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7
Primary Production

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Overview

- Aquatic primary producers—benthic algae, macrophytes, and phytoplankton—play a key role in the trophic support of stream ecosystems.

- Primary production depends on many factors, including light, nutrients, temperature, streamflow, and herbivores. Light is often limiting in small forest streams, which may receive less than 5% of full sunlight. With increased light, photosynthesis can increase up to a level of light saturation, about 20 to 60% of full sunlight, depending on species and acclimation conditions. Phosphorus and nitrogen are often limiting in more open streams.

- Grazing of live tissues and collecting of autochthonous detritus (i.e., from in-stream primary production) are the main avenues of energy flow from primary producers to consumers. At higher trophic levels, salmonids feed mostly on invertebrate drift produced through autochthonous pathways regardless of the input of allochthonous organic matter (i.e., produced outside the stream).

- Within a watershed, production is typically low in the headwaters because of shade from forest canopy, and high in more open, mid-order streams and rivers. In a large (9th-order) watershed, 1st- to 3rd-order streams may produce only 10 to 20% of the total annual gross primary production, despite having over 80% of total stream length.

- Watershed uses can have varied effects on aquatic primary production. Removing riparian canopy and increasing nutrients will often increase productivity leading to greater production of invertebrates and fish.

- Effects of watershed uses, however, should be viewed from a long-term perspective and in the context of associated changes in physical habitat. Maintaining healthy stream habitats and biodiversity can be accomplished by managing for naturally functioning streams with diverse energy sources.

Introduction

Aquatic primary production is a basic source of energy for stream ecosystems. Production by green plants and algae is called *primary production* because it constitutes the only significant energy gateway into the earth ecosystem. Algae and aquatic plants, together with allochthonous organic matter (i.e., produced outside a stream), provide trophic support for invertebrates, fish, and other animals that make up the diverse communities in running waters. Past ideas about stream ecosystems often downplayed the significance of autochthonous (i.e., produced in stream) primary production and emphasized the dependence on allochthonous energy sources, particularly litter from streamside vegetation (Minshall 1978). More recently, ecologists have pointed out the importance of autochthonous primary production, not only in open, nonforested sites, but even in small, forested streams usually perceived as depending on forest litter as the

primary energy source (Bilby and Bisson 1992, Chapter 15 this volume).

Aquatic primary production is sometimes underrated because of the small amount of algae and plants typically present in a stream compared to the much larger amount of stored allochthonous organic matter. However, a small algal biomass can support a much larger biomass of consumers because of rapid turnover (in hours to days) (McIntire 1973, Lamberti et al. 1989, see Hershey and Lamberti this volume). In contrast, turnover of allochthonous detritus is much slower, measured in years or decades (Naiman 1983). Autochthonous organic matter is also more nutritious than allochthonous matter (Anderson and Cummins 1979), and high aquatic primary production, occurring seasonally, can significantly enrich the detritus pool for invertebrate consumers (Hawkins et al. 1982).

Primary production has an important role in both stream productivity and in mediating impacts of watershed uses. Land uses affect primary production by altering riparian vegetation, nutrients, and other habitat features and have consequences at a stream's highest trophic levels. Increased primary production after a disturbance sometimes completely masks otherwise detrimental effects of decreased habitat quality (Hawkins et al. 1983). In order to conserve or restore stream productivity and biodiversity, it is important to understand how land uses affect aquatic primary production.

This chapter describes primary production in streams—the typical forms of algae and plants, environmental factors and energy gateways into the food web, distribution in watersheds, and effects of watershed uses.

Forms and Typical Species

Aquatic primary producers in streams and rivers occur in three common forms: benthic algae, macrophytes, and phytoplankton. Benthic algae are attached to the stream bottom and submerged debris. Macrophytes include angiosperms rooted in the stream bottom, mosses, and other bryophytes. Phytoplankton consists of algae suspended or freely floating in water. The relative abundance of these three types differs with stream size, gradient, and exposure to sunlight.

Benthic Algae

Benthic algae covering stream substrates have two general forms: microscopic, unicellular algae (especially diatoms) that form thin layers on stream substrates (Figures 7.1a and 7.1b); and macroalgae (green, blue–green and red algae) that grow as filaments, sheets, or mats (Figures 7.2a and 7.2b). Benthic algae typically occur with bacteria and fungi in an assemblage called periphyton, which usually also includes inorganic sediments and organic matter as an integral part of this complex association. Macroalgae such as *Ulothrix* form the primary matrix of algal mats, giving the mat its basic structure, but diatoms (e.g., *Achnanthes*) are also an important component (Figure 7.3). The macroalgae often dominate in low-gradient, open streams, whereas diatoms usually dominate in higher-gradient, shaded streams (Minshall 1978). Streams frequently contain a variety of surfaces and microhabitats for different kinds of algal assemblages. Even the backs of snails are seasonally important for certain specialized algae (Stock and Ward 1991).

