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**Canadian
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Volume 49 • Number 3 • 1992

Pages 540–551

Canada



Fisheries
and Oceans

Pêches
et Océans

Allochthonous versus Autochthonous Organic Matter Contributions to the Trophic Support of Fish Populations in Clear-Cut and Old-Growth Forested Streams

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Bilby, R. E., and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. *Can. J. Fish. Aquat. Sci.* 49: 540-551.

Annual organic matter inputs and production of stocked coho salmon (*Oncorhynchus kisutch*), coastal cutthroat trout (*O. clarki clarki*), and shorthead sculpin (*Cottus confusus*) from spring through early autumn were monitored for 2 yr in two headwater tributaries of the Deschutes River, Washington. One site was bordered by old-growth coniferous forest; the other was an area clear-cut without buffer strips 7 yr before the study. Allochthonous organic matter (terrestrial origin) dominated inputs to the old-growth site and contributed $\sim 300 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, while autochthonous organic matter totaled $\sim 100 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. In the clear-cut site, autochthonous inputs contributed $\sim 175 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, but allochthonous inputs contributed only $\sim 60 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ owing to loss of riparian vegetation. Although combined allochthonous and autochthonous inputs were almost twofold greater in the old-growth site, fish production was greater in the clear-cut site. Production of coho salmon and shorthead sculpin during early summer was largely responsible for differences between sites. Fish populations appeared to depend upon food derived from autotrophic pathways during spring and summer in the presence or absence of forest canopy, a hypothesis supported by analysis of coho stomach contents and the similar ratios of autochthonous inputs and fish production between the two streams.

Pendant 2 ans, on a étudié l'apport de matière organique et la production annuels de saumon coho (*Oncorhynchus kisutch*) d'élevage, de truite fardée côtière (*O. clarki clarki*) et de chabot à tête courte (*Cottus confusus*) (et ce du printemps au début de l'automne) dans deux tributaires d'amont de la rivière Deschutes, dans l'État de Washington. Le premier site était ombragé par un peuplement mûr de conifères tandis que le second avait été coupé à blanc, sans création de zone tampons, sept ans avant la réalisation de la présente étude. Au premier site, la matière organique allochtone d'origine terrestre était la composante principale de l'apport, soit $\sim 300 \text{ g}\cdot\text{m}^{-2}\cdot\text{an}^{-1}$, tandis que la matière organique autochtone totalisait $\sim 100 \text{ g}\cdot\text{m}^{-2}\cdot\text{an}^{-1}$. Au deuxième site, l'apport autochtone s'élevait à $\sim 175 \text{ g}\cdot\text{m}^{-2}\cdot\text{an}^{-1}$, mais l'apport allochtone n'atteignait que $\sim 60 \text{ g}\cdot\text{m}^{-2}\cdot\text{an}^{-1}$ à cause de la perte de végétation ripicole. Même si les apports allochtone et autochtone combinés étaient presque deux fois plus élevés au premier site, la production de poisson était supérieure au deuxième site. La production de saumon coho et de chabot à tête courte au début de l'été expliquait en grande partie cette différence. Au printemps et à l'été, les populations de poisson semblaient dépendre d'aliments dérivés de réseaux autotrophes, un présence ou en l'absence d'un couvert forestier. Cette hypothèse est étayée par les résultats d'une analyse des contenus stomacaux de saumons cohos et les rapports semblables des apports autochtones et de la production de poisson entre les deux cours d'eau.

Received October 29, 1990

Accepted October 4, 1991

(JA776)

Reçu le 29 octobre 1990

Accepté le 4 octobre 1991

Organic matter budgets of small streams flowing through forested watersheds are dominated by inputs of terrestrial material (Fisher and Likens 1973; Naiman and Sedell 1979; Cummins et al. 1982; Triska et al. 1982). This dominance is caused by high input rates of material from allochthonous sources coupled with suppression of autochthonous production by heavy shading from terrestrial vegetation (Gregory 1980). Removal of riparian vegetation through timber harvest reverses the relative importance of allochthonous and autochthonous organic sources by stimulating primary production and decreasing inputs of terrestrial organic matter (Hansmann and Phinney 1973; Stockner and Shortreed 1976; Murphy et al. 1981; Gregory et al. 1987).

Greater autochthonous production and decreased inputs of terrestrial materials influence consumer trophic levels within the stream (Murphy and Meehan 1991). Invertebrates that con-

sume autochthonous energy sources benefit from improved food resources when more sunlight reaches the stream channel, nutrient concentrations are elevated, and algal growth is stimulated (Weber 1981; Kirchofer 1984; Murphy 1984; Wallace and Gurtz 1986; Perrin et al. 1987). Overall, invertebrate production may increase after logging (Wallace and Gurtz 1986; Behmer and Hawkins 1986), due in part to the generally higher protein content and digestibility of algae and algal-based detritus than most incoming terrestrial plant material (Triska et al. 1975) and to a change in community composition from predominantly univoltine detritivores to multivoltine grazers and collector-gatherers (Gregory et al. 1987).

Increased density, biomass, and production of salmonids in streams flowing through clear-cut areas have also been documented (Murphy and Hall 1981; Hawkins et al. 1983; Bisson and Sedell 1984), but enhancement of food resources after for-

oxygen-temperature probe fitted into the wall of the chambers. All incubations took place between 10:30 and 14:00 PST. Light intensity during an incubation period was recorded every 0.5 h with a dome solarimeter. A photosynthetic quotient of 1.2 was used to convert change of oxygen concentration to amount of fixed carbon (Wetzel and Likens 1979). The total amount of fixed organic matter was estimated by dividing the carbon values by 0.47 (Vollenweider 1974). Measurements in each stream were taken at about 10-d intervals during spring and summer months. Photosynthesis during autumn and winter was measured less frequently.

Solar input to the streams was extrapolated from light measurements taken near Olympia, Washington, at the mouth of the Deschutes River (Cinquemani et al., U.S. National Oceanic and Atmospheric Administration undated report). Measurements from Olympia, 50 km from the study area, were applied directly to the clear-cut site. However, the forest canopy over the old-growth site reduced incoming solar radiation, necessitating a correction. Decreased light inputs to the old-growth stream were estimated by comparing light intensity measurements taken simultaneously with a dome solarimeter at the old-growth site and the clear-cut site under different cloud cover conditions.

Primary production was estimated from regressions of gross photosynthesis against light intensity, a procedure used for other small forested streams by Murphy (1984). Regressions were developed for each site during each of three intervals: July-October, November-February, and March-June. These time intervals corresponded to periods of similar water temperature and discharge regimes. During the July-October period, water temperatures were relatively warm and streamflow was low and stable. From November to February, water temperatures were low and streamflows tended to be high and extremely variable; nearly all major freshets occurred at this time of year. Water temperature and streamflows from March to June were intermediate relative to the two other periods.

