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Role of microbes in pelagic food webs: A revised concept

In recent years, research focused on the organisms of the "microbial loop" (Pomeroy 1974; Azam et al. 1983) has resulted in a significant body of data on trophic interactions involving microbes within pelagic food webs. From this mass of information, we believe that a revised concept of pelagic food web structure is beginning to emerge. In our opinion, the microbial loop should now be considered as a component (and integral) part of a larger microbial food web, which includes all pro- and eucaryotic unicellular organisms, both autotrophic and heterotrophic. From this standpoint, the entire microbial food web, not simply phytoplankton, supports the metazoan food web (Fig. 1). Thus, the "link or sink" controversy, i.e. the debate concerning the relative importance of the microbial loop as a source of food for the metazoan food web or as a sink for fixed carbon via respiratory losses (e.g. Ducklow et al. 1986; Sherr et al. 1987), becomes a nonissue. Even though most of

the primary production may be respired within the microbial food web, the microbial food web is at the same time *the* ultimate food resource for metazooplankton.

A more detailed look at transfers of fixed carbon within the microbial food web and from microbes to metazoans is presented in Fig. 2. In this diagram we have decomposed the microbial food web into phytoplankton and the heterotrophic organisms of the microbial loop. The original conception of the microbial loop of Azam et al. (1983) was as a processor of nonliving organic matter via bacterial uptake, followed by protozoan grazing of bacteria. However, there are so many direct links between algae and heterotrophic microbes (Sherr et al. 1986; see Fig. 2) that, from a total systems standpoint, the microbial loop cannot be considered separately from the rest of the microbial food web. Instead, heterotrophs can be viewed as responsible for repackaging parcels of fixed carbon (e.g. bacterial and algal cells) into larger parcels and for recovering fixed carbon (e.g. dissolved and particulate organic matter), which otherwise might be lost to the food web. Repackaging pathways also include uptake of bacteria by mixo-

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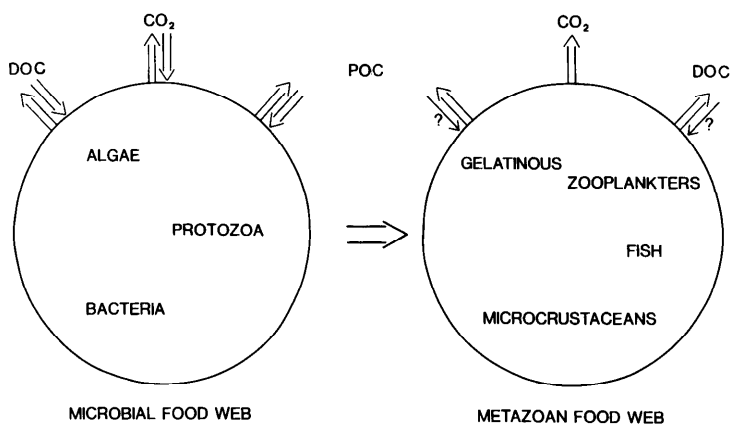
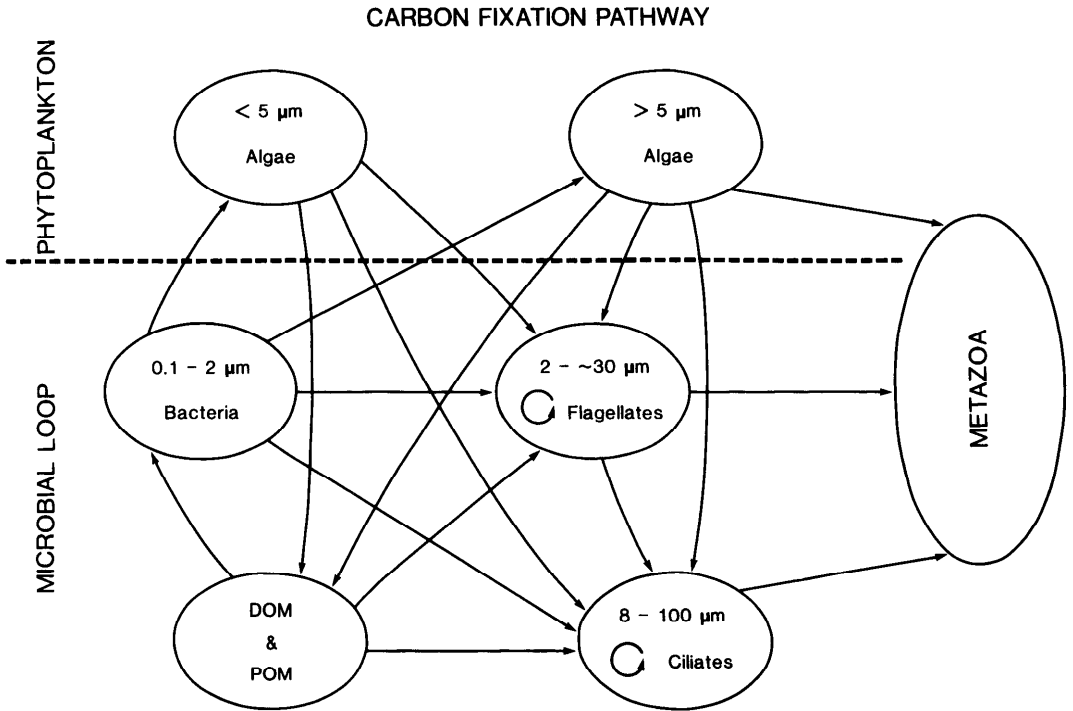


