Reports

Top Predators in the Southern Ocean: A Major Leak in the Biological Carbon Pump

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Primary productivity in the Southern Ocean is approximately 3.5 gigatons of carbon per year, which accounts for nearly 15 percent of the global total. The presence of high concentrations of nitrate in Antarctic waters suggests that it might be possible to increase primary production significantly and thereby alleviate the net accumulation of atmospheric carbon dioxide. An analysis of the food web for these waters implies that the Southern Ocean may be remarkably inefficient as a carbon sink. This inefficiency is caused by the large flux of carbon respired to the atmosphere by air-breathing birds and mammals, dominant predators in the unusually simple food web of Antarctic waters. These top predators may transfer into the atmosphere as much as 20 to 25 percent of photosynthetically fixed carbon.

IT HAS BEEN SUGGESTED THAT THE high primary production of the Southern Ocean (1–4) could be further increased by the addition of iron (5) to take advantage of the generally high concentrations of dissolved nitrate (6). The result would be to increase the activity of the biological carbon pump and to sequester atmospheric CO_2. However, little consideration has been given to the ultimate fate of this carbon as it is transferred through the Antarctic marine food web. Principal components of this food web are phytoplankton (P); macrozooplankton (Z), mainly copepods and krill; fishes and squid (F); birds and mammals (B); the microbial loop (L); and the sinking flux of organic carbon to the benthos (f). We modeled the annual mean flux of carbon through this food web, considering bird and mammal respiration, a term previously neglected. The structure of the model (Fig. 1) reflects available knowledge of trophodynamic relations in the food web of the Southern Ocean (7).

Relative fluxes of carbon in our model depend only on transfer coefficients between trophic levels; absolute fluxes are driven by the magnitude of primary production, which need not be specified. Total photosynthetically fixed carbon (P) flows through a succession of trophic compartments, x. P_x is the proportion of production by compartment $x - 1$ that enters compartment x. P is

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initially partitioned between the zooplankton (P_Z) and the microbial loop (P_L) compartments (Fig. 1), on the assumption that the sinking flux of algal cells and the production of dissolved organic carbon during photosynthesis are negligible (8, 9):

$$P_L + P_Z = P = 1 \qquad (1)$$

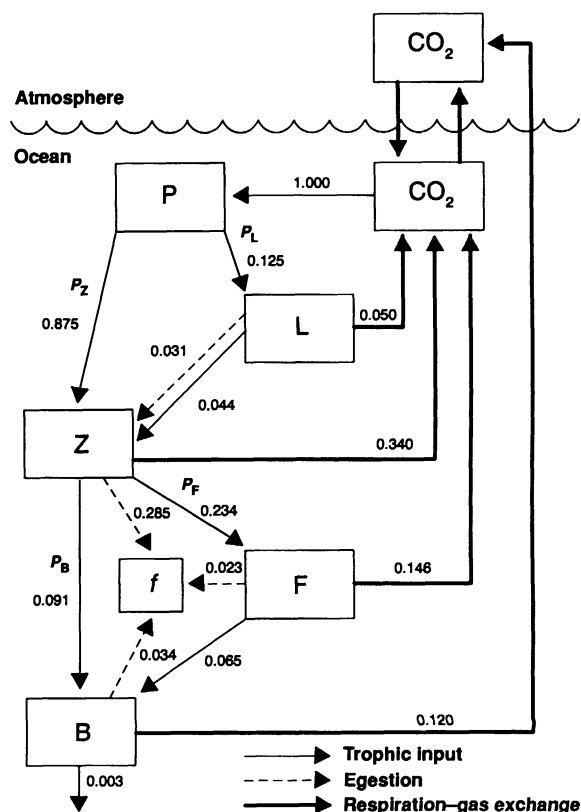The rate of carbon transfer through compartment x is controlled by growth (G_x),

Fig. 1. Antarctic marine food web structure and model output values for the reference scenario, for an initial photosynthetic carbon fixation of 1 unit. Primary production (P) is partitioned into a fraction consumed by macrozooplankton (P_Z), and the remainder is consumed by the microbial loop (P_L); macrozooplankton consume the entire production of the microbial loop, as well as all fecal matter produced by protozoa (12). Production of macrozooplankton is partitioned into a fraction consumed by fishes and squid (P_F), and the remainder is consumed by birds and mammals (P_B); birds and mammals are assumed to consume the production of fishes and squid. All fecal matter is assumed to sink to the benthos, represented by f. The CO_2 produced by respiration of birds and mammals is presumed to enter the atmosphere directly, without opportunity for gas exchange with seawater; CO_2 respired by all other biota is assumed to go directly into seawater.

