RELATIVE IMPORTANCE OF ALLOCHTHONOUS VS. AUTOCHTHONOUS CARBON SOURCES AS FACTORS LIMITING COHO SALMON PRODUCTION IN STREAMS

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ABSTRACT

Organic matter inputs from allochthonous and autochthonous sources were related to fish production rates over two years in an experiment in which coho salmon Oncorhynchus kisutch were stocked into an old-growth coniferous forested stream and a nearby stream flowing through a 7-yr old clear-cut. Both streams contained natural populations of cutthroat trout Oncorhynchus clarki and shorthead sculpins Cottus confusus. In the old-growth site, allochthonous input from riparian vegetation was approximately three times greater than organic matter fixed through autotrophic production. In the clear-cut site the reverse was true, but total organic inputs (allochthonous plus autochthonous) at the clear-cut site were about 50% lower than at the old growth site. Overall, however, the stream in the clear-cut exhibited the highest rates of primary production, and the relative difference in gross photosynthesis between the two streams proved to be nearly identical to observed differences in salmonid production. Coho salmon, in particular, appeared to be limited by food derived from autotrophic pathways at both sites, regardless of riparian conditions. The trophic dependence of juvenile coho salmon on autochthonous carbon sources has been widely overlooked in salmonid enhancement programs.

INTRODUCTION

Carbon budgets of small streams flowing through forested watersheds are dominated by inputs of terrestrial organic matter (Fisher and Likens 1973; Naiman and Sedell 1979; Cummins et al. 1982; Triska et al. 1982). This dominance is based upon a high delivery rate of allochthonous material to the stream coupled with suppression of primary production as the result of heavy shading of the channel by terrestrial vegetation (Gregory 1980). Removal of riparian vegetation by logging may reverse the relative importance of allochthonous and autochthonous inputs due to stimulated primary production and a decrease in the amount of terrestrial litter (Gregory et al. 1987). Such changes influence consumer trophic groups within the stream. Where more sunlight reaches the stream surface, invertebrates specialized to use autotrophically-based energy sources become more abundant (Gurtz and Wallace 1986) and there is often an overall increase in invertebrate production (Wallace and Gurtz 1986; Behmer and Hawkins 1986) that may, in part, be related to the higher nutritional quality of organic material produced by autochthonous processes (Triska et al. 1982; Gregory et al. 1987).

Elevated summer density, biomass, and production of salmonid fishes in streams flowing through clear-cut areas in western North America has been demonstrated by Murphy et al. (1981), Hawkins et al. (1983), Bisson and Sedell (1984), and Bilby and Bisson (1987). These authors have suggested that changes in salmonid productivity are related to greater food availability caused by changes in benthic species composition and increased invertebrate production that accompanied riparian canopy removal. Other factors that have been suggested to contribute to higher salmonid production in open streams include elevated water temperatures (Hartman et al. 1987), enhancement of feeding efficiency (Wilzbach 1985; Wilzbach et al. 1986), and differential patterns of migration (Bilby and Bisson 1987). The relative importance of these factors in limiting salmonid production and the ways in which they interact are not well understood.

This paper compares differences in organic matter sources, amounts, and seasonal timing of inputs over a 2-yr period in a stream flowing through an old-growth coniferous forested watershed with a stream in a nearby watershed that had been clear-cut seven years prior to study initiation. By contrasting organic matter inputs, the dynamics of fish populations in the streams (coho salmon Oncorhynchus kisutch, coastal cutthroat trout Oncorhynchus clarki [formerly Salmo clarki], and shorthead sculpin Cottus confusus) could be examined relative to differences in the form and amount of energy resources available in each stream. The comparison provided new insight into factors limiting the production of food organisms for juvenile coho salmon rearing in headwater areas.

METHODS

The streams were located in the headwaters of the Deschutes River in western Washington (46°43'N, 122°23'W). Details of the study reaches are given in Bilby and Bisson (1987). Most of the 255-ha upper Deschutes River watershed was clear-cut logged in 1974-1975 and replanted with Douglas-fir and noble fir in 1975-1976. Old-growth coniferous forest covering the adjacent 850-ha West Fork Creek watershed was undisturbed at the time of the study and contained Douglas-fir, western redcedar, and western hemlock. Two fish species, cutthroat trout and shorthead sculpin, resided naturally in these streams. During the two years of this study, juvenile coho salmon were released in each study section. Releases took place on June 15, 1982, and again on May 5, 1983. The difference in stocking time, and as a result, size at stocking, was dictated by availability of coho salmon at the hatchery. Virtually all coho salmon that remained in the study reaches smolted after one year; therefore, only one age-class was present in the streams at any given time. We intentionally stocked higher densities in 1982 than in 1983 to test the effects of initial density on habitat use and emigration (Bilby and Bisson 1987).

