

# Constraints on the Productivity of Coho Streams

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The question of which factors regulate productivity in small streams has been addressed for most trophic levels in the past decade. Nutrient limitation of primary productivity has been a common observation in experimental studies and surveys. Various experimental studies have also indicated that food regulation of benthic populations is a frequent check on productivity. Other studies have shown that for coho, and other salmonids, growth and survival may be co-limited by benthic productivity and instream habitat. If potential productive capacity of coho streams is limited by trophic transfer rates from the benthos, then management that promotes benthic productivity would be advised. Such techniques as stream fertilization and preservation of instream structure which retards the export of detritus and nutrients are valuable management tools. These properties should hold whether trophic transfer from benthos to fish is donor-controlled or strongly interactive.

## INTRODUCTION

Lotic salmonids such as coho salmon rely heavily on drifting and benthic macroinvertebrates for food. A diverse array of studies suggest that salmonid density and growth, and hence productivity, are limited, at least in part, by food supply (Warren et al. 1964; Chapman 1966; Mason 1976; Johnston et al. 1990; Deegan and Peterson 1992). Density and growth of stream fishes is often correlated with measures of invertebrate biomass (Warren et al. 1964; Hawkins et al. 1983); unfortunately productivity of benthic organisms is seldom measured. Territorial behaviour of stream salmonids is often closely linked to availability of prey (Slaney and Northcote 1974; Dill et al. 1981), and fish will occupy locations in the stream which can be predicted on the basis of food delivery rates in terms of drift (Hughes and Dill 1990). Either food or habitat, (i.e., instream cover) are considered to limit the density or biomass of salmonids, and may be co-limiting; many of these same themes have been considered in a paper by Mundie (1974) in which he considered how the productive capacity of nursery streams could be augmented for the production of juvenile salmonids. In this paper we wish to emphasize recent research on limitation of the productivity of salmonid prey organisms and to point out that instream complexity may also play a role in affecting abundance of the macroinvertebrate food base of lotic salmonids. If indeed salmonid productivity in streams is in part limited by food supply then the question of what limits benthic productivity becomes a critical question.

During the past 15 years evidence has been accumulating which shows that many trophic pathways in streams leading to salmonid production are limited by resources. Many studies have shown that primary productivity is strongly nutrient limited on scales from small, nutrient-amended pots or containers (Pringle 1987), to whole streams (Peterson et al. 1985; Perrin et al. 1987). Furthermore there is strong coupling between periphyton productivity, and grazer biomass (Feminella and Resh 1991; McCormick and Stevenson 1991), (i.e., strong and rapid feedback between trophic levels). In many streams, especially smaller systems, detritus derived from litterfall in the surrounding watershed contributes substantially to system-wide productivity (Cummins et al. 1983). A variety of studies have demonstrated that detritus, in its many forms (coarse particulate organic matter, fine particulates, dissolved organic carbon) also frequently limits productivity of populations which are dependent on these resources (Mundie et al. 1983; Richardson 1991; Richardson and Neill 1991; Richardson and Mackay 1991). Predacious macroinvertebrates are a common component of stream ecosystems but their relative role in the trophic transfer to coho salmon or as net energetic sinks is unknown.

In this paper we briefly review the evidence for limitation of productivity at most trophic levels in stream ecosystems. The observation of limits to productivity of trophic levels leading to the nutrition of coho salmon in streams has important implications for the community structure and energy flux within stream communities. There are many important questions regarding the way stream ecosystems function, particularly regarding the nature of the population interactions between coho and their prey, and the nature of the feedback processes between trophic levels. Tests of the effects of salmonid predation on benthic communities have produced results that range from largely donor-controlled (i.e., the fish have little or no direct effect on depression of their prey populations), to strong population dynamical interactions between fish and their prey. In the former scenario salmonids would have little impact on their prey populations, and in the latter case insectivorous fish would contribute to their own self-limitation through exploitative competition and resource depression. It is unlikely that the interaction is either at one extreme or the other, but little is known about the range of conditions under which these predator-prey population dynamics might be more or less strongly coupled. We will discuss the relevance of this question to instream management for production of coho salmon. Regardless of how predator and prey interact in a population dynamics sense, the rate of productivity of prey will in large part determine the carrying capacity of stream-dwelling salmonids where prey supply is limiting. While we make some sweeping generalizations in this paper, we appreciate that nature is never so straightforward. Nevertheless our conclusions are generally supported by the evidence, and we hope to promote the search for general processes and relationships in stream ecosystems.