ingestion (I_x), egestion (E_x), and respiration (R_x), which are related by

$$G_x = I_x - E_x - R_x \qquad (2)$$

Each parameter may be expressed as a function of the assimilation efficiency $([I - E]/I$, or $a)$ and the gross growth efficiency $(G/I$ or $K_1)$. Thus, each term in Eq. 2 can be evaluated for each compartment as shown in Table 1. It is assumed that all growth in compartment $x - 1$ is consumed at higher trophic compartments. Estimates of a, K_1, and P_x based on values reported in the literature are given in Table 2. Mean values are arithmetic averages of the number of available measurements for each parameter. Minimum and maximum values for each parameter are calculated as the mean $\pm$ 1 SD and are defined, respectively, as those values that either minimize or maximize the flux of CO_2 to the atmosphere.

Primary production is assumed to be partitioned between macrozooplankton and the microbial loop in the proportion 0.87:0.13 for the reference scenario. In open waters of the Southern Ocean the microbial loop may be more important; however, recent measurements in coastal Antarctic ecosystems suggest that the carbon flux through the microbial loop is low (10, 11). For sensitivity analysis in our model, we assumed a range of 0.8:0.2 to 0.95:0.05 for P_Z:P_L (Table 2). Fecal production by the microbial loop is assumed to be ultimately consumed

Trophic Input
Egestion
Respiration–gas exchange

Table 1. Equations describing the flow of carbon between trophic compartments in terms of physiological rates. G_{x-1}, growth of compartment $x - 1$; P_x, proportion of G_{x-1} entering compartment x; a_x, assimilation efficiency of compartment x; K_{1x}, gross growth efficiency of compartment x.

Ingestion:	$I_x = G_{x-1} P_x$
Egestion:	$E_x = (1 - a_x) I_x$
Respiration:	$R_x = (a_x - K_{1x}) I_x$
Growth:	$G_x = (K_{1x}) I_x$

by zooplankton (12).

The ratio of macrozooplankton production consumed by fish and squid to that consumed by birds and mammals (P_F:P_B) was calculated from information on the dietary composition of consumers and on the relative production of the principal macrozooplankton (krill and copepods). Krill and copepod biomass are estimated to be approximately equal (13). A conservative assumption would be that their production is

Table 2. Values of the parameters used in the model. Maxima and minima, calculated as mean value ± 1 SD, are those values that respectively increase or decrease the estimate of CO_2 flux to the atmosphere. All parameters are dimensionless. Reported values of assimilation efficiency (a) are based on a recent summary of measurements for bacteria and protozoa (29), on 98 measurements in 39 species of marine invertebrates (30), and 23 measurements in 13 species of marine fishes (30) and are based on the assumption that the high value for birds and mammals is equal to that for birds (31), the low value is equal to that for Southern Ocean blue and fin whales (32), and the mean is halfway between. Reported values for gross growth efficiency (K_1) are based on a recent review for bacteria and protozoa (29), on 8 measurements for two species of Arctic copepods (30) and measurements for each of 7 larval stages of Antarctic krill (33), on measurements for 14 species of fish (30), and on the mean of measurements on birds (34), Southern Ocean whales (32), seals (18), and mammals in general (34). The protocol for selecting values of P_x is described in the text.

Param-eter	Value			Reference
	Mean	Maxi-mum	Mini-mum	
K_{1B}	0.017	0.016	0.019	(18, 32, 34)
K_{1F}	0.276	0.362	0.190	(30)
K_{1Z}	0.342	0.472	0.211	(30, 33)
K_{1L}	0.350	0.600	0.100	(29)
a_B	0.785	0.810	0.760	(31, 32)
a_F	0.900	0.980	0.820	(30)
a_Z	0.700	0.870	0.530	(30)
a_L	0.750	0.600	0.900	(29)
P_B	0.281	0.375	0.238	(13–19)
P_F	0.720	0.625	0.763	(13–19)
P_L	0.125	0.050	0.200	(10, 11)
P_Z	0.875	0.950	0.800	(10, 11)

also equal. Approximately 35% of krill production is consumed by fish and squid, and the remainder is consumed by birds and mammals (14). In the model, birds and seals are assumed to eat no zooplankton other than krill (15–18). Thus, of the homeotherms, only whales consume copepods. Whales are estimated to consume 10% of the krill production (14) and, from the dietary composition of various whale species in the Southern Ocean (19–22), we assume that whales also consume 10% of the copepod production. Taking these arguments together, we find that our maximum estimate of the consumption of zooplankton by birds and mammals results in a value of P_F:P_B equal to 0.63:0.37 (Table 2). The balance of copepod production is then taken up by fish and squid. However, copepod production may be double or perhaps as much as triple krill production (23). Applying the assumed partitioning of krill and copepod production between poikilotherm and homeotherm compartments to these production estimates results in the mean and minimum P_F:P_B ratios given in Table 2.

