

The role of the microbial loop in Antarctic pelagic ecosystems

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The paradigm of the pelagic food web organization in Antarctic waters is undergoing fundamental revision due to recent evidence that large fractions of material and energy flow through the microbial food web. We suggest that, because of the unique Antarctic ecosystem conditions, the microbial food web performs some roles that are fundamentally different from those in oligotrophic temperate and tropical waters: 1) during winter, bacterial production, at the expense of slow-turnover DOM (dissolved organic matter) from the previous summer, could be a significant factor in the survival of overwintering animal populations; 2) microbial regeneration of ammonium in nitrate-replete Antarctic waters may spare the reductants necessary for nitrate assimilation and thus enhance primary productivity of deep-mixed light-limited phytoplankton; and 3) the small diatoms and phytoflagellates which dominate the Antarctic pelagic primary production are apparently directly digestible by the metazoan herbivores, whereas cyanobacteria which dominate the primary productivity in lower latitude oligotrophic waters are not digestible by the metazoan herbivores. These roles performed by the microbial loop may, in part, explain why Antarctic waters, in contrast to the lower latitude oligotrophic waters, have high levels of tertiary productivity despite low primary productivity.

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Introduction

The classical notions of pelagic food web organization in Antarctic waters are undergoing fundamental revision (Hewes et al. 1985). For long it had been believed that material and energy flows occurred dominantly along a linear food chain: large diatoms → krill → whales, seals, birds, etc. The idea of a simple and short food chain was appealing because it was consistent with the widely held perception of very high tertiary production in Antarctic waters. Recent evidence suggests, however, that a large fraction of primary production is due to pico- and nanoplankton rather than large diatoms. Brökel (1981) showed that small (<20 µm) phytoplankton comprised 73% of the chlorophyll *a* and 83% of the primary production in an extensive areal coverage between the Bellingshausen Sea and South Georgia. Hewes et al. (1983), after performing a comprehensive circumpolar sampling, showed the generality of the results of Brökel (1981) regarding the significance of small autotrophs (the dominance of pico- and nanoplanktonic autotrophs is, however, not the case in coastal blooms; Holm-Hansen et al. 1989).

A second departure from the classical view is the realization that Antarctic waters are oligotrophic in terms of primary production in spite of the high residual nutrients. We use the term “hypoproductive” in describing these waters in order to distinguish them from the oligotrophic waters in lower latitudes where low primary productivity is due to low nutrient concentrations. Primary productivity rates for the region are on the order of 100–300 mg C m⁻² d⁻¹ (Holm-Hansen et al. 1977; Brökel 1981; El-Sayed & Taguchi 1981), which is comparable to lower latitude oligotrophic regions.

The focus on the small organisms and the hypoproductive view of the Southern Ocean has now uncovered a dynamic microbial food web with potential for substantial energy and material transfer. Previous notions that Antarctic waters are too cold to permit bacterial growth (Sorokin 1971) have been refuted by measurement of bacterial abundance and growth rates which have been found to be comparable to measurements from lower latitude open ocean waters (Hodson et al. 1981; Hanson et al. 1983; Fuhrman & Azam 1980; Azam et al. 1981; Rivkin 1991). Two questions are now being asked: How can the microbial

food web be incorporated into the structure and dynamics of the Antarctic pelagic food web and, given the unique physicochemical characteristics of the Antarctic ocean, is the ecosystem role performed there by the microbial loop different from that in the lower latitude oligotrophic waters?

This paper suggests that the microbial loop in Antarctic waters performs some roles that are fundamentally different from roles performed in lower-latitude oligotrophic waters. We believe that this is due to the unique ecosystem conditions which include high residual nutrients, extreme seasonality of solar radiation, and the wind-driven deep mixing of the plankton. Finally, we propose ways of integrating the microbial loop activities with the Antarctic pelagic ecosystem dynamics. We have taken the liberty of generalizing from the limited amount of available data for the purpose of stimulating discussion and formulating new testable hypotheses.

