Stream Community Response to Nutrient Enrichment
Author(s): Richard A. Cole
Source: *Journal (Water Pollution Control Federation)*, Vol. 45, No. 9, Annual Conference Issue (Sep., 1973), pp. 1874-1888
Published by: Water Environment Federation
Stable URL: http://www.jstor.org/stable/25037979
Accessed: 17/09/2009 22:32

Stream community response to nutrient enrichment

RICHARD A. COLE

INORGANIC ENRICHMENT of streams with nutrient salts produces roughly predictable biological and physical changes. The addition of nutrient salts to streams commonly results from the decomposition of organic wastes either in the stream or in wastewater treatment plants. Better understanding of the biological responses to inorganic enrichment is required to identify reliable indexes for the appropriate management of inorganic residues.[1] Hooper[2] has indicated the need for further evaluation of potential biological inorganic enrichment indexes that include primary productivity, community metabolism, biomass, species composition, and diversity. Many of the data accrued on these community parameters have been derived from studies of undisturbed ecosystems so that the effects of rapid enrichment on community structure and function are often predicted rather than observed.[3] No previous studies have simultaneously observed the responses of all these parameters to stream enrichment. The purpose of this study was to examine the effect of inorganic enrichment with particular reference to the impact of a change in the structure of the primary producer assemblage on community structure and function.

STUDY STREAM

As part of the Susquehanna River watershed, Spring Creek drains 370 sq km of rolling farmland in central Pennsylvania. The stream originates from numerous limestone springs that maintain moderately high alkalinity and moderate temperatures. Total alkalinity varies inversely with discharge between 150 and 200 mg/l, and the temperature rarely drops to 0°C or exceeds 22°C. The mean seasonal discharge varies from about 0.2 to 0.5 cu m/sec in the headwaters to 2.0 to 10.0 cu m/sec near the mouth.

Several municipalities lie in the Spring Creek drainage system (Figure 1). A small town, Oak Hall, is situated a few kilometers downstream from the major spring sources of the stream. Nutrient salts from Oak Hall septic systems, barns, and a small cannery probably reach the stream, but this minor enrichment does not cause obvious changes in concentrations of oxygen, phosphorus, or nitrogen. This part of the stream supports a reproducing brown trout population, and primary producers are mostly periphytic algae with submerged macrophytes restricted to the edges of pools.

Effluent from the State College wastewater treatment plant enters Spring Creek by way of a tributary, Thompson Run, about 4 km below Oak Hall. The effluent from the treatment plant has an average biochemical oxygen demand (BOD) of about 40 mg/l (50 percent resulting from nitrification) and total suspended solids (SS) average about 30 mg/l (20 mg/l volatile SS). An average of 0.15 cu m/sec of effluent is discharged by the plant. This contributes 5 to 20 percent to the discharge of Spring Creek. Apparently, the water quality of the effluent improves as it travels the 4 km to Spring Creek. McDonnell and Blain[4] found that carbonaceous BOD remained low in Spring Creek below this source of enrichment, but nutrient concentrations increased. Below the confluence, BOD averaged 1.0 to 2.2 mg/l, while above the confluence it averaged 0.9 to 1.0 mg/l. Oxidized nitrogen in Spring Creek increased from an average of 1.6 mg N/l above the confluence to 2.6 mg N/l below

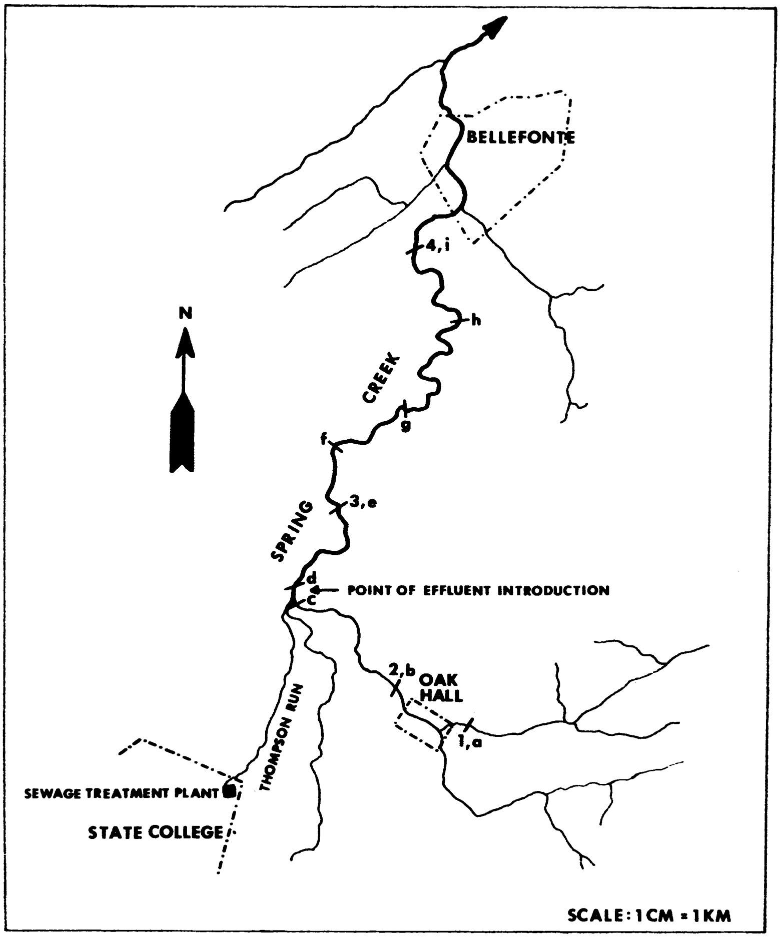

FIGURE 1.—Map of the study area. Letters indicate macrophytic sampling sites and numbers indicate the sites sampled for the other parameters.

the tributary, while Kjeldahl nitrogen remained about the same (0.4 mg N/l) in both areas. Orthophosphate increased markedly from an average of 0.05 to 3.0 mg/l.

After individual septic systems were replaced by the municipal wastewater treatment plant in 1958, macrophytes largely replaced periphytic algae in the riffles below the confluence, and severe diurnal fluctuations in oxygen concentration occurred during the growing season. Trout disappeared from several kilometers of affected stream except where large springs entered.

