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Stream ecosystem research in a watershed perspective

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With 2 figures and 2 tables in the text

Introduction

In has now become increasing clear that characteristics of stream ecosystems are intimately tied to the nature of their watershed (HYNES 1975). Until recently, however, research directed at stream ecosystems was largely confined to individual segments or small watersheds, seldom being extrapolated to a wider perspective. Due primarily to the pioneering work of VANNOTE et al. (1980), research on lotic ecosystems has recently shifted from studies of stream segments to studies of biological and physical longitudinal profiles as streams gradually coalesce to form large rivers (see for example, SEDELL et al. 1978; NAIMAN & SEDELL 1979 a, b, 1980). This river continuum concept may be referred to as a "second dimension" in our understanding of the characteristics of streams as they flow from headwaters to the sea. Research on lotic ecosystems is now on the verge of progressing to a "third dimension", by giving breadth to the previous studies of longitudinal changes, through careful watershed analyses of stream size, length, numbers, discharge, and gradient within the entire drainage network.

Gross physical analyses of large watersheds are relatively easy to accomplish, and when combined with studies of stream segments of various orders, can be a powerful tool for understanding the basic structural and functional processes of large and seemingly complex ecosystems. When physical and biological studies are combined, the relative importance, abundance, activity, and distribution of biological components can be readily examined at the watershed level. By not considering the entire watershed, overemphasis is often placed on certain aspects relative to their proportion within the watershed, both in terms of quantity and quality. As a consequence, longitudinal and latitudinal perspective, which covers the total drainage network, is lost.

For this short paper we have chosen three examples from our studies in Quebec, Canada, and Washington, U. S. A., to demonstrate how physical analyses can be combined with biological studies to produce a clearer understanding of large watershed ecosystems. These examples include export of organic carbon, distribution of periphyton production, and the relative abundance and distribution of quality habitat for salmonid fishes.

Site descriptions

Studies in Quebec are centered on the Moisie River (9th order; area = 19,811 km^2) and the Matamek River watersheds (6th order; 673 km^2), about 25 km east of Sept Iles. Both rivers discharge into the Gulf of St. Lawrence. The area is Precambrian Shield with virgin stands of black spruce (*Picea mariana;* 47 %) and balsam fir (*Abies balsamea;* 44 %). The trees are of mixed ages but most are > 60 years old. Disturbances are < 1 % of each watershed, and nearly all are > 50 yrs old. Winters are long and severe with a mean annual temperature of 1 °C. There is a strong spring freshet in April—May when nearly 75 % of the annual discharge occurs. Mean annual discharge of the Moisie River is 466 m$^3 \cdot s^{-1}$; for the Matamek River it is 22.1 m$^3 \cdot s^{-1}$.

In Washington the South Fork of the glacially fed Hoh River meanders over a broad, gravel-floored, flood channel on the Olympic Peninsula. This temperate rain forest is old-

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growth spruce *(Picea sitchensis)* and western hemlock *(Tsuga heterophylla)* $\leq$ 260 yrs old. The study area was divided into sections consisting of the main river channel; subsidiary channels to the main river located within the active exposed floodplain; tributaries resulting from spring networks on the flat valley floor and from tributaries draining the valley slopes which continue across geological terraces to the main river; side slope streams originating from run-off on the sleep valley walls; and upper side slope streams with steep gradients and high velocities (SEDELL et al. 1980).

Materials and methods

With minor modifications, annual periphyton production was estimated by methods described by NAIMAN & SEDELL (1980). This is a chamber technique utilizing a diel oxygen curve to measure metabolic parameters. Particulate seston concentrations $> 0.5\ \mu m$ were measured by filtering 4 l of water onto a preweighed and ashed Gelman A/E glass filter, ashing the filter and sample for 2—4 hr at 525 °C, and then reweighing the sample. Samples were assumed to be 50 % carbon. Dissolved organic carbon (DOC; $\leq 0.5\ \mu m$) was measured by persulfate oxidation (MENZEL & VACCARO 1964).

Watersheds were characterized from Canadian Department of Energy, Mines, and Resource, and U. S. Geological Survey topographic maps (scale = 1 : 50,000) for stream order (STRAHLER 1957), number and length of each stream order, and for spatial distribution of streams. Results were randomly checked in the field for accuracy. Stream widths were determined either from aerial photos taken by the Quebec Ministry of Lands and Forests (scale: 1 : 15,000) or by measurement of a large number of transects. Physical stream survey techniques were used to rate channel and bank stability and pool quality (DUFF & COOPER 1976; PFANKUCH 1975). The stability method is based on a visual rating of 15 physical factors which yields a qualitative, objective ranking. Pool classification is largely based on surface area, maximum depth, and extent of vegetative cover. Debris obstructions were counted directly and rated for their role in bank stability, providing fish habitat, and in flow deflection.