### PRIMARY PRODUCTION

In all but the most eutrophic streams primary productivity is limited by the concentration of nutrients (phosphorus or nitrate) or light levels. Among the first to comment on this observation was Huntsman (1948) who added bags of agricultural fertilizer to Atlantic salmon streams in New Brunswick and observed increased algal biomass. Since then nutrient limitation of instream primary production has been shown to be common. Demonstration of nutrient limitation has been shown across a variety of scales including small pots or containers (Pringle 1987), flow-through troughs (Peterson et al. 1983; Bothwell 1989; Hart and Robinson 1990; Perrin 1991), and whole-stream fertilization (Peterson et al. 1985; Perrin et al. 1987).

Periphyton accrual rates are quite sensitive to nutrient concentrations in stream water (Bothwell 1989; Perrin 1991). In most instances where some form of nutrient amendment has been used there have been large increases in growth rates of periphyton and total biomass. Very small increments in the concentration of limiting nutrients (phosphorus or nitrate) can result in large relative increases in biomass-specific growth rates. Nevertheless the potential for increased algal growth rates may only be saturated at very high nutrient concentrations as demonstrated in trough studies (Bothwell 1989; Perrin 1991). One hypothesis for the high concentrations necessary for saturation of periphyton growth rate is the concentration gradient required for diffusion of nutrients into a thick layer of periphyton. In spite of the knowledge of the effects of nutrient addition on periphyton growth and accrual rates, there is little known about long-term effects on systems, or the duration of fertilization necessary to see a system-wide enhancement of primary productivity. There is no direct knowledge of the relationships between instantaneous growth rates, longer-term productivity, standing crop, and nutrient spiralling for stream periphyton; much of the approach to stream fertilization is based on assumptions about these relationships derived from lake studies.

## HERBIVORES

The interaction between herbivores and periphyton is the best studied of all trophic interactions in streams in terms of understanding the rates and net impact of the interaction and the intensity of feedback. Because of the tight coupling of these two trophic levels one predicts that this interaction should be very sensitive to fluctuations in nutrient concentrations and scouring effects of discharge variation. In many plant-herbivore interactions intermediate levels of grazing may reduce biomass but actually increase productivity through increased turnover due to more rapid nutrient cycling. There is little evidence of this in streams, perhaps because of the difficulties measuring the spiralling of nutrients and their different forms (e.g., particulate or dissolved). However, there are studies showing that herbivory can reduce shading by senescent cells thereby increasing chlorophyll-specific productivity (McCormick and Stevenson 1991).

Grazers are able to depress standing stocks of algae and also show density dependent effects of such resource depression by reduction in growth, fecundity, or survival rates (Hart 1987, Hill and Knight 1987, Lamberti et al. 1987; Hart and Robinson 1990; Feminella and Resh 1991). The evidence for tight coupling of the population interactions of herbivorous macrozoobenthos and algae strongly supports the hypothesis that rates of primary production will limit population size and biomass of grazing macroinvertebrates. Nutrient additions which stimulate periphyton productivity have been shown to enhance demographic parameters of grazer populations by the amelioration of resource-based density dependent effects. Nutrient additions have led to increased grazer biomass, growth rates, and survival (Hershey et al. 1988; Hart and Robinson 1990; Mundie et al. 1991; Perrin 1991; Richardson and Rosenfeld - unpub. data). These studies and others indicate a strong coupling of nutrients, periphyton productivity, and grazer productivity.

## DETRITUS

Detritus derived largely from riparian litterfall is an important component of the energy base of stream communities, and in heavily shaded streams 80% or more of the available fixed energy comes from this source (Cummins et al. 1983). Earlier studies had shown correlations between the biomass of detritus and detrital consumers (Egglishaw 1964). Detrital materials are generally divided into two size fractions, based on particle size (e.g., those > 1.0 mm in diameter and those < 1.0 mm), which closely corresponds to the types of microfauna associated with them and to the feeding morphologies (and therefore species) which feed on certain particle types. Consumers of large particles are often called "shredders" and fine particle feeders are called "collectors".