Input of allochthonous organic matter to each of the streams was monitored with six litter traps suspended 1.5 m above the stream surface at randomly selected locations. In addition, six traps were placed on the banks adjacent to the channel with their mouths facing upslope to sample organic matter entering the streams by blowing or sliding along the forest floor. Traps were emptied monthly from June 1982 through May 1984. Input from herbaceous vegetation growing within the margins of the channel or overhanging the streams less than 1.5 m above the water surface was estimated from plots. Rooted vascular plants growing within the high flow channel margins were collected to a height of 1.5 m at 10 randomly spaced 1-m^2 plots, assuming that all plant material so collected would be delivered to the stream at some time each year. Vegetation overhanging the channel less than 1.5 m above the water surface was sampled by selecting 10 1-m long sections of the high flow bank at each site and collecting all non-woody material above ground level to a height of 1.5 m, again assuming that all organic matter would be delivered to the stream each year. Samples were returned to the lab, oven dried at 60°C and separated into six categories: wood, moss and lichens, needles, leaves, flowers and fruit, and miscellaneous. The miscellaneous category included items such as insects, frass, and unidentifiable material. This fraction was never more than 1% of the sample weight. The material in each category was then redried and weighed. Following weighing, subsamples were selected for ashing at 500°C. Organic matter was determined by weight loss on ignition.

We measured autochthonous production with *in situ* light and dark photosynthesis-respiration chambers (Bott et al. 1978). Flow in the chambers was regulated by two submersible pumps that were run continuously throughout incubation periods. Trays filled with gravel from the streambed and left undisturbed in the stream for a minimum of three weeks were placed in the chambers and incubated from 0.5-2.0h, depending upon the rate of oxygen production. Dissolved oxygen was measured with an oxygen-temperature probe fitted into the wall of the chamber. All incubations took place between 1030 and 1400 hours PST. Light intensity immediately above the light chamber was recorded each half hour during an incubation period with a dome solarimeter. A photosynthetic quotient of 1.2 was used to calculate gross photosynthesis during each trial (Wetzel and Likens 1979). Total amount of fixed organic matter was estimated by dividing the values for carbon by 0.47 (Vollenweider 1974). Measurements in each stream were taken approximately every ten days during the spring and summer months. Estimates of photosynthesis during autumn and winter were made less frequently. Total light input to the streams over the two year study period was estimated from light measurements taken near Olympia, Washington, at the mouth of the Deschutes River (Cinquemani et al., NOAA undated report).

Autochthonous production for the streams was estimated by employing regressions of primary production against light intensity, a procedure used for other Pacific Northwest streams by Murphy (1984). The curves were developed for each stream during each of three time periods throughout the year: July through October, November through February, and March through June. These time intervals corresponded to characteristic periods of similar water temperature and discharge regimes. During the July through October period, water temperatures were relatively warm and flows were low and stable. From November through February, water temperatures were low and flows tended to be high and extremely variable. Nearly all major precipitation events and flood flows occurred at this time of year. Water temperature and flows from March through June were intermediate to the two other periods.

Organic matter inputs to the study reaches by fluvial transport were separated into three categories based on particle size. Dissolved organic matter (DOM) was material less than 1um in diameter, fine particulate organic matter (FPOM) ranged from 1um to 1mm, and coarse particulate organic matter (CPOM) was material larger than 1mm. Fluvial organic matter samples were collected during 1984 only. Because differences in fluvial inputs between the two streams were found to be relatively small and could not be clearly related to fish population dynamics, they will not be discussed in detail.