The various growth forms of periphytic algae are related to their function in primary production, nutrient uptake, and protection from grazing (Steinman et al. 1992). Growth forms include branched or unbranched filamentous forms (e.g., *Draparnaldia* and *Oedogonium*); branched filaments in a gelatinous or mucilaginous matrix (e.g., *Batrachospermum*); plate-like colonies of cells in a gelatinous matrix (*Tetraspora*); and prostrate forms (e.g., *Stigeoclonium* basal cells and several diatoms). Carbon fixation and nutrient uptake are directly related to the alga's surface-to-volume ratio (Steinman et al. 1992) and are highest in branched filamentous species and lowest in gelatinous species. Gelatinous filamentous algae are least vulnerable to grazers, whereas loosely attached diatoms and unbranched filaments are most vulnerable (Lamberti and Resh 1983, Steinman et al. 1992).
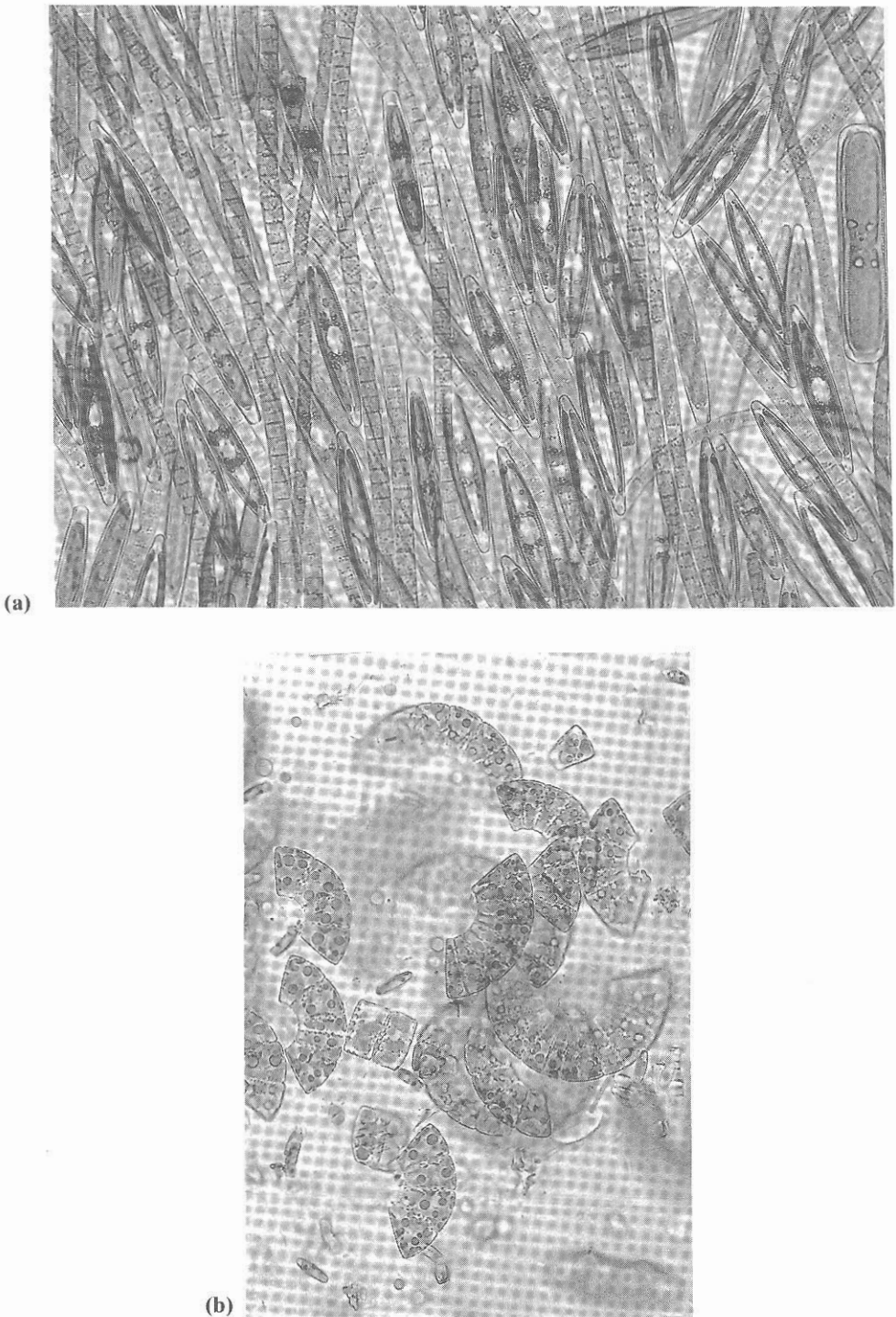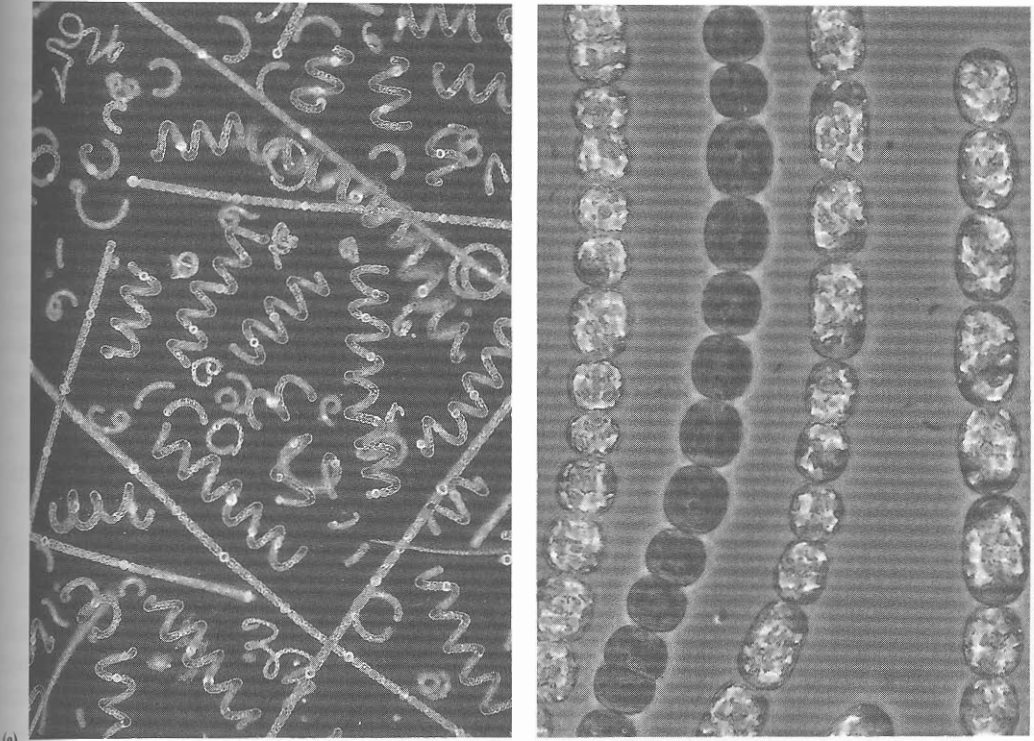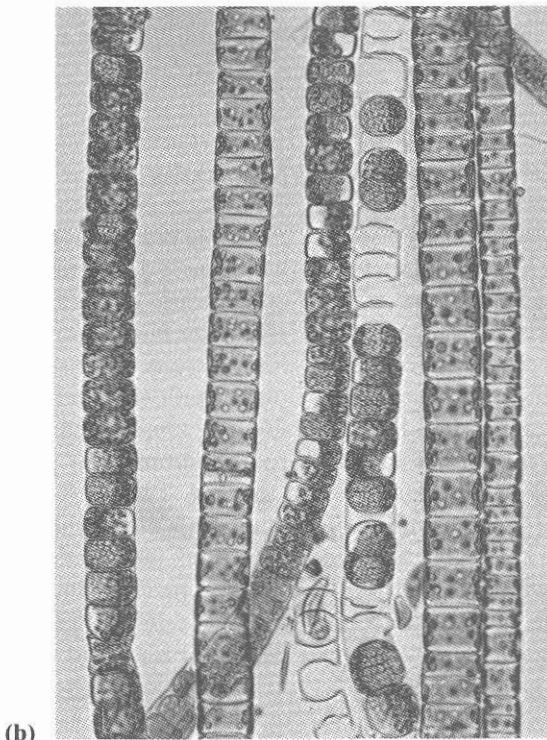
FIGURE 7.1. (a) The cigar-shaped diatom *Navicula* is a large genus with many common species occupying a broad range of habitats in fresh and salt water. (b) The benthic diatom *Meridion* forms fan-shaped colonies. It is common in headwater streams, sometimes occurring as a brown scum on the stream bottom. (Photos: Canter-Lund and Lund 1995 with permission).
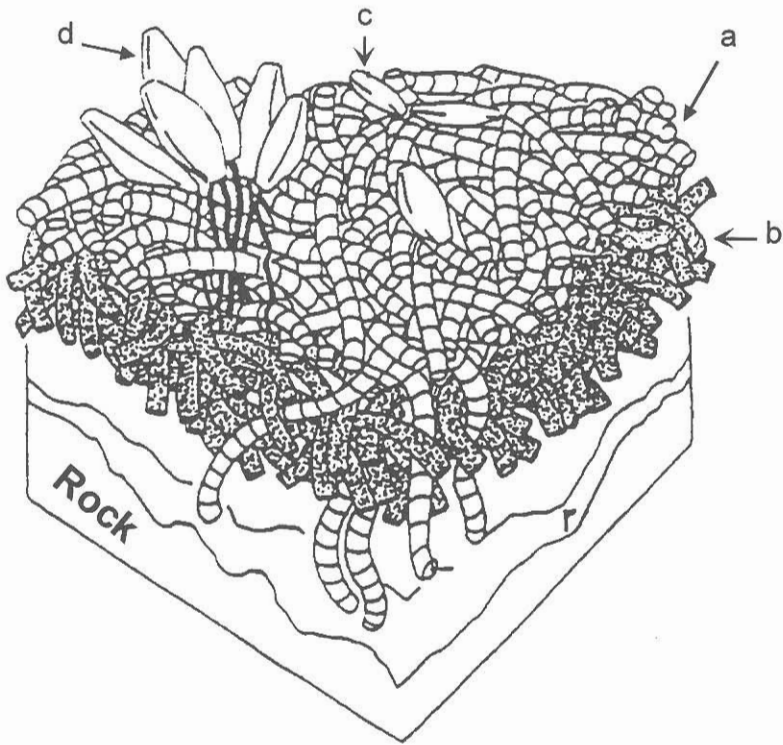
FIGURE 7.3. Drawing of an Oscillatoria mat on rock substrate, showing upper metabolically active filaments (a), lower dead algal filaments (b), loosely attached diatoms (c), and stalked diatoms (d) (Stock and Ward 1991 with permission).

Dominant species and growth forms usually change seasonally in response to changes in light, temperature, and streamflow. Seasonal changes are usually gradual. Major species tend to wax and wane in a succession of broad peaks, with long periods of overlap (Wehr 1981). Benthic algae often consist of permanent taxa that are always present, with certain taxa being seasonally dominant (Walter 1984). Filamentous green algae (e.g., *Ulothrix*) often dominate in spring and early summer, giving way to other green and blue–green algae (e.g., *Oedogonium, Pectonema, Phormidium*) in early autumn, and then to mainly diatoms in winter (Wehr 1981, Walter 1984). Overlying the gradual seasonal succession are rapid changes resulting from sudden increases in discharge during freshets. Species susceptible to export accumulate during periods of low streamflow but are exported during the next storm (Rounick and Gregory 1981, Steinman and McIntire 1990).

Macrophytes

Principal macrophytes include the angiosperms which have differentiated roots, leaves, and vascular tissue. They have four main growth habits: emergent plants rooted below water with aerial leaves (e.g., *Pontederia*); floating attached plants with submerged roots (e.g., *Nymphaea*); floating unattached plants (e.g., *Lemna*); and rooted submerged plants (e.g., *Potamogeton*) (Riemer 1984). A river may be lined by emergents along shore, have floating plants in protected water, and have submerged plants midstream. Vascular macrophytes are most abundant in low-gradient streams with open canopy (Fisher and Carpenter 1976).

Besides angiosperms, bryophytes (mosses and liverworts) can be important in both densely shaded headwater streams (Steinman and Boston 1993) and large rivers (Naiman and Sedell 1980, Naiman 1983). Characteristic

genera include the moss *Fontinalis* and the leafy liverwort *Porella*. Often the same bryophyte species that occur submerged in streams also grow terrestrially along shore (Glime and Vitt 1987). Mosses have several characteristic growth forms, including clumps with long, free-floating filaments, and in fast water, short filaments that appear to be sheared by flowing water and bedload (Brusven et al. 1990). Mosses are perennial, taking several years to accumulate (Naiman and Sedell 1980), and they are sensitive to substrate instability (Englund 1991). Hence, they are often most abundant in fast water on stable boulders and bedrock (Suren 1991, Steinman and Boston 1993).