During the early 1960's, stream flow in central Pennsylvania decreased in response to drought, but the output from the treatment plant remained nearly the same. At that time, macrophytes were abundant below the effluent source all the way to the city of Bellefonte. Since then, average stream discharge has increased, and macrophytic growth has receded upstream, presumably in response to dilution of the effluent. As a result, the lower reaches of Spring Creek above the city of Bellefonte recovered from conditions that promoted macrophytic growth.

PROCEDURES

Sampling. Sampling was designed to compare sites in the stream that were physically similar. To reduce the sampling error, physically similar areas that represented the majority of conditions found in the stream were delineated and sampled randomly. Much of the stream was comprised of riffles with water velocities between 30 and 60 cm/sec, depths between 15 and 30 cm, and rubble sizes between 2 and 15 cm in greatest dimension. The remaining area of the stream was composed primarily of pools with extensive accumulations of sediments along the edges. These areas had low water velocities, less than 10 cm/sec. Water depths usually ranged from 10 to 30 cms over 15 to 25 cm of fine sediments.

Standing crops of macrophytes were estimated at nine sites (Figure 1) in the stream during August 1966, the time of maximum standing crops. All macrophytes were removed from duplicate, 1-m wide transects at each site and then drained and weighed. The drained wet weight per hectare was calculated after the percentage of stream area occupied by macrophytes was visually estimated.

Gross primary productivity and community respiration were estimated from diurnal changes in dissolved oxygen concentrations between two sampling stations as described by Odum.[5] The azide modification of the Winkler method was used to analyze oxygen concentrations at 2 to 4 hr intervals above and below the source of enrichment from State College. Reaeration coefficients were calculated with the formula described by Owens *et al.*[6] Respiration was assumed to be constant throughout the 24-hr period. Measurements were made above and below the source of enrichment from State College at Stations 2 and 3 (Figure 1). Station 3 was situated in an enriched zone of maximum oxygen fluctuation where standing crops of macrophytes were relatively large.

Both the sedimented edges of pools and riffles were sampled for macroinvertebrate numbers, weights, diversity, and distribution of species at Stations 2 and 3. Riffles were also sampled at Station 1, above a potential nutrient source at Oak Hall, and at Station 4, 10 km below Station 3 where the stream had recovered from conditions that promoted macrophytic growth. Station 4 therefore, represented a zone of recovery from upstream enrichment.

Six benthic samples were taken from each of the two pool-edge stations with an Ekman dredge (230 sq cm) about once a month (total = 132 samples). Samples taken within a season were pooled to determine seasonal means. The collected sediments were then sieved with 1-mm mesh before the samples were sorted. Riffles were sampled with a modified Surber sampler that had galvanized metal sides, a screened front, and 1-mm mesh netting. The relatively large mesh size was selected because fine material in the sediments rapidly plugged smaller mesh sizes and decreased the sampling efficiency. Sets of 12 samples, each 230 sq cm, were taken from the four riffle stations during each season (total = 192 samples).

All macroinvertabrate samples were preserved in 75 percent isopropyl alcohol and later sorted to species and counted under a microscope. Because tubificids were so abundant in pool edges, numbers were estimated from determinations of average and total ash-free dry weights and the numbers of species were estimated from subsamples. Average ash-free dry weights were estimated for each of the species found during each season, and the total ash-free dry weights per sample were calculated by multiplying the number of species times the estimated mean weight of the species. Ash-free dry weights were determined after burning dried samples in a muffle furnace at 600°C for 1 hr.

Fish were sampled by electrofishing from areas near Stations 2 through 4 during the fall of 1967. Numbers per size class were estimated using the removal methods described by Zippin.[7] Mean wet weights were estimated from samples of each size class and the total standing crop in weight was calculated.

Diversity index. An index of diversity ($\bar{H}$) described by Patten[8] and Wilhm and Dorris[9] was obtained from the samples collected. The equation used to calculate $\bar{H}$ was the Shannon-Wiener formula for cal-

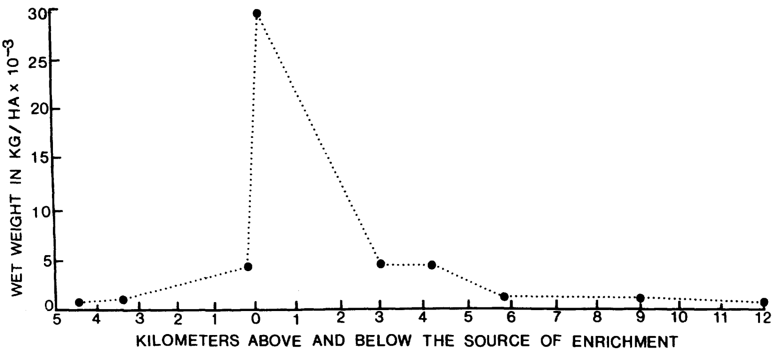

FIGURE 2.—Distribution of the standing crops of macrophytes in Spring Creek during August 1966.

culating information:

$$\bar{H} = -\sum_{i=1}^{S} \frac{N_i}{N} \log_2\left(\frac{N_i}{N}\right)$$

in which the proportion of the total abundance made up by each species (N_i/N) is multiplied by its logarithm and summed for all species (s). $\bar{H}$ is 0 when only one species is present and increases from 0 as the probability of placing an individual into a particular species decreases from certainty. The degree of uncertainty is determined by the interaction of two variables, the number of species and the evenness of the species' abundances. An estimator of $\bar{H}$ is currently a popular measure of diversity because it at least attempts to account for the relative contribution of each species to the community as well as the number of species found in the community.[10] Very rare species contribute little to the total value of the index. This is an advantage over other indexes because rare species are frequently overlooked in sampling. Incomplete identification of species particularly affects indexes that depend greatly on the number of species.

In this study, the population values (N_i/N) were estimated by sampling to give $\bar{d}$ as an estimator of $\bar{H}$. Both numbers and weights were used to represent abundance.

A measure of the evenness of species' frequencies was obtained using a formula given by MacArthur.[11] Whenever all the species present are equally abundant, the number of species, S, is equal to the log base used taken to the $\bar{d}$ power, that is $S = 2^{\bar{d}}$. The relative deviation from evenness, the species equitability, can be obtained from $2^{\bar{d}}/S$.