Transfer of bacterial production to protozoa and metazoa

In temperate and tropical waters bacterial carbon demand is equal to roughly one-half of the primary production which becomes dissolved and follows the idealized pathway: DOM → bacteria → protozoa → metazoa (Azam et al. 1983; Cole et al. 1988). In this pathway bacteria salvage the energy lost to the particulate food web as DOM and potentially transfer it to tertiary consumers. In Antarctic waters the DOM-based bacterial production could be a source of food for metazoa during summer, and particularly during the dark winter in the absence of primary production. Bacterial production during the austral spring and summer in open ocean waters is in the range of 1 to few mg C m⁻³ d⁻¹ (Azam et al. 1981; Hanson et al. 1983) while the rates in coastal waters can be higher. In Antarctic waters microflagellates and ciliates avidly consume bacteria (Garrison et al. 1986; Lessard & Rivkin 1986; Buck & Garrison 1988). Marchant & Nash (1986) found that krill can ingest organisms in the size range of flagellates and ciliates (few to few tens µm) although large diatoms are preferred (Holm-Hansen & Huntley 1984). Some of the bacterial production could thus be potentially available to metazoa, including krill. From work in temperate and tropical waters, it is commonly believed that

bacterial biomass is largely mineralized within the multitrophic level microbial loop (Ducklow et al. 1985). However, others (King et al. 1980; Azam & Ammerman 1984; Crocker et al. 1991) found that bacteria can be directly utilized by some specialist metazoa (e.g. pelagic tunicates) and by "unintentional bacterivores" which may ingest aggregated or particle bound bacteria. While direct measurements in Antarctic waters have not been made, metazoa such as salps and krill may feed on free, particle-bound and aggregated bacteria.

Digestibility of phytoplankton by metazoa: consequences for trophic transfer efficiency

An interesting, and possibly important, contrast should be noted here between the Antarctic and the temperate or tropical food webs in low productivity regions. Antarctic waters do not harbor cyanobacteria of the genus *Synechococcus* (Marchant et al. 1987; Letelier & Karl 1989) which is responsible for a significant, even dominant, portion of the primary production in oligotrophic waters (Li et al. 1983; Platt et al. 1983). The Antarctic pico- and nanophytoplankton are mainly small diatoms or phytoflagellates. Metazoan herbivores apparently cannot digest *Synechococcus* (Silver & Bruland 1981; Silver & Alldredge 1981; Johnson et al. 1982); their production must be channeled through protozoa, which can digest *Synechococcus*, to the higher trophic levels. This additional step in energy transfer would reduce the total energy transferred to the higher trophic levels. On the other hand, the small diatoms and phytoflagellates which constitute the nanoautotrophic biomass in Antarctic waters are presumably ingested as well as digested by the herbivores including the krill (Marchant & Nash 1986). Thus, a part of the pico- and nanophytoplankton production in the Antarctic waters might be transferred directly to the larger grazers. This difference may, in part, explain why the Antarctic waters have higher levels of tertiary productivity, despite low primary productivity. Digestibility of the dominant primary producer (as in the Antarctic waters) should hardly be surprising; indeed, it is the indigestibility of the often-dominant primary producer (*Synechococcus*) in the temperate and tropical waters which seems intriguing. In any event, the con-

sequence may be that in Antarctic waters the grazing food chain is qualitatively (enzymatically?) better equipped to utilize the primary production and thus to support a high tertiary production.

Temporal variation in phytoplankton-bacteria coupling

Because of the extreme seasonality of solar radiation (and therefore of carbon reduction) in Antarctic waters, the significance of bacterial production for the food web also varies seasonally. Rivkin (1991) showed that in McMurdo Sound, Antarctica, bacterial production ($30\text{--}90\text{ mg C m}^{-2}\text{ d}^{-1}$) in the early Spring (August–October) was in fact 22 to 36-fold greater than the primary productivity. If we assume a 50% assimilation efficiency, then the bacterial carbon demand would be 44 to 72-fold greater than the primary production. Bacterial production was not unusually high, but the primary production prior to the bloom was extremely low ($1.2\text{--}2.8\text{ mg C l}^{-1}\text{ d}^{-1}$). The situation was dramatically reversed as the phytoplankton bloom started in mid-November and primary production completely dwarfed bacterial production (10 to 190-fold). However, the shift from virtually unmeasurable primary production to a strong bloom is an ice edge and coastal waters phenomenon; open ocean waters apparently do not experience a significant spring bloom.