Fluvial Inputs

Organic matter contributed to the study reached by fluvial transport was separated into three categories based on particle size. Dissolved organic matter (DOM) was material <0.001 mm diameter and was measured as DOC, fine particulate organic matter (FPOM) ranged from 0.001 to 1.0 mm, and coarse particulate organic matter (CPOM) was material >1.0 mm. Fluvial transport samples were collected during 1984, with the exception of two months when the sites were not accessible. Grab samples were analyzed for DOC with an infrared gas analyzer after digesting an aliquot of filtered water with $K_2S_2O_8$ (Menzel and Vaccaro 1964).

FPOM concentration was measured in water samples drawn with automatic pump samplers (1-mm-mesh intakes) and chosen to represent concentration changes over the full range of flow conditions during the study period. FPOM samples were filtered through precombusted and preweighed glass fiber filters and dried at 60°C. After reweighing to determine the total weight of particulate material, filters were ashed at 500°C and organic matter content was determined by weight loss on ignition.

CPOM was sampled by placing 1-mm-mesh drift nets in the streams at a wide range of flows. During periods of low discharge, nets sampled the entire flow of the stream for up to 24 h. Volume of water passing through the net was equivalent

to discharge when the entire streamflow was being sampled. During freshets, a 55-cm-wide net was placed in the channel from 1 to 30 min. Volume of water sampled was determined by measuring flow through the net at the start and end of a collection period using a current velocity meter. CPOM samples were dried, separated into the five categories used for litter samples, weighed, and then the litter categories were recombined. A subsample was drawn from each sample for determination of organic content through weight loss on ignition.

Fisher (1977) and Cummins et al. (1982) have discussed difficulties in comparing fluvial inputs of particulate organic matter with inputs from other sources in stream reaches of unequal length. Because the lengths of our study sites were not equal, the relative importance of material transported into the sites from upstream sources varied. Input from terrestrial vegetation or from primary production was dependent upon the surface area of the sites whereas fluvial inputs were dependent only upon organic matter concentration and stream discharge and were not significantly influenced by the area of the sites. However, relative differences in the availability of fluvially transported material to the stream's biota were indexed by computing mean monthly organic matter concentrations, weighted for flow, at each site. Relationships between CPOM and FPOM concentration and discharge were developed over a wide range of flow conditions at each study site. The mean monthly concentration of particulate organic matter transported to the sites was calculated from average daily values based on the relationship between concentration and discharge and weighted by mean daily flow.

We also monitored discharge, stream temperature, and nutrient concentrations. Daily streamflow at the sites was estimated by correlating readings on rated staff gauges with simultaneous readings on a nearby stream with a similar flow patterns and equipped with a gauge height recorder. Electronic thermographs recorded daily maximum, minimum, and mean water temperatures. Grab samples of nutrients (nitrate-N, ammonia-N, Kjeldahl-N, and total P) were collected monthly and analyzed by standard methods (American Public Health Association et al. 1975).

Fish Populations

Two species resided naturally in the streams, coastal cutthroat trout (*Oncorhynchus clarki clarki*) and shorthead sculpin (*Cottus confusus*). Cutthroat trout were found by Bisson and Sedell (1984) to be more abundant in the Upper Deschutes River than in West Ford Creek during the late 1970s. Bilby and Bisson (1987) also reported that cutthroat trout and shorthead sculpin densities and biomasses were significantly greater in the clear-cut than in the old-growth site during the 3 yr prior to this study.

Juvenile coho salmon (*Oncorhynchus kisutch*) of hatchery origin (South Puget Sound stock from the Washington Department of Fisheries Puyallup River hatchery) were released at each site on June 15, 1982, and May 5, 1983. The number of fish was adjusted for differences in site area so that identical initial densities (number per square metre) were planted into the streams (Bilby and Bisson 1987). However, the total number, time of stocking, and size of coho fry changed from 1982 to 1983. Difference in stocking time and size at stocking was determined by availability of fry at the hatchery. Stocking densities of coho in 1982 were approximately $16 \text{ fry} \cdot \text{m}^{-2}$, while stocking densities in 1983 were approximately $9 \text{ fry} \cdot \text{m}^{-2}$. Sub-

samples of planted fry indicated that there was no difference in initial size or condition factor between the sites in either year (t -test, $p < 0.01$). Average weight of coho fry at release was 1.88 g in 1982; in 1983, fish averaged 0.75 g.

Our purpose in stocking was to evaluate the response of juvenile coho to differences in organic matter sources independent of differences in recruitment rates between the two streams. Changes in stocking density from 1982 to 1983 permitted examination of compensatory effects of population pressure on survival and growth. Although we could not control the abundance of resident trout and sculpins at the outset, the ability to stock coho above a natural barrier (Deschutes Falls) facilitated a comparison of production rates in streams where initial populations were under strict experimental control. In doing so, we were forced to assume that hatchery coho fry would respond in the same manner to conditions in the streams as would naturally produced fry, an untested assumption.

Fish populations were censused in early summer and early autumn. Efforts to obtain midwinter population estimates failed owing to high streamflow and inability to assess the sites. Therefore, our results extended over only part of the annual cycle, albeit the period when most growth occurred. We found (Bilby and Bisson 1987) that the majority of juvenile coho rearing in the sites in early autumn emigrated from the streams with the onset of winter conditions (high discharge and low temperatures), a pattern consistent with observations elsewhere in the Pacific Northwest of coho salmon moving from headwater streams to favorable winter habitat lower in the drainage system (Peterson 1982; Brown and Hartman 1988). A survey of the winter distribution of coho salmon in the Deschutes River in 1984 (P. A. Bisson, unpubl. data) located large numbers of fish downstream in small, spring-fed tributaries and sloughs along the flood plain. Although it would have been preferable to describe the production of coho salmon in our headwater study sites throughout the year, we feel that spring and summer measurements accurately reflected most of the relative contribution of allochthonous and autochthonous organic matter to this species while rearing in headwater streams.

Randomly selected pools and riffles (habitat units) within the streams were electrofished three times and the number of fish present in each habitat unit was estimated using the removal summation technique of Carle and Strub (1978). Fork lengths were measured to the nearest millimetre, and all fish were returned to the channel unit from which they had been collected. Total numbers of fish in the entire reach were estimated by multiplying the average density for a given type of habitat by the total surface area of that habitat type present in the study section (Bilby and Bisson 1987). Biomass estimates were based on length-weight regressions established from 30 fish selected randomly from each site on each sample date. When fewer than 30 individuals of a species were available for length-weight determinations, all fish were used.

Downstream movements were monitored with fish traps at the lower end of each study site. Actual mortality was calculated as the difference between the estimated population size and the number of downstream migrants. Production estimates (Chapman 1978) assumed that instantaneous daily rates of growth and "mortality" (actual mortality plus emigration) were exponential.