RESULTS

Plants and community metabolism. High abundances of macrophytes were associated with the source of enrichment from State College (Figure 2). Above the enrichment from State College, macrophytes grew only in silted pool edges and periphyton dominated the riffles. Below the effluent, macrophytes dominated both pool edges and riffles most of the year, but they decreased in relative importance downstream from the confluence with the tributary that carried the effluent from State College. Macrophytic abundances were greatest in late summer and least during winter. Further downstream, near Station 4, macrophytes were no more abundant at the time of this study than they were below Oak Hall at Station 2.

Three species of macrophytes succeeded each other during the year as the dominant plants. *Elodea canadensis* was the only macrophyte commonly found in isolated beds during the winter. *Chara* sp., a macrophytic alga, occupied the stream riffles with periphyton during spring but never grew in the silted pool edges. As *E. canadensis* and *Chara* sp. increased in abundance, sediments accumulated at their bases. During early summer, *Potomogeton*

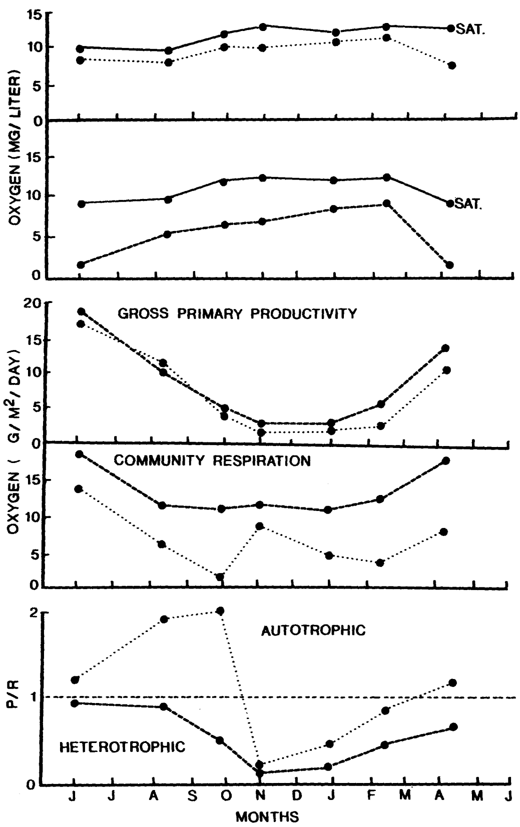

FIGURE 3.—Deviation from saturation concentration of the predawn oxygen concentration, gross primary productivity and community respiration, and P:R ratios. The dotted lines represent values obtained above the source of enrichment and the dashed lines below the source.

crispus grew rapidly in the accumulated sediment, and *Chara* sp. died out under the thick plant beds that developed. By the end of summer the total macrophytic standing crop reached an annual peak with *P. crispus* dominating both *E. canadensis* and periphyton. During the fall, *P. crispus* died out while *E. canadensis* remained in isolated patches. Silt held by the plants eroded from the stream bed as plant standing crops decreased, and high water washed out most of the remaining silt the following spring.

Predawn concentrations of oxygen (Figure 3) were always lower in the grossly enriched reach dominated by macrophytes at Station 3 than above the effluent from State College at Station 2. The lowest concentration of oxygen (below 3 mg/l) occurred at Station 3 during summer when water temperatures and community metabolism were greatest.

Community respiration was considerably greater and gross primary productivity was consistently higher at Station 3, the reach dominated by macrophytes (Figure 3). Both above and below the effluent from State College, productivity exhibited a seasonal pattern that varied directly with the length of day and water temperature. Like productivity, respiration varied with the length of day except in late fall when it sharply increased following the autumn leaf fall into the stream. There was no obvious association of increased respiration with the seasonal accumulation of macrophytic biomass.

The ratio of total primary productivity to community respiration (*P*:*R*) was always less than 1 at Station 3 where the macrophytes were abundant (Figure 3), indicating that the greatly enriched community consumed more than was produced.[5] Above the effluent from State College, *P*:*R* values were greater than 1 during the seasons when terrestrial leaf litter did not contribute to the heterotrophic demand for oxygen. Much of the unconsumed autochthonous production was probably exported downstream. This export, along with sediments eroded from the watershed, probably contributed to the sediment that accumulated downstream about the base of macrophytes and partly explains why *P*:*R* ratios were usually less than 1 where macrophytes dominated.

Macroinvertebrates. There were 84 species representing 16 orders of macroinvertebrates found in Spring Creek (Table I). Gross enrichment from State College apparently reduced the number of species by about one-half in pool edges and riffles. More than half the species found in pools were also found in riffles. Of the macroinvertebrates found in the riffles and pool edges below the effluent from State College, only five species totaling nine

TABLE I.—Number of Macroinvertebrate Species per Order Found in Sections of Spring Creek

Order	Stations								Total Number of Different Species
	Riffles					Pool edges			
	1	2	3	4	Total	2	3	Total	
Tricladida	1	1	1	1	1	1	1	1	1
Nematoda	—	—	—	—	—	—	1	1	1
Oligochaeta	3	4	2	4	4	6	6	6	6
Hirudinea	—	1	1	—	2	1	1	1	2
Gastropoda	1	2	2	1	5	3	4	4	6
Isopoda	1	1	1	1	1	1	1	1	1
Pelecypoda	1	1	—	—	1	1	1	1	1
Amphipoda	1	1	—	1	1	1	1	1	1
Plecoptera	1	—	—	—	1	—	—	—	1
Ephemeroptera	6	7	—	—	8	3	—	3	9
Odonata	—	—	—	—	—	2	—	2	2
Hemiptera	—	—	—	—	—	1	—	1	—
Megaloptera	1	1	—	—	1	—	—	—	1
Trichoptera	10	11	2	2	11	—	—	—	11
Coleoptera	3	2	1	1	3	5	—	5	6
Diptera	22	14	17	11	29	17	8	19	34
Total	51	46	27	22	68	42	24	46	84

individuals were not found above the effluent. The small reduction in the number of species found below Oak Hall may have resulted from minor enrichment at the town.

