déclenchement des migrations. Quand l'ensemencement avait lieu à des densités élevées, les alevins émigrants étaient plus petits que les résidents. Par contre, quand les alevins étaient ensemencés à de faibles densités, l'émigration après la pointe initiale de déplacement vers l'aval était généralement réduite et il n'y avait aucune différence de taille entre les émigrants et les résidents. La production dans le bassin versant faisant l'objet d'une coupe rase était plus élevée que dans le bassin versant à peuplement mûr. Un nombre proportionnel moins élevé de poissons ont émigré du cours d'eau à peuplement mûr mais quand les densités étaient élevées, la mortalité à cet emplacement dépassait celle observée dans le bassin versant faisant l'objet d'une coupe rase où le taux d'émigration plus élevé était possiblement lié à la rareté des mares. Quoique le bassin versant à peuplement mûr offrait de meilleures zones de croissance, il semblait contenir moins de nourriture comme le portent à croire des taux de photosynthèse bruts qui sont 50 % moins élevés que ceux observés dans le bassin versant faisant l'objet d'une coupe rase. Les niveaux trophiques semblent donc fortement influer sur la production de cohos tandis que le séjour volontaire était plus fortement touché par la qualité de l'habitat.

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Large numbers of coho salmon (*Oncorhynchus kisutch*) frequently emigrate from natal streams after emerging from spawning redds (Chapman 1962). Downstream movement of these fry tends to be greatest immediately after emergence, but often continues at a lower level throughout the summer and autumn. The timing and magnitude of emigration are driven by environmental factors whose influences are known from only a few case studies and which apparently are not consistent from stream to stream. Emigration was originally believed to be the result of accidental displacement of fish that failed to find hiding places among the stream's stony substrate at night and were unable to maintain a visually oriented feeding station (Hoar 1958). However, recent evidence has pointed to the existence of a wide variety of environmental cues that facilitate increased downstream movement. The nature and importance of such cues has received widespread attention because emigration coho from nursery streams may account for more than half of the initial fry

population. The survival to maturity of presmolt emigrants that enter salt water is believed to be very low (Mason 1975; Crone and Bond 1976; Washington 1981; Holtby and Hartman 1982), although some emigrants establish themselves in lower stream reaches if suitable habitat can be located (Chapman 1962; Mason 1969; Scrivener and Andersen 1984).

The factors influencing downstream movement of coho fry include both physical and biological conditions. Chapman (1962) noted that initial coho fry densities may exceed a stream's carrying capacity, and aggressive behavior among individuals competing for feeding territories results in downstream displacement of subordinates. Mason and Chapman (1965) demonstrated a positive correlation between level of aggression and fry emigration from artificial stream channels, and Chapman (1962) found that fry emigration rate was proportional to the initial population density in three Oregon streams. However, in Carnation Creek, a relatively short Vancouver Island stream prone to severe freshets, fry movements were principally associated with freshets and most of the fish leaving the vicinity of spawning areas were transported completely out of the stream system (Hartman et al. 1982). In addition to being associated with population pressure and discharge peaks, coho fry movements have coincided with lunar phases (Mason 1975), temperature change (Keenleyside and Hoar 1954; Chapman and Bjornn 1969; Hartman et al. 1982), and turbidity increase (Noggle 1978; Berg 1982; Sigler et al. 1984). Downstream movements may also result from volitional attempts to locate suitable overwintering habitat (Bustard and Narver 1975a, 1975b; Peterson 1982; Tschaplinski and Hartman 1983).

Research to date has focused on wild populations. However, stocking of hatchery coho fry has become common, especially in watersheds where escapement of adult fish is below the number needed to fully seed the system or where habitat above barriers is perceived to be underutilized. It is unknown if hatchery fry exhibit the same emigration patterns as wild fish, or if their movement is triggered by similar environmental cues. The impact of logging on emigration and production is also not fully understood. Hartman et al. (1982) found that clear-cut logging along Carnation Creek caused increased water temperatures and earlier emergence of coho from spawning gravel in the spring. As a result, emigration began earlier in the year, but resident fry gained the advantage of a longer growing season. Higher salmonid production rates in other open-canopied streams in the Pacific Northwest have been attributed to a variety of causes, including increased autotrophic production resulting from more sunlight reaching the channel (Murphy et al. 1981; Weber 1981; Hawkins et al. 1983; Walter 1984; Duncan and Brusven 1985), increased water temperature (Narver 1972; Osborn 1980), and increased foraging efficiency (Wilzbach 1985). The objective of our study was to identify the important environmental clues triggering the emigration of hatchery coho fry stocked in an old-growth coniferous forested watershed and a clear-cut watershed and to relate the patterns of downstream movement to differences in summer production between the two sites.

Study Area

The study was conducted in the headwaters of the Deschutes River system (46°43′N, 122°23′W), which drains the foothills of the Cascade Mountains of western Washington. West Fork Creek (the old-growth site) drains an 850-ha watershed consisting of undisturbed coniferous forest dominated by Douglas-fir, western hemlock, and western red cedar. Most of the watershed of the adjacent 255-ha upper Deschutes River study site (the clear-cut site) was logged in 1974–75 and replanted with Douglas-fir in 1975–76. The riparian zone of this stream is dominated by small willows, red alder, salmonberry, and herbaceous vegetation. Differences in discharge between the two streams are less than would be expected based on differences in drainage area due to greater precipitation in the clear-cut watershed. Mean annual discharges at the clear-cut site were 0.65 $m^3 \cdot s^{-1}$ in 1982 and 0.64 $m^3 \cdot s^{-1}$ in 1983. Corresponding values for the old-growth site were 1.12 $m^3 \cdot s^{-1}$ in 1982 and 1.11 $m^3 \cdot s^{-1}$ in 1983.

TABLE 1. Habitat composition of the study streams, following the classification system of Bisson et al. (1982).