Several studies have experimentally demonstrated that shredders are severely limited by the quantity and quality of detrital materials (Otto 1974; Mundie et al. 1983; Richardson 1991). The demographic effects of supplementing detrital resources to benthic macroinvertebrates are increased growth rates, increased survival, and reduced per capita rates of emigration, similar to the results found with grazers. These changes lead to increased benthic densities and biomass of consumers of coarse particulate detritus. The timing of leaf litter inputs creates seasonal shortages for populations of shredders and may be the main regulator of population dynamics and productivity (Richardson 1991). The type and magnitude of litter inputs are obviously related to the riparian canopy and this group of consumers may be quite sensitive to manipulations of riparian zones under certain land use practices.

Fine particle consumers, including both collectors and filterers, show relations between density and measures of the supply of fine detritus in suspension or in the benthos (Richardson and Mackay 1991; Richardson and Neill 1991). The patterns of association with collectors and their food supply come in

the form of correlations between seston concentration and the density of collectors. Another often observed pattern which is consistent with seston concentration determining population density of collectors is the very high density of filter feeders found in outlets of lakes where seston is both high quality (plankton) and in high quantity (Richardson and Mackay 1991). In general we know less about the population dynamics and limits for this particular trophic grouping of benthos than most other groupings. One of the reasons for this is the complexity of their food resources which span a size range from  $<0.2 \mu\text{m}$  to 1 mm, may be derived from fragmentation of any kind of organic matter or flocculation of dissolved organic carbon, may include live (including algae, bacteria, rotifers, etc) or dead matter, and can vary tremendously with season, hydrograph, etc. Thus it is harder to make broad comments on this trophic grouping.

The microbial loop (i.e., use of dissolved organic carbon by bacteria and protozoa) may be a significant source of secondary productivity in marine and lacustrine systems. Stream ecologists are only just beginning to address the contribution of this flux of energy within stream food webs. This will be a growing area of stream ecology for the foreseeable future.

### THE TROPHIC BASIS OF COHO PRODUCTION AND ITS LIMITATION

It seems that under many circumstances lotic salmonids, such as coho salmon, are limited by their food supply or co-limited by space which provides access to food or cover. Increased density of benthos due to addition of dissolved sucrose resulted in increased growth of cutthroat trout in an Oregon stream (Warren et al. 1964). Supplemental feeding of juvenile coho salmon by direct addition of dead euphasiid shrimp to stream enclosures led to increased growth and lipid storage in one study (Mason 1976). Johnston et al. (1990) have shown increases in the size of coho and steelhead following whole-stream fertilization, putatively as a result of increased benthic productivity. Other studies have shown that young coho compete for space, which may be considered as a proximate resource for gaining access to food (Chapman 1966). Increase in food supply reduces the space which an individual defends (Slaney and Northcote 1974) in accordance with models of economically defensible area. Social dominance in the defense of feeding areas by some lotic salmonids is based on the value of the space for access to drift (Hughes and Dill 1990).

In medium-sized streams (orders 3-5) primary production may be the most important source of fixed organic carbon for higher trophic levels (Minshall 1978; Vannote et al. 1980). Regardless of the food web organization of communities in such streams, the productivity of higher trophic levels will be an increasing function of productivity of primary producers or detrital biomass. There are few studies which illustrate the relation between system productivity and fish productivity. In a descriptive study of southern Ontario streams Bowlby and Roff (1986) found positive correlations between measures of biomass of zoobenthos and salmonid biomass.

The available evidence strongly supports the hypothesis that coho young are co-limited by food supply and available habitat (which provides access to food). Given this view we then need to address the question of what affects the food supply rate to coho in natural streams. The essence of this question then is what limits the production and delivery of prey derived from the benthos and what is the nature of the interaction with coho salmon? We discuss these issues in a general sense below.