Phytoplankton

True riverine phytoplankton, or "potamoplankton," are normally restricted to slow-flowing rivers and sloughs and do not usually occur in small streams. Nearly all suspended algae in small streams are detached and drifting cells of benthic algae (Swanson and Bachmann 1976), called "tychoplankton" (Reid and Wood 1976). Typical potamoplankton of slow-flowing rivers includes Centric diatoms (e.g., *Stephanodiscus*) and small green algae (e.g., *Scenedesmus*). Seasonally, diatoms often bloom in spring as river discharge decreases followed by mixed blooms of green algae and diatoms in summer (Garnier et al. 1995).

For potamoplankton to develop in a river, the retention time must be long enough so that population growth by cell division outweighs the loss by dilution and discharge. At a given site, potamoplankton increase as river dis-

charge declines, whereas suspension of detached cells from benthic algae increases as discharge goes up (Jones and Barrington 1985). These two opposing trends determine the composition and total density of algae suspended in a river.

The Primary Production Process

Driving primary production is the energy of photons from the sun captured as chemical bond energy by a plant's chlorophyll and other photosynthetic pigments (Figure 7.4) (Jorgensen 1977). Photosynthesis takes carbon, usually from carbon dioxide (CO_2) or bicarbonate, and hydrogen from water to fix carbohydrate and release oxygen. The plant uses some of the photosynthetic products for maintenance and either stores the rest or uses it for growth. These products subsequently may be used by other organisms in the food web.

Analogous to the first law of thermodynamics, the energy equation for primary production is

$$GPP = NPP + R$$

where *GPP* is gross primary production, *NPP* is net primary production, and *R* is respiration (McNaughton and Wolf 1973). The net production *NPP* represents the excess energy above the plant's maintenance costs which accumulates as biomass. Net production is what becomes available to other organisms through the food web.

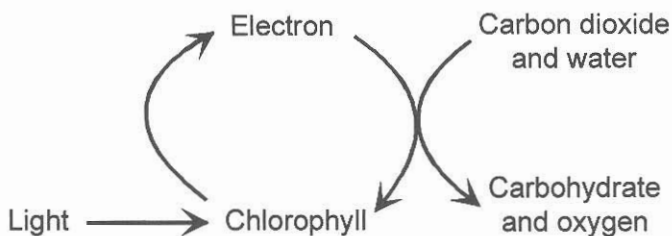The relationship between biomass and production determines the turnover rate at which

FIGURE 7.4. The basic photosynthetic process of green plants and algae, in which photons excite electrons in the chlorophyll molecule, and the resultant energy is used for carbon fixation (modified from McNaughton and Wolf 1973).

the standing biomass is replaced by new biomass production. Standing biomass itself is not necessarily a good measure of potential production because a small biomass with a high turnover rate may support a great abundance of consumers. Periphytic diatoms, for example, may be kept at a low standing biomass by stream scour and invertebrate grazing (Minshall 1978), but because they reproduce rapidly, their production is often many times greater than their standing biomass (McIntire 1973).

Limiting Factors

The rate of primary production in streams is a function of many factors, including availability of light and nutrients, temperature, herbivores, physical characteristics of the stream, and periodic disturbances (e.g., high streamflow). These factors interact with one another, and different ones predominate in different situations. Limiting factors also depend on whether production is expressed per unit algal biomass or unit stream area. In a given stream, for example, biomass-specific production may be limited by light, whereas areal-specific production could be limited by low algal biomass due to grazing (Steinman 1992).

The most common limiting factors for primary production in streams are sunlight and nutrients (Gregory et al. 1987). Low light is usually the first limiting factor in small streams (Hill and Harvey 1990), and low nutrients limit production at higher light levels (Lowe et al. 1986, Perrin et al. 1987, Hill and Knight 1988). Many diatoms, however, are adapted to low light, and areal-specific production may actually be limited by nutrients and grazers even in small shaded streams (Steinman 1992).

Sunlight

Most aquatic plants and algae are adapted to low light intensity (Riemer 1984). The ability to photosynthesize efficiently under low light is advantageous to submerged plants. The critical light level at which respiration equals photosynthesis is known as the compensation point, below which plants and algae would eventually

starve to death because they respire food faster than they produce it.

With increased light, photosynthesis can increase up to the level of light saturation. At higher light levels, photosynthesis may actually decline because of photooxidation of enzymes and chlorophyll inactivation (Jorgensen 1977). The saturation level for many algae and vascular macrophytes is about 30 to 60% of full sunlight (McIntire 1973, Riemer 1984). The saturation level, however, varies depending on species and their acclimation conditions. The light intensity of saturation is positively correlated with ambient light conditions and is in the range of about 100 to 400 μmol quanta m^2/s in 2nd- to 4th-order streams (Boston and Hill 1991). Light saturation for shade-adapted benthic algae from small streams is approximately 20% of full sunlight (Gregory et al. 1987). The important consequence is that more sunlight will not increase primary production if photosynthesis is already light-saturated.

In small woodland streams, dim light under the dense forest canopy usually limits primary production (Gregory et al. 1987, Hill and Knight 1988, Feminella et al. 1989, Hill and Harvey 1990). Light at the surface of forested headwater streams often is less than 5% of full sunlight (Gregory et al. 1987). If light increases by removing riparian vegetation or as streams get larger, algal biomass and production can increase with adequate nutrients.

Nutrients

With sufficient light, primary production usually then becomes limited by nutrients. The mechanism of nutrient limitation in streams is different from that in lakes, where biomass can increase until a nutrient is exhausted (Russell-Hunter 1970). Streams receive a continual supply of nutrients from upstream, but nutrient uptake is limited by the rate of diffusion through the boundary layer around algal cells (Elwood et al. 1981, Klotz 1985). Under this diffusion limitation, nutrient uptake and cell reproduction may be nutrient-limited, even though nutrient supply is continuous. Large rivers, however, may behave like lakes if retention time is long enough for potamoplankton

to deplete available nutrients (Garnier et al. 1995).

Availability of carbon is usually sufficient in streams because of water turbulence and high CO_2 solubility (Wetzel 1975, see Chapter 14 this volume). In some situations, however, free CO_2 in equilibrium with the atmosphere may be inadequate for high rates of photosynthesis. Ability to use bicarbonate instead of CO_2 is an adaptive advantage, particularly for many submerged angiosperms (Wetzel 1975). Aquatic bryophytes, however, may be limited by low CO_2 in alkaline streams because, unlike most other aquatic plants, they utilize only free CO_2 and can not use bicarbonate (Wetzel 1975, Glime and Vitt 1987). In highly calcareous waters above pH 8, free CO_2 concentration is negligible, and carbon species are dominated by bicarbonate and carbonate. Thus, mosses are generally restricted to soft waters of lower pH and abundant CO_2 (Wetzel 1975).

Silica is a required mineral for diatoms but not for most other algae, and diatom cell division stops without it (Werner 1977). The spring diatom bloom of phytoplankton in many lakes and some large rivers may deplete silica to limiting concentrations, after which other algae develop in a silica-limited environment (Wetzel 1975, Garnier et al. 1995).

Phosphorus (P) and nitrogen (N) are the two elements that most frequently limit aquatic primary production and are most commonly implicated in eutrophication from nonpoint source pollution (Riemer 1984). Both nutrients can limit algal growth in unpolluted waters, and adding either or both can increase productivity (Stockner and Shortreed 1978). If light and other factors (such as micronutrients, Patrick 1978), are sufficient, P often will be the first nutrient to become limiting (Wetzel 1975) because, in most fresh waters, P is an order of magnitude less abundant than N (Wetzel 1975).

The major sources of P in unpolluted waters are dust in precipitation and the slow weathering of rock (Wetzel 1975). The P content of groundwater is generally low, even where rocks and soils have high P content, because P-containing minerals are highly insoluble and strongly retained by biological and chemical processes in soil (Wetzel 1975, Mulholland 1992).

Phosphorus is present in natural waters usually in extremely small amounts in many different forms: dissolved as inorganic orthophosphate, suspended as organic colloids, adsorbed onto particulate organic and inorganic sediment, and contained in organic matter (Wetzel 1975). Soluble reactive phosphorus, consisting of ionic orthophosphates, is the only significant form available to plants and algae and constitutes less than 5% of the total phosphorus in most natural waters (Wetzel 1975). Dissolved P is usually in equilibrium with the amount bound to sediments, whose exchange capacity is increased by organic and inorganic colloids. Phosphorus is most available at a slightly acidic pH of 6 to 7. At a lower pH, it combines readily with aluminum, iron, and manganese (Tate et al. 1995), and at a higher pH, it becomes associated with calcium as apatite and phosphate minerals (Wetzel 1975).