	Deschutes River (clear-cut)	West Fork Creek (old-growth)
Midsummer dimensions		
Length (m)	377	451
Area (m^2)	872	1502
Volume (m^3)	120	277
Pool habitat (% total area)		
Backwater	5.6	6.0
Scour	16.1	25.7
Plunge	8.7	23.9
Secondary channel	2.0	2.1
Dammed	0	1.1
Total pool habitat	32.4	58.8
Riffle habitat (% total area)		
Low gradient riffles	23.3	14.7
Rapids	3.3	8.1
Cascades	41.0	18.4
Total riffle habitat	67.6	41.2

Reaches of stream chosen for study were bounded by a fish trap on their downstream end and a falls impassable to upstream movement by salmon fry at the upstream end. The clear-cut study reach was shorter and possessed a smaller stream area and volume than the old-growth reach (Table 1), and it also had a slightly higher gradient. The clear-cut stream channel was nearly devoid of large woody debris, having been cleaned following logging. As a result, the relative abundance of pool habitat in the clear-cut stream was much lower than in the old-growth stream, where the channel was heavily loaded with woody debris. At midsummer stream flows the frequency of pool habitat in the clear-cut site was approximately half that of the old-growth stream. The remainder of the surface areas at both sites consisted of various types of riffles.

Only two fish species resided in the streams naturally, cutthroat trout (*Salmo clarki*) and shorthead sculpin (*Cottus confusus*). Average midsummer biomasses and densities of trout on an areal basis during the three years prior to the experiment were 1.8 times and 2.5 times greater, respectively, in the clear-cut site than in the old-growth site (Bisson and Sedell 1984). Likewise, sculpin biomasses and densities prior to the experiment were highest in the clear-cut watershed, being 3.0 times and 5.3 times greater, respectively, than in the old-growth stream. Neither resident species exhibited migratory tendencies, and over the period of study, very few cutthroat or scuplin entered the fish traps. Therefore, only the emigration patterns of coho are reported here. We do not know to what extent the downstream movement and production of coho in the two

watersheds were affected by differences in the abundance of resident trout and sculpin populations between the old-growth and clear-cut watersheds.

Care should be taken in extrapolating the results of this study in both space and time. Conditions in the streams reflected watershed history, but we studied only single examples of old-growth and clear-cut headwater tributaries. While the watersheds were adjacent to each other, they were not replicates, and the two years in which emigration was monitored were hydrologically dissimilar. For this reason, the results are presented as case studies of two different watersheds in two different years. These limitations must be considered when applying the results of this study to other drainages.

Methods

Coho salmon fry from the Puyallup River Salmon Hatchery were planted in the study streams on June 15, 1982, and again on May 5, 1983. The difference in stocking time and fish size was dictated by the timing of fry availability at the hatchery. In 1982 the initial stocking density was twice the normal stocking rate used by the Washington Department of Fisheries; in 1983, each stream was stocked according to standard procedures, which were based on the standing stocks of wild coho in Oregon coastal streams (Chapman 1965). The two different initial densities were chosen to evaluate the effect of population pressure on survival, growth, and emigration. In 1982, average size at release was 1.88 g whereas in 1983 the fry were much smaller, averaging 0.75 g at stocking. No differences in size or condition factor existed between the fish released into the two study streams, based on subsamples of fry planted at each site.

Movement of fish from the streams was monitored with permanently installed fish traps at the downstream end of each study reach. The fish traps were constructed of steel mesh screening bolted to concrete footings which were, in turn, anchored to bedrock. A single opening in each screen led to a baffled, wooden live-box. The traps were emptied daily for 4 wk immediately after stocking when emigration was heavy. When the initial emigration had subsided, the traps were emptied every 3 d, although on several occasions the traps were left as long as 7 d between checks. On three occasions during 1983, high discharge forced the lid off the live-box in the old-growth site. These occasions occurred 1, 2, and 10 d after stocking during a period of heavy downstream movement of the fish. Therefore, we estimated the number of coho that would have been expected to emigrate on those dates based on the ratio of emigration rates between the old-growth and the clear-cut sites observed the same number of days after stocking in 1982.

Coho remaining in the streams were sampled during summer and fall. Several randomly chosen examples of each habitat type (Table 1) were isolated with blocking nets and electrofished at least three times. The density of fish within individual habitats was estimated by the removal summation technique of Carle and Strub (1978). The total population of coho in the stream was determined by multiplying the average density obtained for each habitat type by the frequency of that habitat type in the study section. Biomasses were based on length–weight regressions derived from samples of 30 fish selected at random from each stream on each date. Mortality was estimated as the difference between the estimated population size and the number of downstream migrants. Emigration was expressed as the percent of the remaining stream population collected in the trap each time the trap was emptied. Such expression facilitated a more appropriate comparison of downstream movement than the absolute number of coho fry leaving the streams. Production estimates followed Chapman (1978) in which instantaneous daily rates of growth and "mortality" (i.e. actual mortality plus emigration) were assumed to be exponential. We further assumed that the distribution of coho during the first measurement interval was reflected in the relative proportions of fish observed in each habitat during the first census, i.e. all fish captured in a particular habitat had actually spent the entire measurement interval there. However, because fish were not individually marked, these assumptions were untested.

Discharge for the two streams was estimated by correlating readings on rated staff gauges with simultaneous readings on a nearby stream with a continuous flow recorder. Recording thermographs were installed in both streams prior to fry stocking and operated continuously throughout the study periods. Average daily water temperature was taken to be the mean of the daily minimum and maximum. Daily turbidity values in the two streams were measured during the study period in 1983. Automatic pump samplers composited four samples drawn at 6-h intervals in one bottle. Bottles were collected monthly and turbidity was measured with a nephelometer.