The dominant species collected from pool edges were the same above (Station 2) and below (Station 3) the source of gross enrichment, but the dominant species of the riffles differed greatly. Along the pool edges, *Tubifex tubifex* dominated, but also common were a sowbug, *Lirceus brachyurus*; a planarian, *Dugesia doratocephala*; two species of snails, *Gyraulus* sp. and *Physa* sp.; and the "bloodworm" midge, *Chironomus* sp. The most abundant species in riffles above the gross enrichment were the mayflies, *Ephemerella rotunda* and *Baetis vagans*; a riffle beetle, *Optioservus* sp.; and a midge, *Prodiamesa* sp. These species were rarely found in the enriched riffles that were dominated by macrophytes (Station 3) where *D. doratocephala*, *Gyraulus* sp., *L. brachyurus*, *T. tubifex*, and another midge, *Psectrocladius* sp., were most abundant. In the enriched section, the pool and riffles contained, except for the midges, essentially the same abundant species. At Station 4, below the reach dominated by macrophytes, the number of macroinvertebrate species remained nearly the same but *L. brachyurus* and a blackfly, *Simulium* sp., were dominant while *Gyraulus* sp., *T. tubifex*, and *D. doratocephala* were rare.

Macroinvertebrates were most abundant in the sediment of pool edges (Table II). Tubificids made up such a large proportion (50 to 98 percent) of the abundances in pool edges that seasonal changes mostly reflected their population changes. The macroinvertebrate biomass above the effluent from State College was consistently high during the year; below the effluent, macroinvertebrate biomass was similar to upstream biomass except in summer when it was obviously (probability of a larger α value <0.01) lower. During the summer, much of the plant production in the enriched section was stored in macrophytic biomass. Compared to areas where attached algae dominated, relatively small amounts of organic matter may have reached the sediments of pool edges during the summer. This could explain the exceptionally low summer biomass of the macro-

TABLE II.—Mean Macroinvertebrate Numbers and Ash-Free Dry Weights Along Pool Edges

Season	n	Station 2		Station 3	
		Number/sq m ± SE*	G/sq m ± SE	Number/sq m ± SE	G/sq m ± SE
Summer	18	62,178 ± 11,127	19.9 ± 1.9	29,637 ± 7,181	5.5 ± 0.9
Fall	18	46,096 ± 7,611	19.8 ± 2.6	41,581 ± 10,062	19.7 ± 3.1
Winter	18	36,034 ± 7,568	19.4 ± 2.5	36,679 ± 10,879	20.7 ± 3.3
Spring	12	24,768 ± 2,967	25.2 ± 3.5	27,090 ± 4,343	21.3 ± 4.1
Mean annual		42,269 ± 7,318	21.1 ± 2.6	33,744 ± 8,116	16.8 ± 2.8

* Standard error of the mean.

invertebrates. During seasons other than summer, macrophytes and terrestrial leaf litter drifted into the pool edges and probably increased food availability to macroinvertebrates.

The diversities ($\bar{d}$ index) along the pool edges above and below the effluent were similar and among the lowest encountered at any of the sampling sites (Table III). Although the number of species in pool edges in the enriched reach at Station 3 was about half that found above the effluent, only rare species that contributed little to the diversity index were not found in the enriched section. This is reflected in the low equitabilities measured both above and in the enriched area. Therefore, the diversity in pool edges was not obviously altered by enrichment from State College.

The abundance of macroinvertebrates in riffles was strongly associated with the type of dominant plants present. Macroinvertebrates were relatively abundant where periphyton dominated and were less abundant where macrophytes had replaced periphyton (Table IV). The differences in the abundance of macroinvertebrates at Stations 1 and 2, both above the enrichment from State College, may have been a result of a small but unmeasured increase in periphyton productivity as a result of minor enrichment from the village of Oak

TABLE III.—Macroinvertebrate Diversity and Equitability in Pool Edges

Seasons	Station 2		Station 3	
	Number/species	Weight/species	Number/species	Weight/species
Summer				
Diversity	0.18	0.61	0.73	1.53
Equitability	0.07	0.06	0.13	0.22
Fall				
Diversity	0.72	1.30	0.63	1.04
Equitability	0.07	0.10	0.10	0.13
Winter				
Diversity	0.55	0.91	0.41	0.63
Equitability	0.07	0.09	0.13	0.14
Spring				
Diversity	0.45	0.94	0.92	0.91
Equitability	0.06	0.08	0.14	0.13
Mean annual				
Diversity	0.48 ± 0.05*	0.94 ± 0.14	0.67 ± 0.10	1.02 ± 0.19
Equitability	0.07 ± 0.01	0.08 ± 0.01	0.12 ± 0.01	0.16 ± 0.02

* Standard error of the mean.

TABLE IV.—Mean Macroinvertebrate Numbers and Ash-free Dry Weight in Riffles.

Season	n	Station 1		Station 2		Station 3		Station 4	
		Number/ sq m ± SE*	G/ sq m ± SE	Number/ sq m ± SE	G/ sq m ± SE	Number/ sq m ± SE	G/ sq m ± SE	Number/ sq m ± SE	G/ sq m ± SE
Summer	12	4,171 ± 408	1.6 ± 0.2	6,708 ± 387	4.2 ± 0.3	5,762 ± 752	3.0 ± 0.8	6,063 ± 1,376	5.2 ± 0.7
Fall	12	5,418 ± 753	2.8 ± 0.6	6,880 ± 1,075	5.4 ± 0.8	5,160 ± 667	3.9 ± 0.5	10,449 ± 3,074	6.1 ± 2.2
Winter	12	6,149 ± 989	5.2 ± 1.0	10,965 ± 1,892	8.9 ± 0.4	2,967 ± 623	1.0 ± 0.2	14,964 ± 2,300	13.2 ± 2.2
Spring	12	7,998 ± 795	4.6 ± 0.7	4,518 ± 365	6.7 ± 0.7	1,978 ± 387	1.9 ± 0.5	4,977 ± 1,312	6.9 ± 1.7
Mean annual		5,934 ± 736	2.4 ± 0.4	7,493 ± 1,866	6.3 ± 0.6	3,967 ± 607	2.5 ± 0.5	9,487 ± 2,015	8.9 ± 1.7

* Standard error of the mean.