Retention of P in streams is mostly a biological process regulated by algae, bacteria, and fungi. Aquatic microflora are capable of rapid uptake of significant amounts of P, as much as 95% within 100 m of stream length (Gregory 1978, Tate et al. 1995). Physical sorption generally accounts for less than 20% of P retention on stream substrates (Gregory 1978, Mulholland 1992) but can be much higher, such as the high sorption by iron oxide in acid streams (Tate et al. 1995). Streams have prolonged periods of net in-stream retention of nutrients punctuated by large net losses during storms (Meyer and Likens 1979). In-stream processes tend to transform nutrients that are transported downstream from inorganic forms to dissolved or particulate organic forms (Meyer and Likens 1979, Mulholland 1992).

The reservoir of N in the atmosphere as free gas (N_2) cannot be used by plants and most algae until N-fixing bacteria or blue–green algae transform it into nitrate or ammonia (Wetzel 1975). Nitrogen occurs in fresh waters in numerous forms: dissolved molecular N_2, organic compounds, ammonia, nitrite, and nitrate. Sources of N include N-fixation, precipitation, surface runoff, and groundwater. Losses of N occur as stream outflow, denitrifi-

cation of nitrate to N_2 by bacteria, and deposition in sediments (Wetzel 1975). Unlike P, N inorganic ions are highly soluble in water and readily leach out of soils and into streams. Concentration of N in stream water often follows a diel pattern, lowest in mid-afternoon and highest after dark, due to varying uptake by benthic algae (Triska et al. 1983).

Ammonia is generated by heterotrophic bacteria as the primary end-product of decomposition of organic matter, either directly from proteins or from other nitrogenous organic compounds (Wetzel 1975). Ammonia in water is present primarily as NH_4^+ and undissociated NH_4OH, which can be toxic. Although ammonia would be a good source of nitrogen for plants and algae, and many can use it at alkaline pH values, most plants and algae grow better with nitrate as their nitrogen source.

Whether N or P limit production depends on their relative and absolute abundance. The optimal N:P ratio for primary production is about 15:1 molar ratio (Elwood et al. 1981). A lower ratio indicates N is limiting; a higher ratio indicates P is limiting. Although a high N:P ratio indicates potential P limitation, this actually depends on the absolute P concentration (Bothwell 1985). Phosphorus limitation begins at a very low concentration ($<4\mu g\,PO_4/L$), and even a small increase above that level can produce a large amount of benthic algal biomass (Bothwell 1989). Growth of benthic algae in typical streams may be P-saturated at less than $1\mu g\,PO_4/L$ because of low temperature ($<15\,°C$) and low algal biomass (Bothwell 1985, Bothwell 1988). More P (up to $25\mu g\,PO_4/L$) may be needed to saturate photosynthesis at higher temperatures and higher algal biomass (Horner et al. 1983).

The optimum N:P ratio also depends on the particular algal species (Rhee 1978). A low N:P ratio (N limitation) favors growth of N-fixing algae, such as the blue–green *Nostoc* and the diatom *Epithemia* which has symbiotic blue–green inclusions (Fairchild and Lowe 1984). Adding P to a river can favor certain taxa, particularly the N-fixers.

Nutrient levels in unpolluted streams vary geographically, depending on geologic parent material (Chapter 4 this volume). Streams with volcanic bedrock generally have low N and relatively high P, and thus are likely to be N-limited, whereas streams with glacial or granitic geology are more likely to be P-limited (Gregory et al. 1987). Streams with sedimentary bedrock, such as dolomite, tend to have the most P (Golterman 1975) and be N-limited. Northern California streams are often poor in N with a low N:P ratio, and are N-limited when canopy is removed (Hill and Knight 1988). In contrast, addition of P to an Alaska tundra river increased primary production because P concentration was very low ($<4\mu g\,PO_4/L$) compared to N (Peterson et al. 1985).

Besides the limiting effects of light and nutrients, other controlling, lethal, and accessory factors (Fry 1947) also influence primary production. Controlling factors, of which temperature is most important, regulate metabolism without actually entering the process. Temperature has little effect on rate of photosynthesis at low light intensity, but under high light, temperature directly affects photosynthesis by essentially raising the level of light saturation (Jorgensen 1977). Turbidity acts as an accessory factor by clouding the water (Lloyd et al. 1987). Streambed scour and invertebrate grazing are lethal factors that reduce areal-specific primary production by keeping algal biomass low (Hill et al. 1992).

Grazing

Natural densities of snails, caddisflies, isopods, minnows, and other grazers can limit primary production by cropping benthic algae to a low biomass (Elwood and Nelson 1972, Gregory 1983, Lamberti and Resh 1983, McAuliffe 1984, Murphy 1984, Power et al. 1988, see Chapter 8 this volume). Effects of grazers on benthic algae are most evident during periods of low streamflow when grazers are concentrated (Hill and Knight 1987, Feminella et al. 1989).

Although intensive grazing can limit areal-specific primary production, moderate grazing often increases biomass-specific production by changing algal structure (i.e., species composition, physiognomy, age, and chlorophyll content) (Lamberti and Resh 1983, Hill and Knight 1987) and by enhancing nutrient supply

by excretion (McCormick and Stevenson 1991). Biomass-specific production is highest when biomass is low because of self-limitation within the algal assemblage (Hill et al. 1992). Ungrazed benthic algae often change from a diatom film to a dense turf of filamentous green algae in which self-shading and reduced circulation cause light and nutrient limitation in lower layers. Growth is then confined to a thin upper layer, whereas lower layers only respire. Grazers thus help to keep benthic algal communities in a productive, early-successional state characterized by low biomass and rapid turnover (Lamberti and Resh 1983, Jacoby 1987).

Grazing affects benthic algal structure because of differential vulnerability of algal species and physical disturbance while feeding. Upper-layer diatoms that are loosely attached to the substrate are most susceptible to grazers, whereas small, adnate diatoms are more resistant (Lamberti and Resh 1983, Hart 1985). Heavy grazing converts benthic algae from filamentous types with diverse overstory to less-diverse, closely attached diatoms (Jacoby 1987). Grazers also affect the benthic algal assemblage by disturbing substrate surfaces (Sumner and McIntire 1982), which reduces abundance of loose-layer diatoms (Hill and Knight 1987).

Coevolution of algae with grazers has resulted in grazer-resistant algal species that depend on grazers to control their competitors. The characteristics that help certain algae resist grazers—toughness, unpalatability, mucilage, or protective growth form—also slow their growth and make them more susceptible to being overgrown by faster-growing, less-resistant species (Power et al. 1988).

Effects of grazing on benthic algae depend on the grazer species (Lamberti et al. 1987). The caddisfly *Dicosmoecus*, for example, possesses robust mandibles that can remove most algae except for basal holdfast structures. The snail *Juga* has a fine-toothed radula that is effective at removing diatoms and filamentous algae. Mayflies, having delicate brush-like mouthparts effective for harvesting diatoms rather than long filaments, tend to have little effect on benthic algal structure (Jacoby 1987).

Energy Flow

Energy flow from aquatic primary producers involves several output processes to various consumer compartments (Figure 7.5). Aquatic net primary production is the source of autochthonous organic matter in a given reach. It is also the source of part of the allochthonous
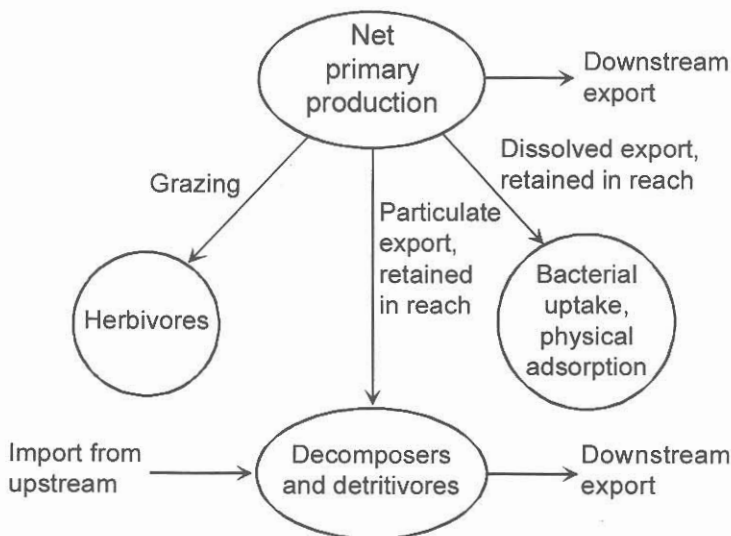