Gross photosynthesis by stream periphyton was measured approximately every 10 d using light and dark watertight rectangular chambers (66 × 31 × 8 cm) fitted with submersible recirculating pumps (Bott et al. 1978). Trays of streambed substrate (40 × 25 cm) that had been left undisturbed in the streams for at least 3 wk were placed in the two watertight chambers, which were submerged during the measurement period (0.5–2 h, depending on the rate of oxygen production). All measurements were taken between 10:30 and 14:00 PST and probably represent peak daily production rates. Light intensity immediately above the chambers was recorded every half hour during the incubation period with a dome solarimeter. Dissolved oxygen concentrations were measured with an oxygen–temperature probe that was fitted into the wall of the chamber. Gross photosynthesis was calculated from the change in dissolved oxygen concentration during the incubation period using a photosynthetic quotient of 1.2 (Wetzel and Likens 1979).

Results and Discussion

Seasonal Patterns of Emigration

During both 1982 and 1983, coho exhibited elevated emigration rates for about 2 wk after stocking; however, emigration from the clear-cut site continued at a higher rate for a slightly longer period of time (Fig. 1). In 1982, approximately 42% of the coho fry left the stream in the clear-cut in the first 14 d after stocking, while 37% moved out of the old-growth site. For 1983, these values were 69% from the clear-cut and 55% from the old-growth. During July and August 1982, emigration rates remained relatively low, usually $>1\% \cdot d^{-1}$ (Fig. 1A). Downstream movement of fish, although infrequent, was generally higher from the clear-cut than the old-growth watershed during this period although several small peaks of emigration were seen in both streams. Substantial increases in downstream movement occurred in mid-September and early October. The mid-September emigration rates were the highest observed in 1982, excluding those immediately after stocking. The emigration rates in October were somewhat lower than those of

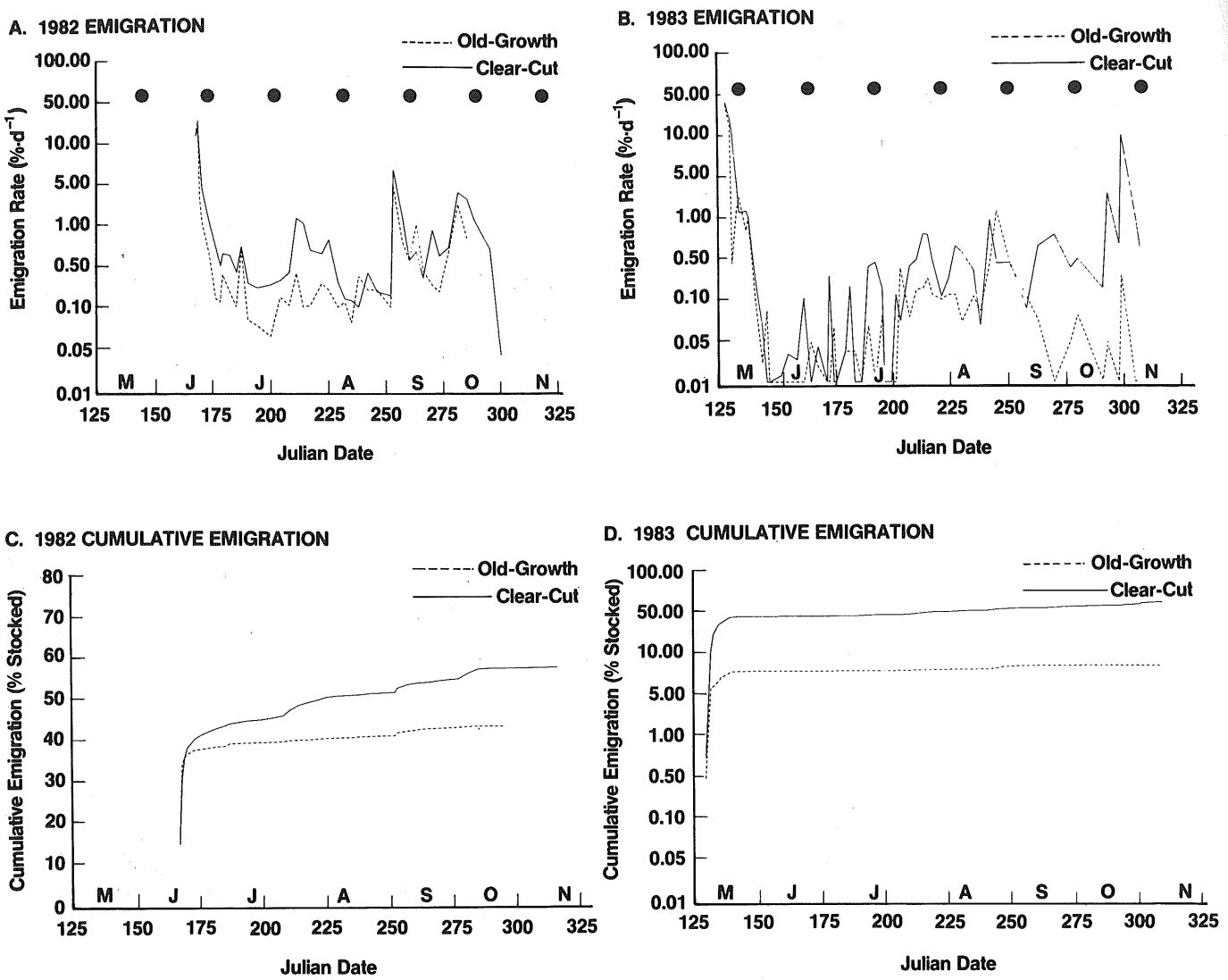

FIG. 1. (A) Emigration, as percent of resident population per day, of coho salmon from the study sites during 1982. Rates are plotted on a logarithmic scale. Solid circles indicate a new moon. (B) Coho emigration during 1983. (C) Cumulative emigration during 1982, expressed as the cumulative percent of the number of fish initially stocked in the study sites. (D) Cumulative emigration during 1983.

September but were still substantially elevated over July and August values.

Overall emigration from the two streams in summer 1983 was lower than in 1982 (Fig. 1B). Downstream movement continued to be higher from the clear-cut than the old-growth site. Very little emigration took place in June and July, with some small increases in emigration in August. Increased movement from the old-growth watershed occurred in early September, with a slight rise noted at the same time in the clear-cut site. Emigration from the old-growth site declined after the early September increase; however, coho in the clear-cut stream displayed high levels of downstream movement throughout mid- and late-October.