The respiration of birds and mammals, R_B, as a fraction of the carbon fixed by photosynthesis (P), can be expressed by the general equation:

$$R_B = (a_B - K_{1B})\{K_{1B}[(1 - a_B)P_L + P_Z$$
$$+ K_{1L}P_L][P_B + (K_{1F}P_F)]\} \quad (3)$$

R_B was calculated for the mean values of parameters in Table 2. We calculated minimum and maximum estimates for R_B, substituting into Eq. 3 the mean parameter values ± 1 SD, as appropriate. Other terms in the model, the rates of ingestion, egestion, growth, and respiration at each trophic level, were calculated for scenarios corresponding to the mean, minimum, and maximum rates of R_B (Table 3). We also estimated the sinking carbon flux as a fraction of the photosynthetically fixed carbon, corresponding to f (24), which includes all losses due to grazing but which considers as negligible those losses due to sinking of algal cells (8) and production of dissolved organic carbon (9). Closure of the model is given by:

$$R_B + R_F + R_Z + R_L + E_B$$
$$+ E_F + E_Z + G_B = 1 \quad (4)$$

In the reference case, R_B is expected to return to the atmosphere about 12% of the photosynthetically fixed carbon as CO_2, with minimum and maximum values of 22.5 and 5.0%, respectively. The most important terms affecting R_B in the model are K_{1Z}, P_L:P_Z, and P_F:P_B. Sensitivity analysis showed that the gross growth efficiency of zooplankton, K_{1Z}, was far more influential

than any other term. Model estimates of the annually averaged f range from 0.18 to 0.41, which is comparable to direct estimates of new production for Antarctic ecosystems (25, 26).

On the basis of our model, as much as 0.86 gigaton of carbon as CO_2 could be returned to the atmosphere per year through Antarctic bird and mammal respiration (4, 27). This represents the average annual efflux of CO_2 from the ocean due to respiration of birds and mammals, but there are likely to be distinct temporal and spatial inhomogeneities to the efflux related to the timing of maximum feeding activity and foraging range. Adélie penguins, crabeater seals, and baleen whales are not only the principal consumers of macrozooplankton, but they also constitute the large majority of bird and mammal biomass in the Southern Ocean. All of these species have their peak feeding period during the austral spring and summer (October to February). Adélie penguins may forage offshore, but not in the open sea (16). Crabeater seals tend to be associated with pack ice and thus would forage near the ice edge and under the ice (18). Baleen whales, except the minke, generally do not proceed far south of the ice edge (20).

These distributions suggest that respiration of air-breathing predators will be most concentrated relatively near the Antarctic continent and the few polar islands. It is in such nearshore regions that the greatest atmosphere-ocean disequilibrium in pCO_2 has been observed for 1 to 2 months during the spring bloom of phytoplankton (26, 27).

Table 3. Model output values of respiration (R_x), egestion (E_x), growth (G_x), and ingestion (I_x) at each trophic level. Output values are expressed as a fraction of the total primary production, if we assume mean parameter values (Table 1) or those parameter values required to maximize (Max) or minimize (Min) respiration by birds and mammals (R_B). Also included is the predicted f for each scenario. Mean output values are shown graphically in Fig. 1.

Parameter	Mean	Max	Min
R_B	0.120	0.225	0.050
R_F	0.146	0.182	0.085
R_Z	0.340	0.398	0.268
R_L	0.050	0.000	0.160
E_B	0.034	0.054	0.016
E_F	0.023	0.006	0.024
E_Z	0.285	0.130	0.395
E_L	0.031	0.020	0.020
G_B	0.003	0.005	0.001
G_F	0.065	0.107	0.026
G_Z	0.325	0.472	0.177
G_L	0.044	0.030	0.020
I_B	0.156	0.284	0.068
I_F	0.234	0.295	0.135
I_Z	0.950	1.000	0.840
I_L	0.125	0.050	0.200
f	0.319	0.184	0.411

During such bloom periods, the seawater-to-atmosphere flux we quantify in this model will enhance the already large pCO_2 gradients that exist. Furthermore, because the O_2 used in bird and mammal respiration is derived from the atmosphere rather than from the ocean, the anticipated Redfield O_2:CO_2 relations (28) will also be affected. This phenomenon may be a characteristic feature of especially productive Antarctic marine ecosystems caused by seasonally intensive feeding and respiration of highly concentrated birds and mammals. We conclude that the CO_2 respired by birds and mammals may represent a significant inefficiency in the ability of the Southern Ocean to act as a carbon sink. We suggest that similar determinations be made for birds and mammals in other oceans to assess their global role in the biological carbon pump.