Hall. Unlike the effect of State College enrichment, which produced a change from periphyton to macrophytes, periphyton remained dominant. At Station 4, where periphyton also dominated, the abundance of macroinvertebrates was similar to that found below Oak Hall at Station 2.

The mean annual diversity was greatest in riffles above Oak Hall, intermediate and similar in the riffles just above and below the effluent from State College, and lowest downstream from the enriched area where macrophytes were no longer present (Table V). At the two riffle stations above State College, equitability was higher at Station 1 than at Station 2, and the difference in diversity was nearly all dependent on the lower equitability. Even though the number of species was much lower, the diversity in the reach at Station 3 was slightly but not markedly lower than at Station 2. This resulted because the species equitability at Station 3 was relatively high. Diversity was lowest in the riffles at Station 4 because the number of species and the species equitability were both low.

Seasonal changes of macroinvertebrate abundance in the enriched area were associated with seasonal changes in macrophytic abundance. Seasonal changes in the abundance and diversity of macroinvertebrates in all the riffles dominated by periphyton seemed to be associated with the growth and emergence of the dominant insects. In the enriched reach, the abundance of macroinvertebrates was greatest and the diversity least in the summer and fall when macrophytes were most abundant. Most of the insects emerged during spring and summer; consequently, they did not contribute to the decline in abundance from fall to

TABLE V.—Macroinvertebrate Diversity and Equitability in Riffles

Season	Station 1		Station 2		Station 3		Station 4	
	Number/ species	Weight/ species	Number/ species	Weight/ species	Number/ species	Weight/ species	Number/ species	Weight/ species
Summer								
Diversity	3.17	3.18	2.86	2.90	2.14	2.14	1.40	0.60
Equitability	0.32	0.50	0.27	0.29	0.24	0.24	0.26	0.10
Fall								
Diversity	3.69	3.88	2.73	2.68	1.59	1.60	1.25	0.77
Equitability	0.38	0.43	0.25	0.23	0.27	0.27	0.20	0.09
Winter								
Diversity	3.27	3.61	2.16	2.69	2.53	2.74	1.67	1.31
Equitability	0.28	0.36	0.14	0.20	0.34	0.39	0.18	0.14
Spring								
Diversity	3.91	3.88	3.22	2.21	2.78	2.17	0.93	0.45
Equitability	0.32	0.35	0.28	0.14	0.57	0.38	0.17	0.13
Mean annual								
Diversity	3.51 ± 0.17*	3.79 ± 0.29	2.74 ± 0.23	2.62 ± 0.12	2.26 ± 0.26	2.16 ± 0.12	1.31 ± 0.15	0.78 ± 0.30
Equitability	0.32 ± 0.02	0.41 ± 0.02	0.24 ± 0.02	0.22 ± 0.01	0.38 ± 0.07	0.32 ± 0.02	0.20 ± 0.02	0.13 ± 0.02

* Standard error of the mean.

TABLE VI.—Fish Abundance, Diversity, and Number of Species in the Studied Reach

Species	Station 2		Station 3		Station 4	
	Number/ha	Kg wet weight/ha	Number/ha	Kg wet weight/ha	Number/ha	Kg wet weight/ha
Salmo trutta	1,224	175.0	5	1.0	497	94.0
Exoglossum maxillingua			12	0.3	191	3.0
Notemigonus crysoleucas			7	0.1		
Notropis cornutus			12	0.2	67	1.4
Notropis hudsonius					25	0.3
Pimephales notatus					97	0.4
Pimephales promelas			435	3.0		
Rhinichthys atratulus	4,687	19.0	3,432	13.0	3,054	14.0
Rhinichthys cataractae	1,858	14.0	5,635	20.0	9,315	44.0
Semotilus atromaculatus			892	24.0	205	7.0
Catostomus commersoni	1,467	384.0	1,783	232.0	2,247	331.0
Hypentelium nigricans					23	3.1
Lepomis gibbosus			297	1.1		
Cottus cognatus	109,574	266.0	53	0.1	5,906	25.0
Total	118,810	858.0	12,563	294.8	21,627	524.1

winter. *Gyraulus* sp. and *D. doratocephala* were particularly abundant when macrophytes were abundant. *T. tubifex* became most abundant in the fall when silt accumulation was greatest. The relatively high abundance of these species contributed to the low species equitability and diversity found during summer and fall.

Fish. More species of fish were collected from below the effluent than from above the source of enrichment (Table VI). None of the species present above the effluent was eliminated by changes associated with the enrichment. However, the sculpin, *Cottus cognatus*, and brown trout, *Salmo trutta*, which were relatively numerous above the enrichment, survived only in spring seeps in the enriched section. These two species were much more widely distributed at Station 4. In this sense, the area represented by Station 4 had recovered from enrichment effects other than the change from macrophytes to periphyton.

The total weights of fish were greatest above the gross enrichment at Station 2, lowest in the enriched reach at Station 3, and intermediate at Station 4. The differences in fish weight between Station 4 and Station 2 were almost entirely a result of differences in the weights of trout and sculpins, which were not quite as abundant at Station 4.

The $\bar{d}$ index of fish numbers was higher at Stations 3 and 4 than at Station 2 (Table IV). More species were present below the source of enrichment from State College, but, more importantly, species equitability increased because the relatively abundant sculpins were reduced by factors associated with enrichment. When weights were used to calculate the $\bar{d}$ index, it was lowest at Station 3 because the sucker, *Catostomus commersoni*, was relatively numerous and, therefore, species equitability was low.

Discussion

The biological indexes to enrichment summarized by Hooper [2] are derived from community structure and function changes that follow increased nutrient availability. These include changes in gross primary productivity, community respiration, biomass, consumer efficiencies, species composition, and diversity.

In Spring Creek above State College, enrichment probably occurred at low levels that were difficult to detect by casual observation. Below State College, however, the introduction of nutrients produced obvious and sometimes unexpected changes in stream communities. The following discussion concerns the application of various biological indexes to enrichment with particular reference to the impact of macrophytes, compared with periphyton, on community structure and function.