Fish populations were censused during spring, summer, and autumn; efforts to obtain mid-winter population estimates failed owing to high streamflow and inability to access the sites. Randomly selected habitats within the streams (see Bilby and Bisson 1987) were repeatedly electrofished and the number of fish present in each of the sampled habitat units was estimated using the removal summation technique of Carle and Strub (1978). Total fish populations in the entire reach were estimated by multiplying the average density for a given habitat type by the total surface area of that habitat type present in the study section. Biomass estimates were based on length vs. weight regressions established from subsamples collected at each sample date. Ages of both salmonids and sculpins were estimated from length frequency distributions. Movements of coho salmon from the sites were monitored with fish traps at the downstream end of each study reach. Actual mortality was figured 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.

Dietary habits of coho salmon (obtained by stomach flushing) were sampled during June and July of 1982 in order to determine if there were differences in food organisms selected by fishes in the two sites. Thirty coho salmon were selected at random from each stream for dietary analysis. Invertebrates found in stomach samples were assigned to functional groups according to Merritt and Cummins (1978). Differences in taxonomic composition and functional grouping of the invertebrate drift in both streams were also examined. A series of six 24-h drift samples were taken from August 19 through August 22, 1984. Fish stomach and invertebrate drift samples were taken only once during the study, and then not simultaneously. Therefore, we considered them a crude approximation of the distribution of invertebrate functional groups in the diet and of the food items available to the coho salmon in the two streams. Nevertheless, the proportion of each functional group in the diet enabled us to draw some inferences about the relative contribution of different carbon sources to the energetics of coho salmon populations.

RESULTS AND DISCUSSION

ORGANIC MATTER INPUTS

Terrestrial litter input to West Fork Creek was far greater than to the Deschutes River (Figure 1). Highest levels of litter in the old-growth site occurred in November during both years of the study; however, terrestrial organic matter entered the stream in substantial quantities throughout the year. The clear-cut site also displayed a pronounced seasonal trend in litter input. November was also the highest input month for this stream, but input rates were nearly an order of magnitude less than those observed in West Fork Creek. Litter input was very low at other times of year in the Deschutes River, especially during winter.

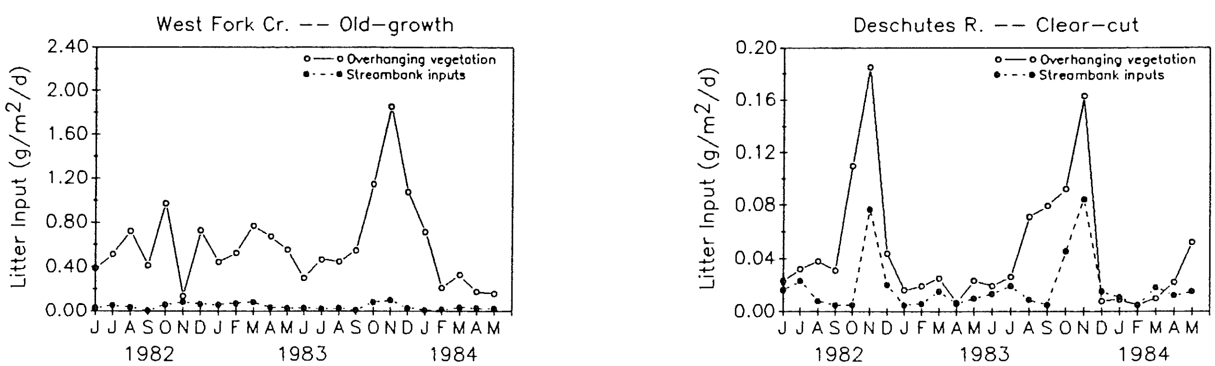

Figure 1. Seasonal changes in allochthonous organic inputs to the old-growth forested site (West Fork Creek) and the clear-cut site (Deschutes River). Open circles denote inputs of litter from vegetation overhanging the stream; solid circles denote inputs from the streambank.

The sharply defined seasonal pattern of litter input to the Deschutes River resulted from a predominance of deciduous vegetation growing along the stream. Leaves were the most common type of litter collected in traps at the clear-cut site. This material typically fell from terrestrial vegetation in an autumn pulse. While some litter from other sources was captured over the year, it made only a minor contribution to the total input to the Deschutes River. The more evenly distributed input of litter to West Fork Creek resulted from greater diversity in the sources of organic matter and temporal separation in peak periods of litter production by the different sources. Like the clear-cut site, the old-growth stream also displayed an autumn peak in leaf input. Needles were an important component of autumn litter, but they entered the stream throughout the year at fairly high levels, comprising the most important component of litter inputs during spring and summer. In winter, woody debris (limbs, bark, etc.) dominated inputs to the old-growth system.

