Food web connections: Links and sinks

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ABSTRACT

Multivorous food webs potentially connect secondary production of microorganisms to metazoan consumers. The actual amount of carbon flux from microorganisms to metazoans is dependent on assimilation efficiency, the length of food chains, the chemical and physical nature of available organic matter, connectivity, and retentiveness. Ruminant nutrition appears to be the most efficient in transferring organic carbon from a microbial food web to metazoans. Phytotelmata (small water bodies contained by plants) contain little-studied microbial food webs that support a metazoan community. Salt marshes, though productive, have major losses of carbon to microbial loops in sediments and additional losses in the detritus food web. In the more productive of the ocean systems, there may be a tradeoff for metazoan consumers between direct consumption of large phytoplankton and consumption of larger protozoans that are feeding on picophytoplankton. Low-productivity central ocean systems may be dominated by this latter food web structure in which the microbial food web is an inefficient intermediary between most of the primary production and metazoan consumers.

The microbial loop [3], although inherently complete within itself, usually is a subset of the larger food web that includes metazoans [18]. Situations have been documented in which consumption of heterotrophic components of the microbial food web apparently provides a vital link in metazoan nutrition (e. g. [22, 23]. Metazoans are also competing with bacteria and protozoans for nutrition [25]. This review explores how much energy metazoans can extract from microbial food webs. Respiratory energy losses in long food chains dissipate energy. Also, the ability of various microbial and metazoan components to utilize organic materials depends on connectivity within the system. Connectivity can be influenced by the size, chemical composition, and physical location of products of primary and secondary production. Utilization of production, primary or secondary, also depends on system retentiveness which may be limited, for example, by losses to a deep and essentially disconnected benthos.

The system which appears to maximize return to metazoans from a microbial food web is ruminant nutrition. There are ruminant-like marine organisms, but the rumen systems of cattle and sheep are the best understood. The anaerobic environment of a rumen makes for inefficient bacterial production but a good transfer of nutrition to metazoans, since the metazoan consumes labile dissolved organic carbon directly. The cow conserves nitrogen by returning urea to the rumen to be recycled through bacteria. Efforts to improve ruminant efficiency have shown that a major loss of energy is to protozoans in the rumen. They are an unnecessary step in the food chain, and they compete directly with the ruminant

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for bacteria and starch grains that either can utilize [19]. Elimination of protozoans could double yield in cattle from 35% to 70-80% [2]. The success of the ruminant results from a minimal number of trophic transfers, high connectivity, and relatively high retentiveness.

Food webs in phytotelmata (tree holes, pitcher plants, and bromeliads) are a favorite subject of population ecologists who ignore the ubiquitous microbial components. Cochran-Stafira and von Ende [10] have discovered the microbial food web in pitcher plants but do not provide us with an analysis of carbon flow. To evaluate carbon flux in phytotelmata, I developed a STELLA-based model of a tropical bromeliad containing heterotrophic bacteria, nanoflagellates, ciliates, mosquito larvae, and a predatory insect larva. Tropical phytotelmata may also contain all stages in the life history of several copepods, crabs, and frogs. I set a steady input of 3 mg C d^{-1} of litter into a 40 ml phytotelm, based on literature data [24]. Assuming that bacteria must process the litter, and that mosquito larvae eat only protozoans, 7-15% of litter carbon is converted to mosquitoes, depending on assumptions about food web connections. Any direct consumption of bacteria by mosquitoes would further increase their yield. This is a luxuriant and efficient system relative to lakes, and it is a detritus-based system with essentially no benthos. Retentivness is high, but mosquitoes and their predators depart as adults and become part of a larger terrestrial food web.

Salt marshes are detritus-based with major benthic processes, most of the primary production being intertidal grasses. Of an annual production in southeastern U. S marshes of 800 g C m^{-2} d^{-1}, about 1% is directly grazed by insects. About half of the primary production in salt marshes consists of roots and rhizomes, less than 5% of which ever enters estuarine water [14]. Roots and rhizomes are utilized in the anaerobic sediments by sulfate-reducing bacteria and, to a lesser extent, by methanogens whose products are almost completely oxidized to CO_2 before reaching the sediment-water interface [5]. Because most estuarine metazoans do not intercept the products of fermentation and bacterial biomass as ruminants do, marsh sediments are a nearly closed microbial loop. The only exceptions are some burrowing organisms having sulfide-reducing symbionts [8]. Much of the primary production that is not isolated in sediments takes chemical forms that are relatively refractory for most metazoans and accessible only through a detritus food web consisting of many trophic transfers. To better cope with this, a number of marsh-dwelling metazoans have developed quasi-ruminant digestive processes involving symbiotic microorganisms that transfer labile organic matter more effectively to the metazoan hosts [12, 13]. This undoubtedly increases the success of metazoans in a system dominated by microbial processes.