Stomach contents were sampled by flushing during June and July 1982 to determine differences in types of food organisms selected by coho salmon in the two sites. Thirty coho fry were selected at random from each stream for food analysis. Stomach

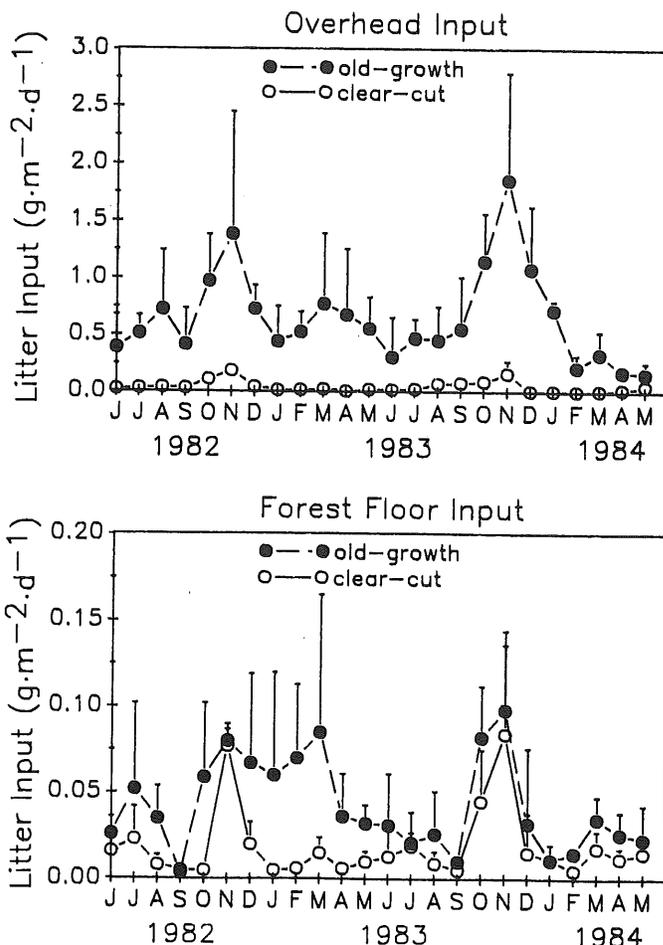


FIG. 1. Monthly input of terrestrial litter (mean \pm 1SD) to the study sites from June 1982 through May 1984.

samples from all fish were combined prior to sorting and identification. Classification of stomach contents included only items that were mostly intact; invertebrate fragments, exuviae, and unidentifiable items were not counted. Invertebrates in stomach samples were assigned to functional groups according to Merritt and Cummins (1978).

Differences in taxonomic composition and functional groups in the invertebrate drift of both streams were also examined. Six 24-h drift samples were taken from August 19 through August 22, 1984. Several rectangular drift nets of 202- μ m mesh were placed together in riffles so as to sample as much of the streamflow as possible. Nets were emptied every 2 h over the 24-h sample period.

Fish stomachs and invertebrate drift were sampled only once during the study, and then not simultaneously. We therefore considered them only a crude approximation of the proportions of different invertebrate functional groups available to coho salmon in the two streams. Because samples were limited, comparison of the actual abundance of invertebrates at the sites was not attempted. Nevertheless, the proportion of various groups in the diet enabled us to draw some inferences about the relative contribution of different organic matter sources to the trophic support of coho salmon populations.

Results

Allochthonous Inputs

The amount of terrestrial litter collected in the suspended traps was significantly greater (t -test, $p < 0.05$) at the old-

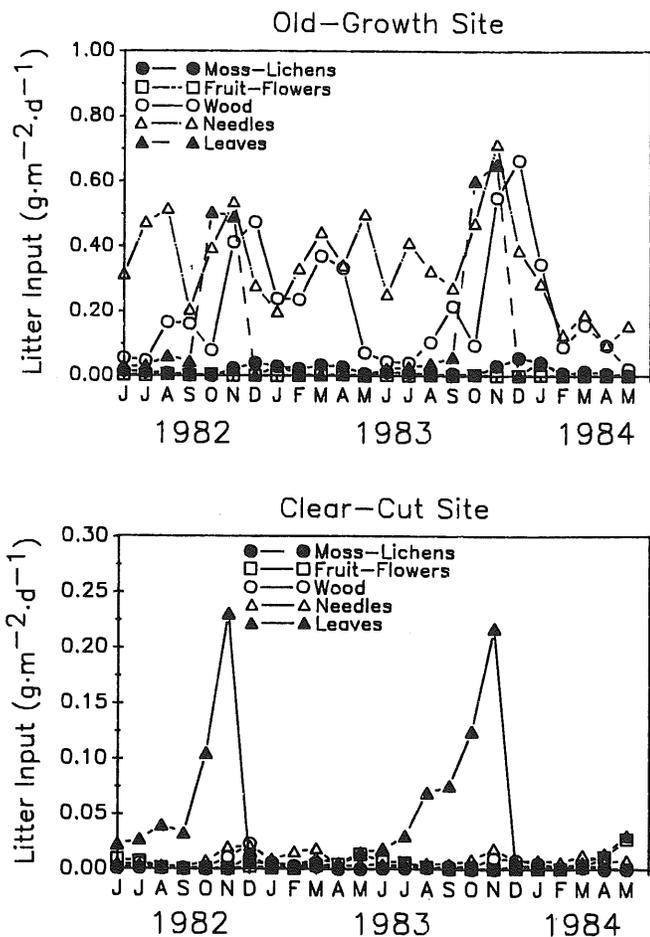


FIG. 2. Composition of terrestrial litter entering the study sites from June 1982 through May 1984.

growth site than at the clear-cut site at all times (Fig. 1). The greatest amounts of litter entered the streams in autumn. However, relatively large quantities entered the old-growth site throughout the year, while nearly all litter input to the clear-cut from overhead vegetation occurred over a short period.

Inputs of organic matter blowing into the streams along the forest floor were also significantly greater ($p < 0.05$) at the old-growth site than at the clear-cut site, but differences between the two streams were less for this material than for litter from the vegetative canopy (Fig. 1). There was a clear seasonal trend in the delivery of forest floor litter to the stream in the clear-cut watershed, with a peak in November of both years. Litter entering the old-growth site from the forest floor also tended to be greater in the autumn, but seasonal input differences were less distinct.

Leaves were the most common type of material collected in litter traps at the clear-cut site (Fig. 2), where most litter entered the stream in autumn. All other categories of terrestrial litter made only minor contributions to the clear-cut stream. The pattern of litter input essentially was dominated by autumn leaf fall from deciduous trees and herbaceous plants. A more constant input of allochthonous material to the old-growth site resulted from the greater diversity of litter sources and from temporal separation of peak periods of different types of litter production (Fig. 2). Leaves and needles were important components of autumn litter in the old-growth site, but this material was delivered to the stream throughout the year and

TABLE 2. Summary of organic matter inputs to the two study sites from allochthonous and autochthonous sources.

Source	Organic inputs ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$)			
	Clear-cut site		Old-growth site	
	1982-83	1983-84	1982-83	1983-84
Allochthonous inputs				
Litterfall	16.9	16.2	245.9	222.7
Forest floor	6.0	7.7	18.4	12.5
In-stream vegetation ^a	36.3	36.3	60.7	60.7
Total	59.2	60.2	325.0	295.9
Autochthonous inputs				
Primary production	185.3	166.9	111.1	108.8
Total inputs	244.5	227.1	436.1	404.7

^aInput values for herbaceous vegetation growing in the channel and overhanging vegetation less than 1.5 m above the water surface were determined for 1983-84 only. This value was used for both years of the study.

