

Organic Matter and Trophic Dynamics

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Overview

- This chapter examines the sources of nutrients and organic matter in streams, the mechanisms by which organic materials are physically and biologically transformed as they pass from small to progressively larger channels, and the trophic processes by which organic matter supports consumer organisms.

- Organic matter is incorporated into stream ecosystems through two general pathways: autotrophy, the production of new plant material through photosynthesis; and heterotrophy, the assimilation of organic matter by consumers.

- Material derived from photosynthesis can come from within the stream (autochthonous production) or from terrestrial sources (allochthonous production). Depending on the type of input, organic matter is utilized by a variety of consumer groups whose mode of feeding is adapted to different physical states of organic materials.

- Inputs of coarse particulate organic matter (CPOM) to headwater streams are transformed through processes of microbial decomposition, consumption by macroinvertebrates, and physical abrasion to fine particles and dissolved organic matter, which are utilized by aquatic communities downstream.

- The relative abundance of different types of producer and consumer organisms changes from small headwater streams to large rivers in response to the availability and character of organic matter inputs, as well as storage and transport processes.

- Using salmonid fishes as a focus of the discussion, differences in productivity between streams can often be explained by variations in the types and availability of food resources. For populations of anadromous salmonids in the Pacific coastal ecoregion, productivity is strongly influenced by seasonal shifts in organic matter origin. Autotrophic processes dominate in spring and summer, whereas heterotrophic processes dominate in autumn and winter.

- Human activities depriving streams of nutrients and organic matter or reducing the capacity of aquatic communities to store and process these materials (e.g., removal of streamside vegetation, loss of coarse woody debris, and reduction of salmon carcasses) often lead to changes in the trophic system that ultimately impair salmonid productivity. Anthropogenic nutrient enrichment may enhance trophic processes that support the production of undesirable organisms.

Introduction

Just as the characteristics of flowing water—velocity, turbulence, temperature, sediment, and solute content—influence the distribution and abundance of plants and animals in streams, so too the movements and transformations of organic matter influence the composition and productivity of different members of the aquatic community. Whether the goal is protecting invertebrates and salamanders in a small stream or maximizing the yield of

commercially valuable fishes in a large river, knowledge of both physical processes and trophic dynamics is needed for effective management. This chapter reviews the sources and transformations of organic matter in flowing water ecosystems and examines some impacts of human activities on organic matter pathways supporting the production of important aquatic resources. Although processes discussed are shared by river systems throughout the world, many examples are drawn from western North America, where much of the research on trophic dynamics has examined factors contributing to the support of salmonid fishes.

The following information is meant to provide a very general overview of organic matter and trophic dynamics in streams of the Pacific coastal ecoregion. Two important references contain more detailed and comprehensive information about organic matter and trophic dynamics in rivers. The first, H.B.N. Hynes' *The Ecology of Running Waters* (Hynes 1970), is a treatise of exceptional depth and breadth summarizing much of what was known about stream ecology up to that time. It is still an invaluable reference for any aquatic scientist. The second and more recent book, J.D. Allan's *Stream Ecology: Structure and Function of Running Waters* (Allan 1995), describes many newer advances in knowledge of lotic ecosystems, for example, the paradigm that riverine communities are structured from headwaters to mouth by a changing pattern of organic matter sources and nutrient transformations. Together, these two works provide a wealth of information and references.

Organic matter and nutrient transformations in streams are often discussed in the context of aquatic productivity. Warren (1971) defined the concept of productivity as the capacity of an ecosystem to generate a product of interest. Productivity is measured by the survival and growth of members of a population under a certain set of conditions; the population's actual performance—its production—is limited by properties of the ecosystem in which its members reside. The nature and timing of organic matter and nutrient inputs usually exert a powerful influence on the capacity of streams

and rivers to produce different species. Measurement of ecosystem productivity and measurement of ecosystem "health" or "integrity," using parameters such as species composition, may be quite different. It is possible for species diversity to be low in streams that are highly productive for certain taxa. Conversely, species diversity may be relatively high in unproductive streams because of a variety of physical and biological factors, as well as time lags for recovery and colonization of competitively dominant organisms after a disturbance (Patrick 1975, Power 1990, Wootton 1996).

Movements and transformations of organic matter influence the productive capacity of rivers for salmonids. Fishes are frequently taken as indicators of stream productivity and aquatic health, but other organisms often dominate secondary production and may be far more sensitive indicators of aquatic integrity (Karr 1991, Chapter 20, this volume). Nevertheless, fish production has generally been studied more widely than production of other aquatic taxa. A comparison of salmonid fishes in rivers throughout the world (Table 15.1) reveals that annual production (the product of average population biomass and mean individual growth rates over a year expressed as new tissue produced per unit of area) varies greatly from stream to stream. Production of salmonids is relatively low in most streams world wide, but a few streams are very productive (Figure 15.1), although not as productive as streams supporting warm-water species where annual production can exceed $100 \text{ g/m}^2/\text{yr}$ (Naiman 1976).

Many factors influence productivity. Physical characteristics of the stream environment affect a population's abundance, hence its production. Food availability also influences productivity (Chapman 1966); the 10-fold difference in salmonid production between the most and least productive sites in Table 15.1 would be difficult to explain strictly on the basis of differences in physical habitat among the rivers. In many instances, large differences in the capacity of streams to produce salmonid fishes, or other consumer organisms, are strongly related to availability of food resources (Le Cren 1969, Warren 1971, Gregory et al. 1987).

TABLE 15.1. Production estimates of salmonid populations in streams ranked within each species from approximately highest to lowest.

Species location	Production (g/m ² /yr)	Reference
Brown trout (<i>Salmo trutta</i>)		
Horokiwi Stream, New Zealand	54.7 ¹	Allen (1951)
Black Brows Beck, England	12.2–33.9	Elliott (1985)
Candover Brook, England	13.4–28.7	Mann et al. (1989)
Tadnoll Brook, England	20.0	Mann et al. (1989)
Granslev a, Denmark	12.6–25.7	Mortensen (1982)
Bisballe baek, Denmark	18.8	Mortensen (1977a)
Duhonw Stream, England	10.5–19.8	Milner et al. (1978)
Orred baek, Denmark	10.0–18.6	Mortensen (1977b)
Docken's Water, England	12.1	Mann (1971)
River Tarrant, England	12.0	Mann (1971)
Walla Brook, England	11.6	Horton et al. (1968)
Black Brows Beck, England	10.0	Le Cren (1969)
Shelligan Burn, Scotland	6.7–12.7	Egglishaw and Shackley (1977)
Hinaki Stream, New Zealand	8.9	Hopkins (1971)
Hinau Stream, New Zealand	8.5	Hopkins (1971)
Chwefru Stream, England	6.9–9.3	Milner et al. (1978)
Bere Stream, England	2.6–12.9	Mann (1971)
Kingswell Beck, England	7.4	Le Cren (1969)
Valley Creek, Minnesota, USA	<0.1–13.2	Waters (1983)
Marteg Stream, England	5.9–6.0	Milner et al. (1978)
Loucka Creek, Czechoslovakia	1.7–8.6	Libosvsky (1968)
Hall Beck, England	5.2	Le Cren (1969)
Nether Hearth Sike, England	5.0	Le Cren (1969)
Devils Brook, England	4.8	Mann (1971)
Bidno Stream, England	3.2–6.0	Milner et al. (1978)
Blackhoof River, Minnesota, USA	4.4	Waters et al. (1990)
Nunn Creek, Colorado, USA	3.4–5.2	Scarnecchia and Bergersen (1987)
Appleworth Beck, England	3.0	Le Cren (1969)
Cow Creek, Colorado, USA	1.4–1.8 ²	Scarnecchia and Bergersen (1987)
Normandale Creek, Ontario, Canada	1.4 ³	Gordon & MacCrimmon (1982)
Atlantic salmon—<i>Salmo salar</i>		
Shelligan Burn, Scotland	5.5–12.6	Egglishaw and Shackley (1977)
Duhonw Stream, England	6.3–11.0	Milner et al. (1978)
Bere Stream, England	7.2	Mann (1971)
Chwefru Stream, England	5.7–5.9	Milner et al. (1978)
Marteg Stream, England	2.4–6.9	Milner et al. (1978)
Bidno Stream, England	1.9–6.9	Milner et al. (1978)
Catamaran Brook, New Brunswick, Canada	2.1–5.1	Randall and Paim (1982)
Little River, New Brunswick, Canada	2.2–2.7	Randall and Paim (1982)
Meo River, Quebec, Canada	0.5	Leclerc and Power (1980)
Chinook salmon (<i>Oncorhynchus tshawytscha</i>)		
Lemhi River, Idaho, USA	3.0	Goodnight and Bjornn (1971)
Orwell Brook, New York, USA	0.6 ⁴	Johnson (1980)
Coho salmon (<i>Oncorhynchus kisutch</i>)		
Schultz Creek, Washington, USA	5.7–21.6 ¹	Bisson et al. (1988)
Flynn Creek, Oregon, USA	6.0–16.2 ²	Chapman (1965)
Deer Creek, Oregon, USA	5.4–12.7 ³	Chapman (1965)
Needle Branch, Oregon, USA	4.9–11.5 ⁵	Chapman (1965)
Hoffstadt Creek, Washington, USA	2.7–10.3 ⁴	Bisson et al. (1988)
Herrington Creek, Washington, USA	2.3–9.7 ⁴	Bisson et al. (1988)
Orwell Brook, New York, USA	2.7 ⁴	Johnson (1980)
Tye Creek, Alaska, USA	0.6–2.0 ⁴	Dolloff (1986)
Toad Creek, Alaska, USA	0.6–1.0 ⁴	Dolloff (1986)
Bush Creek, British Columbia, Canada	0.9	Tripp and McCart (1983)