With the exception of deep aquifers, the ocean is near the extreme of biologically dilute aquatic systems. For the open ocean, Legendre and Rassoulzadegan [18] define a continuum of food web structure characterized by four types ranging from the classical herbivorous food web through the ‘multivorous’ and microbial food webs to the nearly closed microbial loop of bacteria and flagellates. In this scheme, the contribution of microorganisms to metazoan nutrition may approach zero at both extremes - a purely grazing food chain or a pure microbial loop - and should be greatest in the multivorous situation. Since productive environments, such as spring blooms and Ekman upwellings are commonly assumed to be dominated by the grazing food web, the contribution of microorganisms to metazoan nutrition in those systems is often assumed to be small.

However, a new analysis by Legendre and Rassoulzadegan [these Proceedings] suggests that most productive situations involve multivorous food webs. Also, the flow analysis of McManus [20] and the empirical results of Ohman and Runge [22] and Rivkin et al. [27] show that zooplankton can switch from feeding on large phytoplankton to protozoans.

Productive regions of the ocean, such as upwellings, contain multiple sources of nutrition for a microbial food web. Jumars et al. [16] emphasized the role of soluble organic matter in zooplankton feces and munchates as bacterial substrates. Productive pelagic systems also contain large populations of organic aggregates which are accumulations of dead phytoplankton, munchates, feces, atmospheric fallout, and aggregates of DOC [1, 28]. Solubilization of aggregates by attached bacteria releases labile DOC into bulk water, supporting free-living bacteria [4]. In highly productive pelagic systems an active transfer of organic carbon is occurring through a microbial food web, linked at both ends to metazoans. A recent model of upwellings highlights the direct input of primary production of picophytoplankton to microbial food webs. Elaborating on Moloney's model, Carr [7] shows that in many upwelling regimes the microbial pathway determines total carbon uptake and grazing rates. As others have shown empirically, primary production of pico- and nanoplankton goes on at a steady rate even when nutrient concentrations permit larger phytoplankton with higher V_{max} to bloom, and picoplankton have a rapid turnover into flagellates and ciliates [26]. However, a well-developed microbial food web may not necessarily produce a major transfer of carbon to metazoans. A single inefficient trophic transfer could greatly limit throughput, and this may be happening in less-productive ocean systems where the multivorous food web gives way to a more microbially dominant food web [11].

A major issue in evaluating trophic transfers from protists to metazoans is the question of assimilation efficiency of the bacteria and protozoans. The assumption that bacterial assimilation efficiency is around 50% seems to be giving way to recognition that efficiency is exceedingly variable [15]. In productive coastal waters and estuaries the range may be on the order of 20-50%, but in the open ocean, even in spring blooms, much lower values are reported: 5% in a spring bloom [17], declining to 1-3% in some less productive regions (e. g. [9]).

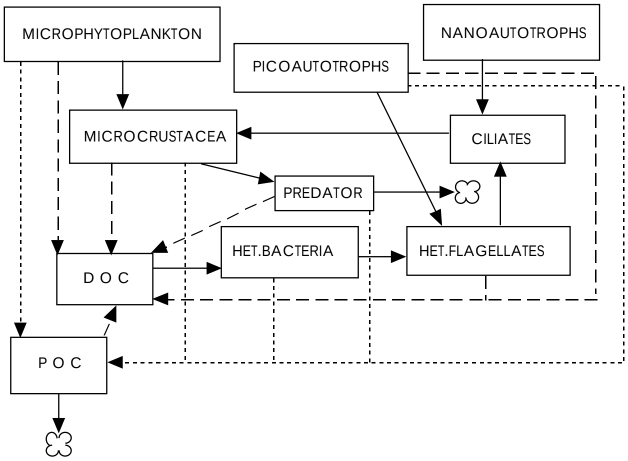

Fig.1. Generic marine food web model used in simulations of the effect of microbial food chain length and microbial gross growth efficiencies on the nutrition of metazoan consumers.

Protozoans have a similarly wide range of gross growth efficiencies [6]. The flow analysis of McManus [20] showed that the flux of carbon to zooplankton from the microbial food web was little influenced by the efficiency of bacteria but was greatly influenced by protozoan efficiencies. His model showed that the potential transfer of primary production to metazoans could be largely through protozoan consumption of picoplankton.