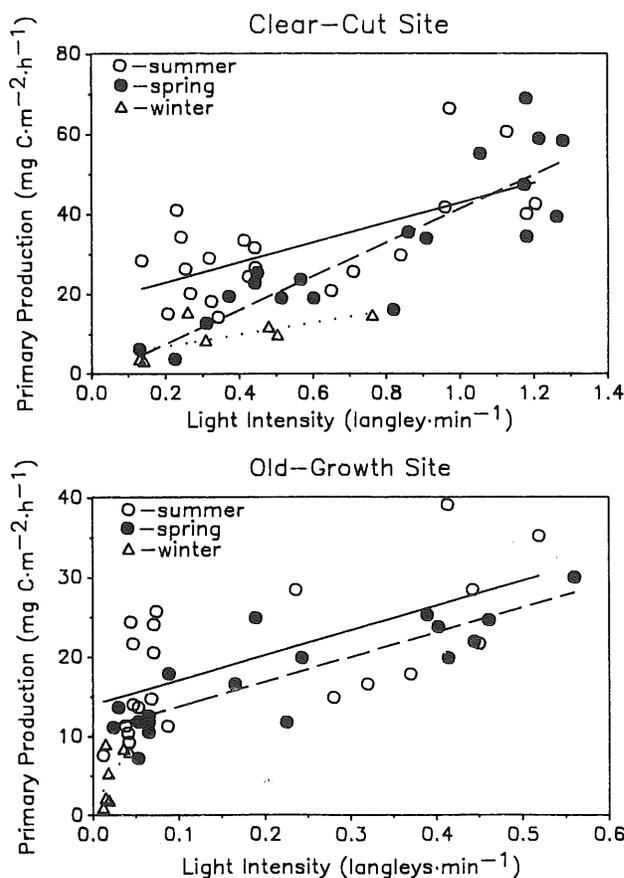


FIG. 3. Relationship between rate of gross primary production (GPP) and light intensity (LI) for the two study streams. Clear-cut site: spring, $\text{GPP} = 42.38(\text{LI}) - 0.89$ ($r^2 = 0.77$); summer, $\text{GPP} = 24.96(\text{LI}) + 18.02$ ($r^2 = 0.44$); winter, $\text{GPP} = 14.83(\text{LI}) + 4.02$ ($r^2 = 0.48$). Old-growth site: spring, $\text{GPP} = 31.09(\text{LI}) + 10.69$ ($r^2 = 0.74$); summer, $\text{GPP} = 31.25(\text{LI}) + 14.00$ ($r^2 = 0.40$); winter, $\text{GPP} = 176.26(\text{LI}) + 1.09$ ($r^2 = 0.37$).

was the most abundant type of litter in spring and summer. During winter, small pieces of wood were the most common type of litter input in the old-growth system.

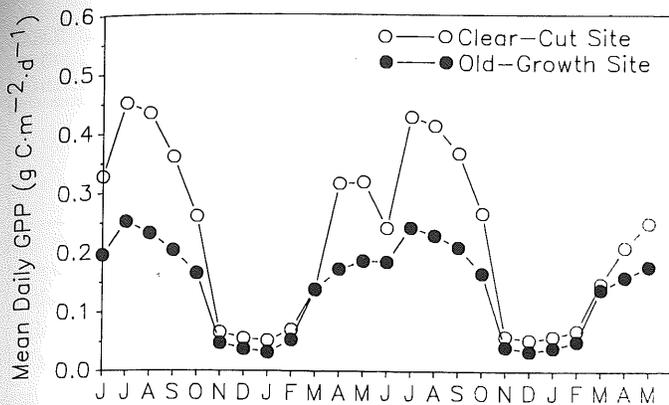


FIG. 4. Average daily primary production (GPP), by month, at the two study sites from June 1982 through May 1983.

Vegetation growing within or overhanging the channel less than 1.5 m above the water surface was an important source of the terrestrial organic matter at the clear-cut site (Table 2), where the proportion (60%) of allochthonous inputs contributed by in-channel and overhanging vegetation was nearly twice the amount from other sources. While the amount of this type of organic matter entering the stream was actually greater at the old-growth site, input from in-channel and overhanging vegetation was relatively less important (20%) due to the greater amounts of litter from other sources. Substantially more material was delivered to the old-growth stream by this pathway, however, than was delivered by transport across the forest floor.

Autochthonous Inputs

The relationships between gross primary production and light intensity at the clear-cut site differed significantly among spring, summer, and winter (Fig. 3, analysis of covariance, $p < 0.001$). Seasonal variations in water temperature, discharge, and a shift from green algae in spring to diatoms in summer were likely responsible for this difference. The relationships between gross primary production and light intensity were also significantly different among seasons at the old-growth site (Fig. 3, $p < 0.05$), but seasonal differences were somewhat less apparent than at the clear-cut site. The algal community in the old-growth stream was always dominated by diatoms. Total organic matter fixed by primary producers was calculated using estimated solar inputs (from climatological data) and the seasonal regressions between gross primary production and light intensity (Fig. 3).

At both sites, the amount of organic matter produced by autochthonous production was lowest during winter when there was relatively little difference in photosynthetic activity between the streams (Fig. 4). Highest levels of primary production occurred during summer, when the greatest differences between the old-growth and clear-cut sites were noted. Gross primary production was approximately twofold greater in the clear-cut than in the old-growth stream from April to October. Production of autochthonous organic matter was also relatively high during spring but dropped rather quickly in autumn. Rates of photosynthesis were similar for the two sites from November through March.

In spring, a dense growth of green algae, dominated by *Ulothrix* sp. and *Prasiola* sp., developed at the clear-cut site.

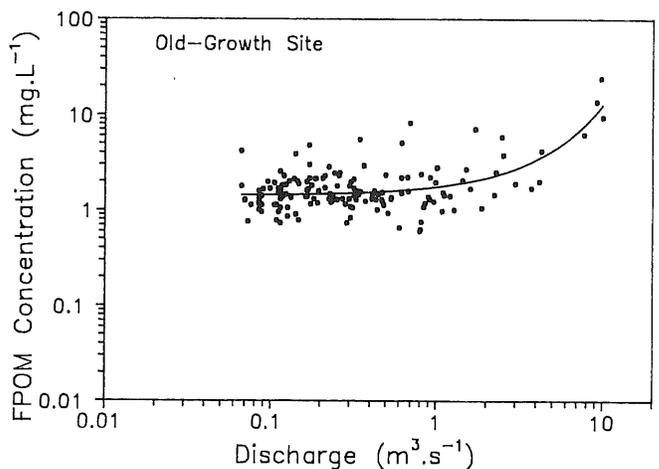
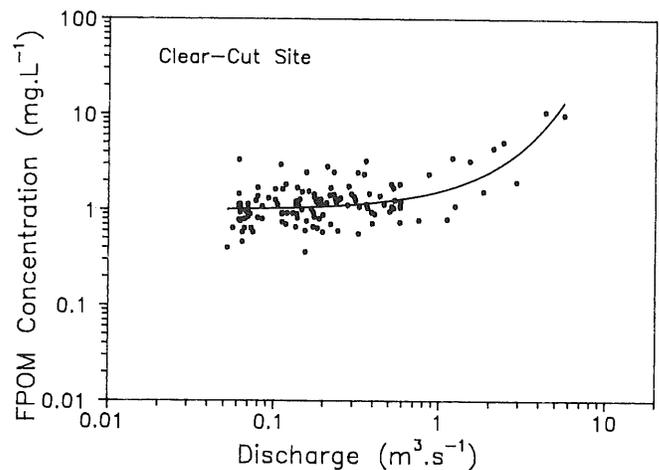


FIG. 5. Relationship between the concentration of fine particulate organic matter (FPOM) and discharge (Q) at the study sites. Clear-cut site: $\log_{10}(\text{FPOM}) = 0.203(Q) - 0.004$ ($r^2 = 0.63$); old-growth site: $\log_{10}(\text{FPOM}) = 0.096(Q) + 0.052$ ($r^2 = 0.61$).

