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Autotrophy in Stream Ecosystems

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The tempo of investigations in lotic ecology has increased in recent years, and considerable advances are being made, particularly in the areas of system structure and function. However, most of the information to date has been derived from deciduous forest streams where the import of organic matter from outside the system is the predominant feature. Little has been done to test the hypotheses derived from these systems against information obtained from other lotic systems in different vegetational regimes (biomes) or arising along a single river system from its source to the sea.

The purpose of this paper is to examine the relative contribution from allochthonous and autochthonous sources of energy in streams. It is my belief that the idea of a general dependency of streams on allochthonous organic materials has been overemphasized. I will present an alternative hypothesis that in many cases autotrophy is of primary importance in maintaining the structure and function of flowing water communities. The supporting evidence for such an idea is limited, probably because most of the relevant studies to date have concentrated on small streams located in deciduous-forested areas of the world and not because of any scarcity of autotrophic-based communities.

The arguments concentrate on two main points: First, in a number of streams, autotrophic production is the major or sole source of fixed carbon supplied to the system. Second, primary production plays a fairly important role in the economy of streams previously considered to be "heterotrophic." I will also comment on the fate of these autochthonous materials in streams.

AUTOTROPHY: THE PREDOMINANT ENERGY SOURCES IN MANY STREAMS

Many of my ideas on the importance of autotrophy in streams have been generated by our work on Deep Creek (Minshall et al. 1971, 1972, 1973, 1975, 1978). Deep Creek is a small stream located in southern Idaho in the northern cool-desert of the Great Basin. It is a productive hardwater stream (mean alkalinity 137 to 263 mg/L as $CaCO_3$). Over the four physiographic sections studied, mean width ranged from 1 to 6 m, mean depth from 10 to 60 cm, and mean discharge from 0.06 to 0.7 m^3/sec. The predominant streamside vegetation is sagebrush (*Artemisia tridentata*) and grass.

Energy budgets for several sites along Deep Creek (Table 1) indicate that allochthonous contributions are trivial and that autotrophs supply most of the organic matter that sustains the remainder of the system. Thus, a diverse and productive community is being maintained by autotrophic production (Fig. 1).

TABLE 1. Energy budgets for Deep Creek, Idaho (kcal/m^2/yr). Values in parentheses are subtotals.

Station	1	2	3
ALLOCHTHONOUS LITTER INPUT	2.4	60.9	12.2
AUTOTROPHIC PRODUCTION	3131.6	5915.4	12,271.9
Macrophytes			
Net*	(170.5)	(308.3)	(532.9)
R_{12}†	(453.1)	(1184.6)	(2020.4)
Periphyton			
Net*	(1681.0)	(2882.0)	(6313.0)
R_{12}†	(827.0)	(1540.5)	(3406.0)
COMMUNITY RESPIRATION	2884.0	6171.0	12,010.6
Microbial	(119.4)	(511.0)	(328.1)
Invertebrate	(204.3)	(210.0)	(830.4)
Plant			
Macrophytes	(906.3)	(2369.1)	(4040.1)
Periphyton	(1654.0)	(3081.0)	(6812.0)

*Does not include losses due to leakage of dissolved organic matter, breakage and sloughing, or grazing.
†R_{12} = 12 h respiration.