To further evaluate the effects of microbial food chain length and microbial assimilation efficiencies on transfer of organic carbon to metazoan consumers, I constructed a STELLA carbon model of a typical marine food chain with arbitrary inputs of primary producers at three hiererchical sizes (Fig. 1). The model was run for 100 days, iterating approximately hourly, and the model outputs for the final 50 days were then averaged. Four runs were made in which 50% of the primary production was by microphytoplankton, 25% by nanophytoplankton, and 25% by picoautotrophs (Table 1). In the first, gross growth efficiency (GGE) of all microorganisms was 50%. In the second, GGE of bacterioplankton was 5%, in the third, protozoan GGE was 5%, and in the fourth, all microbial GGE was 5%. The results in general confirm those of McManus [20]. The largest and best source of organic carbon for metazoans is, as expected, microphytoplankton, but at a uniform microbial 50% GGE ciliates are potentially 26% of metazoan food. Reducing bacterioplankton GGE to 5% has little effect, but reducing protozoan GGE to 5% essentially eliminates the transfer of nano- and picoautotrophc carbon to metazoans.

Table 1. Results of STELLA simulations of rates of organic carbon production by microorganisms and copepods with varying inputs of primary production at three hierarchical sizes and varying gross growth efficiencies of the microorganisms. Column 1 is fraction of primary production that is microphytoplankton (see text).*

	Efficiency		Percentages of Net Primary Production			
Microphyto-Plankton (%)	Bacteria	Protozoa	Bacteria	Heterotrophic Nanoflagellates	Ciliates	Copepods
50	50	50	21.0	21.6	17.4	31.9
50	5	50	2.1	12.1	13.6	28.3
50	50	5	18.1	3.0	1.6	17.5
50	5	5	1.9	1.8	1.6	17.5
10	50	50	13.9	28.9	24.9	22.7
10	5	50	1.4	22.5	22.3	20.6
10	50	5	14.1	8.8	3.5	9.1
10	5	5	0.8	4.1	1.9	4.9

* Columns 2 and 3 are gross growth efficiencies of bacteria and protozoa. Columns 4 -7 are percentages of secondary production of heterotrophic bacterioplankton, heterotrophic nanoflagellates (HNAN), ciliates, and copepods as fractions of primary production.

In a second set of model runs, 10% of the primary production is by microphytoplankton, 45% by nanophytoplankton, and 45% by picautotrophs. This simulates conditions late in the history of a bolus of upwelled water or conditions in a less productive region. With GGE of all microorganisms at 50%, 71% of potential metazoan nutrition is from ciliates. If bacterial GGE is reduced to 5%, 69% of potential metazoan nutrition is from ciliates, but this drops to 26% when protozoan GGE is 5% and to 16% when all microbial GGE is 5%. The model thus suggests that in less productive situations, where production of microphytoplankton is small, the assimilation efficiency of protozoans feeding directly on pico- and nanoautotrophs is a critical factor in supplying food for metazoans. The model is insensitive to large changes in the amount of production of heterotrophic bacteria, so, unlike the Mc Manus flow analysis, heterotrophic bacteria do not appear to be a significant link to metazoans. Theirs is the longest food chain. The assimilation of pico- and nanoautotrophs by protozoans does appear to be a potentially significant link to metazoa, and some validation of this is the demonstration by Legendre and Rassoulzadegan [these Proceedings] that multivorous planktonic food webs are the most common kind of food web and also the most stable.

Examination of a broad range of examples of food webs suggests that the amount of connectivity in multivorous food webs is high. How effective these connections are in providing nutrition to metazoans depends on the structure of the web and the efficiency of trophic transfers. Probably the typical detritus or aggregate food web contains more trophic transfers than we usually incorporate into models. From Moloney et al. [21] onward, models are condensed size-hierarchies containing heterotrophic bacteria, flagellates, and ciliates. Within these categories in the real ocean many food chains on separate and only partially parallel paths may co-exist. How well the condensed models simulate that reality is debatable. In order to evaluate quantitatively the contribution of microbial food webs to metazoans in the sea, we need more detailed models in concert with more empirical studies of microbial processes in the real ocean, especially of protozoan efficiency under natural conditions. Understanding microbial food webs in the ocean is a formidable project, and further descriptive microbiology is needed to help us fill out models for better simulations of the total food web. Would this post-modern natural history be worth the cost? I would argue that the only information that is not useful is information we do not yet know how to use. The efficiency of cows is being increased with accumulated knowledge. Increasing the efficiency of other food webs is simply a longer-term project.

Acknowledgments

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