Pediatric patient samples obtained from St. Jude Children's Hospital included the following: patient 9907 (Ph^1-negative T-cell ALL), 9913 (Ph^1-negative common ALL), 9453 (Ph^1-positive pre–B cell ALL), 9312 (Ph^1-positive common ALL with a deletion of the short arm of chromosome 9), 9254 (Ph^1-positive common ALL), 9378 (Ph^1-positive pre–B cell ALL) and 9556 (Ph^1-positive common ALL). Patients obtained from UCLA included the following: 045-14-02 (adult Ph^1-positive, pre–B cell ALL), 146-03-37 (Ph^1-positive blast-crisis CML), 143-57-16 (Ph^1-positive blast-crisis CML), and 133-68-56 (Ph^1-positive accelerated CML).

14. S. Clark *et al.*, unpublished data.

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Technical Comments

Bacteria: Link or Sink?

Ducklow *et al.* (*1*) conclude from an experimental study of an enclosed water column at Loch Ewe, Scotland, that bacteria were not a link (that is, a food source) to higher order consumers in the planktonic food web. We strongly disagree that "the results have great importance for our understanding of the structure and function of marine planktonic ecosystems."

First, one cannot generalize from a single "link or sink" experiment. It will be necessary to carry out many such tracer studies in different parts of the sea representing a variety of trophic states, and to have a detailed characterization of the planktonic assemblage of each, before we can begin to discover the importance of the microbial loop in marine food webs. Ducklow *et al.* do not provide information about the components of the planktonic assemblage, that is, heterotrophic microorganisms, phytoplankton, and zooplankton, at the time of their experiment. In addition, the work carried out 9 years previously (*2*) that was cited in support of the statement that "The plankton community . . . was an assemblage of bacteria, protozoans . . . typical of the . . . Scottish sea lochs in mid- to late spring" in fact contained no data on bacterioplankton or protozoan numbers. Without information on the relative abundances and production rates of organisms of the microbial loop, that is, bacteria and protozoa, compared to those of the phytoplankton and metazooplankton assemblages, one cannot properly interpret the results of the experiment.

Second, the experimental study of Parsons *et al.* (*3*), briefly mentioned by Ducklow *et al.*, provided direct evidence that bacteria can be a link in marine food webs. Addition of small quantities of glucose (1 to 5 mg per liter) to enclosed water columns enhanced bacterial production, which in turn significantly increased the total abundance of benthic larvae and gelatinous zooplankton compared to a control treatment with predominantly phytoplankton production.

Third, the speculation of Ducklow *et al.* that production of cyanobacteria as well as of bacteria may not be utilized in marine food webs is not supported by the results of their study. Cyanobacteria in the sea have an average cell volume of 0.5 μm^3 (*4*), while the average cell volume of marine bacteria is 0.07 μm^3 (*5*). The larger cyanobacterial cells are likely to be grazed more effectively than are bacteria by marine pelagic ciliates (*6*), which are abundant in the sea and are a known food source for metazooplankton (*7*). Iturriaga and Mitchell (*4*) demonstrated with autoradiography that protozoa in the size range of 10 to 50 μm actively grazed $^{14}CO_2$-labeled cyanobacteria in surface waters of the oligotrophic North Pacific Ocean. They also showed that carnivorous metazoans incorporated the label, implying at least a two-step transfer of cyanobacterial carbon in the food web.

Finally, results from a similar bag experiment previously carried out in the same system, in which the fate of phytoplankton production was assessed by monitoring the distribution of ^{14}C in the water after a spike of radiolabeled bicarbonate was added (*8*), showed that, at the end of 10 days, the herbivorous zooplankton (68-μm and 250-μm size fractions) had incorporated only 1.2% of the ^{14}C activity present in the phytoplankton (*8*). Since this apparent trophic transfer from algae to zooplankton is of the same small magnitude as that reported by Ducklow *et al.* for the transfer of bacterial production to larger organisms, it is misleading to single out bacteria as a sink.

Ducklow *et al.* are correct in stating that further ecosystem-scale experiments should be done in order to address the question of bacteria as a link or sink for organic carbon in marine food webs. Their results, based on a one-season experiment carried out in a coastal ecosystem atypical of most of the world ocean, have not settled the matter.

EVELYN B. SHERR
BARRY F. SHERR
University of Georgia Marine Institute, Sapelo Island, GA 31327
LAWRENCE J. ALBRIGHT
Biological Sciences Department, Simon Fraser University, Burnaby, British Columbia V5A 156, Canada