(Continued)

TABLE 15.1. *Continued*

Species location	Production (g/m ² /yr)	Reference
Banon Creek, British Columbia, Canada	0.6	Tripp and McCart (1983)
Normandale Creek, Ontario, Canada	0.5 ³	Gordon and MacCrimmon (1982)
Rainbow trout (<i>Oncorhynchus mykiss</i>)		
Bothwell's Creek, Ontario, Canada	13.2	Alexander and MacCrimmon (1974)
Big Springs Creek, Idaho, USA	10.4	Goodnight and Bjornn (1971)
Blackhoof River, Minnesota, USA	9.6	Waters et al. (1990)
Normandale Creek, Ontario, Canada	5.6 ³	Gordon and MacCrimmon (1982)
Dale 1 Creek, Colorado, USA	4.5–5.4 ²	Scarnecchia and Bergersen (1987)
Dale 2 Creek, Colorado, USA	3.0–3.8 ²	Scarnecchia and Bergersen (1987)
Lemhi River, Idaho, USA	2.4	Goodnight and Bjornn (1971)
Valley Creek, Minnesota, USA	<0.1–4.5	Waters (1983)
Orwell Brook, New York, USA	0.9 ⁴	Johnson (1980)
Cutthroat trout (<i>Oncorhynchus clarki</i>)		
Little Green Creek, Colorado, USA	2.2–3.6	Scarnecchia and Bergersen (1987)
Roaring Creek, Colorado, USA	2.3–3.3	Scarnecchia and Bergersen (1987)
Right Hand Fork, Colorado, USA	1.5–3.6	Scarnecchia and Bergersen (1987)
Upper Deschutes River, Washington, USA	1.1–2.1 ⁴	Bilby and Bisson (1987)
West Fork Creek, Washington, USA	0.4–2.5 ⁴	Bilby and Bisson (1987)
Bush Creek, British Columbia, Canada	0.4–2.1	Tripp and McCart (1983)
Berry Creek, Oregon, USA	0.5	Nickelson (1974)
Banon Creek, British Columbia, Canada	0.1–0.8	Tripp and McCart (1983)
Brook trout (<i>Salvelinus fontinalis</i>)		
Big Spring, Pennsylvania, USA	30.0	Cooper and Scherer (1967)
McCreavy Creek, Colorado, USA	12.6–18.4	Scarnecchia and Bergersen (1987)
Lawrence Creek, Wisconsin, USA	9.3–10.6	Hunt (1966)
Valley Creek, Minnesota, USA	2.5–16.7	Waters (1983)
Kaikhosru Creek, Quebec, Canada	6.1–6.6	O'Connor and Power (1976)
Larry's Creek, Pennsylvania, USA	5.8	Cooper and Scherer (1967)
Caribou River, Minnesota, USA	5.8	Waters et al. (1990)
Cow Creek, Colorado, USA	4.9–6.5 ²	Scarnecchia and Bergersen (1987)
Porcupine Creek, Colorado, USA	4.8–4.9	Scarnecchia and Bergersen (1987)
Dale 2 Creek, Colorado, USA	4.4–5.7 ²	Scarnecchia and Bergersen (1987)
Indian Creek, Colorado, USA	4.4–5.2	Scarnecchia and Bergersen (1987)
Dale 1 Creek, Colorado, USA	4.0–4.9 ²	Scarnecchia and Bergersen (1987)
Gallienne Creek, Quebec, Canada	3.7–3.9	O'Connor and Power (1976)
Sherry Creek, Quebec, Canada	1.4–4.1	O'Connor and Power (1976)
Me'o River, Quebec, Canada	1.9	O'Connor and Power (1976)
Davis Creek, Colorado, USA	1.7–1.9	Scarnecchia and Bergersen (1987)
Tchinicaman Creek, Quebec, Canada	1.5–1.6	O'Connor and Power (1976)
Guys Run, Virginia, USA	0.5–1.9	Neves and Pardue (1983)
Dolly Varden (<i>Salvelinus malma</i>)		
Toad Creek, Alaska, USA	0.3–0.8 ^{4,6}	Dolloff (1983)
Knob Creek, Alaska, USA	0.1–0.8 ^{4,6}	Dolloff (1983)
Aha Creek, Alaska, USA	0.3–0.5 ^{4,6}	Dolloff (1983)
Tye Creek, Alaska, USA	0.1–0.9 ^{4,6}	Dolloff (1983)

¹ Many scientists believe this figure to have been an overestimate. Le Cren (1969) suggested an alternative estimate of 38 g/m²/yr while Chapman (1966) suggested 45 g/m²/yr.

² Biomass ratios of different species from Scarnecchia and Bergersen (1987: Table 7, p. 322) were used to estimate each species' contribution to total annual production (Table 5, p. 321).

³ Brown trout and rainbow trout production were estimated from Figure 4 (p. 466) of Gordon and MacCrimmon (1982).

⁴ The interval over which production was estimated was less than 1 year, but included the late spring and summer growth period when much of the annual production takes place.

⁵ The production interval was 14 months for each cohort.

⁶ The estimate did not include production of age 0+ fish.

From Hanson and Waters 1974 and Chapman 1978.

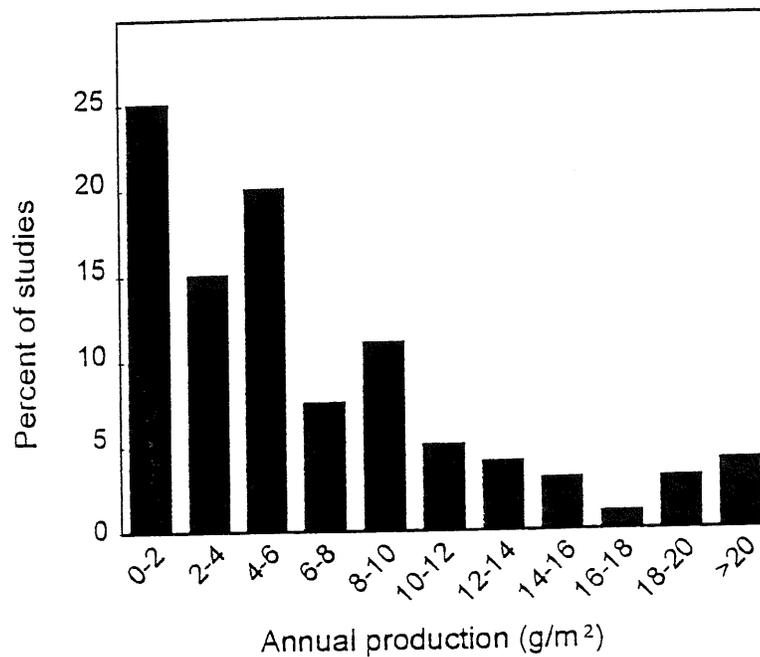


FIGURE 15.1. Distribution of estimates of annual production of salmonid fishes in streams of the world (based on 92 studies from Table 15.1 [Hanson and Waters 1974, Chapman 1978]).

Food availability as a factor limiting the production of stream-dwelling fishes is often overlooked by habitat managers. Most projects designed to improve the production of salmonids involve manipulating elements of the physical habitat such as logs or boulders, placing structures to prevent streambank erosion, or planting trees and shrubs to increase shade (NRC 1992 and 1996, Hunt 1993). Although these projects may remedy habitat damage caused by human activities, they usually do not address the food web contribution to production. Given the potential gains in productivity that can accompany increased food availability, consideration of the trophic system is critical to managing aquatic resources in rivers. Ignoring this important component imposes significant constraints on the effectiveness of restoration (Gregory et al. 1987, NRC 1992).

