sufficient to meet bacterial needs (let alone the needs of other consumers) to one in which bacterial needs are very much less than available carbon, thereby solving the budgetary problems discussed in the closing paragraphs of Scavia and Laird's paper. Similarly, an explicit consideration of the recycling of organic carbon by consumers may help to explain apparently excessive demands of consumers in other ecosystems, especially retentive systems such as the open ocean.

David Strayer

Institute of Ecosystem Studies
The New York Botanical Garden
Box AB
Millbrook 12545

References

Fahnenstiel, G. L., and D. Scavia. 1987. Dynamics of Lake Michigan phytoplankton: Primary production and growth. Can. J. Fish. Aquat. Sci. **44:** 499–508.

Humphreys, W. F. 1979. Production and respiration in animal populations. J. Anim. Ecol. **48:** 427–453.

Jordan, M. J. 1985. Bacteria, p. 246–250. *In* G. E. Likens [ed.], An ecosystem approach to aquatic ecology: Mirror Lake and its environment. Springer.

———, G. E. Likens, and B. J. Peterson. 1985. Organic carbon budget, p. 292–301. *In* G. E. Likens [ed.], An ecosystem approach to aquatic ecology: Mirror Lake and its environment. Springer.

Scavia, D., and G. L. Fahnenstiel. 1987. Dynamics of Lake Michigan phytoplankton: Mechanisms controlling epilimnetic communities. J. Great Lakes Res. **13:** 103–120.

———, and G. A. Laird. 1987. Bacterioplankton in Lake Michigan: Dynamics, controls, and significance to carbon flux. Limnol. Oceanogr. **32:** 1017–1033.

Schroeder, L. A. 1981. Consumer growth efficiencies: Their limits and relationships to ecological energetics. J. Theor. Biol. **93:** 805–828.

Strayer, D., and G. E. Likens. 1986. An energy budget for the zoobenthos of Mirror Lake, New Hampshire. Ecology **67:** 303–313.

Limnol. Oceanogr., 33(5), 1988, 1220–1224

On the role of bacteria in secondary production

Our recent work on the role of heterotrophic bacterioplankton in Lake Michigan (Scavia et al. 1986; Scavia and Laird 1987) has led to the assertion that bacterial secondary production is high relative to autotrophic primary production. We found that annual areal bacterial carbon demand was about equal to that supplied through phytoplankton net production; in the summer epilimnion, however, that demand was much greater than contemporary phytoplankton supply. We concluded our second paper with two uncomfortable observations. First, because bacterial carbon demand was approximately equal to organic carbon supply, carbon demand by consumers, other than bacteria, could not be met by phytoplankton production (or the estimates of phytoplankton and/or bacterial production were wrong). Second, bacterial carbon demand that was greater than phytoplankton supply in the summer epilimnion suggested a temporal disequilibrium, where bacterial summer demand is met partially by winter and spring algal production. Strayer's (1988) reanalysis of our data sheds important light on the commonly assumed restriction that secondary consumption must be equal to or less than primary production. He demonstrates that because organic carbon can cycle within the food web, this restriction is false. I agree with his reassessment and recognize that, because of this relaxed and more appropriate limit to secondary production, our first uncomfortable observation is more acceptable.

This reanalysis is important because highly retentive, autotrophically driven Lake Michigan certainly supports a rich and productive array of secondary consumers in addition to bacteria. It is also important for other large systems. Recent reports of very

---

Acknowledgments

GLERL Contribution 622.

I thank H. Ducklow, G. Fahnenstiel, G. Laird, and H. Vanderploeg for reading an earlier draft of this manuscript.

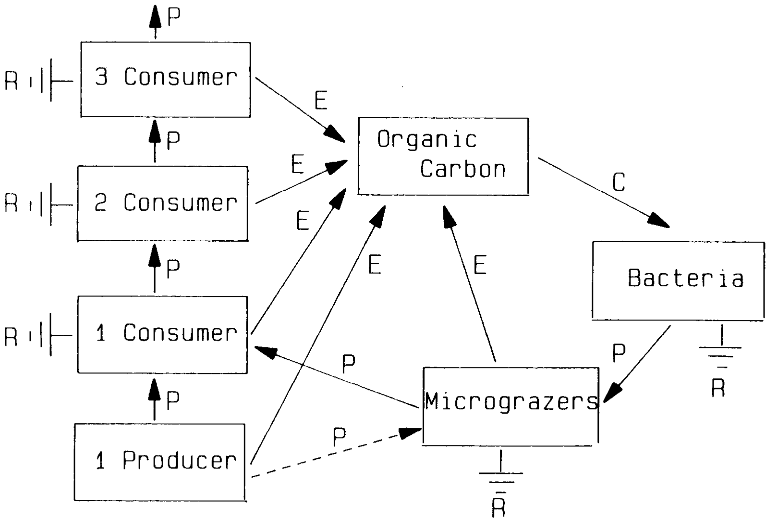

Fig. 1. Schematic diagram of carbon flow through a consumer community with bacteria as a means of sequestering otherwise lost carbon. Arrows represent flow of organic carbon, *R* represents respiratory loss, *P* represents production (=consumption), *E* represents organic release, and *C* represents consumption.