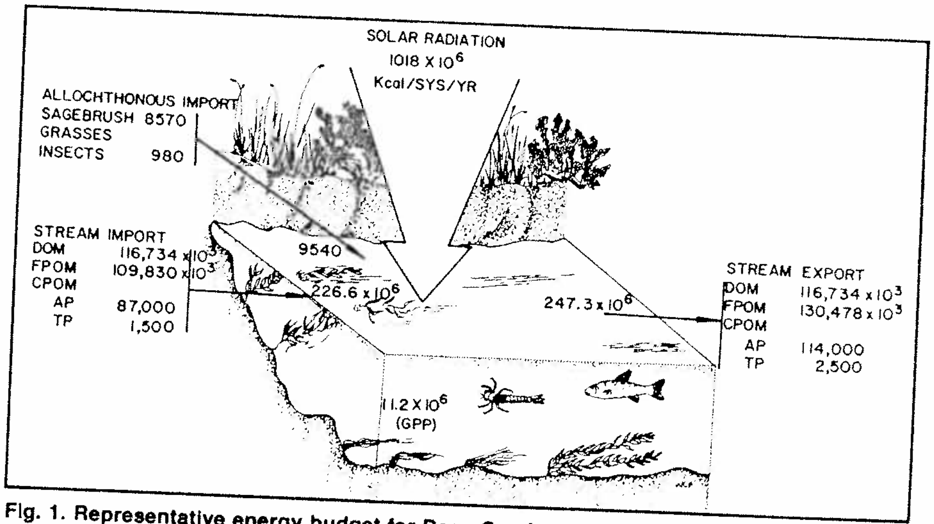

Fig. 1. Representative energy budget for Deep Creek, Idaho (Station 3) in kcal per system (783 m^2) per year. The material in transport is largely autochthonous: dissolved organic matter (DOM), fine particulate organic matter (FPOM), and coarse particulate organic matter (CPOM) categories are shown. AP = aquatic plant, TP = terrestrial plant, GPP = gross primary productivity.

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TABLE 2. Comparison of energy contributions from endogenous (as net primary production) and exogenous (litter fall) sources (in kcal/m²/yr). In the more complex systems (i.e., other than spring sources), fluvial transport may provide an additional source of energy. However, the origin of this material varies with different streams. For example, in Bear Brook, total allochthonous input is 6029 kcal, of which fluvial transport accounts for 3358 kcal. In Deep Creek, fluvial transport is 92 × 10^3 to 290 × 10^3 kcal, all but about 10% of which is autochthonous.

Location	Source of fixed energy		Reference
	Endogenous	Exogenous	
Bear Brook, NH	5	2260	Fisher & Likens 1973
Root Spring, MA	660	2350	Teal 1957
New Hope Creek, NC	660	2140	Hall 1972
Fort River, MA	1525	1920	Fisher 1977
Cone Spring, IA	1070	630	Tilly 1968
Rattlesnake Creek, WA	1820	1100	Cushing 1978*
Deep Creek, ID 1	1850	2	
2	3310	60	
3	6850	10	
Thames River, England	6000	140	Mann et al. 1970
Silver Springs, FL	8830	490	Odum 1957
Tecopa Bore, CA†	11065	0	Naiman 1976

*C. E. Cushing, Battelle Pacific-Northwest Laboratories, Richland, WA, personal communication, January 1978.
†A thermal spring.

Ideally, evaluation of the relative importance of autotrophy and heterotrophy in stream systems would involve comparison of the amounts contributed by each source. However, published data are limited and are restricted largely to deciduous forest regions (Table 2). In these forested watersheds from 3% to 40% of the total fixed energy input is contributed by autotrophy. In streams in nondeciduous forests and large rivers (e.g., Thames R.), the conditions are reversed, and autotrophic production outweighs the heterotrophic contribution by a substantial margin.

To generate additional data for comparison, I compiled a list of values on gross primary productivity for various streams (Table 3). I included only those studies for which annual estimates of productivity are available in order to incorporate seasonal differences in primary productivity. Moreover, I considered only relatively unpolluted streams to avoid the criticism (Hynes 1969) that the values tabulated by Odum (1956) (showing the high productivity of flowing waters) are biased by the inclusion of enriched streams. Finally, I used gross primary production values (rather than net) to permit inclusion of a larger number of studies. However, even if generous adjustments for respiration are made to obtain estimates of net production (say R = ~ 50%), many of the values (11 out of 14) are comparable to the amounts of allochthonous detritus entering streams (~ 4.2 to 21.5 kcal/m²/day, Petersen and Cummins 1974).

All the intermediate and high values for primary production in Table 3 are associated with high levels of insolation accompanying an "open" canopy. Because of the role played by light in determining the relative importance of autotrophy and heterotrophy in streams, several investigators (Cummins 1974, Fisher and Likens 1973, Vannote 1977) have suggested that small headwaters are basically heterotrophic but that larger flowing waters should exhibit a trend toward autotrophy. The tendency for headwater streams to derive most of their fixed carbon from outside the system seems to be true for heavily forested regions. However, in the more "open" semi-arid regions of the western United States, the effect of shading can be negligible even in these small streams.