Trophic Pathways

Autochthonous and allochthonous, two major sources of organic matter, fuel lotic ecosystems. Autochthonous organic matter is generated by

autotrophic members of the aquatic community (Table 15.2) that synthesize organic matter from inorganic materials in the presence of sunlight through the process of photosynthesis (Minshall 1978). On the other hand, organic inputs to lotic ecosystems that originate from terrestrial plants and animals, or organic materials of marine origin, are termed allochthonous inputs (Table 15.3). The relative abundance of these types of organic matter plays a key role in structuring the biotic community of the stream (Vannote et al. 1980) and influences nutrient dynamics of the system (Newbold et al. 1981 and 1982).

Autotrophic Production

Important autotrophs in rivers include vascular plants (principally aquatic angiosperms), bryophytes (mosses and liverworts), periphyton and phytoplankton (green and red algae), some bacteria (principally blue-green algae), and protists (diatoms, yellow-brown algae, and euglenoids). Periphyton refers to algae growing on the stream bottom; phytoplankton refers to algae suspended in the water column. The

TABLE 15.2. Major types of autotrophs and heterotrophs in streams.

Autotrophs		Heterotrophs	
Group	Growth forms	Group	Feeding types
<i>Macrophytes</i> (flowering plants, mosses and liverworts)	Emergent	<i>Microheterotrophs</i> (bacteria, fungi, protozoans, and micrometazoans)	Microbial decomposers
	Floating-leaved		Suspension feeders
	Free-floating		Grazers
	Submergent		Predators
	Crustose		Shredders
<i>Periphyton</i> (diatoms, green algae, blue-green algae, euglenoids, yellow- brown algae, red algae)	Prostrate	<i>Macroinvertebrates</i> (all larger invertebrate metazoans)	Gougers
	Stalked/short filamentous		Suspension feeders/filterers
	Filamentous		Collector-gatherers
	Filamentous with epiphytes		Grazers
	Gelatinous		Predators
<i>Phytoplankton</i> (algae, protists, and cyanobacteria)	Sloughed periphyton	<i>Aquatic vertebrates</i> (fishes and amphibians)	Herbivore-detrivore
	True phytoplankton		Benthic invertebrate feeder Surface/drift feeder Generalized invertevore Planktivore Omnivore Piscivore Parasite

From Berkman and Rabeni 1987; Allan 1995, Merritt and Cummins 1996a.

former category dominates primary production in swiftly flowing streams while phytoplankton often dominates in slow moving, large rivers (Vannote et al. 1980). A more complete discussion of the structure and function of autotrophs in flowing waters is found in Chapter 7.

Through photosynthesis, autotrophic production creates new plant material within the stream itself. Part of this material is consumed by herbivorous animals, including a wide vari-

ety of micro- and macroinvertebrates, fishes, and larval amphibians. Some of the plant material becomes senescent and dies, after which it may settle into the stream substrate and become part of the detrital pool, or it can be carried downstream by the current. In either event, dead plants serve as a food source for detritivorous animals as well as bacteria and fungi, which form important links in heterotrophic organic matter pathways.

TABLE 15.3. Size classes and examples of different categories of organic matter.

Category	Abbreviation	Size range (μm)	Example
Dissolved organic matter	DOM	<0.45	Leaf leachate
Fine particulate organic matter:	FPOM	>0.45-<1.000	
Ultrafine	UPOM	0.45-25	Bacteria
Very fine	VPOM	25-45	Pollen
Fine	FPOM	45-100	Macroinvertebrate feces
Small	SPOM	100-250	Algal detritus
Medium-large	MPOM	250-1.000	Very small leaf fragments
Coarse particulate organic matter	CPOM	>1.000	Needles; dead aquatic animals

Allochthonous Organic Matter and Heterotrophic Production

Heterotrophic organisms derive energy from organic matter, living or dead, much of which may ultimately derive from outside the stream (Table 15.3). Important heterotrophs in flowing waters include large and small organisms: microbes (bacteria and fungi), protozoans and micrometazoans that consume mostly dead organic matter, and animals (macroinvertebrates and vertebrates) that feed on living or dead organic matter—the most conspicuous of which are usually insects (Table 15.4) (Chapter 8). In heavily forested headwater streams, heterotrophic production is supported primarily by terrestrial organic matter, while in open

river channels heterotrophic production can be supported by autochthonous detrital pathways (Vannote et al. 1980).

Inputs of allochthonous material are highly seasonal. Dissolved organic matter (DOM) (Table 15.3) enters river networks throughout the year but may be particularly significant during early fall rains or in periods of spring snow melt (Triska et al. 1984, Naiman et al. 1992). Fine particulate organic matter (FPOM) enters rivers in great quantities during flooding (Welcomme 1979). Coarse particulate organic matter (CPOM) varies widely in size, from needles and leaves entering rivers during autumn to large woody debris entering stream channels during major storms (Naiman and Sedell 1979). Carcasses of anadromous

TABLE 15.4. Functional groups of aquatic insects, their food and feeding mechanisms, examples of taxa, and typical food size.

Functional group	Subdivision of functional group		Example taxa	Food particle size (μm)
	Dominant food	Feeding mechanism		
Shredders	Living vascular hydrophyte plant tissue	Herbivores: chewers and miners of live macrophytes	Trichoptera: Phryganeidae, Leptoceridae	>1,000
	Decomposing vascular plant tissue and wood: coarse particulate organic matter	Detritivores: chewers, wood borers, and gougers	Diptera: Tipulidae, Chironomidae	>1,000
Collectors	Decomposing fine particulate organic matter	Detritivores: filterers or suspension feeders	Trichoptera: Hydropsychidae Diptera: Simuliidae	<1,000
	Decomposing fine particulate organic matter	Detritivores: gatherers or deposit feeders (includes surface film feeders)	Ephemeroptera: Ephemeridae Diptera: Chironomidae	<1,000
Scrapers	Periphyton: attached algae and associated material	Herbivores: grazing scrapers of mineral and organic surfaces	Trichoptera: Glossosomatidae Coleoptera: Psephenidae Ephemeroptera: Heptageniidae	<1,000
Predators (engulfers)	Living animal tissue	Carnivores: attack prey, pierce tissues and cells, and suck fluids	Hemiptera: Belostomatidae	>1,000
	Living animal tissue	Carnivores: ingest whole animals or parts	Plecoptera: Perlidae Odonata	>1,000

From Merritt and Cummins 1996a, 1996b.

fishes, a major source of allochthonous material to many coastal watersheds in the Pacific coastal ecoregion, become available during adult spawning periods (Kline et al. 1990 and 1993, Bilby et al. 1996) which may be very short in some rivers or nearly year-round in others.

Organic Matter Processing

A generalized model of a riverine trophic pathways (Figure 15.2) shows some important pathways of organic matter as it is consumed, stored, and excreted by members of different functional groups. The flow of materials through different pathways is strongly influenced by position along the stream network (Vannote et al. 1980). In a heavily shaded 1st-order stream in the western Cascade Mountains of Oregon, Triska et al. (1982) found the organic budget dominated by inputs of terrestrial litter (mostly wood fragments and detritus >10cm diameter) which comprised over 80% of the organic standing crop (Table 15.5). Detritus entered the stream as litterfall

from overhanging vegetation and through lateral movement along the forest floor. Microbial respiration accounted for much of the community outputs, but a considerable amount of organic material was exported from the stream as small particles or dissolved organic matter. Primary production was very low under the dense forest canopy of this headwater stream. Community respiration (microbial plus aquatic plant plus macroinvertebrate respiration) far exceeded photosynthesis by algae and moss (Table 15.5).