Community metabolism. Odum [5] suspected that enriched reaches of streams are among the most productive on earth. The gross primary productivity of Spring Creek above and below the effluent from State College was less than that reported by Odum [5] for other enriched streams. Productivity in Spring Creek did not seem to be greatly stimulated by nutrient addition from State College. However, both productivity and respiration will be underestimated if macrophytes store oxygen produced by photosynthesis in internal lacunae and respire oxygen without releasing much to the surrounding water.[12] Also, nighttime respiration probably decreases with decreased concentrations of oxygen, and the calculation of total respiration using night values probably yields underestimates of both respiration and productivity.[13] Community metabolism, therefore, was probably much greater than measured below State College where macrophytes were dominant.

Odum's [5] conclusion that inorganically enriched reaches normally will have high $P:R$ ratios does not apply to many streams that have been invaded by macrophytes. The $P:R$ ratios were 1 or less in the reach of Spring Creek that was dominated by macrophytes. Similar ratios are described for streams dominated by macrophytes by Odum,[5] using the data of Butcher *et al.*[14] and Owens and Edwards.[13] Macrophytes indirectly cause relatively low $P:R$ ratios because of at least two general responses to the decreased stream velocities brought about by thick beds of plants. First, as Owens and Edwards[13] concluded, the respiratory component of community metabolism can be markedly increased by biologically active sediments that are deposited where velocities are slowed. Second, decreased velocities also decrease the diffusion gradients of nutrients to plants,[15] contributing to a decrease in productivity efficiencies. As a result of these indirect effects on stream velocity, communities dominated by macrophytes will usually have lower $P:R$ ratios than communities of the same metabolic level that are dominated by algae.

The $P:R$ ratios were higher than 1 in reaches dominated by periphyton except after the input of terrestrial leaf litter in late autumn and winter. Decomposition of leaf litter probably also contributed to winter heterotrophy in the reach dominated by macrophytes. Oxygen demand from leaf litter has been observed in other streams [16] and should be considered as a potentially important determinant of $P:R$ ratios not directly related to enrichment. The use of productivity estimates or $P:R$ ratios as a measure of community response to enrichment may be satisfactory where gross enrichment occurs but probably lacks the sensitivity to reveal minor enrichment.

Biomass and consumer efficiency. Biomass commonly increases following enrichment [17] as a result of increased productivity or decreased consumption or both. Bartsch and Ingram [18] illustrated that the biomass of both algae and benthic consumers increases following inorganic enrichment. The response of fish to enrichment is less predictable [19] because of their mobility, their trophic position in the community, and their variable tolerance to diurnal oxygen fluctuations. However, if primary productivity is increased without generating limiting low oxygen concentrations, the biomass of fish is expected to increase. In Spring Creek, the biomass of primary producers where macrophytes dominated was obviously high, but the abundances of macroinvertebrates and fish were relatively low compared with both upstream and downstream reaches where periphyton was dominant. Wilhm [20] also found lower invertebrate biomass associated with the vegetated part of a spring. As in other investigations,[21] there was no evidence that actively growing macrophytes were consumed by aquatic animals.

Primary consumers in Spring Creek riffles were apparently less capable of consuming macrophytes than periphyton.

Odum[22] has suggested that decreased consumption efficiencies can indicate gross enrichment. The reduced abundance of fish and macroinvertebrates in the reach dominated by macrophytes suggested that the net productivity of most consumers and the consumptive efficiency of at least the primary consumers in the riffles declined because macrophytes dominated. The abundance of invertebrates in pools may have been less affected by macrophytic dominance because decaying macrophytes reached the pools after the growing season.

Riffle invertebrates were more abundant below Oak Hall than above it, probably because food availability was greater and not because of reduced predation. Although fish abundance was not estimated above Oak Hall, it is doubtful that the fish abundance exceeded that found below Oak Hall. Scherer[23] found similar abundances of suckers, the dominant fish by weight, above Oak Hall in 1964. Invertebrate predation was, if anything, greater below Oak Hall because *Hydropsyche slossonae*, primarily a secondary consumer,[24] became relatively abundant. Although it is likely that the productivity of periphyton was stimulated by the minor enrichment, the sampling techniques available are not refined enough to identify small changes in consumer efficiencies in natural streams.

Species composition. All species of macroinvertebrates found in the grossly enriched reach were probably derived from the original benthic communities, but many of the aquatic insects normally associated with well aerated riffles were rare in the enriched reach. Diurnal oxygen fluctuations during the summer were probably great enough to kill many of the insects. Species normally associated with pool edges appeared in the riffles where many of the aquatic insects had been eliminated. This change in species composition in the riffles of grossly enriched streams is a commonly recorded response to organic enrichment[25,26] and is attributed to lower oxygen concentrations, increased sedimentation, and other changes produced by active decomposition. Any minor enrichment from Oak Hall may have eliminated a few rare species but otherwise had little effect on the species composition other than to increase the relative abundance of a few species.

The greater number of fish species found below the source of enrichment from State College probably resulted more from the increased size of the stream than from the enrichment. The discharge of Spring Creek nearly doubled where the effluent from State College entered the stream. Thompson and Hunt[27] directly correlated the number of species found with the size of streams. The brown trout and slimy sculpin seemed to be indicators of the gross enrichment but not the minor enrichment. They probably responded negatively to high diurnal fluctuation of oxygen. Downstream from the grossly enriched stretch, the number of species remained high, and the sculpin and trout were common. This also indicated that the size of the stream and not enrichment was responsible for the high number of fish species below the source of enrichment from State College.

Diversity. Species diversity, as calculated by the Shannon-Weiner formula, has been considered one of the best indicators of altered environments.[2,9] Diversity is generally expected to decrease following any recognizable alteration of an ecosystem and, therefore, should be a good biological indicator for most forms of water pollution.

The diversity of macroinvertebrates inhabiting riffles decreased below a possible source of minor enrichment but did not markedly change below a source of gross enrichment. Changes in environmental stability, predictability, and rigor all should have operated to decrease the diversity[28] in the enriched reach. Cultural enrichment is likely to be a highly unpredictable ecological event for communities inhabiting a spring-fed stream. Environmental stability was decreased by strong diurnal oxygen fluctuations and the seasonal change in the benthic habitat from high standing crops of macrophytes in the summer to periphyton-covered rubble in the winter. Environmental rigor was increased by low, predawn concentrations of oxygen that occurred during the growing season. Primary productivity increased, but contrary to Margalef's [3] proposal, diversity did not decrease as a result of species taking advantage of increased food availability and interrupting competitive interactions. Predation, which also maintains diversity,[29] was depressed by gross enrichment. The only change apparently acting to increase diversity in the grossly enriched stretch of Spring Creek was increased habitat diversity [30] or spatial heterogeneity.