high heterotrophic bacterial carbon demands from Chesapeake Bay (Malone et al. 1986; Ducklow and Peele 1987) and the Sargasso Sea (Fuhrman et al. 1987), for example, can be reconciled more easily with autotrophic supplies if one allows organic carbon to cycle. Although I agree with his conclusion, Strayer's theoretical framework—a linear food chain—leads to a second conclusion that I intend to show is incorrect. He suggests that temporal disequilibrium need not be invoked to explain balanced summer epilimnetic fluxes because recycled organic carbon satisfies the demand. My reanalysis, with a more appropriate model, supports our original contention that sources other than contemporary phytoplankton production are needed to balance bacterial organic carbon demand in the summer epilimnion.

Strayer's analysis is not invalid, but it is applied to an inappropriate, linear system. Bacteria do not fit neatly into a linear food chain. They ingest neither primary producers nor consumers directly and, therefore, they cannot be characterized as any of the consumers depicted by Strayer's model (his figure 1). The bacterial loop is adjunct to the main autotrophic path. Bacteria make their living by taking advantage of the byproducts of the autotrophic food web—they get what leaks from it. Figure 1, here, is a better representation of the unique position bacteria (actually any organo-osmotrophs) hold in the carbon cycle.

Before proceeding with budget calculations for the system depicted in Fig. 1, I consider certain conditions of the model. Strayer's assumption of 60% growth efficiency for all consumers is too generous. Bacteria may be that efficient (e.g. Calow 1977; Cole et al. 1982), but microbial grazers are less efficient, and the metazoa are even less so. My analysis, which may still be generous, allows 60% for bacteria, 40% for micrograzers, and 20% for all others. It also admits consumer release of organic carbon because it is clear that not all carbon ingested (I) and lost from potential biomass production (P) is lost as CO_2. For my analysis, the split between organic (E) and inorganic (R) carbon loss is based on the assumed 20% growth efficiency (P/I) and a typical crustacean assimilation efficiency ($1 - E/I$) of 50% (e.g. Comita 1972; Porter et al. 1982; Parsons et al. 1984; Peters and Downing 1984). Assuming instead values of 40 or 60% does not change the conclusions that follow. Although the relative availabilities of particulate and dissolved organic carbon certainly differ, my analysis does not distinguish between the two forms.

Table 1. Partial organic carbon annual areal budget for Lake Michigan (g-C m^{-2} yr^{-1}). Input is 232 g and nonrespiratory loss is 8 g based on data from Scavia and Fahnenstiel (1987) and Fahnenstiel and Scavia (1987).

Production directly available (%)	0*	10	20	0	10	10
Consumer assimilation efficiency	—	50	50	50	40	60
Summed secondary consumption	560*	697	695	698	843	581
Bacterial consumption†	—	235	249	222	312	175

* From Strayer 1988.
† Measured as 237±80 (Scavia and Laird 1987).

This simplification should not affect the analysis because only a small percentage of primary production is buried in Lake Michigan's sediment each year (Eadie et al. 1984) and there is no clear annual trend in concentration of either form. Thus, on the relatively long time scales of my analysis, all of the released organic material is used by the heterotrophic community.

A second important factor in the following analysis is the portion of primary production immediately available to bacteria. This direct shunt can be from phytoplankton excretion or nonpredatory mortality (e.g. autolysis). Rates of direct excretion are low for Lake Michigan (Laird et al. 1986), as well as other Great Lakes (e.g. Lee and Nalewajko 1978). We have shown (Scavia and Fahnenstiel 1987) through comparison of algal production, sedimentation, and grazing rate measurements that nonpredatory mortality is not likely to be a dominant factor in the algal dynamics of Lake Michigan. Thus, for the calculations below, I assume 10% of primary production enters the available organic pool directly. Assumptions as different as 0 and 20% do not change the conclusions.

I first consider water-column annual rates (g-C m^{-2}, Table 1). With the assumptions stated above, I calculate organic supply to bacteria to be 147.4 g after one "pass" through the traditional food web. Assuming 60% growth efficiency for bacteria and subsequent consumption by bacterivores, the second pass of this recovered carbon through the food web produces 55.1 g available for reassimilation by bacteria. Continuing this procedure until 99% of the original carbon is respired (Table 1) indicates, as in Strayer's analysis, that summed secondary consumption is much greater than primary production and that measured bacteria carbon demand fits well within total consumer demand. This situation allows significant production by zooplankton and other secondary consumers.