Production of autochthonous organic matter was greater in the Deschutes River than in West Fork Creek, due to higher light levels reaching the stream channel in the clear-cut watershed. In both streams, the lowest rates of autotrophic production were measured in winter (Figure 2) when temperatures were low, daylight was short, and there was frequent scouring of the bed by high flows. From November through March, little difference in gross primary production existed between the sites. The greatest differences occurred during summer in both streams, with primary production at the clear-cut site contributing nearly twice the autochthonous organic matter to the stream than was produced at the old-growth site in this period. Autotrophic production was also relatively high in both streams during spring, but differences between the two sites were not as great as those measured during summer.

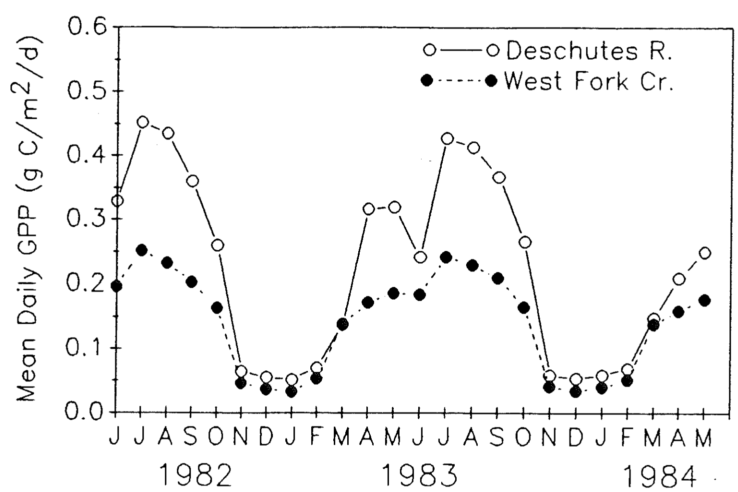

Figure 2. Seasonal changes in gross primary production (GPP) in the clear-cut site (open circles) and the old-growth site (solid circles).

There was a distinct change in the composition of the algal community between spring and summer at the clear-cut site. During the spring a dense growth of green algae occurred, dominated by <u>Ulothrix</u> sp. and <u>Monostroma</u> sp. The green algae disappeared by early June, and diatoms formed the majority of the algal community through the summer. Conditions responsible for the dominance of green algae in the Deschutes River during spring were not clear; however, the appearance of these algae corresponded with fairly stable flows, low water temperatures, and relatively high light intensities. In addition, there may have been more nutrients available at this time of year due to flushing of accumulated materials from the snowpack, coupled with lack of nutrient uptake by terrestrial plants (Likens et al. 1977). Some green algae were also noted at the old-growth site in spring, but diatoms remained the dominant component of the algal community year-round in West Fork Creek.

Overall, the two study reaches differed considerably in the forms, amounts, and timing of organic matter inputs. Total autochthonous production in the Deschutes River was about 70% greater than in West Fork Creek during 1982-1983, and approximately 50% greater during 1983-1984 (Table 1). In contrast, allochthonous inputs to the old-growth site were approximately five-fold greater than to the clear-cut site. Organic matter from autochthonous production at the old-growth site was only about 35% of that derived from allochthonous production. At the clear-cut site, however, autochthonous production accounted for about three times the amount of organic matter derived from terrestrial sources.

Table 1. Summary of organic matter inputs to the two study sites from allochthonous and autochthonous sources.

Organic matter source	Deschutes River clear-cut ($g/m^2/y$)		West Fork Creek old-growth ($g/m^2/y$)	
	1982-1983	1983-1984	1982-1983	1983-1984
<u>Allochthonous</u>				
Litterfall	17	16	246	223
Forest Floor	6	8	18	13
Overhanging and Instream Vegetation*	36	36	60	60
Total Allochthonous	59	60	325	296
<u>Autochthonous</u>				
Primary Production	185	167	111	109

* Input values for overhanging and instream herbaceous vegetation were determined for 1983-1984 only and were applied to 1982-1983.