Although much of the allochthonous organic material in headwater streams enters as CPOM, it is converted through a variety of mechanisms (Figure 15.3) to FPOM. Microbial colonization takes place rapidly after CPOM enters the stream, forming a layer of bacteria and fungi on its surface. As this layer forms, it also includes a polysaccharide matrix inhabited by protozoans, micrometazoans, and early instars of macroinvertebrates such as midges and copepods. Microbial decomposers consume DOM leached from CPOM, and it is this rich layer of microbes, small animals, and organic

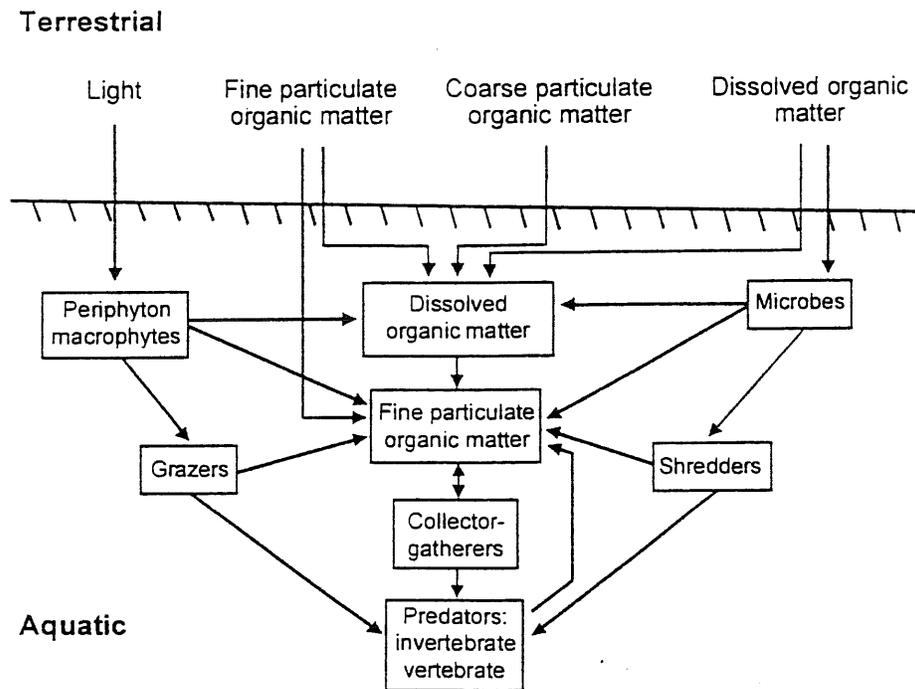


FIGURE 15.2. Generalized food web for low- to mid-order forested streams (from Hildrew et al. 1987, Allan 1995).

TABLE 15.5. Annual organic matter budget for a 1st-order stream in the H.J. Andrews Experimental Forest of western Oregon from 1973-1974.

Inputs			Standing crop			Outputs		
Category	kg/y	%	Category	kg/y	%	Category	kg/y	%
Litterfall	161-170	22-33	Large detritus (>10 cm)	8,692-8,698	82-83	Particulate organic	37-245	11-32
Throughfall	41-57	7-8	Small detritus (10 cm to 1 mm)	1,382-1,535	13-15	Microbial respiration	183-186	24-55
Lateral movement	200-333	41-43	Fine particulate organic matter (FPOM) (<1 mm to 75 µm)	87	1	Macroinvertebrate respiration	2	0.3-1
Gross primary production:			Ultrafine detritus (<75 µm to 45 µm)	233	2	Primary producer respiration:		
Algae	<1	0.1-0.2				Algae	<1	0.1-0.3
Moss	23	3-5				Moss	15	2-4
Dissolved organic matter	64-206	13-26	Primary producer biomass	31	0.3	Dissolved organic matter	96-310	28-41
			Macroinvertebrates	0.8-1	<0.1			
Total	490-790		Total	10,432-10,585		Total	337-756	

From Triska et al. 1982.

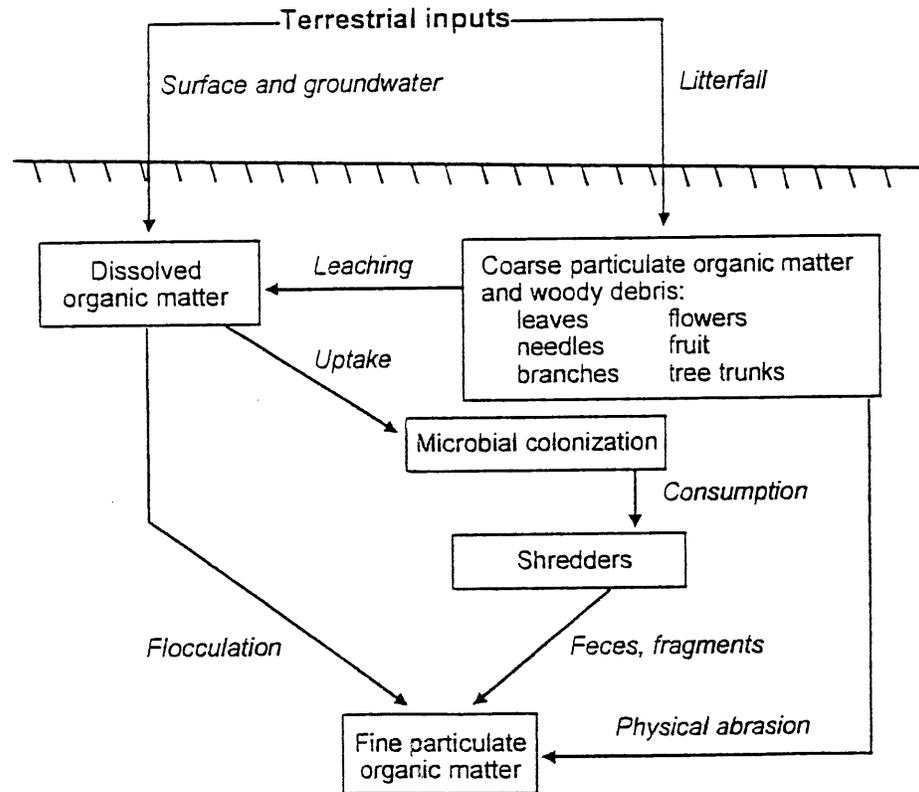


FIGURE 15.3. Processes through which coarse particulate organic matter (CPOM) and dissolved organic matter (DOM) are converted to fine particulate organic matter (FPOM) (from Cummins and Klug 1979, Allan 1995).

substances that provides the main food source to macroinvertebrates specialized for feeding on terrestrial foliage and woody debris (shredders). Dead aquatic macrophytes can also be processed in this way. In the digestive tracts of shredder macroinvertebrates, CPOM is converted to FPOM, which is excreted. Shredders actually derive most of their food value from the microbial coating on CPOM, not from the plant material itself (Anderson and Sedell 1979). In addition to conversion of CPOM to FPOM by macroinvertebrates, FPOM can be formed by the flocculation of DOM and by the physical breakdown of larger particles as they are carried by the stream or pulverized by bedload movement (Figure 15.3).

As headwater streams come together to form larger channels, the relative importance of allochthonous and autochthonous inputs changes significantly (Figure 15.4). In a comparison of community structure and organic matter pathways among 1st-, 3rd-, 5th-, and 7th-order streams in the McKenzie River system of Oregon, Naiman and Sedell (1980) found that autotrophic production exceeded heterotrophic consumption (i.e., the ratio of gross photosynthesis to community respiration, P/R , was greater than one) in both 5th- and 7th-order streams during all seasons. Respiration exceeded photosynthesis in the 3rd-order stream only during winter, but on an annual basis the 3rd-order stream was predominantly heterotrophic ($P/R < 1$) because it contained a very large pool of detritus accompanied by considerable microbial respiration. The balance between allochthonous and autochthonous pathways gradually shifted from a strongly heterotrophic-based stream community in the headwaters to an autotrophic-based community in the larger streams. For the McKenzie River, this shift from aquatic communities in which P/R is less than one to those in which P/R exceeds one occurred in channels of approximately 3rd- to 5th-order (Hawkins and Sedell 1981).

The hypothesis that the relative balance of photosynthesis and respiration shifts downstream in a predictable pattern in response to changing organic matter sources and increasing light reaching the channel is an important part

of the river continuum concept (RCC, Vannote et al. 1980). This hypothesis suggests that the species and functional composition of plant, invertebrate, and vertebrate communities changes according to the physical template of the stream and its valley as well as its sources of organic matter. According to this hypothesis, small headwater streams are dominated by large-bodied shredder and collector-gatherer macroinvertebrates (i.e., those invertebrates specialized for consuming CPOM of terrestrial origin). Mid-order streams, only partially shaded, have a much more significant component of grazing organisms specialized for feeding on periphyton. Large rivers are dominated by three distinct trophic communities: detritivores feeding on fine particulate organic matter that had been consumed and excreted by organisms upstream, phytoplankton and zooplankton, and aquatic macrophytes and their associated fauna along the riverine-streams edge. The role of floodplains as an important source of fine particulate organic matter for larger rivers was recognized (Minshall et al. 1985) after the original formulation of the river continuum concept by Vannote et al. (1980).

Overall, the river continuum concept predicts that low-order streams in forested landscapes should have a very low P/R ratio and a high ratio of coarse to fine particulate organic matter (CPOM/FPOM), reflecting heavily shaded conditions and inputs of coarse material from the surrounding riparian zone. In mid-order streams, the model predicts that P/R should reach a peak and CPOM/FPOM should decline, reflecting an abundance of periphyton and conversion of CPOM to FPOM in the headwaters. In high-order streams, CPOM/FPOM should be very low and P/R should decline somewhat because of heterotrophic processing of floodplain-derived detritus. The river continuum concept predicts that biological diversity should be greatest in mid-order streams because of the wide variety of organic inputs.