Unlike Strayer's analysis, mine also provides an estimate of bacterial carbon consumption. If we assume that 10% of primary production is immediately available for assimilation, calculated bacterial consumption is 235 g (Table 1). This estimate is 249 g if 20% is made immediately available and 222 g without any direct shunt from primary producers. Assumptions of 40 or 60% consumer assimilation efficiency and 10% direct shunt, yield bacteria carbon demands of 312 and 175 g, respectively. All calculated estimates are within 1 SD of our previously reported empirical estimate of 237±80 g. This portion of the analysis agrees with Strayer's and demonstrates that summed consumer demand can be considerably higher than carbon input and that bacterial demand can be met by autotrophic production on an annual water-column basis in Lake Michigan.

I now consider the same calculations for the summer epilimnion, the region pre-

Table 2. As in Table 1, but for summer epilimnion (g-C m^{-2} $summer^{-1}$). Input is 29.4 g and nonrespiratory loss is 9.4 g.

Production directly available (%)	0*	10	20	0	10	10
Consumer assimilation efficiency	—	50	50	50	40	60
Summed secondary consumption	50.1*	62.2	62.0	62.4	75.9	51.9
Bacterial consumption†	—	21.0	22.0	19.8	27.9	15.6

* From Strayer 1988.
† Measured as 43.8±14.8 (Scavia and Laird 1987).

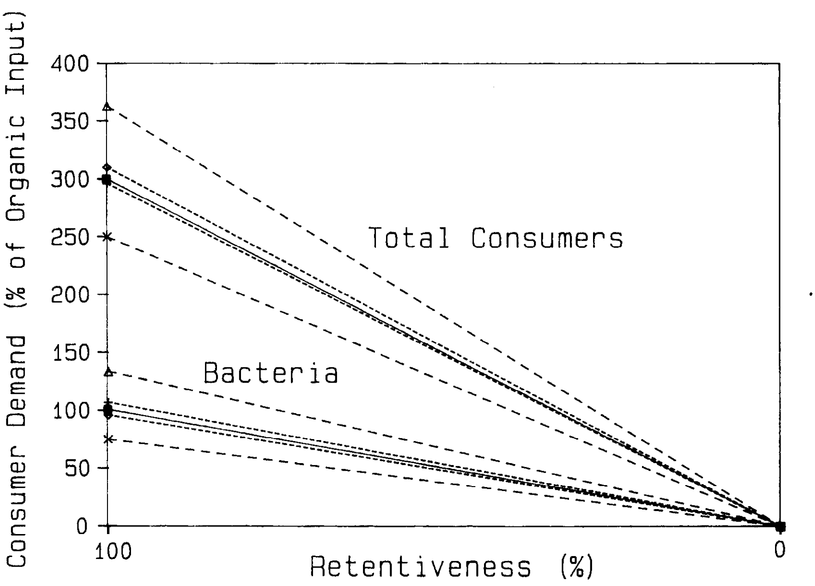

Fig. 2. Consumer carbon demand, expressed as a percentage of total organic carbon input, as a function of system retentiveness [(inputs − nonrespiratory losses)/inputs]. Solid line represents calculations with a consumer assimilation efficiency of 50% and primary production shunt to bacteria of 10%. Dashed lines represent calculations with assimilation efficiencies of 40 and 60%. Dotted lines represent calculations with production shunts of 0 and 20%.

senting a serious imbalance between organic carbon supply and bacterial demand in our empirical studies. With the same assumptions as above, I calculate a summed consumer demand of 62.2 g (Table 2), again higher than net inputs and capable of including both our measured bacterial demand (43.8 ± 14.8 g) and carbon demands of other consumers. This result is similar to Strayer's, but it differs in an important way when I calculate bacterial carbon demand. On the basis of the model presented here, only 21.0 g could be consumed by bacteria before all of the carbon produced in, but not sedimented from, the epilimnion was respired. That demand varies between 15.6 and 27.9 g over the range of coefficient values used above (Table 2). None of these values approaches the empirical estimate of 43.8 g. It appears that, given the constraint that bacteria must get their carbon as a byproduct of the autotrophic food web, the amount of carbon made available to them in the summer epilimnion is insufficient to balance the measured demand. A source, in addition to processes of the summer epilimnion, is needed. This analysis supports our original contention (Scavia and Laird 1987) that there must be a temporal disequilibrium between organic carbon supply and summer demand.

I now turn to the more general case and consider the relationship between summed secondary consumption, bacterial consumption, and total organic carbon input with respect to system retentiveness. Within the constraints of uncertainty in the assumed consumer assimilation efficiency (50 ± 10%) and the portion of primary production that is shunted directly to bacteria (10 ± 10%), it is clear (Fig. 2) that summed secondary consumption can be much greater than organic input. In fact, the lower, more reasonable growth efficiencies used here result in more recycling and thus even greater consumption than that suggested in Strayer's analysis. My analysis also suggests that bacterial demand can approach a value equal to total organic input and yet constitute only a third of the total demand in highly retentive systems.