I reorganized the values from Table 3 according to occurrence in major bioclimatic zones (Table 4). The results show that the high values are associated with the grassland and desert regions and the larger, more open forest streams of the deciduous and semi-arid Rocky Mountain areas. These encompass a substantial geographic area; if the findings can be extrapolated to other streams in these regions, they suggest a serious oversight in the formulation of stream ecosystem generalizations up to the present time. Many of the streams in the grassland and desert areas are wooded and the allochthonous inputs substantial. But in a large number of cases, water stresses limit streamside woody vegetation, and within-stream autotrophic sources predominate on an annual basis. The foregoing evidence suggests that in the larger streams of forested areas and in streams of all sizes in major portions of the arid and semi-arid lands, autotrophy plays the major role in their trophic economy.

AUTOTROPHY IN "HETEROTROPHIC" STREAMS

Comparison of standing crops possibly has misled some workers to believe that apparent small amounts of aquatic plants are insufficient to sustain the consumer segment of the community. For example, in a study of Morgan's Creek, Kentucky, I suggested, on the basis of biomass present, that periphyton constituted an insignificant amount of the total available food resource and, consequently, did not play an important role in the economy of the stream (Minshall 1967). Other investigators have employed similar logic.

However, McIntire (1973) used a simulation model of periphyton dynamics to show that small standing crops of periphyton are capable of supporting relatively large standing crops of consumer organisms. This is due to rapid turnover

TABLE 3. Mean annual gross primary productivity.

Location	kcal/m²/day	Canopy	Reference
Bear Brook, NH	0.03	closed	Fisher & Likens 1973
Berry Creek, OR	0.2–2.2	closed	Warren et al. 1964
Root Spring, MA	2.0	closed	Teal 1957
New Hope Creek, NC	2.8–13.8	closed	Hall 1972
Cone Spring, IA	6.1	open	Tilly 1968
Fort River, MA	6.3	open	Fisher & Carpenter 1976
Rattlesnake Creek, WA	10.0	open	Cummins et al. 1978
Logan River, UT	11.9	open	McConnell & Sigler 1959
Deep Creek, ID	8.6–33.6	open	Minshall, G.W. (unpublished)
River Arakawa, Japan	22.1	open	Tominaga & Ichimura 1966
Skeleton Creek, OK	47.6	open	Prophet & Ransom 1974
Silver Springs, FL	57.0	open	Odum 1957
Tecopa Bore, CA	60.6	open	Naiman 1976
Blue River, OK	10.5–74.5	open	Duffer & Dorris 1966

TABLE 4. Mean annual gross primary productivity.

Biome	kcal/m²/day
Deciduous forest	
Closed canopy	0.03–13.8
Open canopy	6.30–22.1*
Coniferous forest	
Coastal	0.20– 2.2
Rocky Mtn	12.00–14.0
Desert	8.00–34.0*
Grassland	6.10–74.5

*Excluding Silver Springs, FL, and Tecopa Bore, CA, as atypical.

rates of algae in comparison with slower turnover rates of animals and occurs even under conditions of low light intensity (550 ft-c.). At these low light levels the model predicted that biomasses (expressed by McIntire as grams glucose/m^2) of periphyton could support consumer biomasses ranging from 115 to 120 g. As McIntire observed, "A periphyton biomass of 10 g/m^2 or less is scarcely visible to the casual observer, and in streams where biomasses of this magnitude occur it is easy to conclude that the consumer organisms are supported almost entirely by allochthonous organic matter."

McIntire's model suggests that such an assumption could be erroneous, and that it is bioenergetically feasible for a very low periphyton biomass to support relatively large populations of primary consumers. Similarly, Elwood and Nelson (1972) found that grazing rates of snails nearly equaled periphyton net-production rates in Walker Branch, Tennessee.

A related argument to that based on the observation of low periphyton standing crop states that, because of the patchiness of aquatic vegetation and its scarcity during critical times of the year, the autotrophic production is too unreliable to sustain the benthic consumer community. For example, Hynes (1961) speculated that a lull in invertebrate herbivore activity during the summer in the Afon Hirnant was due to the general dependence of the benthic fauna on autumn-shed leaves as a source of food. He further stressed (Hynes 1963, 1969) that the whole biocoenosis in a normal stream, with respect to the animals' diet, life cycle, and longitudinal distribution, is geared to the annual allocation of leaf-fall. However, other workers (e.g., Chapman and Demory 1963, Coffman et al. 1971, Koslucher and Minshall 1973) have shown that the invertebrates are opportunists, feeding on whatever is available. Substantial evidence (Minshall 1968, Sweeney and Vannote 1978) suggests that the autumnal peak in invertebrate activity in temperate streams is a temperature-directed phenomenon and not primarily associated with leaf input.