FIGURE 7.5. Energy-flow pathways for net primary production in a stream reach.
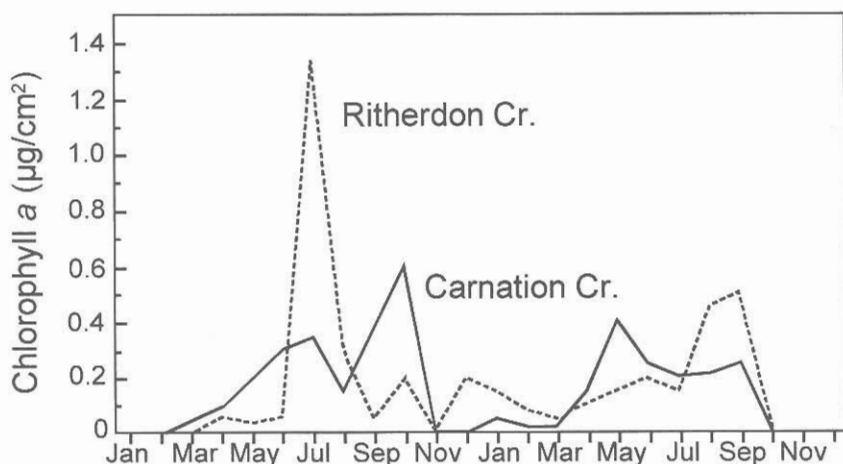
FIGURE 7.6. Seasonal growth of benthic algae, as measured by amount of chlorophyll *a*, in Carnation Creek (old-growth forest) and Ritherdon Creek (clear-cut without buffer) on Vancouver Island, British Columbia. Carnation Creek sites received 5 to 47% of available light; Ritherdon Creek received 72% of available light. (modified from Stockner and Shortreed 1976. Reprinted by permission of Kluwer Academic Publishers).

input, the part produced upstream by algae and aquatic plants and transported into the reach via streamflow. Energy flows out of net primary production through excretion of dissolved organic matter, grazing, and decomposition of particulate organic matter. Of these, the principal avenues of energy flow from primary producers are through direct grazing of living tissues and collecting of autochthonous detritus.

Different forms of aquatic plants and algae vary in the seasonal patterns of production and mortality that influence timing of energy flow and relative importance of grazing and detrital pathways. Benthic algae often show two seasonal peaks: in spring before vegetation leafs out and in autumn after leaves have fallen (Figure 7.6) (Minshall 1978, Sumner and Fisher 1979). The decline later in autumn is due to declining light and temperature and scour by seasonal storms (Rounick and Gregory 1981). Macrophyte biomass and production are highest in mid-summer and decline sharply in fall (Figure 7.7). Macrophytes are not grazed extensively, and biomass accumulates until plants die in late summer and autumn (Mann 1975, Minshall 1978). Macrophyte detritus decomposes quickly (50% weight loss the first

week; Anderson and Sedell 1979), and most decomposition occurs near the site of production (Fisher and Carpenter 1976).

The Grazing Pathway

The amount of net primary production consumed by grazers is frequently considered negligible (e.g., Stockner and Shortreed 1976, Bothwell 1989), but in many common situations, grazing is an important pathway of energy flow. Abundance of grazers depends on stream size, as predicted by river continuum theory. For example, in western Oregon, invertebrates that scrape benthic algae make up only 1 to 12% of total invertebrates in 1st-order streams, but almost 25% in 3rd- to 7th-order streams (Figure 7.8) (Hawkins and Sedell 1981). This relative abundance indicates the importance of grazing in energy flow in the different stream orders.

In general, benthic diatoms provide the most nutritious food source for stream herbivores. Diatoms tend to have higher nutritive quality (Patrick 1978) and are more readily assimilated than other algae (Lamberti et al. 1989). Stream invertebrates most commonly reject filamentous and gelatinous algae (Gregory
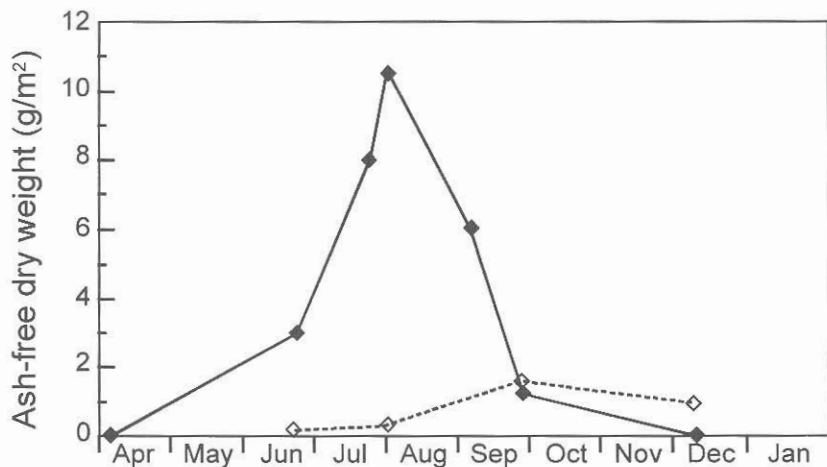
FIGURE 7.7. Living biomass (◆—◆) and downstream export (◇---◇) of vascular macrophytes (*Potamogeton*, *Callitriche*, and others) in the Fort River, Massachusetts (modified from Fisher and Carpenter 1976 with permission).

1983, Steinman et al. 1992). Live macrophytes generally are not consumed because of their tough cell walls, lignified structures, and low N content (Gregory 1983).

Consumption of living benthic algae by grazers varies depending on season, streamflow, and other factors. Although invertebrate grazers potentially have profound effects on benthic algae, they are usually prevented from having major effects because of periodic disturbances from storm events that significantly reduce their abundance (Steinman and McIntire 1990). Both plants and animals are regulated to some degree by catastrophic events. The major "reset mechanism" in lotic ecosystems, high streamflow, occurs several times per year (Naiman et al. 1992), a frequency similar to algal generation (Steinman and McIntire 1990). The marked spatial heterogeneity in current, light, and substrate of streams
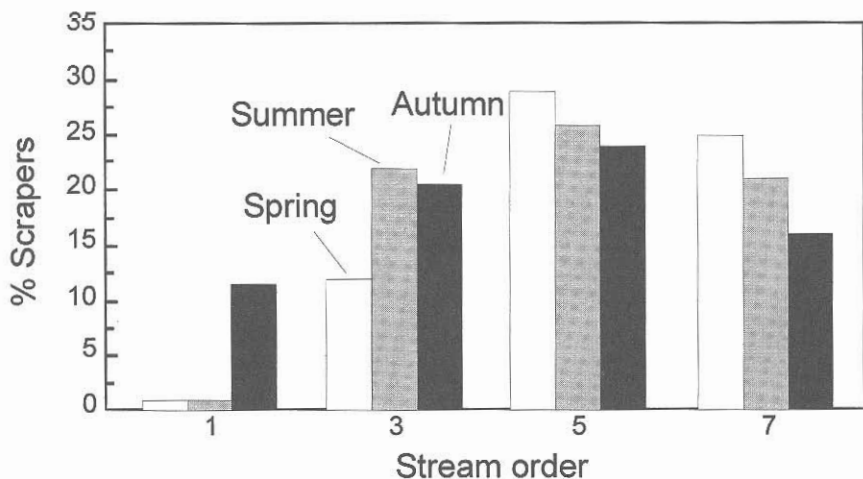

FIGURE 7.8. Relative abundance of the scraper functional group of macroinvertebrates in spring, summer, and autumn in relation to stream order in the McKenzie River basin, Oregon (modified from Hawkins and Sedell 1981 with permission).
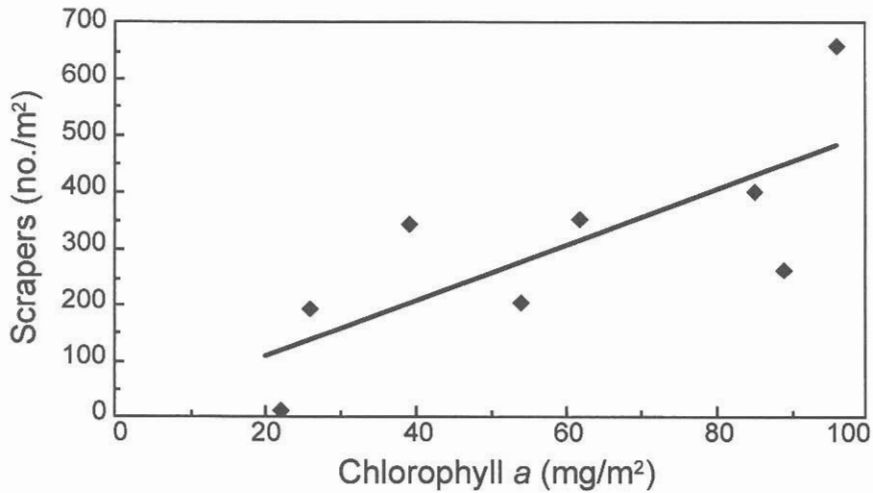
FIGURE 7.9. Density of the scraper functional group of macroinvertebrates in relation to amount of benthic algal chlorophyll *a* on rock surfaces (modified from Hawkins and Sedell 1981 with permission).

can mask grazing effects even when grazer density is high (Hill and Knight 1987). Such fluctuations and heterogeneity prevent grazers from attaining densities that reduce benthic algae (Hill and Knight 1987). In streams with stable flow or during extended dry periods when streamflow and wetted area slowly diminish, grazers can become concentrated enough to significantly impact their food resource.