The relative nutritional value of these organic inputs to higher trophic levels is variable, and is often closely related to rate of decomposition in the stream. In general, autochthonous organic matter (algae) is considered superior to allochthonous organic matter as an invertebrate food source (Gregory et al. 1987). Algae was produced in substantially greater quantities at the clear-cut site than at the old-growth site. There is also a wide range in the decomposition rate of different types of terrestrial organic matter. Herbaceous plants, as well as fruits and flowers, tend to decompose most rapidly, followed in turn by leaves from deciduous trees, needles, and wood. Based on the abundance of litter of deciduous origin, allochthonous inputs to the clear-cut site were dominated by relatively high quality material, while inputs to the old-growth site were dominated by relatively low quality needles and wood. However, while terrestrial inputs to the Deschutes River were of high quality, the total input of this material, including litter of deciduous origin, was greater at the old-growth site.

Differences in fluvial organic matter inputs were not as striking. DOM inputs were roughly similar in the two systems. FPOM concentrations were slightly higher at the old-growth site during low-flow periods, while CPOM concentrations were higher at the clear-cut site during high-flow periods. Total input of all three size classes of fluvial organic material tended to be greatest in the old-growth stream, due primarily to higher streamflows at this site. Fluvial inputs peaked during winter. This pattern was especially true for CPOM and FPOM components, where the majority of the total annual input often occurred during a few days of elevated discharge.

FISH PRODUCTION

Overall, fish production was greater in the clear-cut site than in the old-growth site (Table 2). Coho salmon dominated the production of all fish species in both streams. In 1982, when high densities were stocked, coho salmon production was sustained by higher average biomass. In 1983, when lower densities were stocked, coho salmon production at both sites was sustained by high growth rates. Cutthroat trout production in the Deschutes River and West Fork Creek differed relatively little. In the clear-cut site, production of coho salmon exceeded that of cutthroat trout by a factor of 4-5 in both years. In the old-growth site, production of the two species was approximately equal in 1982, but was 10-fold greater for coho salmon in 1983. Shorthead sculpin production was lowest of the three fish species, due primarily to low growth rates.

Table 2. Production statistics for coho salmon, cutthroat trout, and shorthead sculpins in the clear-cut Deschutes River site (CC) and the old-growth West Fork Creek site (OG).

Year	Coho salmon		Cutthroat trout		Shorthead sculpin		All species	
	CC	OG	CC	OG	CC	OG	CC	OG
1982								
Density (no./m^2)	2.13	1.67	0.15	0.12	0.95	0.28	3.23	2.07
Biomass (g/m^2)	9.21	7.25	2.28	1.79	3.58	0.93	15.06	9.97
Growth rate (%/d)	0.35	0.33	0.32	0.47	0.19	0.19		
Production (mg/m^2/d)	39.2	13.6	10.5	12.7	5.8	1.6	55.5	27.9
(g/m^2/yr)			2.1	2.5				
1983								
Density (no./m^2)	0.57	0.87	0.12	0.24	0.41	0.35	1.10	1.46
Biomass (g/m^2)	2.15	2.37	1.54	3.29	2.46	1.28	6.14	6.94
Growth rate (%/d)	1.10	0.88	0.41	0.05	0.13	0.20		
Production (mg/m^2/d)	28.7	22.5	5.8	2.1	3.1	3.3	37.6	27.9
(g/m^2/yr)			1.1	0.4				

FACTORS LIMITING FOOD AVAILABILITY

The importance of autochthonous production to salmonid populations in streams flowing through clear-cut areas has been suggested by other studies in the Pacific Northwest (Murphy and Hall 1981; Hawkins et al. 1983; Bisson and Sedell 1984; Bilby and Bisson 1987). Gregory et al.(1987) have speculated that salmonid production is likely to benefit more from food resources based on autotrophic than on heterotrophic pathways. Our results support this hypothesis, particularly for juvenile coho salmon, whose production rates were consistently greater in the clear-cut than the old-growth site in spite of five-fold greater inputs of allochthonous organic material to the stream in the old-growth forest (Table 1). If detrital pathways based on processing of terrestrial organic inputs were responsible for the majority of food available to coho salmon, as suggested by Mundie (1974), West Fork Creek should have exhibited superior production. This, however, was not the case. We also noted that the average ratios of both coho salmon and total salmonid production in the clear-cut site to the old-growth site closely approximated the ratio of their primary production rates (Table 3).