Another argument for the inadequacy of the primary producers has been their presumed lack of availability during the crucial fall-spring period of benthic invertebrate development and growth (Hynes 1963). However, a number of investigators have documented high levels of periphyton development during this same period (Cushing 1967, Douglas 1958, Dunn 1976, Fisher and Sumner 1976, Gumtow 1955, Minshall et al. 1973). Our Deep Creek results also show that what is produced during the summer as autotroph biomass (mainly macrophytes) is made available to the consumers throughout the remainder of the year as *autochthonous* detritus. This situation is similar to that found for temperate-zone *Spartina* saltmarshes (Pomeroy 1970).

Misinterpretation of existing photosynthesis-respiration data also has contributed to a misunderstanding of the importance of the *in situ* primary producers. Some investigators (e.g., Hynes 1969) contend that most studies made since publication of Odum's 1956 work reveal community respiration to be greater than photosynthesis. On this basis, they have concluded that normal rivers and streams are net consumers of organic matter, most of which is allochthonous. Recent tabulation of some 40 published photosynthesis-respiration (P/R) ratios (by James T. Brock of our laboratory) has shown that the reported values are almost equally divided between those indicating heterotrophy and those indicating autotrophy.

Furthermore, the conclusion that streams showing P/R values less than 1 are heterotrophic and, thus, *not* dependent on autochthonous sources meets with at least two difficulties. First, high primary productivity (and P/R's $>$ 1) may occur for only relatively brief periods (1 to 2 months) during a year and, yet, yield enough plant matter to sustain the system over the remainder of the year. Intuitively, we tend to associate high primary productivity with large plant standing crops. Frequently, however, this is not the case. The peak in growth for macrophytes is in the spring or early summer (Westlake 1965). For periphyton, the peak commonly is in the early spring and/or fall (Cushing 1967, Flemer 1970, Gumtow 1955, Marker 1976a). In both cases, maximum standing crops usually are found at other times (Fisher and Sumner 1976, Flemer 1970, Marker 1976b, Tominaga and Ichimura 1966, Westlake 1965), commonly in late summer or late fall.

A second difficulty occurs in the use of P/R data to determine stream trophic conditions. Although a P/R ratio of less than 1 may be indicative of primarily allochthonous-dominated conditions when a closed system or only part of the community is being considered, care must be exercised in interpreting the results when open systems or community metabolism are being examined. Data presented by Tominaga and Ichimura (1966, Fig. 13) illustrate this point very well.

Fisher and Likens (1973) have pointed out that P/R ratios alone do not give a complete picture of system energetics. The amount of imported and exported organic matter must also be included. In systems where import is less than or equal to export, the P/R ratio will tend to be less than 1 even if the system is predominantly autotrophic! For example, if all of the organic matter entering the system and fixed within it is consumed during the year, and allochthonous subsidies are only a small part of the total organic loading (10% or less), then the mean annual P/R would be less than 1 even though the system is predominantly (~ 90%) autotrophic. Consequently, community P/R values less than 1 alone do not provide convincing evidence for dependence on allochthonous sources.

FATE OF AUTOTROPHICALLY DERIVED MATERIALS

If autotrophy can be important, what then is the fate of this material? Consider a simple conceptualization of a stream ecosystem (Fig. 2). The first case illustrates a heterotrophic stream with organic inputs arising mainly from outside the system and with generally low aquatic plant biomass. The second situation shows an autotrophic system with little or no organic input from outside. Consideration of the seasonal pattern of periphyton and vascular plant standing crops indicates that two main growth habits occur:

- low (or high[1]) productivity—high standing crop associated with vascular

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[1] The *Podostemum* beds studied by Nelson and Scott (1962) showed high standing crops, but the rate of productivity was also high.