These results have implications for bacteria-phytoplankton coupling and food web dynamics. During winter as well as during the pre-bloom period, bacterial production could contribute to the energy needs of protozoa as well as of larger animals. Further, Marchant (1990) proposes that choanoflagellates (which are eaten by krill) can directly utilize high molecular weight (>4000) polysaccharides. The possible significance of DOM in supporting Antarctic pelagic food webs raises the question of the source of DOM during this dominantly heterotrophic period.

It is generally assumed from work in temperate and tropical waters that DOM is derived from phytoplankton or detritus by various mechanisms of exudation or solubilization. The extremely low chlorophyll *a* and primary productivity in the pre-bloom waters make phytoplankton a minor contributor to the DOM and suggest that detrital sources of bacterial substrates may be more

important. Possible sources include the slow-turn-over DOM components carried over from the previous summer, and DOM and POM derived from the generally rich sea-ice communities. It thus appears that strong seasonality of both bacteria and phytoplankton production may involve temporally and perhaps also spatially loose coupling between primary production and bacterial utilization of organic matter via the accumulation of DOM during the summer and its utilization during winter and early spring. The implicit assumption here is that a significant fraction of the DOM pool turns over very slowly, with turnover times on the order of months rather than days. Long-lived DOM might include some polymers (e.g. complex carbohydrates) that are not readily hydrolysed. Conceivably, some easily utilizable substrates when bound to (or conjugated with) "humic" or "fulvic" material might also become less readily accessible and thereby constitute a "nutritional buffer". If this idea is correct it would have important implications for energy supply for metazoa during winter.

Remineralized nitrogen as an energy source

Nutrient regeneration is an important role of the microbial loop in the productivity mechanisms of the oligotrophic waters since it reduces the gravitational loss of nitrogen contained in sinking organic matter. In the Antarctic waters, which generally have very high concentrations of plant nutrients sustained through physical processes, the role of the microbiota in reducing nitrogen loss via sinking would seem unimportant. However, nitrogen remineralization to ammonium could enhance primary production by conserving energy within the depth range of growing phytoplankton. One hypothesis which attempts to explain why the nutrient replete Antarctic waters have only modest primary productivity is that it is light-limited; wind-driven deep mixing reduces the mean irradiance experienced by the cells (Holm-Hansen et al. 1989). It has been shown (Rönner et al 1983; Koike et al. 1986) that in Antarctic waters 50–85% of the nitrogen demand for primary production is satisfied by the regenerated ammonium despite the presence of $15\text{--}30\text{ }\mu\text{mol l}^{-1}$ nitrate. The preference for ammonium over nitrate is a well-known phenomenon from a number of studies in Ant-

arctic waters and elsewhere (see Dortch 1990 for review). Ammonium uptake spares the reduction potential which the phytoplankton would otherwise use to reduce nitrate to ammonium since up to one third of the reducing power produced by photosynthesis can be required to reduce nitrate (Lasoda & Guerrero 1979; Syrett 1981). Preference for ammonium over nitrate is generally maximal at low light conditions (but see Thompson et al. 1989). So, the microbial loop in Antarctic waters causes saving of reductant and potentially enhance carbon fixation through nitrogen remineralization by a fundamentally different mechanism than in temperate or tropical oligotrophic waters. Ammonium oxidation and carbon fixation by chemoautotrophic bacteria could be an additional input into Antarctic food webs as reported for waters below the Ross Ice Shelf, Antarctica (Horrihan 1981).

Synthesis

The emergent role for the microbial loop in the Southern Ocean as compared to lower latitude oligotrophic waters include the absence of a competitive advantage over the grazing food chain for the dominant autotrophic nanoplankton due to the qualitative difference of the nanoplanktonic autotroph in Antarctic waters (absence of *Synechococcus*). A second ecosystem role of the microbial loop is to channel DOM into the particle phase of the food web via bacterial production, potentially enhancing energy supply to metazoa. This function of the microbial loop takes on added significance in Antarctic waters during the dark winter when primary production is absent and all secondary production is presumably supported by a detritus based food web. This role is diminished during the austral summer where primary production greatly exceeds bacterial production. Finally, in low latitude oligotrophic waters, which are nitrogen-depleted, the microbial loop serves to efficiently remineralize nutrients and thereby tends to reduce nitrogen loss through sinking of organic matter. In Antarctic waters conservation of energy, not the conservation of nitrogen in the upper waters, may be a critical factor in regulating primary production.

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