An examination of the composition of animal communities from different parts of the McKenzie River system in Oregon generally supports this hypothesis (Hawkins and Sedell

1981). Approximately 75% of the densities of macroinvertebrates in the 1st-order tributary were shredders and the rest were mostly predators (Figure 15.4). In the 3rd-order stream, shredders were still a dominant functional group but grazers and collectors assumed greater importance. Grazers and collector-gatherers became the dominant feeding guilds of the 5th-order stream while shredders were reduced to less than 10% of the densities. In the 7th-order stream, collector-gatherers assumed dominance. Interestingly, in all stream sizes predators comprised about one-fourth of the total standing crop, although the composition

shifted from macroinvertebrate and amphibian dominated predator species in headwater streams to communities dominated by predatory fishes in the larger channels.

A number of investigators have tested the river continuum concept in both temperate and tropical streams, although tests of the concept in high-order river basins are relatively few because so many large rivers have been dammed. Minshall et al. (1985, 1992) tested predictions of the RCC model in Idaho's Salmon River, a free-flowing 8th-order drainage system. They found that communities fit expectations in some respects: shredders dominated CPOM-

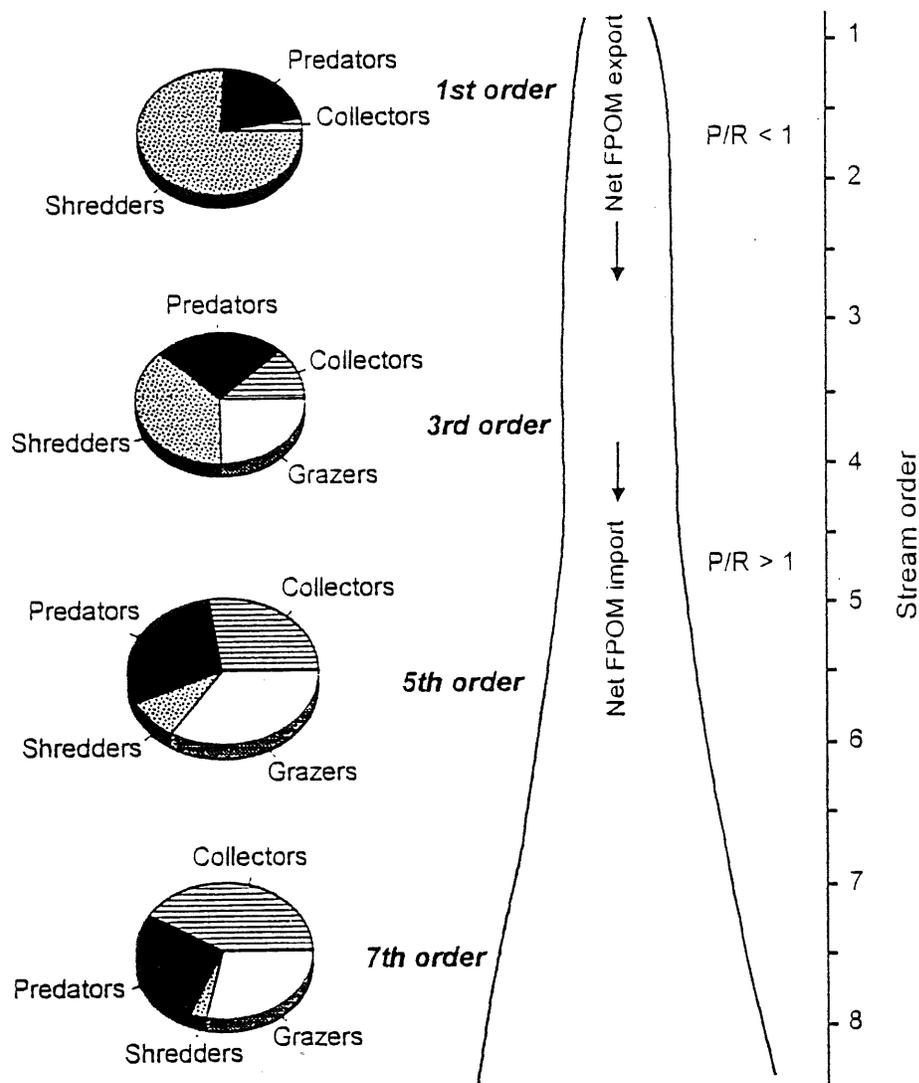


FIGURE 15.4. Changes in the relative importance of allochthonous and autochthonous inputs and the abundance of different functional groups of aquatic

organisms in the McKenzie River system, Oregon, from 1st- to 7th-order stream channels (data from Hawkins and Sedell 1981).

rich headwater channels, periphyton photosynthesis was greatest in mid-order reaches, and FPOM and heterotrophic consumption by collector-gatherers dominated the largest streams. Some functional groups, however, did not conform to predictions. This was attributed to anthropogenic disturbances in the Salmon River basin which reduced CPOM inputs in the headwaters and increased sediment caused by hillslope erosion. In New Zealand streams, Winterbourne et al. (1981) were unable to associate community composition with functional group proportions suggested by RCC. They suggested that a hydrologic regime prone to frequent disturbance could change communities in ways that were not easily predictable, but there has been some debate over whether Winterbourne et al. (1981) used the concept correctly. Overall, the river continuum concept has been useful in describing general changes in organic matter inputs and processing from small headwater streams to large floodplain rivers, but there appear to be many deviations from specific predictions of the model in response to local conditions (Statzner and Higler 1986, Statzner et al. 1988, Allan 1995).

Organic Matter Storage and Nutrient Spiraling

Without processes for storing organic matter in stream channels, much of the material would be rapidly carried downstream without being incorporated into the aquatic community. Storage mechanisms are somewhat different for each of the principal organic matter classes: DOM, FPOM, and CPOM. DOM can be stored in ponded water created by wetlands and beaver dams (Naiman and Melillo 1984) or in hyporheic water deep within the substrate of the stream network (Stanford and Ward 1992). These "reservoirs" of DOM are important nutrient sources for the stream and the release of DOM from them often depends on flow (Triska et al. 1989, 1990).

CPOM enters stream channels seasonally or during large disturbances such as landslides, fires, or floods. The ability of channels to retain this material is strongly influenced by their fluvial-geomorphic character (Gregory et al.

1991). CPOM storage is often greatest in low-gradient, alluvial river systems and least in tightly constrained, bedrock-dominated channels (Sedell and Swanson 1984, Montgomery and Buffington 1993). Large woody debris plays an essential role in the retention of both CPOM and FPOM (Bilby 1981, Harmon et al. 1986, Chapter 13, this volume). As a rule, hydraulically complex streams store more CPOM than streams with simplified channels (D'Angelo et al. 1993).

FPOM can be stored in interstitial spaces in coarse sediments of the streambed, in backwaters formed by eddies, and adjacent to large structural elements of the channel such as large woody debris and boulders (Cushing et al. 1993). Storage capacity for FPOM is largely a function of stream power, a hydrological measure of the capacity of the stream to do "work" defined as a function of the shear stress at the bed and the mean velocity of the stream in cross section (Gordon et al. 1992). The greater the stream power, the greater the tendency to suspend and transport FPOM, which is negatively buoyant but nevertheless has a low specific gravity and is easily carried by the current. Characteristics of the channel that either decrease shear stress or reduce the average velocity of the flowing water will increase FPOM storage capacity. Turbulence plays a significant role in keeping FPOM in suspension: highly turbulent streams have greater FPOM transport capacities.

Organic matter and inorganic nutrients cycle back and forth between biologically incorporated, stored, and fluvially transported states as they are taken up and subsequently released (Figure 15.5). The term nutrient spiraling has been applied to the path traced by nutrients as they are assimilated by living organisms, returned to the stream by decomposition, respiration or excretion, and eventually reincorporated into the aquatic community further downstream (Webster and Patten 1979). Procedures for calculating the rate at which nutrients travel downstream are outlined in Webster and Ehrman (1996). Soluble nutrients are termed conservative if their concentration does not change through biotic or abiotic uptake processes (e.g., chloride, which is usually