Fig. 1. Simplified revised conceptual model of pelagic food webs in which the microbial food web, including all unicellular organisms, supports the metazoan food web. Particulate organic carbon—POC; dissolved organic carbon—DOC.



FIXED CARBON REPACKAGING & RECOVERY PATHWAYS

Fig. 2. Trophic interactions within the microbial food web, which is separated here into phytoplankton and "microbial loop" (i.e. bacteria and protozoa) components. Note the many direct links between heterotrophic and autotrophic microbes, including ingestion of phytoplankton by flagellates and ciliates and ingestion of bacteria by mixotrophic algae. The curved arrows in the flagellate and ciliate compartments indicate further predator-prey interactions within these broad classes of organisms. In this model, production of $< 5\text{-}\mu\text{m}$ algae is accessible to metazoa only after being "repackaged" into larger protozoan cells.

trophic algae (Porter 1988) and ingestion of smaller microbes by chloroplast-containing ciliates (Stoecker et al. 1987*b*; Laval-Peuto and Rassoulzadegan 1988). With respect to recovery pathways, one of us (E. Sherr in press) has recently found that heterotrophic flagellates are capable of ingesting and assimilating high molecular weight polysaccharide at relatively low concentrations, which suggests that protozoa as well as bacteria could be involved in channeling dissolved organic matter back into the food web.

Metazoans would utilize the food resources of the microbial food web primarily by grazing phytoplankton, colorless flagellates, and ciliates $\geq 5\ \mu\text{m}$. For those systems in which most photosynthesis is carried out by cells too small for metazoans to effectively consume (usually $< 5\ \mu\text{m}$: Sherr et al. 1986), e.g. oligotrophic ocean waters and

coastal waters after the spring phytoplankton bloom, the main trophic links to the metazoa would be via phagotrophic flagellates and ciliates (Fig. 2).

Strong supporting evidence for this concept of the structure of pelagic food webs comes from several recent reports of significant grazing, either postulated or directly measured, of metazooplankton, especially microcrustaceans, on phagotrophic flagellates and ciliates in various marine and freshwater systems (Gifford 1986; Sheldon et al. 1986; Frost 1987; Gifford and Dagg 1987; Sanders and Porter 1987; Stoecker and Egloff 1987; Stoecker et al. 1987*a,c*; Roman et al. 1988; Turner et al. 1988).

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Editorial comment on submission of comments concerning printed comments

My clustering of the preceding four comments, that all arrived within a narrow interval, is inflammatory by design. I do not agree completely with all the recommendations made, nor do I expect that readers will. My opinion, however, is that each of the comments has merit beyond semantics. If I am correct, this disparity of opinion is one sign of a healthy and rapidly moving field of science. I am particularly impressed that current excitement about the microbial loop recognizes the distinction between salt

water and freshwater so poorly. I suspect that each reader will find some bone of contention, however, and thus I feel compelled to offer some guidelines to avoid wasted submissions.

I would suggest that due to the mechanical difficulty of using two issues of *L&O* simultaneously the publication transfer efficiency (e) for comments is decidedly $< 10\%$. If a value of $v = 1.0$ is assigned to the initial comment, then one can see from the standard solution of the geometric series