

Carbon and the Antarctic Marine Food Web

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33. We thank R. Tsien, W. Horne, L. Elferink, J. Pevsner, and S. Bajjalieh for discussions and critical reading of the manuscript; R. Kelly, L. Reichardt, and W. J. Nelson for provision of antibodies; A. Randall for preparation of hippocampal neuron cultures (*21*); and K. Miller for providing bacterially expressed p65-IIs (*18*). Supported by the National Institute of Mental Health. N.C. is a Medical Scientist Training Program trainee supported by NIH grant 2T32G07365.

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TECHNICAL COMMENTS

Carbon and the Antarctic Marine Food Web

M. Huntley *et al.* present (*1*) a model of an Antarctic marine food web and suggest that top predators in the Southern Ocean are responsible for a large efflux of carbon into the atmosphere, up to 20 to 25% of primary production. These values are probably an order of magnitude too large because Huntley *et al.* have used an oversimplified food web and invalid assumptions and parameter values.

In the model (*1*), phytoplankton respiration is not accounted for, and all calculations refer to net rather than total primary production, which elevates the estimated contribution of all heterotrophs to the carbon flux. Net primary production, or photosynthetically fixed carbon (*P*), is apportioned between macrozooplankton (P_Z) and the microbial loop (P_L). Mean values of 0.875 (sensitivity range 0.08 to 0.95) and 0.125 (0.2 to 0.05) were assigned to P_Z and P_L, respectively. That is, in all situations, it is assumed that the majority (at least 80%) of net primary production is directly channeled to macrozooplankton, with at most 20% entering the microbial loop. It is further assumed (*1*) that all fecal material produced by the microbial loop is ingested by macrozooplankton, bringing the total proportion of net primary production reaching macrozooplankton to 95%. In general, however, much of the carbon fixed during primary production in marine pelagic systems is believed to enter the microbial food web (*2*), and studies in productive coastal regions indicate that macrozooplankton probably consume no more than 20% of primary production (*3*). The relative abundances of protozooplankton and the structure of Antarctic marine food webs are sufficiently similar to those of lower latitude regions (*4*) that the possibility of a grazing pathway dominated by microbes should be incorporated in the model.

The value of P_L in the model apparently was chosen because bacterial production has been measured as 7 to 14% of phytoplankton production near the ice edge in the austral spring (*5*) and because bacteria do not comprise a large fraction of total microbial biomass (*6*). However, this assumes that the only production that enters the microbial loop is that of bacterioplankton. Heterotrophic flagellates, other protozooplankton, and small microzooplankton feed directly on phytoplankton cells of the appropriate size (*4*). Because most chlorophyll in the Antarctic is contained in cells smaller than 20 μm and because krill generally eat particles greater than 30 μm (*7*), a considerable factor may be heterotrophic organisms within the microbial loop grazing on phytoplankton (*4*, *7*, *8*). Carbon flux *through* the microbial food web may be low, but it does not follow that carbon *entering* the microbial food web is also reduced, as assumed in the model.

Values of growth efficiencies and carbon assimilation efficiencies in the model appear to be inappropriately large. This is a result of treating aggregations of organisms as trophic levels, when it would be more appropriate to consider them as food webs. For example, the microbial loop is given a mean growth efficiency (K_L) of 0.35 and comprises bacterioplankton, heterotrophic flagellates, ciliates, and many other protozoa and small zooplankton. Carbon entering this compartment may undergo four or five trophic transfers before being packaged into a form that can be eaten by macrozooplankton. In such a scenario, growth efficiency of the compartment would be expected to be approximately 0.5 to 1.5% (*9*), rather than the 35% assumed by Huntley *et al.*

In all instances, the model overestimates the amount of carbon being transferred to macrozooplankton, which leads to invalid estimates of carbon fluxes in the food web. If revised estimates of parameters are used in the model ($P_Z = 0.20$, $K_L = 0.01$), a different result is obtained, with birds respiring approximately 5% of *net* carbon fixed and the microbial component approximately 60%. Thus, marine birds and mammals probably play a minor role as producers of atmospheric CO_2, especially when compared with microbial plankton.

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9. If it is assumed that growth efficiencies (K) for each trophic transfer within the microbial compartment are 35%, after n trophic transfers, the resulting growth efficiency of the microbial loop will be 0.35^n. Substituting $n = 4$ and 5 gives estimates of K_L of 0.015 and 0.005, respectively.

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Response: C. L. Moloney suggests that we overestimated the potential of Southern Ocean birds and mammals to respire CO_2 to the atmosphere (*1*). On the basis of estimates for the Benguela Current, she has found (*2*) that zooplankton probably use only 20% of the primary production. This would require that 80% of primary production enter the microbial loop. We have no disagreement with these results, which are characteristic of a subtropical environment. However, studies cited in our *Science* report (*3*, *4*) and results from our ongoing Research on Coastal Antarctic Ecosystem Rates (RACER) program (*5*) indicate that less than 10% of primary production enters the microbial loop of South-

ern Ocean waters, particularly in highly productive coastal and ice-edge ecosystems. The exact nature of the apparent suppression of microbial loop processes in eutrophic Antarctic ecosystems remains unresolved but is actively under investigation.

Contrary to models of the microbial loop in Southern Ocean waters as presented by Hewes (6), Moloney, and others, which assume that transfer rates through the microbial loop are similar to those at lower latitudes, our model is based on direct measurements of such rates in Antarctic coastal ecosystems. The spring bloom in these regions persists for several months (7) and is characterized by a dominance of large diatoms among the phytoplankton (8); high rates of new production and particle flux from the euphotic zone (9, 10); a general dearth of heterotrophs, including bacterioplankton (4, 11); and low rates of protozoan grazing (12). Moloney's assumptions about the role of microbial loop processes appear to be inappropriate for these hypereutrophic spring blooms. Her description of an ecosystem dominated by small (less than 20 μm) algae, large populations of microheterotrophs, and numerous trophic levels within the microbial loop does not agree with field observations made in these coastal regions, which are the principal feeding sites of Antarctic birds and mammals.

A challenge to our model would have to demonstrate that the food web structure or the values of nondimensional constants we used are incorrect or that new data produce a significantly different result. We do not consider the extrapolation of data from a subtropical ecosystem to be an adequate replacement for measurements made in the Southern Ocean.

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REFERENCES AND NOTES

1. M. E. Huntley, M. D. G. Lopez, D. M. Karl, *Science* **253**, 64 (1991); Equation 3 in (*1*) should read:
$$R_B = (a_B - K_{1B})\{K_{1Z}[(1 - a_L)P_L + P_Z + K_{1L}P_L][P_B + (K_{1F}P_F)]\}$$
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