We separated emigration of hatchery coho fry into three distinct phases from spring to autumn: (1) massive emigration occurring immediately after release of the fish, (2) a period of little movement that spanned the summer months, and (3) an increase in downstream movement observed during early autumn. The spring and autumn movements appeared to be triggered by different factors. Emigrant fry during the immediate poststocking pulse of movement were smaller than the average size of resident fish (Fig. 2A–2D). This difference in size was consistent with the hypothesis that territorial interactions among recently emerged juvenile coho displace smaller, subordinate individuals (Chapman 1962; Mason and Chapman 1965). Significant differences (paired t-test, $p < 0.05$) between resident and emigrant fish were observed throughout the summer of 1982, the year of high initial population densities. There were no differences between the sizes of residents and emigrants during 1982 in the old-growth watershed. Lack of size differences between emigrant and resident coho during autumn suggested that territorial displacement was not the causative factor, but that a general emigration of the population was taking place.

Environmental Factors Triggering Emigration

The high rate of emigration immediately after stocking could not be attributed to any single environmental cue. Emigration always occurred following release of the fish, reached a peak 1–2 d later, and then declined precipitously afterwards (Fig. 1). Increases in downstream movement during the sum-

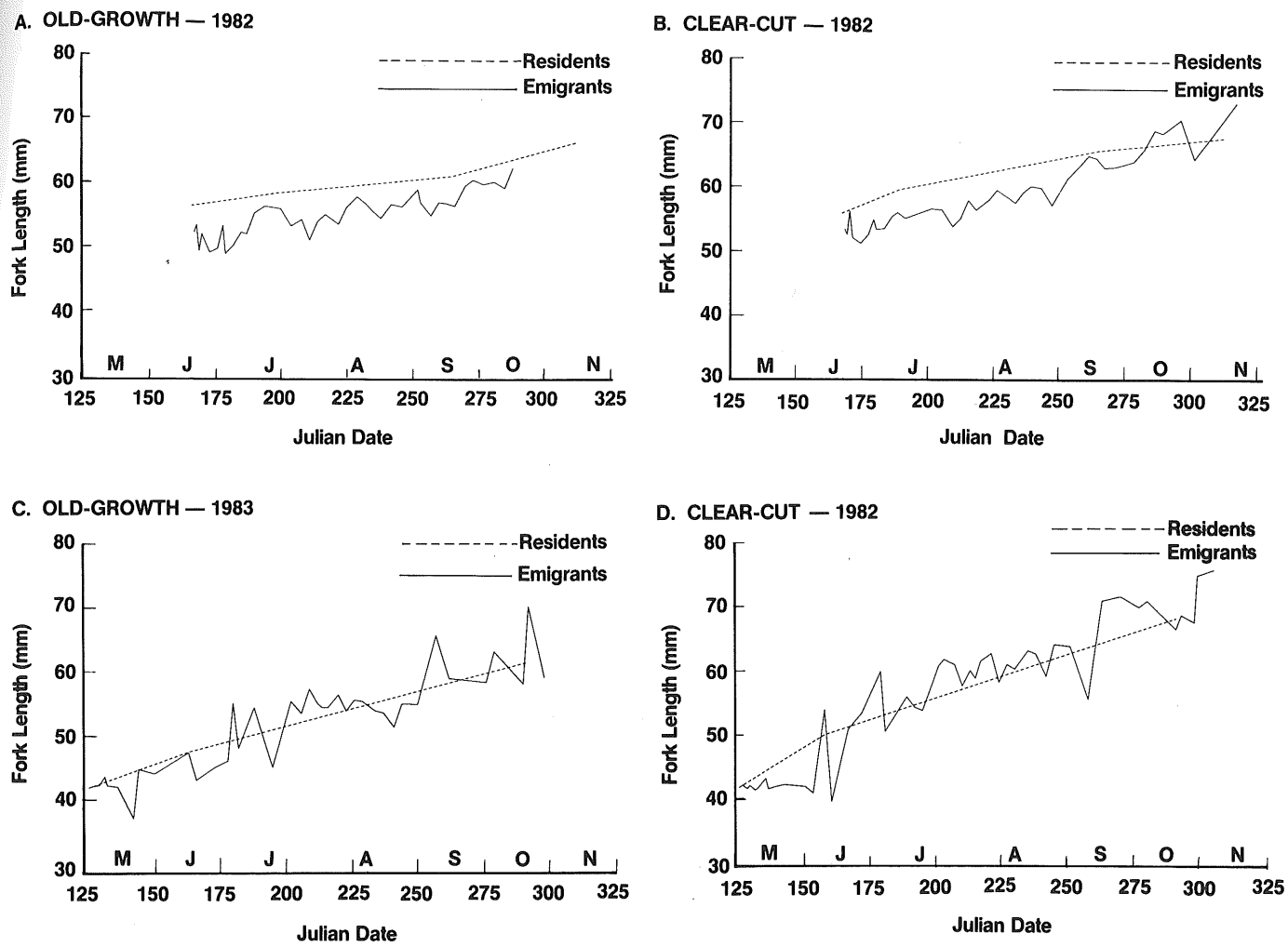

FIG. 2. Average lengths of emigrant and resident coho during (A and B) 1982 and (C and D) 1983.

mer and autumn coincided with flow and temperature changes. Streamflow in the old-growth stream was always higher than in the clear-cut (Fig. 3) owing to the larger watershed area. Substantially higher flows were experienced in 1983 than in 1982, when discharge was very stable throughout the summer. In 1982 peak flows were only 0.18 $m^3 \cdot s^{-1}$ in the clear-cut site and 0.36 $m^3 \cdot s^{-1}$ in the old-growth site. During the unusually wet summer of 1983, these values were exceeded repeatedly and peak mean daily flows were as great as 0.80 and 1.40 $m^3 \cdot s^{-1}$ in the clear-cut and old-growth watersheds, respectively. Freshets were often accompanied by increases in downstream movement of coho fry (Fig. 1A and 1B). This pattern was most evident in the clear-cut site, where increased emigration coincided with moderate flow increases during July and August. Flow changes in the old-growth stream during the summer of 1982 also appeared to coincide with periods of increased emigration, although the pattern was not as pronounced as it was in the clear-cut site due to the overall lower level of fish movement from this watershed. Periods of heavy emigration from both streams in the autumn also corresponded with increases in discharge.