In return, aquatic plants and algae have important consequences on grazer populations (Lamberti and Resh 1983, McAuliffe 1984). Availability of benthic algae regulates the distribution, abundance, and growth of scrapers (Figure 7.9) (Hawkins and Sedell 1981, Gregory 1983). Grazing invertebrates generally compete exploitatively for food (Hart 1987), and competition is most common during periods of summer low streamflow (Hill and Knight 1987). Grazer populations may be food-limited at sites where primary production is severely restricted by dim light (Lamberti et al. 1989) and during periods of stable or low streamflow, even if other factors limit them during other times (Hill and Knight 1987, Hart and Robinson 1990).

The Detrital Pathway

Although grazing is important at times in many streams, much of the biomass produced by aquatic primary producers is typically utilized through detrital pathways after the live or dead algae are exported from the production site (Minshall 1978, Lamberti et al. 1989, Scrimgeour et al. 1991). For example, diatoms that detach from the streambed are strained from the water by filter feeders like the net-spinning caddisfly *Hydropsyche* (Fuller and Mackay 1981) or are collected after they settle by deposit feeders like the chironomid *Paratendipes* (Hawkins and Sedell 1981). Besides exporting particulate detritus, algae also excrete dissolved organic matter that is then taken up by bacteria, a process which is an important energy pathway (Peterson et al. 1985).

Export of benthic algae from production areas to detrital pools results from sloughing, dislodgement by grazers, and scour by flowing water and sediment. Sloughing occurs when underlying layers of algal mats die and pieces float away (Naiman 1976). Dislodgement results when grazers disturb benthic algae while feeding. It can exceed consumption, particularly when algal biomass is high (Lamberti et al. 1989, Scrimgeour et al. 1991). Scour during periodic freshets causes major export of benthic algae, especially in autumn and winter (Rounick and Gregory 1981). Filamentous algae are susceptible to export if currents exceed 50 cm/s (Horner and Welch 1981),

whereas prostrate forms are more resistant to export (Steinman and McIntire 1990). Redd-digging salmon can also cause extensive scour and export (Walter 1984).

To contribute energy to a stream's food web, organic matter from primary production must first be retained in the stream channel so that it can be processed. Export and retention, therefore, largely determine the contribution that aquatic primary producers make to a stream ecosystem. Organic matter and nutrients in stream ecosystems are repeatedly transported, retained, metabolized, and exported in a cycling process called *spiraling* (Newbold et al. 1983, see Chapter 15 this volume). Spiraling describes the coupled processes of cycling and downstream transport of nutrients and organic matter in streams (Mulholland et al. 1983, Newbold et al. 1983). Spiral length represents the average downstream distance traveled in completing one cycle. Streams with short spirals have high retention capacity and efficiently utilize organic matter and nutrients. Both stream channel obstructions and invertebrate collectors help retain particulate autochthonous organic matter.

Although greatly outweighed by allochthonous organic matter of terrestrial origin, autochthonous detritus is important in secondary production, even in heavily forested streams with abundant allochthonous inputs (Bilby and Bisson 1992). Most of the organic matter present in streams is usually of poor nutritional quality (e.g., high carbon-to-nitrogen [C:N] ratio), and large differences in quantity of detritus represent negligible differences in actual food availability (Hawkins et al. 1982). Benthic algae are more nutritious than allochthonous organic matter because of their low C:N ratio and high protein content (Anderson and Cummins 1979). Live algae growing on detritus (Naiman 1983) also augment food quality. Abundance of invertebrates does not correlate well with total amount of organic detritus because invertebrates are usually more influenced by food quality than quantity (Ward and Cummins 1979, Hawkins et al. 1982). However, invertebrate abundance does correlate with the chlorophyll content or respiration rate of detritus (Figure 7.10) (Hawkins and Sedell 1981, Hawkins et al. 1982). Thus, algal detritus is important because it enriches the detritus pool, providing a richer substrate for microbial colonization and invertebrate consumption.

Fish and other predators also benefit from the energy flow from autochthonous organic matter. By the nature of their drift-feeding behavior, juvenile salmonids focus on food from autochthonous pathways. Invertebrates that
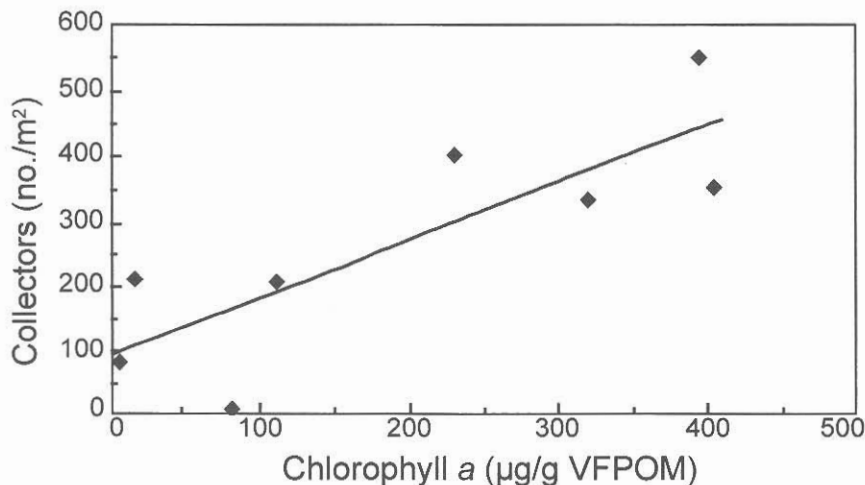

FIGURE 7.10. Density of the collector functional group of macroinvertebrates in relation to amount of chlorophyll *a* in very fine particulate organic matter (VFPOM) (modified from Hawkins and Sedell 1981 with permission).
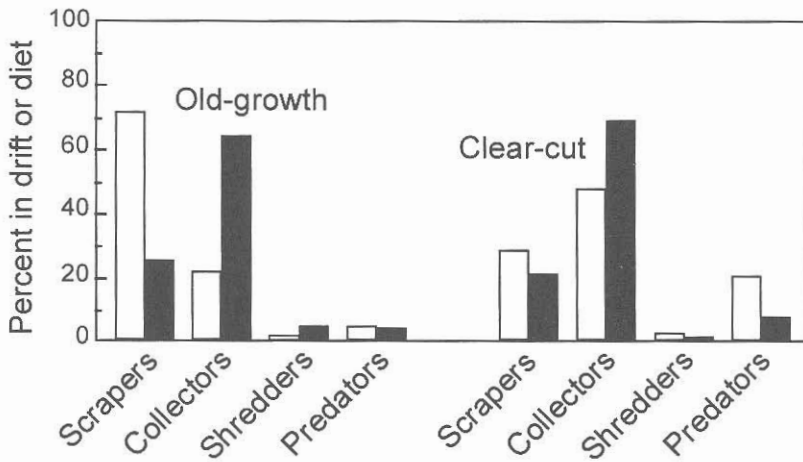
FIGURE 7.11. Percentages of invertebrate functional groups in drift (clear) and coho salmon diet (shaded) in old-growth and clear-cut sections of streams in Washington (modified from Bilby and Bisson 1992, reproduced with permission of the Minister of Supply and Services Canada 1996).

utilize autochthonous production belong mainly to the scraper and collector-gatherer functional groups (Cummins 1974), the groups most frequently eaten by salmonids (Figure 7.11) (Hawkins et al. 1983, Murphy and Meehan 1991, Bilby and Bisson 1992, see Chapter 9, this volume). Insects in these groups (e.g., Baetidae, Chironomidae, Simuliidae) are generally small-bodied and multivoltine, have rapid turnover, and are prone to drift (Waters 1969). In contrast, shredders of allochthonous organic matter (e.g., Limnephilidae) are uncommon in salmonid diets (Figure 7.11) (Jenkins et al. 1970, Griffith 1974). They tend to have only one generation per year, and their advanced instars are often large and armored with wood, shell, or stone cases so that they do not often drift and are hard for fish to ingest. Although the contributions to the diet from both terrestrial and adult aquatic insects are important (e.g., Bjornn et al. 1992), most aquatic insects eaten by juvenile salmon are primarily supported by autochthonous organic matter (Bilby and Bisson 1992). Thus, autochthonous pathways are of overriding importance in the trophic support of juvenile salmonids regardless of the amount of allochthonous material entering the stream.

Distribution of Primary Production in Watersheds

Aquatic primary production changes predictably in response to trends in geomorphology and fluvial processes as streams get larger. These trends in primary production and other ecosystem structures and functions are embodied in the concept of the river continuum (Vannote et al. 1980, Minshall et al. 1983). The river continuum portrays entire drainage networks as integrated ecosystems that change systematically from headwaters to river mouth.