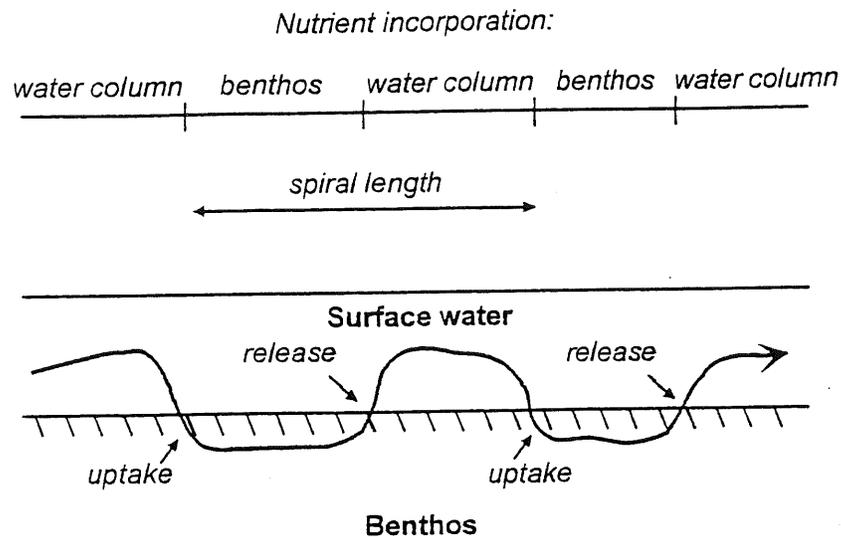


FIGURE 15.5. Two-dimensional nutrient spiraling diagram showing cyclic uptake of nutrients by aquatic biota and subsequent release by remineralization to the water column. The spiral length is the

longitudinal distance traveled by a nutrient atom (e.g., nitrogen or phosphorus) over one complete cycle of uptake and release (from Newbold 1992, Allan 1995).

present in streams far in excess of biological demand), or nonconservative if in-stream processes do alter their concentration (e.g., nitrogen and phosphorus). Models of solute movement can be very complex and require computers to solve systems of differential equations that describe variable stream morphology, groundwater and tributary inputs, transient storage, abiotic processes (adsorption, desorption, precipitation, and dissolution), and biotic exchanges (heterotrophic uptake, plant uptake, leaching, and mineralization). As they are recycled between immobilized (benthic) and remobilized (streamwater) states, nonconservative, biologically important nutrients trace a spiral (Figure 5) whose characteristics can be described by the equation:

$$S = SW + SB \quad (15.1)$$

where S represents spiraling length, SW represents uptake length, and SB represents turnover length. Spiraling length is the linear distance along the stream traveled by a nutrient atom while completing a cycle from biotic to abiotic and back to biotic form. The uptake length is the distance traveled in abiotic form dissolved in the water column, while turnover

length is the distance traveled in biotic form before being remobilized and returned to the water column. Uptake length is the inverse of uptake rate:

$$SW = 1/kC \quad (15.2)$$

where kC represents the rate of biological uptake of the nutrient atom in its abiotic form (Webster and Ehrman 1996).

Transient storage of nutrients in streams with highly retentive characteristics results in relatively short distances traveled downstream at each phase of the cycle of incorporation and release. Conversely, streams with poor nutrient and organic matter retention characteristics possess longer "spirals." Newbold et al. (1981, 1982) constructed a model of the distance traveled by nutrients within the water column and alternately stored in plant and animal components of the ecosystem as they moved downstream. Other investigators have found that a variety of abiotic controls (precipitation and sorption, seasonal hydrologic regimes, severe storms, patterns of subsurface flow) and biotic processes (autotrophic production, sequestration in long-lived or decomposition-resistant organisms, spawning of anadromous fishes, nitrogen fixation and denitrification) govern

the rate of nutrient spiraling (Stream Solute Workshop 1990, Webster and Ehrman 1996). Both standing stock and productivity of members of aquatic communities, including salmonids, are strongly influenced by nutrient dynamics (Mundie 1969, Gregory et al. 1987).

Impacts of Human Activity

It is impossible to describe all of the changes in the trophic system of rivers resulting from anthropogenic disturbances; the reader is once again referred to more comprehensive treatises (Naiman and Decamps 1990, Naiman 1992, National Research Council 1992). Stanford and Ward (1992) summarized several types of human disturbance that disrupt ecological linkages between terrestrial and aquatic ecosystems, alter the concentration of nutrients or toxic substances, or strongly alter aquatic food webs (Table 15.6). Activities resulting in impounded water and regulated streamflows disrupt the downstream movement of dissolved

and particulate organic matter, prevent or inhibit the exchange of sediment and organic matter between the river and its floodplain, reduce the exchange of water between the stream and hyporheic flows, and create sediment and nutrient sinks in the drainage. Water pollution alters the transformations (flux rates) of materials within aquatic food webs by reducing or eliminating some members of the aquatic community, accelerates the rate of eutrophication, or results in sedimentation that reduces organic matter storage within the substrate. Introductions of exotic species frequently alter trophic pathways in aquatic food webs and change the biomass and production of different trophic groups (Li et al. 1987).

Human Activities and Cascading Trophic Systems

Effects of species introductions, faunal changes caused by pollution, or harvest of fishes and invertebrates may generate changes throughout a stream's trophic system. Organisms near

TABLE 15.6. Categories, examples, and effects of some common types of anthropogenic disturbances that alter the trophic dynamics of lotic ecosystems.

Category	Examples	Effects
Stream regulation	Dams, water diversions, dredging, diking, revetments	Lotic reaches replaced by reservoirs: loss of upstream-downstream continuity, migration barriers, flood and nutrient sink, stimulates biophysical constancy in downstream environments Channel reconfiguration and simplification: loss of lateral connectivity, removal of large woody debris, isolation of riparian and hyporheic components of floodplains Diversion of water to other river basins: loss of particulate organic matter, dewatering of stream channels, introduction of exotic species, increases in pollutant concentrations
Water pollution	Point source discharges of industrial wastes, nonpoint source runoff from agriculture, urban, highway, and forestry development, airborne pollutants	Deposition of airborne pollutants: eutrophication, acidification Deposition of waterborne pollutants: toxicity, eutrophication Accelerated erosion: sedimentation of stream substrate, eutrophication
Food web manipulations	Introduction of exotic plants and animals, harvest of fishes and invertebrates, aquaculture	Harvest of fishes and invertebrates, aquaculture and hatcheries: biomass and production shifts, loss of marine- or lake-derived nutrients from anadromous or adfluvial species Introduction of exotic species: species displacement, cascading trophic effects

From Stanford and Ward 1992.

the apex of lotic food webs, usually vertebrates or large-bodied invertebrates, can significantly impact the abundance of their prey. If prey are herbivorous, the influence of predation by a carnivore on herbivores can influence the standing crop of algae in the stream. These "top-down" changes are called *trophic cascades*. In streams where aquatic communities are structured by density-dependent processes (competition, predation), experiments by Power and her associates (Power 1984, Power et al. 1985, Power 1990, 1992) have shown that changes in predator populations influence the abundance of grazers, which in turn regulate the biomass of periphyton. For example, Power (1990) manipulated the summer food web of pools in a northern California river in which the community consisted of a relatively large predator (juvenile steelhead trout [*Oncorhynchus mykiss*]) that consumed other fishes and large predatory invertebrates, two small fish species (roach [*Hesperoleucas symmetricus*] and stickleback [*Gasterosteus aculeatus*]) that fed primarily on small invertebrates, predatory invertebrates (larval damselflies [Lestidae]) that also consumed small invertebrates, and a periphyton community dominated by a filamentous green alga (*Cladophora*), diatoms, and a blue-green alga (*Nostoc*). When fish were present, damselflies and other small predators were limited and midge (Orthoclaadiinae) populations flourished, grazing the periphyton community to a thin layer on the boulder-cobble substrate. When fish were experimentally removed, invertebrate predators increased, grazing invertebrates declined, and periphyton grew into a thick mat covering the stream bottom.

The strength and importance of cascading trophic interactions such as those described by Power (1990) appear to differ greatly within and among streams and it is possible that in the majority of cases predators do not control the structure and abundance of lower trophic levels. Differences in predator-prey linkages, disturbance regimes, and recruitment of colonizing organisms from upstream sources can obscure cascading trophic interactions (Allan 1995). In a review of experimental predation studies, Cooper et al. (1990) concluded that the

ability of predators to structure lower trophic levels declines with increasing rates of prey recruitment. Hawkins and Furnish (1987) found that grazing can be dominated by herbivores such as snails (*Juga*) that are generally not eaten by vertebrate predators and are thus not affected by predator densities. Physical features of stream channels also influence the strength of trophic cascade effects. For example, Power (1992) was unable to detect strong top-down predator effects on the structure of communities in gravel riffles, which were more complex and may have provided more spatial refugia than the pool community in the earlier study (Power 1990). Feminella and Hawkins (1995) concluded that most studies have shown no or only weak effects of stream predators on herbivores, but often strong effects of herbivores on periphyton. On the other hand, "bottom up" controls based on food resource limitation (reviewed in Allan 1995) appear to exert a strong control over the food web structure of many streams.

Additionally, a stream's disturbance regime may affect the characteristics of its food web. Wootton et al. (1996) presented experimental evidence that scouring floods in northern California strongly influenced the abundance of predator-resistant grazers (a caddisfly [*Dicosmoecus*]). When this large, armored benthic grazer was abundant, algal biomass was lower and densities of predator-susceptible grazers and their predators was likewise reduced. Wootton et al. (1996) found that streams with regulated flows were often dominated by predator-resistant grazers, whereas streams with a natural flow regime, including periodic flooding, possessed more predator-susceptible grazers and thus more insectivorous fishes.