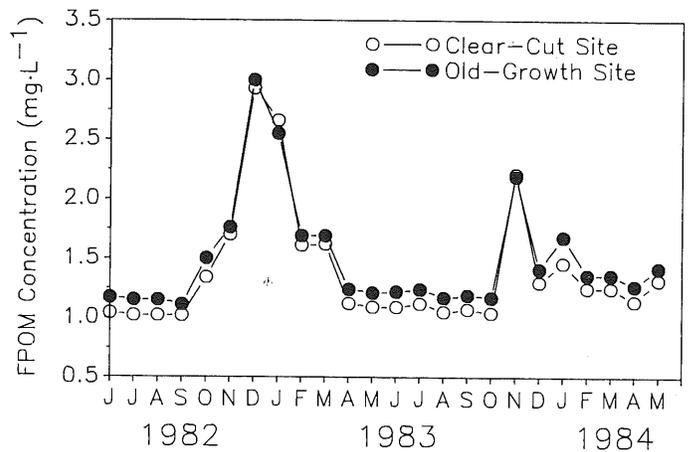


FIG. 6. Mean monthly fine particulate organic matter (FPOM) concentrations, weighted for discharge.

The green algae disappeared by early June, and diatoms dominated the algal community throughout summer and winter. Relatively little green algae was observed in spring at the old-growth site, where diatoms remained the dominant component of the algal community throughout the year.

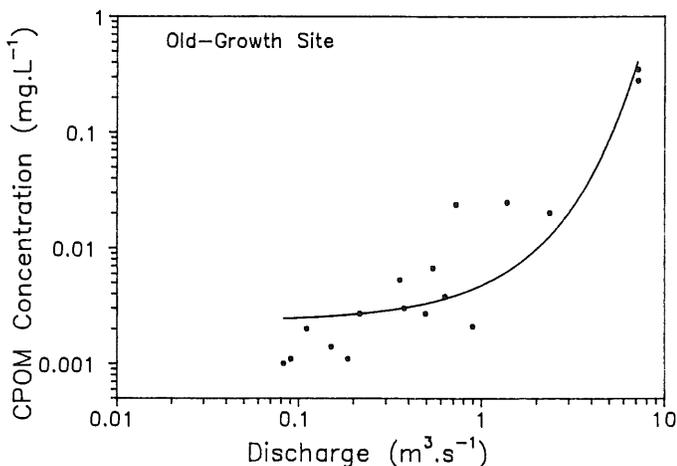
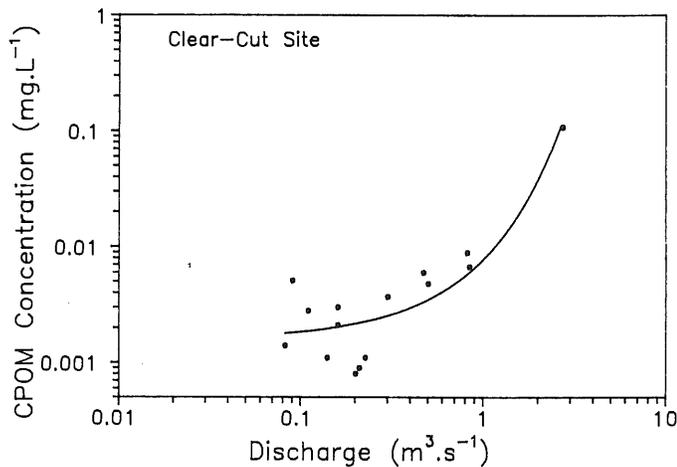


FIG. 7. Relationship between concentration of coarse particulate organic matter (CPOM) and discharge (Q) for the study sites. Clear-cut site: $\log_{10}(\text{CPOM}) = 0.69(Q) - 2.80$ ($r^2 = 0.85$); old-growth site: $\log_{10}(\text{CPOM}) = 0.31(Q) - 2.63$ ($r^2 = 0.82$).

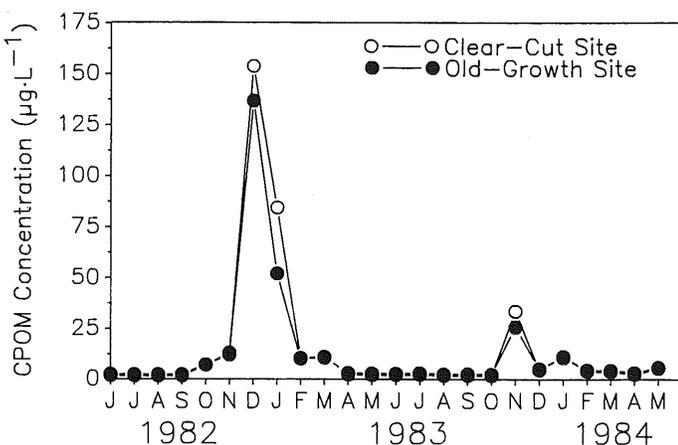


FIG. 8. Mean monthly coarse particulate organic matter (CPOM) concentrations, weighted for discharge.

Fluvial Inputs

Concentrations of DOC in the two streams were similar, averaging 1.31 and 1.21 mg·L⁻¹ at the clear-cut and old-growth sites, respectively. There was no seasonal pattern of DOC con-



FIG. 9. Composition of coarse particulate organic matter (CPOM) collected at the two study sites.

TABLE 3. Concentrations of dissolved nutrients at the two study sites. *Significant differences between sites ($p < 0.05$) as determined by t -tests.

Nutrient species	Mean concentration \pm 1 SE ($\mu\text{g}\cdot\text{L}^{-1}$)	
	Clear-cut site	Old-growth site
Kjeldahl-N	65 \pm 18	59 \pm 11
Ammonia-N	18 \pm 5	20 \pm 6
Nitrate + nitrite-N	9 \pm 1*	22 \pm 4*
Total dissolved P	19 \pm 6	19 \pm 5

centration changes nor any clear relationships between DOC concentration and discharge in either stream. Both streams possessed similar FPOM concentrations at low and moderate flows, with sharp increases occurring only at higher discharges (Fig. 5). As a result, monthly average FPOM concentrations (Fig. 6) were similar at the two sites.