Table 3. Gross primary production, coho salmon production, and total salmonid production in the clear-cut Deschutes River site and the old-growth West Fork Creek site, and their ratios, averaged over the study period.

	Clear-cut	Old-growth	Ratio Clear-cut/old-growth
Gross primary prod. ($mg/m^2/d$)	482	301	1.60
Coho salmon prod. ($mg/m^2/d$)	34	18	1.89
Total salmonid prod. ($mg/m^2/d$)	42	25	1.68

The hypothesis that salmonid populations in both systems were being sustained largely by organic matter of autochthonous origin was also supported by the relatively close correspondence between seasonal peaks of primary production and fish production. Most growth and production of coho salmon and cutthroat trout occurred during spring and early summer when algal growth was at a maximum and input of carbon from allochthonous and fluvial sources tended to be at a minimum. Organic matter of terrestrial origin was present in both streams at this time of year; however, most allochthonous material of high nutritional value (such as herbaceous plants and deciduous leaves from the previous growing season) had likely been processed by the benthic community (Triska et al. 1982; Gregory et al. 1987).

Additional evidence of the reliance of coho salmon on autochthonous carbon sources was provided by the comparison of drift and stomach samples (Table 4). At the time the samples were taken, invertebrate drift at both sites was dominated by organisms belonging to grazer and collector-gatherer functional groups. The principal grazer organisms were mayflies (Baetis spp.), and most of the collector-gatherers in the drift samples were chironomids belonging to the Orthocladiinae. Both taxa rely heavily on algae or algal-based detritus (Lamberti and Moore 1984). Likewise, the frequencies of grazer and collector-gatherer functional groups were very high in coho salmon stomach samples, where together they comprised about 90% of the diet (Table 4). Although sampling was very limited, it therefore appeared that juvenile coho salmon were consuming a large percentage of invertebrates that were supported by autotrophic production in the streams. Shredder organisms, which rely on allochthonous inputs, were poorly represented in both drift and stomach samples.

Table 4. Functional group composition of invertebrates taken from drift samples obtained in August, 1984, and from coho salmon stomach samples obtained in June-July, 1982. Values are expressed as percent of total number.

Invertebrate functional group	Deschutes River clear-cut		West Fork Creek old-growth	
	Drift	Stomach	Drift	Stomach
Grazer	29	21	72	26
Collector-gatherer	48	70	22	65
Shredder	2	2	1	5
Predator	21	7	5	4

Taken together, all lines of evidence strongly support the hypothesis that autochthonous organic matter was an important resource limiting the availability of food, and therefore, production of coho salmon in both the clear-cut and old-growth sites. It is possible that trophic dependence on organic matter of autotrophic origin also extended to the other fish species in these two streams, but lack of site-specific information on the food habits of cutthroat trout and shorthead sculpins prevented us from drawing reasonable inferences. Perrin et al. (1987), in a whole-river enrichment study on Vancouver Island, found that inorganic nutrient additions resulted in a greater increase in the mean weight of coho salmon than did additions of cereal grains. They concluded that increased autotrophic production by nutrient addition results in greater benefit for growth of salmonids in nutrient deficient streams than stimulation of heterotrophic production. Our findings were in substantial agreement with this conclusion.

Over the last decade considerable effort has been expended in projects designed to enhance the rearing capacity of streams for juvenile coho salmon. 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 coho salmon, we are not aware of any instance where habitat enhancement has been shown to increase primary and secondary production. Yet 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; Perrin et al. 1987). Other workers have shown that both overwinter (Hartman et al. 1987) and ocean survival (Bilton et al. 1982; Peterman 1982) of anadromous salmonids improves with larger average size. The benefits to be gained from increased freshwater growth and production would therefore likely include higher smolt yield and, possibly, greater marine survival.

In view of these potential benefits, we suggest that enhancement techniques designed to increase the food supply to stream-dwelling salmonids warrant further investigation. If, as our study indicated, coho salmon production in headwater streams is supported primarily by autochthonous carbon sources, deliberate modification of nutrient concentrations (e.g., through fertilization) and incident light levels (e.g., through manipulation of vegetative canopy) may lead to significant increases in autotrophic production that are passed along to fish populations. The challenge is two-fold: (1) to determine if autotrophic production can be increased to desired levels in a cost-effective and practical manner, and (2) to determine if such increases can be achieved without deterioration in the quality of other environmental components, both on-site and downstream.

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