Fish were captured with a beach seine in the larger rivers and with a 600 v backpack electric shocker in off-channel and tributary sites. Fish were anesthetized with MS 222 (tricaine methanesulfonate), identified to species, fork length measured, and released. Biomass was estimated from length-weight relationships (SEDELL et al. 1980).

Results and discussion

Three diverse examples serve to demonstrate the value of physical watershed analyses to stream research. For this purpose we discuss organic carbon export from watersheds, distribution of periphyton production, and the relative quality of various habitats for salmonid fishes.

Export of organic carbon

The amount of organic carbon exported from watersheds is thought to vary widely and be greatly influenced by vegetation, basin area, hydrographic events, season, and efficiency of terrestrial retention. However, when annual export is scaled to a unit area, it has been found to be surprisingly conservative and can be conveniently used for comparison between biomes, as well as for comparisons among watersheds in the same biome. This has been done for five watersheds in Quebec ranging in area and annual discharge over five orders of magnitude (Table 1). Despite these wide physical ranges the concentrations of particulate organic carbon (POC) and dissolved organic carbon (DOC) rarely vary by more than

Table 1. Preliminary estimate of annual export of organic carbon from various sized watersheds in Quebec.

Watershed	Area (km^2)	POC[a] (mg $C \cdot m^{-3}$)	DOC[a] ($g\ C \cdot m^{-3}$)	Total carbon (g $C \cdot m^{-3}$)	Annual discharge ($m^3 \cdot yr^{-1}$)	Runoff ($m \cdot yr^{-1}$)	Annual export ($g\ C \cdot m^{-2} \cdot yr^{-1}$)
First Choice Creek	0.25	488 ± 70	2.06 ± 0.22	2.55	4.10×10^5	1.64	4.18
Beaver Creek	1.83	875 ± 144	11.52 ± 0.50	12.40	1.04×10^6	0.57	7.05
Muskrat River	207	1201 ± 164	10.43 ± 0.55	11.63	2.65×10^8	1.28	14.89
Matamek River	673	512 ± 29	7.00 ± 0.19	7.51	6.97×10^8	1.04	7.78
Moisie River	19,811	528 ± 76	4.75 ± 0.17	5.28	1.47×10^{10}	0.74	3.92

[a] $\bar{x} \pm SE$

a factor of 3—5 between diverse streams within the same biome. Preliminary estimates of annual export are between 3.92—14.89 g $C \cdot m^{-2}$, depending upon the site, with 81—93 % in dissolved form.

On the average, these results are slightly lower than the 14.18 g $C \cdot m^{-2} \cdot yr^{-1}$ estimated for the productive Amazon River watershed (Richey et al. 1980) and the 14.95 g $C \cdot m^{-2} \cdot yr$ estimated for the Nanaimo River, British Columbia (Naiman & Sibert 1978), and are higher than the 0.29—2.30 g $C \cdot m^{-2} \cdot yr^{-1}$ estimated for several watersheds in the temperate Douglas fir forests of Oregon (Naiman & Sedell 1979 a).

The Amazonian tropical forest, the temperate rain forests of the northwestern United States and western Canada, and the boreal forests of northern Canada range in annual productivity by approximately a factor of four (Leith 1975), which is remarkably similar to the annual range of riverine export of organic carbon from the watersheds. The value of this observation lies in its usefulness for estimating, with a fair degree of confidence, movement of organic carbon from terrestrial ecosystems to oceans at a time when this contribution to the global carbon cycle can only be crudely estimated (Richey et al. 1980). If the range of values reported here for these diverse watersheds are reasonably correct, it should now be a relatively easy task to reliably estimate export from major terrestrial biomes to the oceanic ecosystem using physical measurements of biome size.

Primary production

The distribution of primary production, benthic detritus, and other biological components of streams within a large watershed is not uniform. As an example, it has been shown by Naiman & Sedell (1980) that periphyton production increases in a downstream direction, at least up to the size of a moderately large river. Since > 95 % of all streams are ⩽ 6th order it is thought that most periphyton production occurs in these smaller streams and not in larger rivers which are usually deep and turbid, restricting light penetration.