## TROPHIC TRANSFER MODELS

Several related models of interacting trophic levels predict alternating predator or resource limitation of biomass at adjacent trophic levels, variously known as a top-down model or a trophic cascade (Hairston et al. 1960; Carpenter et al. 1985). The supposedly opposing model is that productivity at each trophic level is simply the amount of energy available at the trophic level below discounted by the efficiency of conversion (the bottom-up model). These models have become tremendously confused since the terms top-down and bottom-up have been applied to biomass, productivity, size-structure, and species composition. The original models were explicitly in terms of biomass and productivity (Hairston et al. 1960). Most systems will have some component of regulation from both nutrient-limited productivity and from the actual trophic structure. This can be viewed as nutrients (or perhaps another basic resource) setting the fundamental rate of productivity and trophic structure fine-tuning the rates. It is not clear what the conditions might be that would result in large versus small effects of trophic structure, but from lake studies results have been quite variable. In productive streams where nutrients are not limiting (e.g., Rand et al. 1992) there may be a more important role for trophic structure affecting system productivity. Nevertheless, in typical coho streams nutrients are frequently limiting and this apparently determines the productivity of many streams.

The importance of these trophic models is in the role of predators (e.g., coho salmon) in regulating their own food supply. There are many reasons why predators may not regulate their prey, nor even have much impact on the biomass or productivity of prey populations (see review in Power 1992). Coho salmon are unlikely to feed extensively on invertebrates while in the stream bottom and instead depend on consuming drifting animals derived from the benthos. If the animals in the benthos represent the population density that can be sustained by their current resource levels, and if coho cannot depress the density of these animals, then the supply of food to coho may be a donor-control process. This follows from the "excess production" hypothesis of Waters (1972) which suggests that drift rate represents organisms in excess of current carrying capacity of resources. Evidence from supplementation of food resources to macroinvertebrates indicate that per capita drift rates decline in response to increased food (Warren et al. 1964, Richardson 1991). It is possible that reduced per capita drift rates in the presence of supplemental food may be a transient effect of excess food. No long-term food enhancement studies over several generations of benthic organisms have been attempted to determine whether the ecosystem would reach another carrying capacity where per capita drift rate would again increase, and the absolute numbers drifting would be much higher. An example of this type of effect can be seen in Richardson (1991) where a multivoltine chironomid apparently reached a new carrying capacity in response to supplemental leaf litter and drift rates subsequently increased. Whether or not drift is so finely tuned to food resource abundance, it does indicate that the rate of transfer of energy from trophic levels in the benthos to drift-feeding coho may be monotonic, decelerating function of productivity at those lower trophic levels. The clear implication of this bottleneck on the transfer of energy from benthos to fish is that productive capacity will be limited by whatever resources (detrital and inorganic nutrients) limit productivity in the benthos. We also know very little about the efficiency of transfer of energy between trophic levels in streams. The bottom line is that increasing productive capacity of coho streams will require more attention to productivity of lower trophic levels and factors affecting the rates and efficiency of energy transfer from benthic populations to juvenile coho.

## MANAGEMENT

One of the typical responses of management agencies to desires to increase productive capacity of streams is to focus on habitat improvement (other papers in this proceedings). While this often leads to increases in density of salmonids the actual mechanism may not be so clear. Manipulation of instream cover for coho can also have important effects on other aspects of the stream community. Instream cover tends to retard the export rate of nutrients and detrital materials by increasing stream retentiveness, and may serve as refuge from hydrologic disturbance for benthic macroinvertebrates as well as salmonids. Several studies have shown that particulate detritus is retained longer in stream reaches with complex bedform, especially woody debris (Speaker et al. 1984; Lamberti et al. 1989; Richardson 1992). Likewise nutrient spiralling distances are reduced in reaches with greater substrate complexity (Lamberti et al. 1989). No one has experimentally addressed the question of how instream complexity affects production of lower trophic levels. However, there are correlations that suggest that instream habitat can affect the densities of benthic organisms. Furthermore, in many streams woody debris, also called snags, provides important habitat for benthos that can increase the areal rates of production.

Productivity of coho will be a function of the rate of productivity and availability of prey derived from populations of benthic macroinvertebrates. A greater focus on the actual mechanisms limiting populations of benthos will lead to a greater appreciation for how to approach the problem of habitat capacity for coho. Techniques such as whole-stream fertilization or bankside management for maintaining litterfall from riparian vegetation are potential means of contributing to the productive capacity of streams through increased benthic productivity. Instream habitat management for complexity and cover may also contribute to increased prey abundance. More study should be addressed to the intensity of population limitation of coho by the supply of food, and its relative role in limiting growth versus the survival advantage of instream cover. Both food and cover are likely to be co-limiting in general and any means that would augment productivity of benthos is likely to alleviate at least one potential source of population limitation for coho salmon.

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