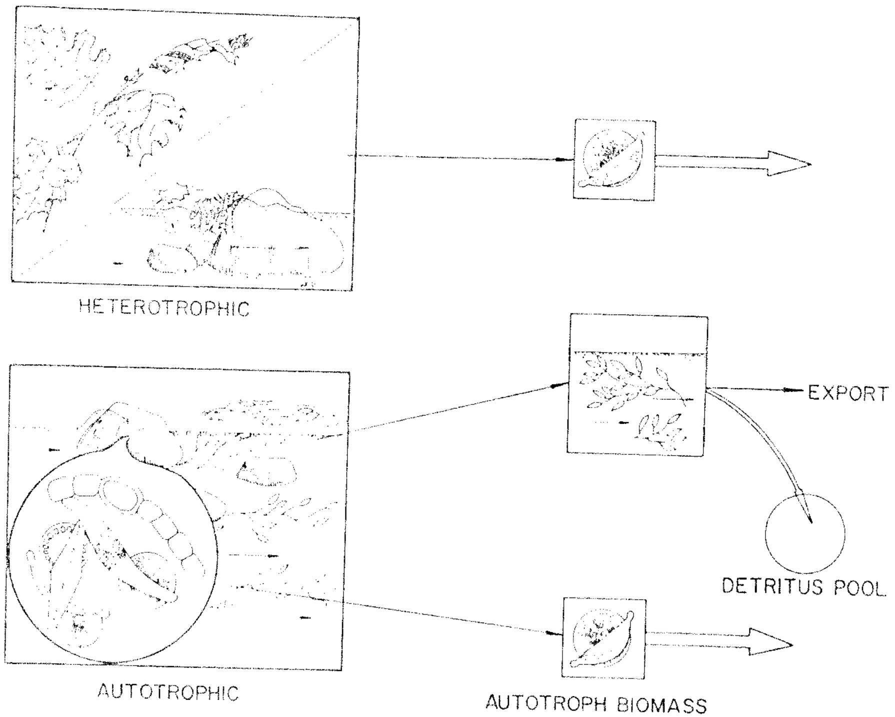

Fig. 2. Conceptualization of relative autotroph standing crops in heterotrophic and autotrophic systems. See text for further explanation.

plants and macrophytic algae; most of the material remains intact until the plant dies and is made available to consumers, mainly as detritus; and

- high turnover—low standing crop associated with periphyton; little detritus accumulates as there is commonly a high level of export, and production is utilized mainly by grazers and filter feeders.

The first type of autotrophic system commonly is associated with low gradient streams; the second with high gradient, mountain streams.

Because practically all of the allochthonous organic matter entering a stream ecosystem is dead, heterotrophic systems are said to have a detritus-based economy. By inference, autotrophic systems have been thought to exist mainly on living materials. Further extension of this logic assumes that because living materials are not present or abundant during certain times of the year, autotrophy must play a secondary role. Consideration of the situation described for macrophytes indicates that such a conclusion may not be valid and illustrates the need to distinguish between the *origin* of the material (autochthonous or allochthonous) and its current *state* (living or dead). Thus, although it is true that streams may differ as to the source of primary organic matter, they may behave quite similarly with respect to its state.

Future research needs to establish the extent to which such differences are important. Although streams may differ with regard to autochthonous and allochthonous inputs, they probably all function with a detritus-based economy. The principles of detritus processing and dynamics may apply to all systems regardless of whether they are classed as heterotrophic or autotrophic.

CONCLUSION

Autotrophy is a viable driving force in the maintenance of community structure and function of a stream. Animal diversity and productivity and community stability in autotrophic streams (Minshall et al. 1973) are comparable to those recorded for heterotrophic ones. Arguments attributing the synchronization of life cycle phenomena in the benthic invertebrates to the autumnal input of allochthonous leaf material (Hynes 1963, 1969, Petersen and Cummins 1974) are not supported by evidence obtained thus far. Full consideration of the total available information does not support the currently held generalization that most, if not all, running waters that have not been significantly altered by man are predominantly heterotrophic. This generalization may be true in specific cases or for certain sized streams over reasonably broad regions but it cannot be accepted as a universal phenomenon. Consideration of the autotrophic nature of lotic systems must be incorporated into the formulation of hypotheses if advancement is to be made in efforts to develop a truly robust theory of stream ecosystem dynamics.

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