CPOM increased slightly with discharge at low and moderate flows but exhibited a dramatic increase during high flows (Fig. 7). Concentrations of CPOM were much lower than those of FPOM in both streams, with values never in excess of 1 mg·L⁻¹ at either site. Average monthly CPOM concentrations, weighted for discharge (Fig. 8), were similar at the two sites.

Woody material was an important component of the CPOM in both streams, accounting for approximately 40 and 50%, respectively, of the total dry weight of CPOM at the clear-cut and old-growth sites (Fig. 9). Deciduous leaves comprised slightly more than half of the CPOM in the clear-cut site, but only 5% of the CPOM in the old-growth site. Conifer needles made up about 40% of the CPOM at the old-growth site, but only about 5% of the CPOM in the clear-cut site. Abundances of other categories of CPOM were approximately the same in both systems.

Concentrations of dissolved nutrients were low at both study sites (Table 3), and no obvious seasonal patterns were apparent from the grab samples. Average nitrate-N concentrations were significantly greater in the old-growth site than in the clear-cut site over the period of study (t -test, $p < 0.05$). Differences in average Kjeldahl-N, ammonia-N, and total dissolved P concentrations between the two streams were not significant. Average atomic ratios of available N:P were 3.7 for the old-growth site and 4.8 for the clear-cut site, thus indicating that N was the nutrient most likely to limit primary production in both streams (Stockner and Shortreed 1978).

TABLE 4. Fish population statistics for the clear-cut (CC) and old-growth (OG) sites for each sample interval. Values are means followed by standard errors in parentheses. Density and biomass are given as terminal values for each interval. Growth rate and production values are estimated averages over the entire interval. Underlined values indicate significant differences (*t*-test, $p < 0.05$).

	Coho salmon		Cutthroat trout		Shorthead sculpin		Total all species	
	CC	OG	CC	OG	CC	OG	CC	OG
July 1982								
Density (number·m ⁻²)	6.1 (1.2)	4.9 (1.2)	0.2 (0.1)	0.1 (0.1)	<u>1.1 (0.3)</u>	<u>0.3 (0.1)</u>	7.4 (1.4)	5.3 (1.2)
Biomass (g·m ⁻²)	12.6 (2.6)	9.2 (2.2)	3.7 (1.5)	1.9 (0.8)	<u>5.2 (1.9)</u>	<u>1.0 (0.3)</u>	<u>21.5 (4.6)</u>	<u>12.0 (2.6)</u>
Growth rate (%·d ⁻¹)	<u>0.43 (0.16)</u>	<u>0.11 (0.06)</u>	0.39 (0.11)	0.60 (0.15)	0.20 (0.13)	0.19 (0.15)		
Production (mg·m ⁻² ·d ⁻¹)	<u>87.8 (27.1)</u>	<u>19.7 (6.1)</u>	12.5 (4.7)	10.3 (1.6)	<u>7.6 (2.9)</u>	<u>1.9 (0.6)</u>	<u>127.2 (24.8)</u>	<u>31.9 (25.8)</u>
September 1982								
Density (number·m ⁻²)	1.9 (0.3)	1.8 (0.5)	0.09 (0.04)	0.11 (0.04)	<u>0.9 (0.8)</u>	<u>0.2 (0.1)</u>	2.9 (0.7)	2.1 (0.5)
Biomass (g·m ⁻²)	5.1 (1.0)	3.7 (0.9)	1.8 (0.8)	2.6 (1.3)	<u>3.4 (0.9)</u>	<u>0.9 (0.4)</u>	10.3 (2.1)	7.3 (1.8)
Growth rate (%·d ⁻¹)	<u>0.41 (0.05)</u>	<u>0.18 (0.04)</u>	<u>0.45 (0.15)</u>	<u>1.10 (0.27)</u>	0.06 (0.10)	0.22 (0.09)		
Production (mg·m ⁻² ·d ⁻¹)	<u>36.1 (7.1)</u>	<u>11.4 (3.2)</u>	12.3 (7.1)	25.0 (7.1)	2.4 (0.5)	2.1 (0.3)	50.8 (13.5)	38.5 (8.7)
June 1983								
Density (number·m ⁻²)	1.2 (0.5)	1.2 (0.3)	0.09 (0.04)	0.15 (0.04)	0.5 (0.2)	0.4 (0.1)	1.8 (0.6)	1.7 (0.3)
Biomass (g·m ⁻²)	1.6 (0.5)	1.4 (0.3)	1.3 (0.6)	2.1 (0.9)	<u>2.4 (1.0)</u>	<u>1.0 (0.3)</u>	5.3 (1.3)	4.6 (1.0)
Growth rate (%·d ⁻¹)	<u>1.9 (0.14)</u>	<u>1.4 (0.12)</u>	0.22 (0.08)	0.09 (0.3)	<u>0.15 (0.13)</u>	<u>-0.54 (0.14)</u>		
Production (mg·m ⁻² ·d ⁻¹)	77.3 (19.6)	54.5 (6.7)	3.3 (1.7)	1.9 (3.8)	<u>3.2 (3.1)</u>	<u>-5.7 (1.8)</u>	<u>83.8 (15.1)</u>	<u>50.7 (3.7)</u>
October 1983								
Density (number·m ⁻²)	0.7 (0.3)	0.8 (0.2)	0.2 (0.1)	0.2 (0.1)	0.3 (0.1)	0.3 (0.1)	1.1 (0.4)	1.2 (0.3)
Biomass (g·m ⁻²)	2.3 (0.9)	2.2 (0.6)	1.3 (0.6)	2.4 (1.0)	1.5 (0.4)	1.3 (0.6)	5.2 (1.1)	5.9 (1.8)
Growth rate (%·d ⁻¹)	0.69 (0.10)	0.86 (0.08)	<u>0.49 (0.08)</u>	<u>0.09 (0.10)</u>	0.16 (0.07)	0.48 (0.30)		
Production (mg·m ⁻² ·d ⁻¹)	13.4 (5.2)	15.1 (2.2)	6.4 (2.1)	2.1 (1.9)	3.1 (0.9)	5.5 (3.1)	22.9 (4.1)	22.7 (5.1)

TABLE 5. Composition of invertebrate functional groups in August 1984 drift samples and in June-July 1982 coho salmon stomach samples.

Group	% of total number			
	Clear-cut site		Old-growth site	
	Drift	Diet	Drift	Diet
Scrapers	29.0	21.1	72.0	26.0
Collector-gatherers	48.1	69.7	21.9	64.6
Shredders	2.4	1.7	1.3	5.1
Predators	20.6	7.3	4.8	4.4

Fish Production

Production of all fish species over the early summer measurement period (Table 4) was greater in the clear-cut site than the old-growth site in both years (*t*-test, $p < 0.05$). In 1982, the average daily rate of fish production during early summer in the clear-cut site was 4.0 times greater than in the old-growth site, while in 1983 fish production in the clear-cut site exceeded the old-growth site by a factor of 1.7. No significant differences in total fish production were observed between the sites from late summer to early autumn.