Theoretical analyses, like that of Strayer's and the one presented here, necessarily require abstraction of nature. The main difference between our approaches is in characterization of the bacterial role in carbon flow. If bacteria are treated similarly to other consumers, as Strayer has done, then imbalances such as that in the epilimnion of Lake Michigan disappear. If bacteria are assigned a more appropriate role, however, as I have tried to do, then significant imbalances remain. For models such as these, it is important that the abstraction be faithful in ways that are critical to the analysis.

I thank Strayer for his contribution to the analysis of carbon flux in Lake Michigan and support his broader thesis that organic carbon cycling allows for a higher limit to secondary production. This broader view allows community consumption to be significantly greater than organic carbon inputs in retentive systems like the Great Lakes and the open ocean and thus may help resolve other apparent imbalances beginning to emerge with respect to heterotrophic bacterial production.

Donald Scavia

Great Lakes Environmental
Research Laboratory
National Oceanic and Atmospheric
Administration
2205 Commonwealth Blvd.
Ann Arbor, Michigan 48105

References

CALOW, P. 1977. Conversion efficiencies in heterotrophic organisms. Biol. Rev. Camb. Phil. Soc. **52**: 385–409.

COLE, J. J., G. E. LIKENS, AND S. L. STRAYER. 1982. Photosynthetically produced dissolved organic carbon: An important source for planktonic bacteria. Limnol. Oceanogr. **27**: 1080–1090.

COMITA, G. W. 1972. The seasonal zooplankton cycles, production, and transformation of energy in Severson Lake, Minnesota. Arch. Hydrobiol. **70**: 14–66.

DUCKLOW, H. W., AND E. R. PEELE. 1987. Bacterial carbon pools and fluxes in Chesapeake Bay plankton, p. 81–85. *In* G. B. Mackiernan [ed.], Dissolved oxygen in the Chesapeake Bay, processes and effects. Maryland Sea Grant Publ. Univ. Maryland.

EADIE, B. J., R. L. CHAMBERS, W. S. GARDNER, AND G. L. BELL. 1984. Sediment trap studies in Lake Michigan: Resuspension and chemical fluxes in the southern basin. J. Great Lakes Res. **10**: 307–321.

FAHNENSTIEL, G. L., AND D. SCAVIA. 1987. Dynamics of Lake Michigan phytoplankton: Primary production and growth. Can. J. Fish. Aquat. Sci. **44**: 499–508.

FUHRMAN, J. A., T. SLEETER, AND C. CARLSON. 1987. Oligotrophic ocean biomass is dominated by nonphotosynthetic bacteria, even in the euphotic zone. [Abstract.] Eos **68**: 1729.

LAIRD, G. A., D. SCAVIA, AND G. L. FAHNENSTIEL. 1986. Algal organic carbon excretion in Lake Michigan. J. Great Lakes Res. **12**; 136–141.

LEE, K., AND C. NALEWAJKO. 1978. Photosynthesis, extracellular release, and glycollic acid uptake by plankton: Fractionation studies. Int. Ver. Theor. Angew. Limnol. Verh. **20**: 257–262.

MALONE, T. C., AND OTHERS. 1986. Lateral variation in the production and fate of phytoplankton in a partially stratified estuary. Mar. Ecol. Prog. Ser. **32**: 149–160.

PARSONS, R. R., M. TAKAHASHI, AND B. HARGRAVE. 1984. Biological oceanographic processes, 3rd ed. Pergamon.

PETERS, R. H., AND J. A. DOWNING. 1984. Empirical analysis of zooplankton filtering and feeding rates. Limnol. Oceanogr. **29**: 763–784.

PORTER, K. G., J. GERRITSEN, AND J. D. ORCUTT, JR. 1982. The effect of food concentration on swimming patterns, feeding behavior, ingestion, assimilation, and respiration by *Daphnia*. Limnol. Oceanogr. **27**: 935–949.

SCAVIA, D., AND G. L. FAHNENSTIEL. 1987. Dynamics of Lake Michigan phytoplankton: Mechanisms controlling epilimnetic communities. J. Great Lakes Res. **13**: 103–120.

———, AND G. A. LAIRD. 1987. Bacterioplankton in Lake Michigan: Dynamics, controls, and significance to carbon flux. Limnol. Oceanogr. **32**: 1017–1033.

———, ———, AND G. L. FAHNENSTIEL. 1986. Production of planktonic bacteria in Lake Michigan. Limnol. Oceanogr. **31**: 612–626.

STRAYER, D. L. 1988. On the limits to secondary production. Limnol. Oceanogr. **33**: 1217–1220.