The relationship between downstream movement and stream-flow differed somewhat between the two summers (Fig. 1C and 1D). In 1983, emigration increased with discharge up to a threshold level which was about 0.15 $m^3 \cdot s^{-1}$ in the clear-cut stream and 0.35 $m^3 \cdot s^{-1}$ in the old-growth site. Above these threshold discharges, downstream movement essentially ceased (Table 2). Flows that triggered the early autumn emigration of coho were, however, below these threshold values. Excluding the emigration rates immediately following stocking and those occurring when streamflow peaks exceeded the threshold, downstream movement from the streams in both years was primarily related to discharge changes (Table 3). There was an increase in the rate of movement whenever a change in daily flow >3% occurred. Flow changes greater than $3\% \cdot d^{-1}$ in early or midsummer elicited a mild increase in fry emigration, but discharge changes of a similar magnitude in early September resulted in much higher emigration rates.

Daily temperature maxima were generally higher and daily minima lower in the clear-cut study stream than in the old-growth site (Fig. 3C and 3D). Average diurnal temperature range during 1982 in the clear-cut stream was 4.7°C compared with 1.3°C in the old-growth stream. During the cooler, wetter summer of 1983, average diurnal temperature range in the clear-cut site was 3.4°C and in the old-growth site was 0.5°C. Midsummer temperature peaks in both streams were greater in 1982 than 1983. Differences in thermal regimes between the two streams were partly a consequence of riparian vegetation. The dense canopy over the old-growth site not only shaded the stream from direct sunlight during the day, but also acted as an

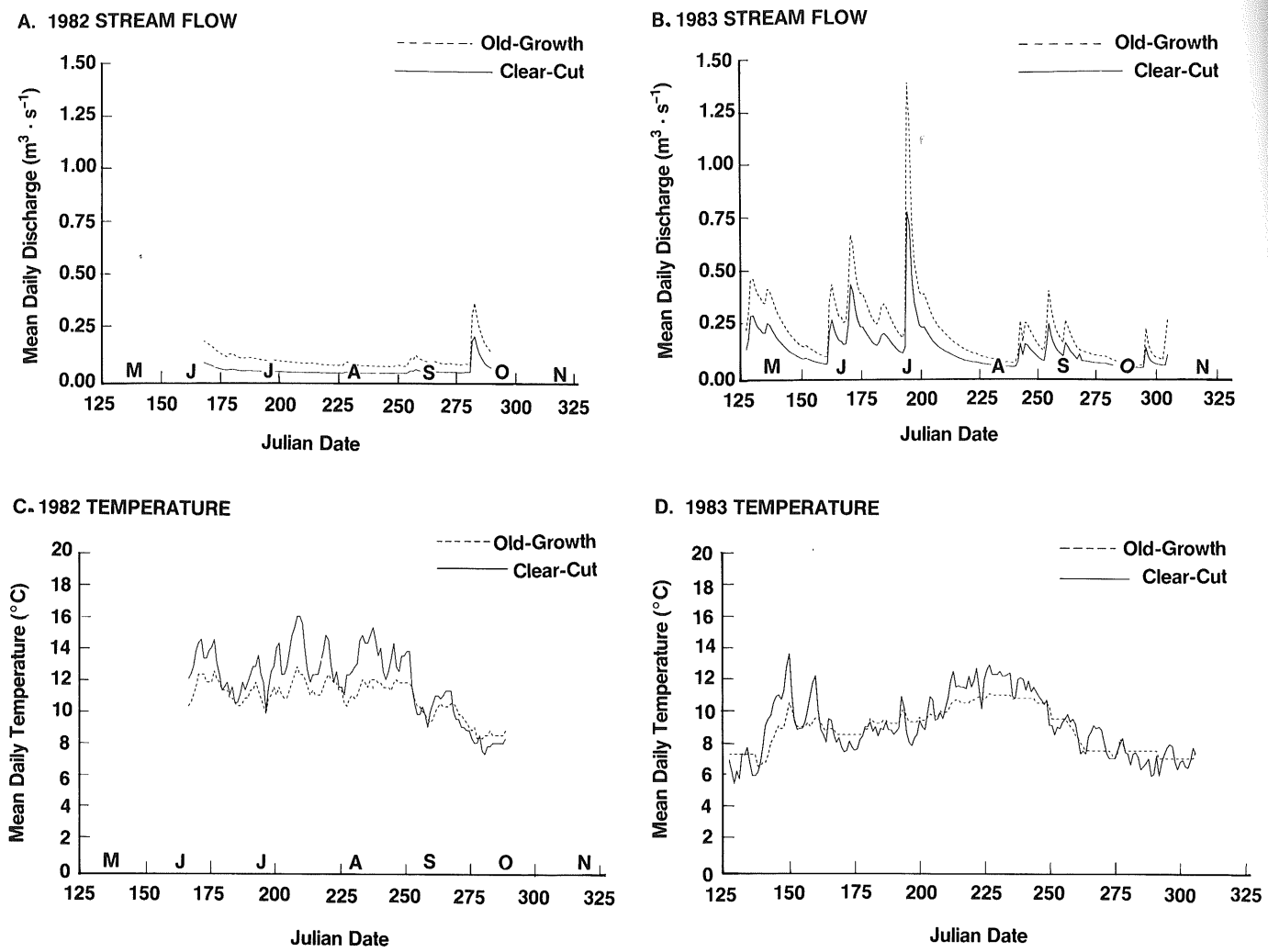

FIG. 3. Estimated (A and B) average daily streamflow and (C and D) average daily temperature during 1982 and 1983.