Production of coho salmon accounted for 30–97% of the total production in the old-growth site and for 59–92% of the total production in the clear-cut site (Table 4). Initial stocking levels of fry influenced coho production rate (Bilby and Bisson 1987). At high stocking densities in 1982, coho production was primarily supported by the relatively large average biomass throughout summer and early autumn. In 1983, the year of lower initial densities, coho production was supported by high

growth rates. In 1982, production of coho was greater in the clear-cut site than in the old-growth site throughout the summer, but in 1983 there was no significant difference in coho production between the streams.

Early summer production of shorthead sculpins was greatest in the clear-cut site in both years (*t*-test, $p < 0.05$), but sculpin production was generally lowest of the three species due to low growth rates (Table 4). Sculpin biomasses were comparable with the two salmonid species, except in 1982 when large numbers of stocked coho fry resulted in high coho biomasses. However, average biomass of shorthead sculpins was significantly greater in the clear-cut site than in the old-growth site in both years (Table 4).

Cutthroat trout production was not significantly different between the clear-cut and old-growth streams during any sampling period. Trout production was lower at both sites in 1983 than in 1982.

Food Habits

Most of the diet of coho salmon during June and July 1982 was composed of invertebrates belonging to scraper or collector-gatherer groups (Table 5). Likewise, invertebrate drift at both sites in August 1984 was dominated by these two functional groups. Principal scraper organisms in both drift and stomach samples were mayflies (*Baetis* spp.). The most abundant collector-gatherers were chironomid larvae belonging to the Orthocladiinae. Both taxa rely heavily on algae or algal-derived detritus as a primary food source (Lamberti and Moore 1984). Invertebrate predators were relatively abundant in drift samples from the clear-cut site; however, the vast majority of predators were mites, which were small and were found only

infrequently in stomach samples. Shredders, which feed primarily on allochthonous organic matter, were rare in both drift and stomach samples. Terrestrial insects did not appear to be important components of coho diets in either stream at this time.

Discussion

Sources and amounts of organic inputs to the clear-cut and old-growth sites were considerably different. Autochthonous production in the clear-cut stream reach was about 70% greater than at the old-growth forested stream during 1982–83 and approximately 50% greater during 1983–84. In contrast, allochthonous input to the old-growth site was approximately five-fold greater than to the clear-cut site (Table 2). Organic matter from autochthonous production at the old-growth site amounted to about 35% of the input from terrestrial vegetation. At the clear-cut site, autochthonous production contributed about three times the amount of organic matter that was delivered from the terrestrial system.

Input rates of various forms of organic matter varied seasonally. Autochthonous production peaked in spring and summer and was likely related to elevated water temperature, high light intensity, extended photoperiod, and relatively stable streamflow. Increased availability of dissolved nutrients has been shown to stimulate algal growth and salmonid production (Johnston et al. 1990), but dissolved N or P concentrations were not greater at the clear-cut site during spring and summer. However, increases in nutrient availability may not have been reflected in the samples if uptake by algae had kept concentrations at low levels (Shortreed and Stockner 1982). Moreover, increases in nitrate-N seen in streams after clear-cutting in the Pacific Northwest (Fredriksen et al. 1975; Brownlee et al. 1988) were not observed in our clear-cut site. In fact, nitrate-N concentrations were significantly below those in the old-growth site, similar to the observed declines in the Carnation Creek, B.C., watershed after logging (Hartman and Scrivener 1990). Reduced nitrate levels in the clear-cut site may have been related to increased uptake by algae (Fig. 4), or alternatively, to increased nitrate uptake by the dense stand of 6-yr-old conifers that had been replanted in the clear-cut watershed (Vitousek and Reiners 1975).

Litter inputs to both sites were greatest in the autumn, although inputs from a variety of vegetation types growing along the stream continued at a fairly high level throughout the year at the old-growth site. Leaves from young deciduous vegetation (willows and alders) next to the clear-cut stream were the predominant source of terrestrial organic matter, yielding a pronounced autumnal peak in litter input (Fig. 2). Fluvial inputs peaked during winter months, when the majority of annual FPOM and CPOM transport often took place during a few days of elevated discharge.

Wood fragments dominated the CPOM component of fluvial allochthonous inputs, comprising 39 and 53% of the CPOM transported by streamflow at the clear-cut and old-growth sites, respectively. In contrast, wood constituted 10% of the litter input from terrestrial vegetation at the clear-cut site and 31% of the terrestrial input at the old-growth site. Net enrichment of wood in CPOM was probably caused by two factors: the lower rate of wood decomposition relative to other types of terrestrial organic matter (Harmon et al. 1986) and lack of tree fall to the streams during the study period. Because there was no tree fall into either reach from 1982 to 1984, measured wood input rates were very low. However, entry of large woody

TABLE 6. Average daily inputs of organic matter from allochthonous and autochthonous sources, average daily production of fishes from spring to early autumn, and the ratios of these values at the two study sites.

	Clear-cut (CC) ($\text{mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)	Old-growth (OG) ($\text{mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)	Ratio (CC/OG)
Annual organic matter inputs			
Allochthonous sources	164	851	0.19
Autochthonous sources	482	301	1.60
Fish production			
Coho salmon	34	18	1.89
Cutthroat trout	8.2	7.4	1.10
Salmonid (both species)	42	25	1.68
Shorthead sculpin	4.5	2.5	1.82
Total (all species)	47	18	1.67

debris tends to be highly episodic in small streams (Bisson et al. 1987), and the absence of significant input during these three years may have resulted in underestimates of actual input rates over longer time periods. Because trees, especially conifers, decompose slowly in streams, woody material can be broken down and exported over periods of decades or more (Harmon et al. 1986). Patterns of storage and transport of wood fragments in Pacific Northwest streams are likely characterized by brief periods of large net gains followed by extended periods of gradual net losses. It appeared that our study took place during one of the latter periods.

Very little leaf material was present in CPOM samples from the old-growth site relative to its abundance in litter traps, indicating that most leaves were retained within the stream reach. Lack of leaf transport through the old-growth stream was probably caused by relatively fast decomposition (Triska et al. 1975; Lamberti and Moore 1984) coupled with retention of leaves by abundant large woody debris (Bilby and Likens 1980). Transport through the clear-cut site was greater because more leaves entered the stream from young deciduous trees growing along the banks and because there was much less large woody debris in the channel to trap incoming leaves. Therefore, a greater fraction of leaves and other terrestrial organic matter was retained in the old-growth site and was available for processing by aquatic invertebrates.

Differences in coho salmon growth rates between 1982 and 1983 (Table 4) suggested that food availability played a major role in controlling production of juvenile coho in the two streams. Coho growth rates were much lower when fish were very abundant than when densities were low. Compensatory growth responses indicated that food availability may have limited coho production more in the old-growth site than in the clear-cut site, an observation similar to findings in other Pacific Northwest streams (Gregory et al. 1987; Hicks et al. 1991). Production in the old-growth reach during the second year exceeded production in the first year in spite of an almost three-fold greater average density of coho in 1982. In contrast, increased growth of coho in the clear-cut site during the low-density year was not sufficient to lead to greater production than in the high-density year, suggesting that compensatory growth limitation occurred to a greater extent in the old-growth stream and that food was probably less abundant there than at the clear-cut site.