We determined for the Quebec sites that annual gross production and net daily metabolism can be estimated from stream order with a fair degree of confidence ($r^2 = 0.71$ and 0.83, respectively) (Fig. 1). These relationships, when combined with data on stream widths, number of streams of various order, and mean lengths of

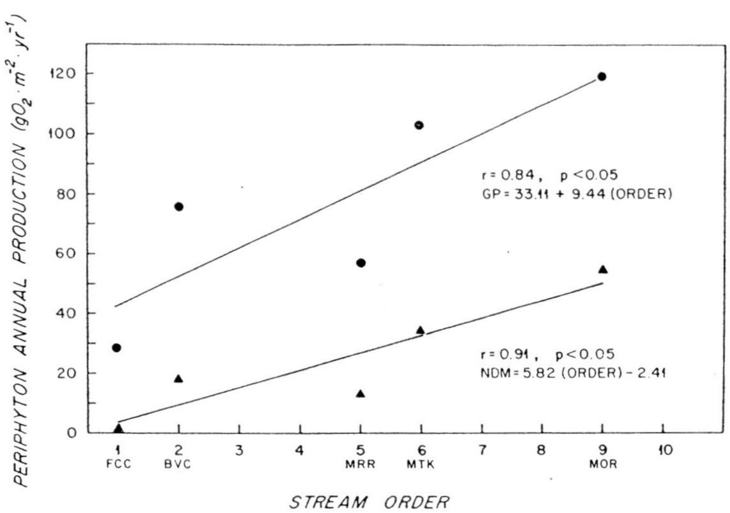

Fig. 1. Annual gross production (●) and net daily metabolism (▲) by periphyton are shown as a function of stream order for the Moisie and Matamek River watersheds in Quebec, Canada. Symbols: First Choice Creek (FCC), Beaver Creek (BVC), Muskrat River (MRR), Matamek River (MTK), and Moisie River (MOR).

each order, give the distribution of periphyton primary production within the watershed (Table 2).

The data have two interesting aspects: despite the overwhelming number and lengths of 1st—3rd order streams (98.8 % of the total number and 87.3 % of the total stream km within the watershed, respectively) they contain only about 18.8 % of the stream surface area for the entire drainage network and yield only 12 % of the annual gross primary production and 7 % of the annual net daily metabolism (Table 2). In contrast, 64 % of annual gross periphyton production and 71 % of annual net daily metabolism for the watershed occurs in streams of 7th—9th order. These latter reaches comprise only 0.02 % of the total stream numbers and only 2.2 % of the total stream length within the watershed, but supply 54 % of the total stream surface area.

These results indicate that significant periphyton production occurs farther downstream than is currently thought and, when coupled with a large surface area devoid of forest canopy, provides a situation where considerable production can occur. To date most studies of periphyton dynamics have been in streams $\leq$ 6th order which have different physical characteristics than the larger rivers. This may suggest that additional research should be conducted downstream where the periphyton must clearly have a significant function in the ecosystems trophic base.

Fish habitat

There exists within a watershed a wide variety of environments available to aquatic organisms; not all of the same quality for a single species. Even though fish faunal gradients along the river continuum have been known for some time (Horwitz 1978), the spatial heterogeneity of fishes within the various geomorphic features of the drainage network has not been generally documented. To investigate

Table 2. Physical characteristics and primary production in the Moisie River Watershed, Quebec (19,811 km^2).

Stream order	No. of streams	% Total	Total length of streams (km)	% Total	Width (m)	Estimated surface area ($m^2 \times 10^6$)	% Total	Annual gross production ($g\,O_2 \cdot m^{-2} \cdot yr^{-1}$)
1	38,770	78.2	16,142	49.9	0.3	4.8	1.8	42.6
2	8,400	16.9	8,249	25.5	1.7	14.0	5.3	52.0
3	1,855	3.7	3,842	11.9	8	30.7	11.7	61.4
4	415	0.84	1,879	5.8	15	28.2	10.8	70.9
5	95	0.19	1,072	3.3	20	21.4	8.2	80.3
6	19	0.04	471	1.5	46	21.7	8.3	89.8
7	7	0.014	340	1.1	150	51.0	19.4	99.2
8	2	0.004	292	0.9	225	65.7	25.0	108.6
9	1	0.002	54	0.2	460	24.8	9.5	118.1
Total	49,564		32,341			2.6×10^8		

Stream order	Annual net daily metabolism ($g\,O_2 \cdot m^{-2} \cdot yr^{-1}$)	Total gross production ($g\,O_2 \cdot yr^{-1} \times 10^8$)	% Total	Total net daily metabolism ($g\,O_2 \cdot yr^{-1} \times 10^8$)	% Total
1	3.4	2.0	0.8	0.2	0.2
2	9.2	7.3	3.1	1.3	1.5
3	15.1	18.9	8.0	4.6	5.4
4	20.9	20.0	8.5	5.9	6.9
5	26.7	17.2	7.3	5.7	6.7
6	32.5	19.5	8.3	7.1	8.3
7	38.3	50.6	21.4	19.5	22.8
8	44.2	71.4	30.2	29.0	33.8
9	50.0	29.3	12.4	12.4	14.5
Total	236.2			85.7	

habitat quality for salmonids we chose the Hoh River system which provides a full range of pristine river conditions.