In a typical forested river continuum, primary production is low in the headwaters, high in mid-order streams and swift rivers, and low again in large, sluggish rivers (Vannote et al. 1980). In small headwater streams, primary production is severely restricted by shade from forest canopy and geomorphic features. Mid-order streams have gaps in the canopy that allow in more sunlight, and benthic algal production increases (Naiman 1983). Finally, in large, sluggish rivers, shade from riparian trees and geomorphic features is insignificant, but water depth and turbidity restrict light penetration, and autotrophs are largely reduced to
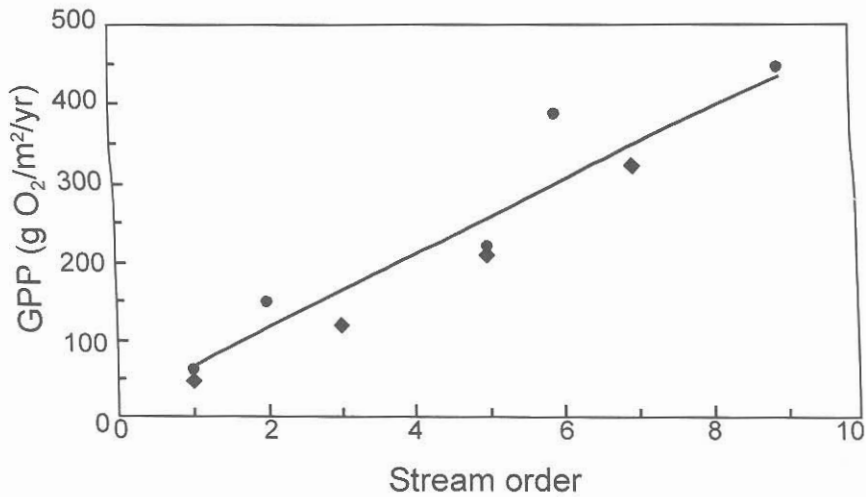
FIGURE 7.12. Total annual gross primary production (GPP) by benthic algae, mosses, and macrophytes in relation to stream order in watersheds in Oregon ◆ and Quebec ●. Production in lower-order streams is mostly by benthic algae; production in higher-order streams is augmented by moss and macrophytes (data from Naiman and Sedell 1980 and Naiman 1983). The regression equation is $Y = 55.7X^{0.93}$; $R^2 = 0.93$.

phytoplankton and macrophytes near shore (Naiman and Sedell 1980). Production, however, may continue to increase in a downstream direction at least up to the size of a moderately large river (Figure 7.12), if not too sluggish and turbid (Naiman and Sedell 1980, Naiman 1983).

Most primary production within a watershed occurs in mid-order and larger streams. The relationship between area-specific primary production and stream order (Figure 7.12) combined with data on surface area of each order give the distribution of primary production within a watershed (Naiman and Sedell 1981, Naiman 1983). For example, in a 9th-order river basin in Quebec, Canada, 1st- to 3rd-order streams contain 23% of the basin's total stream surface area but yield only 16% of the total annual gross production of benthic algae, despite representing 87% of the total stream length (Table 7.1). In contrast, streams larger than 6th order are only 2% of total stream

TABLE 7.1. Distribution of gross primary production (GPP) of benthic algae in the Moisie River basin, Quebec.

Stream order	Stream length (km)	Stream width (m)	Surface area (km²)	Annual GPP per m² (g/O₂/m²)	Total annual GPP	
					(tonnes O₂)	(%)
1	16,142	0.3	4.8	42.6	204	1.2
2	8,249	2.1	17.3	52.0	900	5.3
3	3,842	6.7	25.7	61.4	1,578	9.2
4	1,879	15.6	29.3	70.9	2,077	12.2
5	1,072	30.1	32.3	80.3	2,594	15.2
6	471	51.3	24.2	89.8	2,173	12.7
7	340	80.6	27.4	99.2	2,718	15.9
8	292	119.1	34.8	108.6	3,779	22.1
9	54	168.2	9.1	118.1	1,075	6.3
Total	32,341		204.9		17,098	100.0

Hydrology data, Naiman 1983; production data, Naiman and Sedell 1981, with permission.

length, but account for 35% of total surface area. Because of this large area and open canopy, these large rivers account for 44% of annual gross production of benthic algae for the watershed.

Potential Response to Watershed Uses

Watershed uses have profound multiple effects on aquatic primary production and other functions of stream ecosystems. Timber harvest, livestock grazing, agriculture, urban development, and other activities affect aquatic primary production by altering riparian vegetation, streamflow, sediment, channel structure, and other watershed features. These changes alter the light and nutrient regimes, physical habitat for aquatic plants and algae, and spiraling of autochthonous organic matter through the system.

The most obvious effect on aquatic primary production from land uses that alter riparian vegetation is the result of increased sunlight reaching the stream during early seral stages after disturbance. Canopy removal often causes increased primary production (Lowe et al. 1986) and increased energy flow through the food web leading to greater production of invertebrates and fish (Murphy and Meehan 1991, Bilby and Bisson 1992). Nutrient enrichment of naturally more open, mid-order streams also increases growth and abundance of algae, invertebrates, and fish (Hershey et al. 1988, Johnston et al. 1990). Effects of canopy removal depend on stream size. Larger streams are naturally more open; thus canopy removal has a smaller effect on primary production.

Strong linkages exist between riparian vegetation, light reaching the stream, primary production, microbial respiration, invertebrate production, and ultimately vertebrate production. Increased benthic algal production in open streams is available to higher trophic levels both as live algae and as detritus. The algae enrich the detritus as a substrate for microbes, resulting in increased respiration (Figure 7.13). The abundant microbes and associated live algae improve food quality, encouraging greater invertebrate production (Behmer and Hawkins 1986), which is further increased by a shift in species composition to multivoltine collector-gatherers with fast turnover (Gregory et al. 1987). Finally, increased availability of invertebrate prey leads to greater biomass and production of fish (Murphy et al. 1981, Johnston et al. 1990, Bilby and Bisson 1992).
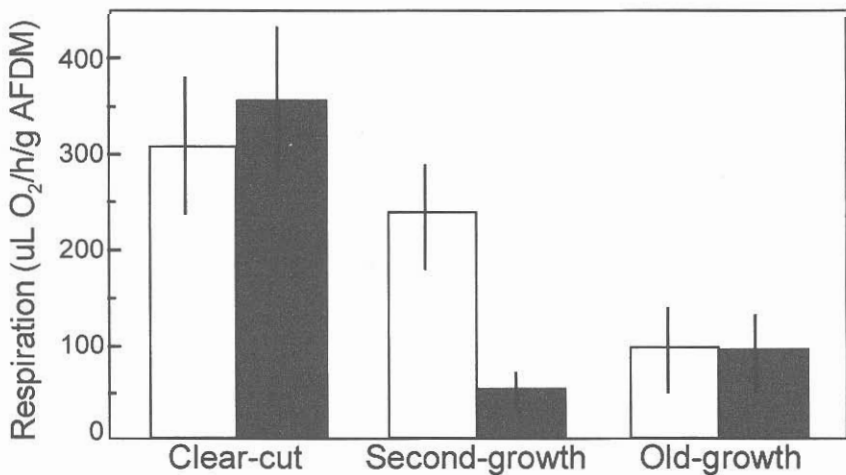

FIGURE 7.13. Respiration rate per g ash-free dry weight (AFDM) of fine particulate organic matter from streambeds in clear-cut, second-growth, and old-growth sites with high gradient (clear) or low gradient (shaded) in western Oregon. Vertical bars are ±1 standard error of the mean (modified from Murphy et al. 1981 with permission).
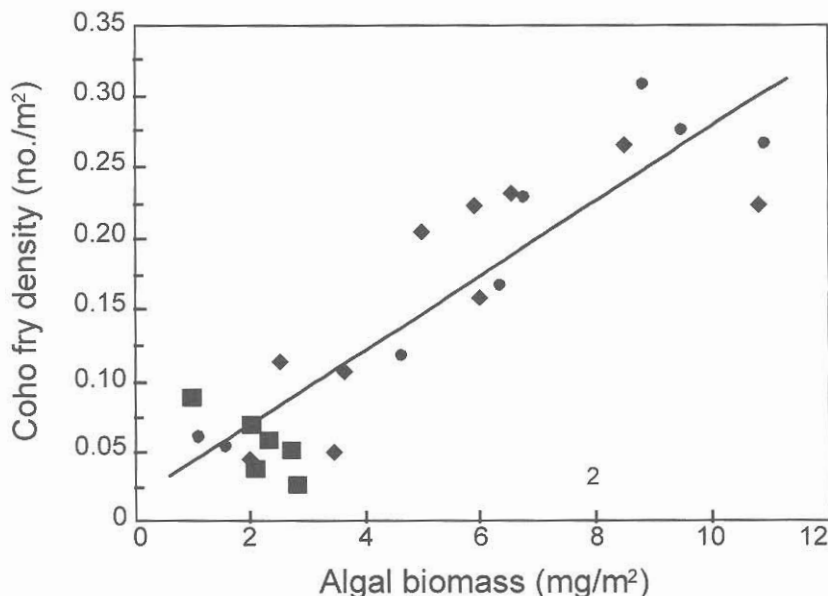
FIGURE 7.14. Relationship between summer density of coho salmon fry and benthic algal biomass (ash-free dry matter) in old-growth ■, buffered ◆, and clear-cut ● reaches of streams in southeast Alaska (modified from Murphy et al. 1984 with permission).