Habitat diversity was increased by macrophytic growth, which created islands of plants and sediments in the exposed rubble. The seasonal fluctuation of species abundances within the three habitat types produced a relatively even distribution of average abundances among species that compensated for the decreased number of species and maintained the mean annual diversity. Similarly, Wilhm [20] found that diversity in a spring was higher in the vegetated portion than the unvegetated, mud-covered portion.

Minor enrichment from Oak Hall was not accompanied by changes in habitat diversity, and the decreased species equitability that occurred may have resulted from increased primary productivity as proposed by Margalef.[3]

Downstream from the enriched reach, dominated by macrophytes, the diversity was very low. When macrophytes receded from the reach after the drought in the early 1960's, periphyton became dominant over the whole stream bed and habitat diversity decreased. Benthic species that had been excluded from the reach during the drought may have been unable to recolonize that stream stretch, if water quality improved, because of pollution barriers upstream and downstream. It is less likely that an unidentified environmental stress continued to inhibit intensively benthic diversification without also affecting the sensitive trout and sculpins. In either case, competitively superior sowbugs and blackfiies are very abundant and equitability is low.

In the pool edges, the relatively great abundance of *T. tubifex* was responsible for low species equitability and diversity. Even though half the species in pool edges disappeared after enrichment, their elimination had little effect on the diversity index because they were initially rare. High flow during spring months churned and displaced the sediment in pool edges creating a uniform environment in which one tolerant species, *T. tubifex*, could maintain a large proportion of the biomass. Above the grossly enriched reach, pool-edge sediment beds appeared as localized enriched parts of the stream with communities similar to those found below the source of enrichment.

The changes in the diversity of fish in relation to enrichment were different for numbers and weights. Harrel *et al.* [31] and Sheldon [32] found that diversity based on numbers increased with the size of the stream. Diversity based on numbers also increased in the enriched part of Spring Creek because the very abundant sculpins were nearly extirpated and species equitability increased. However, when abundance was represented by weight, the diversity dropped in the grossly enriched reach and increased in the recovery zone. As Wilhm [33] pointed out, weight is probably the better ecological measure of abundance. The predicability of this response, based on weight, must remain in doubt until further studies that relate fish diversity to disturbed and undisturbed streams are conducted. Because of their greater size and mobility, fish are not likely to be influenced as much as macroinvertebrates by increased habitat diversity caused by macrophytes.

Wilhm and Dorris [9] have found $\bar{d}$ indexes to be less than 1.0 in heavily polluted streams, between 1.0 and 3.0 in moderately polluted streams, and above 3.0 in unpolluted streams. The range of values that they report are in agreement with the range of values found in Spring Creek, but the degree of stream degradation is not represented adequately by the indexes alone in the areas that had been invaded by macrophytes or in pool edges. Diversity measures may be the only discussed enrichment indicators that are sensitive enough to identify minor changes in communities.

However, these indexes have to be interpreted in relation to the history of the ecosystem being studied and to the dynamics of the major regulators of diversity in order to avoid incorrect conclusions about the degree of environmental alteration.

CONCLUSIONS

Good indexes to detrimental effects from inorganic stream enrichment should be generally applicable, reliable, and specific indicators that are, if possible, sensitive enough to scale predictive rates of change before detrimental effects are realized.[2] None of the community responses investigated in this study is likely to fulfill these requirements, but the variety of community responses to different levels of enrichment in Spring Creek broadly suggests how the responses are interrelated and indicates that a physical response to community change (diurnal oxygen fluctuation) should be investigated further as a suitable index.

The results of this study reinforce previous work that indicated that cultural enrichment could stimulate productivity and decrease consumer efficiencies. Increased productivity can cause diurnal oxygen fluctuations near saturation if the reaeration capacity of the stream is exceeded by oxygen production and consumption by the aquatic community. Changes in the species composition of macroinvertebrates and fish probably occur primarily as a result of night-time oxygen depression. Oxygen-sensitive organisms are the first to disappear. If habitat diversity is not modified by macrophytic invasion, the changes in species composition and deletion of species should be reflected in lower diversity and equitability indexes. Hypothetically, decreased diversity, resulting from species deletion or reduced species equitability, reduces functional consumer specialization and, therefore, consumer efficiency. Communities with depressed consumer efficiencies will export more autochthonous organic matter per gram of organic matter produced than communities with greater consumer efficiencies. This causes a proportionately greater import of organic sediments in downstream reaches and can contribute to an oxygen depression.

Changes in species composition and consumer efficiency are reflected in two common complaints, nuisance growths of plants and depressed game-fish populations. The environmental cause of these resource devaluations may be diurnal oxygen fluctuation.

Diurnal oxygen fluctuation is easily and accurately determined. It should be a good index for extensive stream monitoring if the amplitude of oxygen fluctuation, or more specifically, the lowest daily oxygen concentration, is a sensitive indicator of changes in species composition and community efficiency. The amplitude of oxygen fluctuation should be defined by the level of productivity, community respiration, and reaeration capacity. Any increased community metabolism of a periphyton-based community that does not exceed the reaeration capacity of the stream hypothetically should not cause permanent alterations in species composition or consumer efficiencies once the new metabolic level stabilizes. If macrophytes invade before the reaeration capacity is reached, however, they could cause changes in consumer species composition and consumer efficiency that are unrelated to oxygen fluctuation. However, many of the regulators of reaeration capacity (velocity, depth, bottom roughness, and import and storage of sediments) and nutrient levels probably determine the suitability of the site for macrophytic invasion. Physical conditions that favor macrophytic invasion also cause low reaeration capacities. Therefore, macrophytes may not invade during accelerated enrichment until some time after the reaeration capacity of the stream is overwhelmed by increased periphytic productivity.

To date, evaluation of indexes to stream enrichment rests on field investigations where control is difficult to impossible and results are unavoidably ambiguous. The modes of interaction among community responses to enrichment and diurnal oxygen fluctuation should be examined simultaneously through rigorous experimentation with different levels of nutrient introduction into stream sets with different reaeration capacities.