Human-induced changes in the species composition of stream communities can have dramatic and unanticipated trophic effects, with changes occurring at every trophic level from primary producers to top level consumers (Ross 1991). In many instances the deliberate introduction of a large carnivore has radically altered the structure of lake communities (e.g., the release of Nile perch [*Tilapia nilotica*] into rift lakes of central Africa) (Kaufman 1992). In the Pacific coastal ecoregion, the most exten-

sive changes to riverine ecosystems caused by species introductions have occurred in large, impounded rivers such as the Columbia River and the Sacramento River, where large numbers of exotic species have transformed the food web and largely displaced the native fish fauna from much of the middle and lower river (Moyle et al. 1986, Li et al. 1987).

Loss of Riparian Vegetation

Loss of riparian vegetation, especially trees, has been one of the most pervasive changes to riverine ecosystems resulting from human activities. From the smallest headwater streams to the largest floodplain rivers, riparian vegetation influences organic matter inputs and trophic pathways. Removal of riparian vegetation eliminates a major source of terrestrial organic matter, reduces shade to small streams causing a shift in the autotrophic community, and often leads to streambank erosion that increases fine sediment in the channel. All of these changes affect trophic processes in rivers (Gregory et al. 1991). Loss of riparian trees also reduces the recruitment of large woody debris, which plays an important role in storing sediment and FPOM, provides habitat for aquatic organisms, mediates channel topography, and itself forms an important source of organic matter (Harmon et al. 1986, Ward and Aumen 1986, Bisson et al. 1987, Chapter 13, this volume).

Timber harvesting in riparian zones has been a common cause of riparian alteration in western North America. Overall, removal of trees from riparian zones in forested landscapes has had negative consequences for stream-dwelling salmonids (Hicks et al. 1991) but increases in summer biomass and production of headwater salmonid populations after logging have been reported from enough sites in the Pacific Northwest (e.g., Murphy and Hall 1981, Hawkins et al. 1983, Bisson and Sedell 1984, Bilby and Bisson 1987, Holtby and Scrivener 1989) to suggest that trophic pathways supporting salmonids have actually been enhanced by timber harvest in these headwater areas.

A comparison of the organic matter inputs to paired old-growth forested and clear-cut water-

sheds (Bilby and Bisson 1992) demonstrated that headwater salmonid populations relied primarily on autotrophically based food in summer (Table 15.7). In this study, approximately 90% of the food items consumed by juvenile coho salmon (*Oncorhynchus kisutch*) in both the clear-cut and old-growth streams were organisms supported by autochthonous organic matter sources. Especially prominent in the diets of coho and cutthroat trout (*O. clarki*) were larval midges and baetid mayflies, two invertebrate groups that ingest algae and algal based detritus. Although total organic matter inputs to the stream in the old-growth forest were approximately two times greater than at the clear-cut site, production of fishes in the old-growth forested stream was less than one half that observed at the clear-cut site. Ratios of summer production of two salmonids and a sculpin between the clear-cut and old-growth sites were remarkably similar to the ratios of autochthonous inputs at these streams (Table 15.7), strongly supporting the hypothesis that the fish community was supported by autotrophic food pathways in summer regardless of the condition of the forest canopy.

Similar increases in summer populations of salmonids in the Pacific coastal ecoregion have been reported after losses of riparian vegetation caused by other land uses (e.g., channelization, livestock management) (Chapman and Knudsen 1980). Increased salmonid productivity has apparently been related to greater amounts of light reaching stream channels, stimulating photosynthesis and boosting secondary production of heterotrophs dependent on periphyton. Yet, juvenile salmonids do not always benefit from enhanced autotrophic production following vegetative canopy removal (Gregory et al. 1987). Elevated stream temperature accompanying increased sunlight may favor species better adapted to warmer waters if such species are present in the system. For example, Reeves et al. (1987) found that stream warming after logging in riparian zones led to increased populations of reddsides shiners (*Richardsonius balteatus*), which displaced juvenile steelhead. In warmer streams, shiners became more aggressive and outcompeted steelhead for pre-

TABLE 15.7. Average daily organic matter inputs from allochthonous and autochthonous sources in two 4th-order streams, a clear-cut and an old-growth forested watershed in the Cascade Mountains of Washington: the production of fishes inhabiting these sites from late spring through early autumn; and the ratios of organic inputs and fish production at the two sites.

	Clear-cut (mg/m ² /d)	Old-growth (mg/m ² /d)	Ratio (clear-cut/old-growth)
Annual organic matter inputs			
Allochthonous sources	164	851	0.19
Autochthonous sources	482	301	1.60
Fish production			
Coho salmon (<i>Oncorhynchus kisutch</i>)	34	18	1.89
Cutthroat trout (<i>O. clarki clarki</i>)	8.2	7.4	1.10
Shorthead sculpin (<i>Cottus confusus</i>)	4.5	2.5	1.82

From Bilby and Bisson 1992.

ferred foraging locations. Salmonid production in small forested streams of the Pacific coastal ecoregion generally tends to increase following removal of streamside vegetation at northern latitudes or high altitudes (Dolloff 1983, Holtby and Scrivener 1989). In the southern part of the region most of the enhanced autotrophic production has benefited cyprinid fishes and other species preferring warmer waters (Reeves et al. 1987, R.E. Bilby and B.R. Fransen, Weyerhaeuser Company, Tacoma, Washington, USA, personal communication).

Loss of Salmon Carcasses

Another pervasive effect of human activity in many of the river basins draining to the Pacific Ocean has been a large reduction in the numbers of anadromous salmonids naturally spawning in their natal rivers (Nehlsen et al. 1991). There are a multitude of reasons for declines in the abundance of spawning salmon, including natural as well as anthropogenic causes, but in terms of impact on the trophic system of streams, loss of carcasses has been one of the most significant (NRC 1996). Salmon carcasses appear to influence food pathways supporting rearing juveniles and other stream-dwelling fishes in several ways. First, mineralized nutrients from carcass decomposition stimulate autotrophic production (Richey et al. 1975, Kline et al. 1990, 1993). Second, organic leachates from carcass tissues stimulate microbial uptake

and enhance the heterotrophic food web (Bilby et al. 1996). Third, carcasses are consumed by macroinvertebrates, which in turn may become prey for fishes (Piorkowski 1995). Finally, carcasses, eggs, and alevins are eaten directly by fish. The latter pathway has received relatively little attention, but recent evidence has shown that direct consumption of carcasses, eggs, and alevins provide an extremely valuable food resource for juvenile salmonids during a period when other food resources are scarce (Figure 15.6).

Aside from providing trophic support to salmonids, salmon carcasses serve as vectors of marine-derived nutrients that benefit many other organisms in watersheds. Carcasses are a seasonally important resource for a variety of terrestrial scavengers (Cederholm et al. 1989). Nutrients from carcasses deposited on streambanks and riverine terraces by floods and scavenger activities fertilize riparian vegetation (Bilby et al. 1996). High flows carry carcasses as well as nutrients from their decomposition to lower rivers and estuaries, where they may enhance both autotrophic and heterotrophic production.

To what extent carcass deposition in streams has been reduced relative to predevelopment levels is not well known in most areas. Long-term records of spawning counts are available from only a few streams, and historical runs are usually reconstructed from catch statistics (Bisson et al. 1992). However, in watersheds where fishery policies have emphasized hatch-