TABLE 2. Average emigration rates during 1983 above and below threshold discharges of 0.15 $m^3 \cdot s^{-1}$ in the clear-cut and 0.35 $m^3 \cdot s^{-1}$ in the old-growth sites.

Site	Streamflow ($m^3 \cdot s^{-1}$)	Emigration rate (±1 SD) ($\% \cdot d^{-1}$)
Old-growth stream	≤0.35	0.12 ± 0.23
	>0.35	0.01 ± 0.03
Clear-cut stream	≤0.15	0.72 ± 1.75
	>0.15	0.06 ± 0.11

insulating layer at night, inhibiting heat exchange with the atmosphere and keeping water temperatures slightly warmer than in the clear-cut site. The larger water volume of the old-growth forested stream also contributed to its greater thermal stability.

No clear association was found between changing water temperatures and emigration, although temperature decreases tended to produce higher rates of downstream movement than periods with stable or increasing mean daily temperatures (Table 3). In both watersheds, decreasing temperatures corresponded with emigration rates from 54 to 103% greater than those during periods of stable or rising temperatures; however, these differences were not significant. Although temperature changes alone did not result in significantly increased emigration, increases in the rates of movement during falling temperatures suggested that temperature may have acted together with flow change in triggering emigration. To determine the relative importance of flow change and decreasing temperature, average emigration rates were compared for periods of (1) changing flow and decreasing temperature, (2) decreasing temperature with no change in flow, (3) flow changes with no drop in temperature, and (4) no flow change or temperature decrease (Table 3). In both streams, decreasing temperature combined with daily flow changes >3% elicited the greatest emigration rates. In the old-growth site in 1982, these rates were greater than those observed during periods of either decreasing temperature alone or no flow and temperature change (t-test, $p \leq 0.10$). In the same site during 1983, decreasing temperatures combined with flow changes still produced the greatest average rate of downstream movement, but the average was not significantly different from those of the other flow and temperature conditions. Emigration from the clear-cut stream during changing flows and decreasing temperatures was greater than during periods of decreasing temperature alone or when there was no flow or temperature change (t-test, $p \leq 0.10$).

TABLE 3. Influence of flow change and temperature decreases on average daily emigration rates of coho after the initial pulse of emigration but excluding periods of peak discharge (Table 2).

Conditions	Coho emigration rate (±1 SD) (%·d⁻¹)			
	Old-growth		Clear-cut	
	1982	1983	1982	1983
Flow change >3%·d⁻¹	1.19 ± 0.39	0.18 ± 0.30	1.84 ± 1.79	1.12 ± 2.41
Flow change ≤3%·d⁻¹	0.20 ± 0.15	0.05 ± 0.06	0.46 ± 0.27	0.22 ± 0.25
Decreasing mean daily temperature	0.61 ± 1.19	0.18 ± 0.38	1.11 ± 1.52	0.87 ± 2.39
Rising or stable mean daily temperature	0.39 ± 0.53	0.09 ± 0.11	0.70 ± 0.84	0.55 ± 0.61
Decreasing temperature and flow change <3%·d⁻¹	1.50 ± 2.02	0.27 ± 0.48	2.16 ± 2.45	1.41 ± 3.27
Decreasing temperature and flow change <3%·d⁻¹	0.21 ± 0.16	0.08 ± 0.04	0.56 ± 0.22	0.27 ± 0.25
Rising or stable temperature and flow change ≤3%·d⁻¹	0.94 ± 0.80	0.09 ± 0.12	1.59 ± 1.30	0.69 ± 0.68
Rising or stable temperature and flow change ≤3%·d⁻¹	0.19 ± 0.15	0.09 ± 0.08	0.38 ± 0.23	0.26 ± 0.23

TABLE 4. Emigration and mortality of hatchery coho during the initial pulse phase of emigration (first 10 d after stocking) and during the remaining summer and autumn study period. Mortality estimates assumed exponential death rates and were based on the difference between the known number of emigrants and residents.

	Clear-cut		Old-growth	
	1982	1983	1982	1983
1. Coho stocked				
Total no.	13 090	7700	24 860	14 600
2. Emigration during first 10 d				
Total no.	5 376	5272	9 330	8 035
As % of no. stocked (1.)	41	68	38	55
3. Mortality during first 10 d				
Total	911	468	2 648	1 239
As % of no. stocked (1)	7	6	11	8
4. Resident population after 10 d				
Total no.	6 803	1960	12 882	5 326
5. Remaining emigration				
Total no.	2 091	255	1 617	316
As % of no. stocked (1)	16	3	7	2
As % of init. residents (4)	31	13	13	6
6. Remaining mortality				
Total no.	4 481	1421	11 153	3 823
As % of no. stocked (1)	34	18	45	26
As % of init. residents (4)	66	73	87	72
7. Population at end of study				
Total no.	231	284	112	1 187
As % of no. stocked (1)	2	4	<1	8
As % of init. residents (4)	3	14	1	22

Flow changes occurring without temperature declines resulted in the next highest emigration rates (Table 3), which were greater in both streams in 1982, and in the clear-cut site in 1983, than when temperature alone declined or when there were no flow or temperature changes (t-test, $p \leq 0.05$). In the old-growth site, downstream movements during periods of changing flow did not significantly differ from periods when either temperature decreased or there was no flow and temperature change in 1983. Declining temperatures alone resulted in emigration rates that differed little from those observed when neither temperature nor flow changed. Discharge, therefore, appeared to be the physical factor of overriding importance in

triggering the downstream movement of hatchery coho fry following the initial pulse of poststocking emigration. Our results showed that temperature influenced downstream movement only when accompanied by flow changes.