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Response: Sherr *et al.* (*1*) criticize the design of our study, our interpretation of the results of a previous study (*2*) and of our own, and our conclusions. They imply that because an analogous experimental study of herbivory in a Loch Ewe bag (*3*) also failed to show significant transfer of carbon to zooplankton, both experiments were not performed properly. However, it is clearly shown in (*3*) that, during the earlier study, there was appreciable net primary production only on the three sunniest days. During the major part of the experiment nighttime respiration nearly balanced daytime carbon fixation, and it is thus not too surprising that the herbivores accumulated the label slowly. In contrast, in our experiment there was a rapid and sustained (4-day) accumula-

tion of label in the prey pool, but still no accumulation in the predators. In support of tracer experiments in bags in general, we also offer the following observations. At the same time as the experiment we reported on, we also performed a smaller scale study in a 1000-liter bag using [methyl-^{3}H]thymidine as a tracer of bacterial biomass in the food web. After 10 days only 0.5% of the added tritium initially fixed in the <1-μm size fraction was found in particles >100 μm in diameter. In another study conducted in a similar system at a similar temperature (Friday Harbor, Washington, 11°C), with [^{3}H]leucine as a tracer, there was appreciable transfer of bacterial biomass into zooplankton >53 μm in diameter (12 to 20% of added label) (*4*). In contrast, short-term (1- to 2-hour) studies in in situ incubators have shown that, in a wide variety of coastal and oceanic habitats, zooplankton >64 μm in diameter ingest only a negligible fraction of daily bacterial production (*5*). Finally, we refer the interested reader to the classic study of Armstrong and Harvey (*6*). In constructing a mass balance for phosphate in the English Channel, they observed that only 5% of the nutrient used by the phytoplankton accumulated in the zooplankton. Thus we conclude that neither bag experiments in general, nor the system we studied, nor the tracer we used can account for the nature of our observations. We believe our experiment was valid.

Sherr *et al.* question our citation of another mesocosm study (*2*) in support of our conclusion. Although there was evidence in that study for an increase in zooplankton numbers in response to glucose addition (which stimulated bacterial production), calculations indicate that the increase was small. The additions of glucose to that system were, in fact, large: 5 mg/liter over 0 to 10 m represent a total carbon addition of approximately 10 g m^{-2} day^{-1}, approximately tenfold greater than the primary production. The increase in copepod numbers was about 500 m^{-3}. If one assumes that an adult *Pseudocalanus* sp. has 10 to 20 μg of carbon, there was a biomass increase of 5 to 10 μg of carbon per liter, for a yield of 0.1%. A simple explanation of this small increase is that the zooplankton (or their attached microflora) took up some of the glucose directly, obviating the need to invoke flow through a microbial loop.

We disagree that proper interpretation of the data we presented requires extensive information on the organisms in the food web and their growth and transfer rates, with one exception. If no large zooplankton were present, our observation that label did not accumulate in the larger size fractions would have been trivial. In fact we carried out repeated measurements of the biomass composition in all size fractions on each day of our study and also measured bacterial production routinely (*7*). There were about ten copepods per liter at the end of our study, a concentration similar to that reported earlier (*8*) for Loch Ewe. By comparing day-to-day changes in bacterial abundance with daily production estimates and with occasional dilution experiments to measure rates of bacterivory (*9*), we estimate that protozoan bacteriovores were removing about 50 to 100% of the bacterial production each day. With the addition of these results, we might restate our conclusion as follows: We found little support for either direct transfer of bacterial carbon to zooplankton or for indirect transfer via the microbial loop, in spite of high bacterial production and the efficient removal of that production by bacteriovores.

In our report we implied that the phototrophic cyanobacteria, which are similar in size to the heterotrophic bacteria we studied, may also not serve as an important pathway of carbon through food webs. Sherr *et al.* pointed out correctly that the cyanobacteria can be grazed efficiently by protozoan grazers, as we also suggested for the heterotrophic bacteria. However, recent results from their laboratory (*10*) show that while protozoans ingest cyanobacteria, they sometimes grow only very inefficiently, if at all, on that food source. This result is entirely consistent with our speculation.

Our conceptual models of the structure and functioning of food chains, including microbial loops, are only hypotheses, and only rarely do we have direct evidence of the rates and extent of materials transfer through food webs. An important part of experimental ecology is to test the food chain hypothesis. We do not share the view of Sherr *et al.* (*1*) that, if the results of an experiment fail to fit the hypothesis, then one rejects the experiment or its site. We set up our experiment with the objective of finding transfer of bacterial carbon through a microbial loop to zooplankton, and we would have been pleased to have obtained evidence for that process. We did not obtain such evidence, and our conclusions were based on a single, albeit comprehensive, experiment. At other times and in other places we would certainly expect to see other results. In our view the important issue is not whether the microbial loop exists as a link, but where and when and under what conditions it plays that role. Our report illustrates one direct way of examining the processing and suggests that it may not be universal. We join with Sherr *et al.* in the hope that our report and this exchange of views will result in further such experimentation.

HUGH W. DUCKLOW
Horn Point Environmental Laboratories, Post Office Box 775, Cambridge, MD 21613
D. A. PURDIE
Department of Oceanography, The University, Southampton S09 5NH, England
P. J. LEB. WILLIAMS
Marine Science Laboratory, Menai Bridge, Gwynedd LL59 5EY, Wales
J. M. DAVIES
Department of Agriculture and Fisheries for Scotland, Marine Laboratory, Post Office Box 101, Aberdeen AB9 8D8, Scotland

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