ACKNOWLEDGMENTS

Credits. This study was completed with the aid and advice of many associates. Edwin Cooper was particularly helpful. Others who contributed include Robert Butler, Archie MacDonald, Theodore Wohnsiedler, Niles Kevern, Terry Haines, B. J. Mathis, Curtis Wagner and Thomas Bahr.

Author. Richard A. Cole is a research associate at the Institute for Water Research, Michigan State University, East Lansing.

REFERENCES

1. "Eutrophication: Causes, Consequences, Correctives." Natl. Acad. Sci., Washington, D. C. (1969).
2. Hooper, F. F., "Eutrophication Indices and Their Relation to Other Indices of Ecosystem Change." In "Eutrophication: Causes, Consequences, Correctives." Natl. Acad. Sci., Washington, D. C. (1969).
3. Margalef, R., "Perspectives in Ecological Theory." The Univ. of Chicago Press, Chicago, Ill. (1968).
4. McDonnell, A. J., and Blain, W., "Reaeration Measurements in Eutrophic Streams." *Proc. 22nd Ind. Waste Conf.*, Purdue Univ., W. Lafayette, Ind., Ext. Ser. 129, 1044 (1967).
5. Odum, H. T., "Primary Production in Flowing Waters." *Limnol. & Oceanog.*, **1**, 102 (1956).
6. Owens, M., *et al.*, "Some Reaeration Studies in Streams." *Intl. Jour. Air & Water Poll.* (G.B.), **8**, 469 (1964).
7. Zippin, C., "An Evaluation of the Removal Method of Estimating Animal Populations." *Biometrics*, **12**, 163 (1956).
8. Patten, B. C., "Species Diversity in Net Phytoplankton of Raritan Bay." *Jour. Marine Res.*, **20**, 57 (1962).
9. Wilhm, J. L., and Dorris, T. C., "Biological Parameters for Water Quality Criteria." *BioScience*, **18**, 477 (1968).
10. Pianka, E. R., "Latitudinal Gradients in Species Diversity: A Review of Concepts." *Amer. Nat.*, **100**, 33 (1966).
11. MacArthur, R. H., "Patterns of Species Diversity." *Biol. Rev. Cambridge Phil. Soc.* (G.B.), **40**, 510 (1965).
12. Hartman, R. T., and Brown, D. L., "Changes in Internal Atmosphere of Submersed Vascular Hydrophytes in Relation to Photosynthesis." *Ecology*, **48**, 252 (1967).
13. Edwards, R. W., and Owens, M., "The Effects of Plants on River Conditions, IV—The Oxygen Balance of a Chalk Stream." *Jour. Ecol.* (G.B.), **50**, 207 (1962).
14. Butcher, R. W., *et al.*, "Variations in Composition of River Waters." *Intl. Rev. Gesanten Hydrobiol.* (Ger.), **24**, 47 (1930).
15. Whitford, L. W., "The Current Effect and Growth of Fresh Water Algae." *Trans. Amer. Microscop. Soc.*, **79**, 302 (1960).
16. Slack, K. V., and Feltz, H. R., "Tree Leaf Control on Low Flow Water Quality in a Small Virginia Stream." *Environ. Sci. & Technol.*, 129 (1968).
17. Hynes, H. B. N., "The Enrichment of Streams." In "Euthrophication: Causes, Consequences, Correctives," Natl. Acad. Sci., Washington, D. C. (1969).
18. Bartsch, A. F., and Ingram, W. M., "Stream Life and the Pollution Environment." *Pub. Works*, **90**, (7) 104 (1959).
19. Larkin, P. A., and Northcote, T. G., "Fish as Indices of Eutrophication." In "Eutrophication: Causes, Consequences, Correctives," Natl. Acad. Sci., Washington, D. C. (1969).
20. Wilhm, J. L., "Some Aspects of Structure and Function of Benthic Macroinvertebrate Populations in a Spring." *Amer. Midland Naturalist*, **84**, 20 (1970).
21. Westlake, D. F., "Comparisons of Plant Productivity." *Biol. Rev. Cambridge Phil. Soc.* (G.B.), **38**, 385 (1963).
22. Odum, E. P., "Factors Which Regulate Primary Productivity and Heterotrophic Utilization in the Ecosystem." In "Algae and Metropolitan Wastes," Robert A. Taft, San. Eng. Center, HEW, Washington, D. C. (1961).
23. Scherer, R. C., "Dynamics of Stream Populations of the White Sucker, *Catostomus commersoni* Lacepede." Ph.D. thesis, Pennsylvania State Univ., University Park (1965).
24. Cummins, D. W., *et al.*, "Trophic Relationships in a Small Woodland Stream." *Verh. Intl. Ver. Limnol.* (Ger.), **16**, 627 (1966).
25. Hynes, H. B. N., "The Biology of Polluted Waters." Liverpool Univ. Press, Liverpool, Eng. (1963).
26. Hawkes, H. A., "Biological Aspects of River Pollution." In "River Pollution Its Causes and Effects," Klein [Ed.], Butterworth, Inc., Washington, D. C. (1964).
27. Thompson, D. H., and Hunt, F. D., "The Fishes of Champaign County—A Study of the Distribution and Abundance of Fishes in Small Streams." *Ill. Nat. History Surv. Bull.*, **19**, 1 (1930).
28. Paulson, T. L., and Culver, D. C., "Diversity in Terrestrial Cave Communities." *Ecology*, **50**, 153 (1969).

29. Paine, R. T. "Foodweb Complexity and Species Diversity." *Amer. Nat.*, **100**, 65 (1966).
30. MacArthur, R. H., and MacArthur, J. W., "On Bird Species Diversity." *Ecology*, **42**, 594 (1961).
31. Harrel, R. C., *et al.*, "Stream Order and Species Diversity of Fishes in an Intermittent Oklahoma Stream." *Amer. Midland Naturalist*, **78**, 428 (1967).
32. Sheldon, A. L., "Species Diversity and Longitudinal Succession in Stream Fishes." *Ecology*, **49**, 193 (1968).
33. Wilhm, J. L., "Use of Biomass Units in Shannon's Formula." *Ecology*, **49**, 153 (1968).