Valley wall tributaries make up the bulk (~ 60 %) of the total length of streams while terrace tributaries (~ 15 %), off-channel backwater areas (~ 15 %), and the main river channel (~ 10 %) are relatively minor components of the drainage network within the upper 220 km^2 of the Hoh River basin encompassed by this study. However, when total surface area available is considered, it is the main river channel which provides most of the surface area (~ 50—60 %); valley wall tributaries (~ 20—30 %), terrace tributaries (~ 10 %), and off-channel areas (~ 10 %) are less.

The highest density and biomass of salmonids occurs in the relatively sparse off-channel habitat (Fig. 2). About 60 % of these channels are high quality pools formed by woody debris. In many cases the flood regime had produced an accumulation of woody debris along the edge of the main channel which deflected the flow, thereby producing large backwater pools or alcoves. In these habitats steelhead fry *(Salmo gairdneri)* represented 79 % of the total density and 39 % of the biomass. Coho salmon fry *(Oncorhynchus kisutch)* made up 19 % of the total density

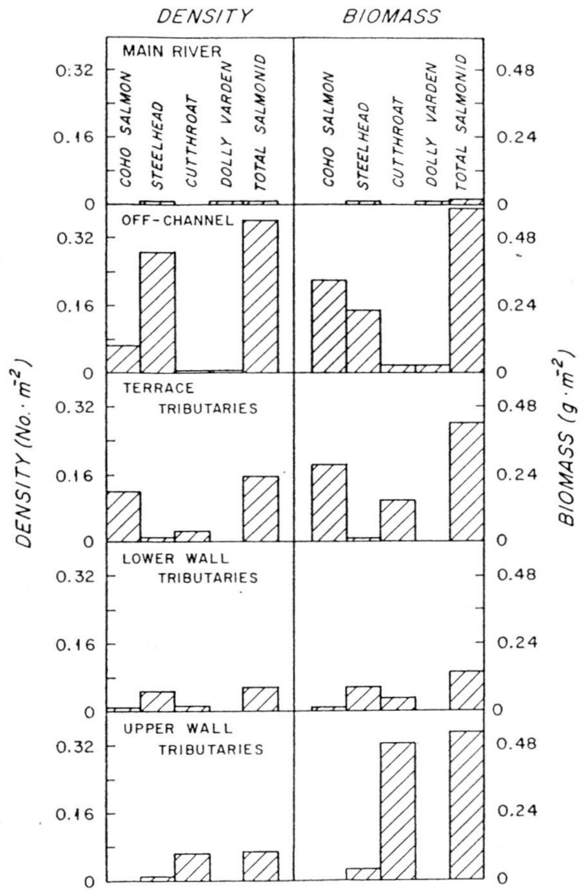

Fig. 2. Density and biomass of salmonids in several habitats of the Hoh River Watershed, Washington, U. S. A.

and 56 % of the biomass (Fig. 2). The second highest density of salmonids are found in the terrace tributaries, yet the fish have less than half the density of off-channel areas. Coho biomass was equal to that of off-channel habitat. Wall tributaries have low density and biomass of coho and steelhead. Upper wall tributaries contained numerous cutthroat trout *(Salmo clarki)*. The main river channel, desite the large surface area, has the lowest salmonid density and biomass of all habitats. In this region total salmonid density is estimated to be < 0.001 fish · m^{-2} and the biomass < 0.01 g · m^{-2}.

Woody debris was found to be a major contributor to habitat quality for spawning and rearing (SEDELL et al. 1980). Its role in forming and maintaining anadromous fish habitat is clearly important, regardless of stream size. This study has significant management implications in that the salmonid productivity of this system is largely dependent upon stable stream networks created and maintained by woody debris, and the salmonids use of the sparse and often abused shallow off-channel habitat. Usually, management protection is more readily provided to streams and main river channels than to less scenic off-channel backwaters and, in addition, the important role of woody debris in creating and maintaining this quality habitat for stream fishes is generally not appreciated.

Conclusion

Studies of stream segments will, of their own accord, produce interesting and often significant results. However, placement of data in larger perspective yields new insights into basic ecosystems processes. Had the physical analyses not been combined with the biological studies, it would have been possible to conclude that (1) annual export of seston varied widely among watersheds, (2) that in a relative sense periphyton production is trophically important only in middle order (3rd—6th) streams because of their abundance and, (3) that high quality off-channel areas created by woody debris were not an especially rare feature of the drainage network. Examples presented here demonstrate that extension of site specific data to watershed dimensions adds perspective to our understanding of these basic ecosystem components. This same approach can be applied to other ecosystem components (e. g., woody debris, detritus, macrophytes, invertebrates, etc.) to produce a three-dimensional picture of their distribution and importance in the watershed. Without this added perspective, it is clear that the overview needed for understanding the dynamics of total watershed ecosystems would be difficult to accomplish.

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