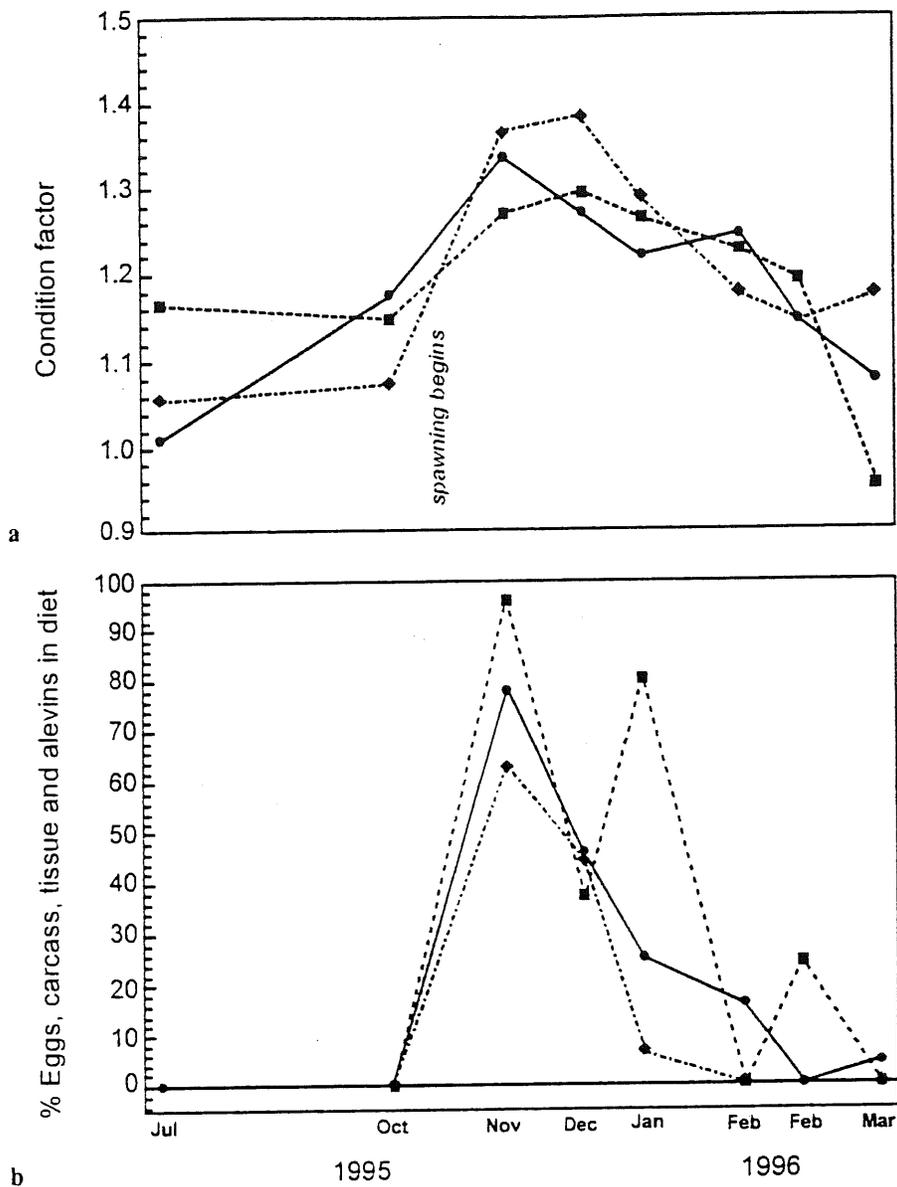


FIGURE 15.6. Influence of spawning by adult coho salmon on a) condition factor (a commonly used measure of overall fish condition or "fatness") and b) diet of juvenile salmonids (steelhead [age 0]-●-; steelhead [age 1]-■-; and coho [age 0]-◆-) in a small

tributary of the Willapa River, Washington (unpublished data of B.R. Fransen, J. Walter, and R.E. Bilby, Weyerhaeuser Company, Tacoma, Washington, USA).

ery production and permitted high fishing rates. numbers of salmon spawning naturally in rivers and their tributaries are typically quite low (Nickelson et al. 1992, Washington Department of Fisheries et al. 1993). In one coastal basin in southwestern Washington state, naturally spawning salmon are estimated to be approximately one tenth of the numbers that spawned in the system earlier in the twentieth century

(NRC 1996). This reduction has deprived the basin of almost 3,000 metric tons (wet weight) of salmon carcass biomass each year. Similar reductions are likely to have occurred elsewhere. For example, estimates of pre-development salmon runs in the Columbia River range from about 8 to 16 million fish annually (Chapman 1986) but current runs total less than two million adults, and most of

these are hatchery-produced fish that will either be caught in fisheries or return to the hatchery of their origin. Very few spawn naturally in the Columbia River basin, relative to the salmon runs that occurred there in the nineteenth century. The significance of this loss for the trophic systems of streams and rivers is seriously underappreciated.

Why Are Some Streams More Productive Than Others?

Consider, again, the question of productivity—the capacity of a stream to produce a product of interest. The chapter began with a comparison of the production of salmonids in rivers throughout the world (Table 15.1). Most streams are relatively unproductive for salmonids; only a few demonstrate high levels of productivity (Figure 15.1). What makes these streams productive, while so many others are not? One hypothesis is that they possess superior physical habitat, but a careful examination of descriptions of study sites reveals that many unproductive streams contain abundant pools and cover, two features often emphasized in assessment of salmonid habitat quality. Some of the most productive streams (e.g., British chalk streams and some spring-fed creeks) tend to have very fine-grained substrates that would be considered distinctly suboptimal for salmonids. Additionally, some of the coldest sites are quite unproductive (e.g., those in Alaska, the coastal rain forests of the Pacific Northwest, the Rocky Mountains of western North America, the boreal forests of eastern Canada). Physical characteristics such as cold water, channel morphology, and coarse substrates, so often identified as key limiting factors in lotic environments, do not appear to be primarily responsible for regulating the productivity of salmon and trout in streams. This is not to discount the importance of habitat, rather to point out that other factors have a powerful influence on productivity.

The most productive streams appear to contain abundant food. Although most of the studies in Table 15.1 have not quantitatively

assessed food availability, productive sites tend to possess hard waters with relatively high inorganic nutrient concentrations; moderate temperatures, especially in spring-fed streams where temperatures are buffered by groundwater inputs year round; relatively low vegetative canopy coverage allowing ample sunlight to reach the streams; and abundant macrophytes and mosses, or dense growths of filamentous algae. These conditions are indicative of high levels of autotrophic production, which may be the most important trophic pathway for aquatic macroinvertebrates preferred by salmonids during spring and summer (Bilby and Bisson 1992). Although there are exceptions, production of salmonids is often more strongly influenced by high growth rates than by dense populations (Warren 1971). Growth rates are a function of food availability, metabolic costs of obtaining and processing food, and density-dependent interactions including competition and predation (Fausch 1984). High growth rates require abundant food resources (Dill et al. 1981), even when physical habitat and water quality are favorable for growth. Population density is mediated by habitat quality but growth rates can be low when densities are relatively high, even in high-quality habitat (Chapman 1966, Mason 1976, Bilby and Bisson 1992, Fransen et al. 1993). For stream-dwelling salmonids, these observations suggest that food availability may be one of the most important factors controlling production.

Further evidence for the importance of food is provided by studies of experimental stream enrichment. Virtually every attempt to increase production by adding inorganic nutrients or organic matter to rivers in the Pacific coastal ecoregion has resulted in increased salmonid production. The most striking increases have come from placing food organisms directly in streams (Mason 1976) or attempting to increase autotrophic production (Johnston et al. 1990, Slaney and Ward 1993). Salmonid production also has been enhanced by increasing heterotrophic pathways (Warren et al. 1964, Mundie et al. 1983, Perrin et al. 1987), but results have not been as obvious. Of course, these studies did not attempt to add so much organic matter or nutrients that the streams suffered

from obvious effects of excessive enrichment characteristic of polluted waters.

Chapman (1966) hypothesized that food would limit production of Pacific coastal salmonids during conditions of summer low flow, and available rearing space would limit production during winter when fish need refuge from high flows. Mundie (1974) speculated that heterotrophic food pathways were generally the most important food resources for juvenile salmon and suggested that it might be possible to create artificial channels in which food organisms available to salmonids could be deliberately enhanced. Based on recent findings, the conclusions of these two seminal papers with regard to the trophic dynamics of Pacific coastal rivers containing anadromous salmonids can be updated. First, available evidence suggests that food availability may limit the productive capacity of streams for salmonids throughout the year, including autumn and winter. Second, autotrophic production is the principal source of trophic support for salmonids during spring and summer, but heterotrophic food pathways dominate during autumn and winter when streams receive inputs of leaves and salmon carcasses. In the spring, as photoperiod lengthens, scouring freshets subside, and stream temperatures warm, salmonids begin to feed primarily on organisms supported by autochthonous production.

If salmonids in Pacific coastal rivers rely primarily on alternating autotrophic and heterotrophic food pathways throughout the year, natural resource managers must consider both sources of organic matter when formulating land use and fishery policies. To attempt to return all streams to a densely forested, heavily shaded condition, for example, would negatively impact autochthonous production, although returning riparian zones to dense, mature conifer forest on a broad regional scale is unlikely to happen in the foreseeable future. On the other hand, benefits of openings in the riparian canopy, such as openings created by natural disturbances, should be acknowledged and included in the planning process for any watershed. In addition, the role of salmon carcasses must be expanded to include their trophic contribution to the stream ecosystem.

To limit the numbers of returning adults strictly to those needed to adequately populate available habitat in the stream network with fry is to misunderstand the notion of carrying capacity and to guarantee that autumn and winter food webs will be impaired. As relationships between salmonid productivity and food pathways become better understood, natural resource managers will be in a much better position to determine what rivers can and cannot produce.

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