Average daily turbidities in 1983 were 1.3 NTU in the old-growth and 1.2 NTU in the clear-cut site with peak values of 5.7 NTU and 5.5 NTU, respectively. These peak values were well below levels known to elicit an avoidance response by coho salmon fry (Berg 1982; Bisson and Bilby 1982; Berg and Northcote 1985), and no relationship between turbidity and downstream movement was observed. Due to the consistently clear water in both streams, it was not possible for us to draw any meaningful conclusions about the influence of water clarity on coho fry emigration. Like Hartman et al. (1982), we also saw no influence of lunar phase on downstream movement of coho fry (Fig. 1A and 1B); however, Mason (1975) found coho fry emigration to increase around the new moon.

Survival, Growth, and Production

The initial emigration rate was greater in 1983 than 1982, despite lower stocking densities (Table 4). In 1983, coho were planted 1 mo earlier and at a much smaller size than those planted in 1982, and the streams experienced marked flow increases in 1983. These factors may have contributed to the relatively high 1983 initial emigration rate. Once the poststocking pulse of emigration subsided, however, downstream movement from both streams remained consistently lower in 1983 than in 1982 when stocking densities were high (Fig. 1; Table 4). During both years, a greater percentage of stocked fish initially moved out of the clear-cut site than left the old-growth site. After the populations had stabilized, emigration from the clear-cut was approximately twice the rate of emigration from the old-growth stream.

Initially, mortality differed little between the study sites, although mortality estimates for the old-growth were slightly greater than those for the clear-cut site in both years (Table 4). During the early period of population decline, emigration accounted for far more fish than mortality. Following population stabilization, mortality became the dominant process and accounted for the majority of coho that disappeared from the streams. In 1982, when initial resident population densities were high, mortality in the old-growth stream was about 20% greater than in the clear-cut stream. At the low population densities of 1983, mortality rates for the two sites were identical. When the initial poststocking phase of movement and the remaining summer period of relative population stability were considered together, emigration generally proved to be more important than mortality in regulating population sizes. This was especially true for the clear-cut site, where emigration accounted for 57 and 79% of the number of coho stocked in 1982 and 1983, respectively. In the old-growth stream, emigration accounted for 57% of the stocked fish in 1983, but only 44% in 1982 when initial densities were high. In both years, only a small number of coho remained at the end of the monitoring period (Table 4), but it was revealing that in each site, more fish remained in the streams during the year when stocking densities were low than when initial densities were high, the most marked difference being in the old-growth site where 10 times as many coho remained at the end of the study during the low stocking density year than during the high-density year.

A possible reason for the increased tendency of coho fry to reside in the old-growth stream was that more suitable habitat was available there than in the clear-cut site. The old-growth stream had a much higher frequency of woody debris than the clear-cut, which had been cleared of nearly all woody debris following logging. Large woody debris is instrumental in the formation of pools in small streams (Swanson et al. 1976), and pool habitat is preferred by coho salmon fry (Hartman 1965; Ruggles 1966; Lister and Genoe 1970; Nickelson and Hafele 1978). Woody debris serves as a source of cover for the fish (Bustard and Narver 1975a, 1975b; Bisson et al. 1982; Forward 1984) and by visually isolating the fry from one another, may reduce aggressive interactions and enable more fish to establish foraging sites in a smaller area of stream than would be possible otherwise (Dolloff 1983). The greater availability of suitable habitat in the old-growth stream may have initially slowed emigration, which in turn led to intense competition for available food and the observed higher mortality rates, particularly in the high-density year. Rapid emigration of coho fry from the clear-cut site may have been a result of lack of pool habitat and cover, which led to competition for the available space.

Production in the two streams reflected differences in the apparent availability of both food and usable rearing space, and the compensatory controls these two resources exerted over the coho populations. In the high-density year (1982), production through mid-September was severalfold greater in the clear-cut site than in the old-growth site (Table 5), largely due to differences in growth rates. In the old-growth site, daily growth rates increased during the autumn. By this time the population had declined to a small fraction of the number of fish originally stocked (Table 4) and the impact of increased growth on production was very small. Total coho salmon production during the 1982 study period was 5.28 $g \cdot m^{-2}$ in the clear-cut stream and 2.05 $g \cdot m^{-2}$ in the old-growth stream; however, this difference in production was not reflected in mean individual weights, which were nearly equal in the two streams at the end of the study.

In 1983, the low-density year, growth during the first month in both streams was greater than during the first month's residence in 1982 (Table 5), but fish in the clear-cut site still grew at a faster rate than those in the old-growth site, although the difference between streams was less than in 1982. Growth rates remained higher than comparable intervals in 1982 throughout the balance of summer and early autumn in both streams. At the end of the 1983 study, coho in the clear-cut site were about 30% larger than those in the old-growth site, based on superior early-season growth. Total production from May to mid-October was 4.63 $g \cdot m^{-2}$ in the clear-cut stream and 3.95 $g \cdot m^{-2}$ in the old-growth stream. Thus, when high densities were stocked in the study streams, production in the clear-cut site was clearly greater than in the old-growth site. At lower stocking densities the clear-cut site still maintained higher production rates than the old-growth stream, but differences between sites were diminished.

The results indicate that the rate of emigration of hatchery coho from the study streams was strongly influenced by habitat quality whereas growth (and consequently production) was primarily related to food availability and population density. The old-growth stream possessed high-quality habitat containing an abundance of pools and cover, and the number of coho remaining at this site after the initial population had stabilized was greater than at the clear-cut site. Growth rates, however, were lower and mortality rates greater in the old-growth site than in the clear-cut site, which suggested that scarce food was

TABLE 5. Growth, biomass, and production of coho in the clear-cut and old-growth streams during 1982 and 1983. Yearly averages are weighted according to length of sampling interval.