Besides increasing primary production, canopy removal also usually reduces inputs of allochthonous organic matter from streamside vegetation (Duncan and Brusven 1985a and 1985b, Gregory et al. 1987, Bilby and Bisson 1992). Increased food quality of detritus derived from autochthonous sources, however, can more than offset the decline in allochthonous sources (Bilby and Bisson 1992).

Higher food quality in open streams mainly benefits certain functional feeding groups: grazers, collectors, and predators (Murphy et al. 1981, Hawkins et al. 1982). Because invertebrates do not respond equally to canopy removal, species diversity may decline (Newbold et al. 1980). Reduced diversity, however, may be a result of increased dominance of certain grazer and collector-gatherers (e.g., *Baetis*, *Nemoura*, and Chironomidae) that consume algae and algal detritus rather than from reduced species richness (Newbold et al. 1980). Within the functional groups that benefit from increased primary production, such as collector-gatherers and invertebrate predators, canopy removal can increase species diversity (Murphy and Hall 1981, Hawkins et al. 1982).

Salmonids and other vertebrates often increase in abundance and growth after canopy removal because of greater food availability (Murphy and Meehan 1991). Where food is limiting and other habitat and population factors are suitable, density of coho salmon fry in summer is directly related to the abundance of algae (Figure 7.14). Evidence suggests higher fry density results from smaller feeding territories (Dill et al. 1981) because of an increase in invertebrate prey (Murphy et al. 1981, Hawkins et al. 1983). In a comparison of energy flow in forested and clear-cut sites (Bilby and Bisson 1992), total fish production was greater in the clear-cut than in the old-growth site, despite the old-growth site receiving five times more terrestrial organic matter. The increase in vertebrate production occurred mainly in spring and early summer, coinciding with the production cycle of benthic algae (Figure 7.15). A similar ratio between the clear-cut and old-growth sites (CC:OG ratio) for both fish and algal production (Table 7.2) indicated that primary production was mainly responsible for supporting fish populations in both sites.
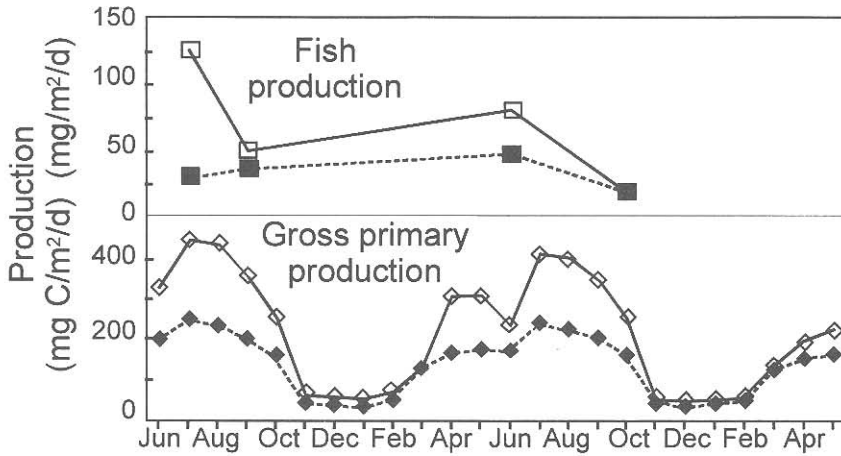
FIGURE 7.15. Seasonal production of benthic algae and fish (coho salmon, cutthroat trout, and shorthead sculpin) in clear-cut □ and old-growth ■ reaches of streams (data from Bilby and Bisson 1992, reproduced with permission of the Minister of Supply and Services Canada 1996).

The overall effects of watershed uses result from the interaction of changes in both trophic processes and physical habitat (Murphy and Meehan 1991). For example, increased aquatic primary production after canopy removal can temporarily mask detrimental effects on physical habitat, such as increased accumulation of fine sediment (Hawkins et al. 1983). In a comparison of paired shaded and open stream reaches with different sediment levels (Hawkins et al. 1983), densities of invertebrates and vertebrates decreased with increased fine sediment in shaded sites, but densities increased independently of sediment in open sites (Figure 7.16). Thus, increased primary production from removing riparian canopy apparently mitigates and sometimes completely masks otherwise detrimental effects associated with decreased habitat quality. As the canopy closes, however, effects of decreased habitat quality may become more evident.

Furthermore, species that are not food-limited do not necessarily benefit from increased primary production. Increased density of salmonid fry in summer, for example, may be nullified by decreased woody debris where winter habitat is the population's limiting factor (Murphy et al. 1986). Studies on coho salmon show increased salmon production after canopy removal, whereas other species may decrease with associated habitat degradation (Hicks et al. 1991, Reeves et al. 1993).

Over the long term, increases in primary production in early seral stages may be outweighed by longer-lasting reductions as a result of increased shade in later seral stages (Murphy and Hall 1981, Sedell and Swanson 1984). Second-growth hardwoods and young conifers produce

TABLE 7.2. Comparison of mean daily input of terrestrial organic matter, net production of benthic algae, and fish production from spring to early autumn in two streams in clear-cut (CC) and old-growth (OG) forest in Washington.

Variable	Clear-cut (mg/m²/d)	Old-growth (mg/m²/d)	CC:OG Ratio
Terrestrial input	164	851	0.2
Net algal production	482	301	1.6
Fish production			
Oncorhynchus kisutch	34	18	1.9
O. clarki	8.2	7.4	1.1
Total salmonids	42	25	1.7
Cottus confusus	4.5	2.5	1.8
Total (all species)	47	28	1.7

Modified from Bilby and Bisson 1992, reproduced with permission of the Minister of Supply and Services Canada 1996.
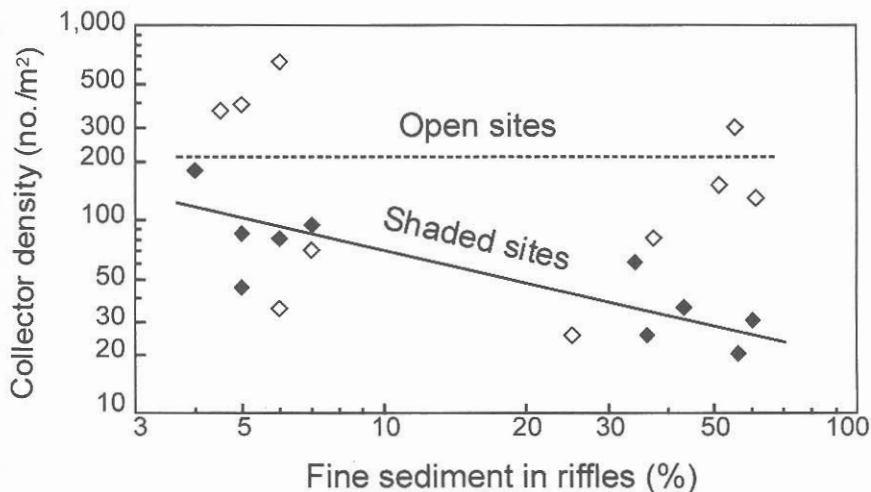
FIGURE 7.16. Relationships between density of the collector functional group of macroinvertebrates and percent fine sediment (<1 mm) in riffles in open ◇ and shaded ◆ reaches of streams in western Oregon and California. The Y-axis is in log scale; the X-axis is in arcsin scale (modified from Hawkins et al. 1983, reproduced with permission of the Minister of Supply and Services Canada 1996).

a denser canopy and lack the canopy gaps common in old-growth forest (Sedell and Swanson 1984, Bjornn et al. 1992). Streams in dense second growth in western Oregon, for example, have lower trout biomass and lower insect species richness than in adjacent old-growth (Murphy and Hall 1981). Besides reduced primary production, second-growth streams often lack important habitat features for salmonids, particularly pools and large woody debris (Bisson et al. 1987). Thus, effects of watershed uses on aquatic primary production need to be viewed from a long-term perspective and in the context of other changes in physical habitat. The focus should expand beyond initial changes, effects in one season, or effects on a single species.

Aquatic primary production plays a key role in the trophic support of stream ecosystems. Opening the canopy surrounding a stream and increasing nutrients often results in a more productive stream for invertebrates and fish. However, the desirability and integrity of stream systems is not solely determined by productivity (Karr and Dudley 1981). Stream organisms are adapted to complex environments, and although an environmental change may increase production, it may also cause undesir-able shifts in community structure and loss of many taxa typical of unmodified streams (Lemly 1982, Hawkins et al. 1983). While enhancing productivity is an important management goal, managing for naturally functioning watersheds and stream ecosystems, with diverse energy sources and full complements of appropriate functional groups, is probably a better approach to maintaining healthy stream habitats and biodiversity.

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