Our results supported the hypothesis that organic matter derived from autochthonous sources is very important to fish

populations even in heavily forested headwater streams. Total fish production in early summer was consistently greater in the clear-cut than in the old-growth site (Table 4), despite approximately five times more terrestrial organic matter entering the stream in the old-growth forest (Table 2). If detrital pathways dependent upon the processing of allochthonous material had been primarily responsible for providing trophic support to the fish (Mundie 1974), greater production should have been recorded at the old-growth site. Further evidence that organic matter of autochthonous origin was primarily responsible for supporting fish populations was seen in similarities of the ratios of fish production and autochthonous input between the clear-cut and old-growth sites (Table 6).

Composition of the invertebrate drift and coho stomach contents, based on limited samples, also indicated that autotrophic pathways were important in trophic support. The majority of invertebrates collected in drift and stomach samples are known to feed on algae or algal-based detritus. Shredders, which rely on terrestrial organic matter, were poorly represented in both the drift and diet of juvenile coho, at least at the time of year when our samples were taken. We noted that about 90% of the invertebrates eaten by coho in *both* the clear-cut and old-growth sites (Table 5) were those supported primarily by autochthonous organic matter. This suggests that autotrophic food pathways are important during summer regardless of the condition of the forest canopy or the amount of allochthonous material entering the streams. At other times of the year, however, terrestrial invertebrates may become a dominant part of the diet (Mundie 1969), thus increasing the relative importance of organic matter of allochthonous origin to fish that reside in headwater streams year-round.

While increased primary and secondary production contributed to increased fish production at the clear-cut site, other factors may have played a role. The clear-cut stream exhibited higher maximum and average daily temperatures than the old-growth stream throughout spring and summer (Bilby and Bisson 1987). Moderate elevations in water temperature have been associated with increased salmonid growth in a small Vancouver Island stream (Holtby 1988; Hartman and Scrivener 1990), although these increases may not necessarily lead to improved survival later in the life cycle (Holtby and Scrivener 1989). In this study, temperatures at the clear-cut site were well within thermal tolerance ranges for salmonids; daily maxima usually ranged from 14 to 16°C and the absolute maximum temperature over the entire study period was 19°C. Average summer temperatures in the clear-cut site generally fell within a range considered optimum for coho salmon growth efficiency (Averett 1969). It is therefore possible that water temperature elevation at the clear-cut site contributed to the increase in salmonid production, although this would not have been likely without a corresponding increase in food availability (Bisson and Davis 1976). In addition, higher light levels at the clear-cut site may have enhanced feeding efficiency by rendering food items more visible (Wilzbach 1985).

Differences in coho salmon emigration after stocking also influenced production, especially at higher stocking rates in 1982 (Bilby and Bisson 1987). Immediately after stocking, fewer coho emigrated from the old-growth site, which contained better physical habitat quality (more pools) than the clear-cut site. This led to higher initial population densities in the old-growth stream and created a situation in which large numbers of fish were competing for apparently scarce food

resources. As a consequence, growth rates of coho in the old-growth site were low in the spring and early summer (Bilby and Bisson 1987). At the clear-cut site, lower initial population densities coupled with apparently elevated food availability led to increased early summer growth rates and higher levels of production than at the old-growth site.

While this study demonstrated the importance of organic matter derived from autochthonous processes to the trophic support of fishes in summer, our results do not indicate whether increased spring and summer fish production in the clear-cut site was followed by increased winter production. Mason (1976) found that juvenile coho survived and grew better in a small stream with summer food supplementation, but that summer gains were lost in the absence of suitable overwintering habitat. Murphy and Meehan (1991) also noted that gains in summer production of salmonids may be lost if overwintering habitat is absent. Relatively few coho remained in either of our study streams at the beginning of the period of heavy winter storms, although more fish were present in the old-growth site at the end of summer than in the clear-cut site. Most coho emigrated from the streams in early autumn when streamflow increased and temperature declined. We estimated that only 0.5–8.1% of the initial number of resident fry, i.e. fish remaining in the streams after the initial pulse of downstream movement following stocking, were actually present in the sites by mid-October (Bilby and Bisson 1987). Thus, the results reflected the relative contributions of allochthonous and autochthonous organic matter sources to fish populations in the spring and summer rearing period, but not to fish production in the overwintering period.

Over the last decade, considerable effort has been expended in projects designed to enhance the rearing capacity of streams for juvenile salmonids. Almost without exception, enhancement procedures have involved manipulations of physical structure (logs or gabions) within the stream channel, or creation of off-channel overwintering areas. While both approaches can potentially increase the carrying capacity of the stream system for salmonids, we are not aware of any instance where habitat enhancement has been shown to increase primary and secondary production. Results of nutrient enrichment or food supplementation studies in streams in the Pacific Northwest have indicated that salmonid production can, under certain conditions, be significantly increased by trophic enhancement, sometimes dramatically (Warren et al. 1964; Mason 1976; Mundie et al. 1983; Johnston et al. 1990). Other workers have shown that both overwinter (Hartman et al. 1987; Hartman and Scrivener 1990) and ocean survival (Bilton et al. 1982; Peterman 1982; Wart and Slaney 1988) of anadromous salmonids improve with larger size. The benefits to be gained from increased freshwater growth and production might include higher smolt yield and, possibly, greater marine survival. However, Holtby and Scrivener (1989) showed that ocean survival was strongly influenced by complex interactions between smolt size, emigration timing, and winter and spring ocean conditions. Since our study did not include winter and ocean phases of the coho salmon life cycle, we are unable to conclude with certainty that increased production of autochthonous organic matter in headwater streams will lead to improved survival of coho salmon to adulthood.

Nevertheless, in view of the potential benefits of increased autotrophic production, we concur with Murphy and Meehan (1991) that management techniques designed to increase the supply of food to stream-dwelling salmonids warrant further

investigation. If, as our study indicated, fish production in headwater streams is supported primarily by autochthonous organic matter sources, deliberate modification of nutrient concentrations (e.g. through fertilization) and incident light levels (e.g. through careful manipulation of vegetative canopy) may lead to significant increases in algal photosynthesis that are ultimately passed along to fish populations. The challenge is twofold: (1) to determine if autotrophic production can be increased to desired levels in a sustained, cost-effective, and practical manner and (2) to determine if such increases can be achieved without concurrent deterioration in the quality of other environmental components such as stream temperature or large woody debris, both on-site and downstream.

Acknowledgments

Funding for this study was provided by the Weyerhaeuser Company. We thank J. Heffner, J. Ward, J. Nielsen, B. Fransen, J. Witkowski, and D. Yoshida for technical assistance and M. Toland for statistical advice. S. V. Gregory, C. J. Perrin, and J. C. Scrivener provided much appreciated comments on an earlier version of the manuscript. The Washington Department of Fisheries donated coho salmon for the experiment and the Washington Department of Wildlife granted us permission to plant them in the two streams.

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