Stream	Sampling interval	Avg. wt. per fish at end of interval (g)	Daily instantaneous growth rate	Average population biomass ($g \cdot m^{-2}$)	Production ($g \cdot m^{-2} \cdot d^{-1}$)
1982					
Clear-cut	June 15 – July 7	2.11	0.0052	20.59	0.108
Old-growth	June 15 – July 18	1.94	0.0010	19.72	0.020
Clear-cut	July 7 – Sept. 21	2.80	0.0037	9.16	0.034
Old-growth	July 18 – Sept. 22	2.20	0.0019	6.09	0.012
Clear-cut	Sept. 21 – Nov. 8	3.10	0.0021	3.01	0.006
Old-growth	Sept. 22 – Nov. 9	3.00	0.0065	2.04	0.013
Clear-cut	1982 weighted averages		0.0034		0.036
Old-growth			0.0032		0.014
1983					
Clear-cut	May 6 – June 7	1.56	0.0249	3.71	0.092
Old-growth	May 6 – June 13	1.25	0.0146	3.63	0.053
Clear-cut	June 7 – Oct. 18	4.25	0.0075	1.77	0.013
Old-growth	June 13 – Oct. 19	3.23	0.0074	2.03	0.015
Clear-cut	1983 weighted averages		0.0109		0.028
Old-growth			0.0090		0.024

TABLE 6. Gross primary production and average light intensities in the two study streams during sunny and cloudy weather in 1983.

Stream	Weather conditions	Mean light intensity during incubation (±1 SD) ($g\ cal \cdot cm^{-2} \cdot min^{-1}$)	Carbon fixation (±1 SD) ($mg\ C \cdot m^{-2} \cdot h^{-1}$)
Old-growth	Sunny	0.32 ± 0.19	26.8 ± 7.6
Old-growth	Cloudy	0.06 ± 0.02	16.6 ± 6.0
Clear-cut	Sunny	1.18 ± 0.08	51.7 ± 12.3
Clear-cut	Cloudy	0.32 ± 0.01	29.5 ± 5.9

being apportioned among more individuals. While food limitation of coho production appeared to be particularly severe in the old-growth watershed, evidence of limiting food resources also existed in the clear-cut stream. In both sites, growth rates were lower at high stocking densities than at low stocking densities (Table 5), and competition for foraging stations may have resulted in the downstream displacement of smaller fish (Fig. 2). Similar size differences between resident and emigrant wild coho fry have been observed in Carnation Creek (Hartman et al. 1982).

Our study streams were probably overstocked with coho fry in 1982; fewer fish remained at the end of the 1982 monitoring period, and their average weights were less than in the following year when only about half as many fish were stocked. In 1983, production of coho in the clear-cut site was similar to the production measured in 1982, yet the initial resident population in 1983 (Table 4) was approximately one third of the number of fish in 1982. Production of coho in the old-growth stream in 1983 was nearly double the total 1982 production, but with less than one half the initial number of residents. Because there was virtually no change in habitat composition or cover in the two streams from 1982 to 1983, we infer that production differences between years were primarily a function of limited food availability coupled with changes in population density.

Although we did not measure food abundance directly, there was additional evidence for increased food resources in the clear-cut watershed. On both sunny and cloudy days, gross primary production in the clear-cut stream was approximately twice that of the old-growth stream (Table 6). From frequent visual observations, it was apparent that the clear-cut stream contained a periphyton assemblage dominated by filamentous green algae that supported numerous grazing insects whereas the periphyton of the old-growth was dominated by epilithic diatoms. It is also possible that algal growth in the clear-cut stream may have been enhanced by slightly increased temperatures and elevated nutrient export from the watershed after logging. The primary production measurements and the observed differences in coho growth between the two streams both support the hypothesis that food was more abundant in the clear-cut site than in the old-growth site during the study period. Our finding that habitat quality exerts a significant influence on the frequency of downstream movement of hatchery coho fry, and hence local population density, while food resources tend to control individual growth rates, and hence production of the population, is in general agreement with results of the Carnation Creek study of wild coho. In Carnation Creek, Scrivener and Andersen (1984) observed that underyearling coho growth in different reaches was negatively correlated with density during summer, even when the relative abundance of fish was low, implying that intraspecific competition for food was taking place regardless of the size of the initial population or the quality of physical habitat. These authors also found that differences in growth between years were density related and that removal of streamside vegetation during logging resulted in summer growth increases that yielded larger fry in early autumn, except in years when adult escapement and subsequent initial fry populations had been unusually high. The larger fry in early autumn were felt to have a greater probability of surviving until smoltification. Tschaplinski and Hartman (1983) showed that more coho fry remained in stream reaches with deep pools, log jams, and undercut banks, which provided

suitable overwintering habitat, than in reaches where pools and cover were lacking; in the latter sites the rate of downstream movement of fry in response to freshets was very high. Although their research was conducted in autumn and winter (the period when our study was ending), the migratory behavior of wild coho fry in response to habitat quality in Carnation Creek appeared to be quite similar in many respects to the behavior we observed in hatchery fish.

The success of hatchery fry outplanting programs, as measured in terms of increased standing stock or smolt yield, is often based on the concept that to realize its production potential a stream must be "fully seeded." We suggest that this concept will require careful definition as well as clarification of management objectives. If full seeding is taken to mean the maximum *number* of fish that can live in a given set of physical conditions in the stream channel, our study indicated that high densities may result in poor growth, possibly at the expense of survival to smolting. We found that the number of fish remaining in the study reaches after stocking appeared to be more a function of habitat quality than of trophic conditions. Where a stream contains abundant pools and cover, we predict that more coho fry will remain in the vicinity of where they are planted than in a stream where these features are scarce, regardless of the availability of food. In streams possessing high quality habitat, it may therefore be desirable to scatter the planting sites along the entire length of the channel in order to ensure an even distribution of fry throughout the drainage. Conversely, single location plants in streams with poor physical habitat can be expected to result in considerable downstream movement, resulting in occupation of suitable rearing areas elsewhere in the system. If full seeding is taken to mean the density that yields maximum *production*, our results showed that greater coho fry production could be achieved, at least in the old-growth site, at a lower density than the maximum number of fish the stream could support. Overstocking a stream in which food resources are severely limited can result in lower growth rates and higher mortality. We conclude that fry planting programs should taken into account the relative availability of food in a stream, not just physical habitat quality, and adjust stocking densities accordingly.

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