REFERENCES AND NOTES

1. W. H. Berger, V. S. Smetacek, G. Wefer, in *Productivity of the Oceans: Past and Present*, W. H. Berger, V. S. Smetacek, G. Wefer, Eds. (Wiley, Chichester, U.K., 1989), pp. 1–34.
2. E. T. Sundquist, *Geophys. Monogr. Am. Geophys. Union* 32, 5 (1985).
3. E. A. Romankevich, *Geochemistry of Organic Matter in the Ocean* (Springer, Heidelberg, 1984).
4. W. O. Smith, Jr., N. K. Keene, J. C. Comiso, in *Antarctic Ocean and Resources Variability*, D. Sahrhage, Ed. (Springer-Verlag, Berlin, 1988), pp. 131–139.
5. J. H. Martin and S. E. Fitzwater, *Nature* 331, 341 (1988); J. H. Martin, *Paleoceanography* 5, 1 (1990).
6. A. L. Gordon and E. J. Molinelli, *Southern Ocean Atlas* (Columbia Univ. Press, New York, 1982).
7. R. M. Laws, Ed., *Antarctic Ecology*, vol. 2 (Academic Press, London, 1984).
8. The loss of algal cells due to sinking during blooms in the Southern Ocean is generally <5% of the net primary production (M. Vernet and D. M. Karl, *Antarct. J. U.S.*, in press; V. Smetacek, personal communication).
9. The production of dissolved organic carbon by Southern Ocean phytoplankton has been placed at <5% of the net primary production [C. Lancelot, G. Billen, S. Mathot, *Belgian Scientific Research Programme on Antarctica, Scientific Results of Phase One (Oct. 85–Jan. 89)* (Science Policy Office of Belgium, Brussels, 1989), vol. 1.
10. G. F. Cota, S. T. Kottmeier, D. H. Robinson, W. O. Smith, Jr., C. W. Sullivan, *Deep-Sea Res.* 37, 1145 (1990).
11. D. M. Karl, O. Holm-Hansen, G. Taylor, G. Tien, D. Bird, *ibid.*, in press.
12. H. Ducklow and A. Taylor, in *Protozoa and Their Role in Marine Processes*, P. C. Reid, C. M. Turley, P. H. Burkill, Eds. (Springer-Verlag, Berlin, 1988), pp. 431–442.
13. G. A. Knox, in *Antarctic Ecology*, M. W. Holdgate, Ed. (Academic Press, London, 1970), vol. 1, pp. 69–96.
14. R. M. Laws, *Am. Sci.* 73, 26 (1985).
15. Approximately two-thirds of Southern Ocean bird biomass is composed of the Adélie penguin (*Pygoscelis adeliae*), which eat krill exclusively; other bird species also rely largely on krill. The dove prion (*Pachyptila desolata*) and the common diving petrel (*Pelicanoides urinatrix*), whose primary food is copepods, make up only a minor part of the bird biomass.
16. J. P. Croxall, in *Antarctic Ecology*, R. M. Laws, Ed. (Academic Press, London, 1984), vol. 2, pp. 533–620.
17. Almost 90% of the Antarctic seal biomass is composed of the crabeater seal (*Lobodon carcinophagus*), whose diet is 90% krill; apart from the fur seal, whose diet is 30% krill, and the leopard seal, which preys upon krill, birds, and seals, other species of Antarctic seals depend primarily on fish and squid.
18. R. M. Laws, in *Antarctic Ecology*, vol. 2, R. M. Laws, Ed. (Academic Press, London, 1984), pp. 621–715.
19. Baleen whales feed on both copepods and krill, but the diets of both minke and sei whales, whose baleen is finer than that of other Southern Ocean balaenopterids, may be predominantly copepods.
20. A. Kawamura, *Sci. Rep. Whales Res. Inst. (Tokyo)* 22, 127 (1970).
21. Odontocetes such as the sperm and killer whales, which are less abundant than baleen whales, prey largely on fish, squid, birds, and other mammals.
22. S. G. Brown and C. H. Lockyer, in *Antarctic Ecology*, R. M. Laws, Ed. (Academic Press, London, 1984), vol. 2, pp. 717–781.
23. R. J. Conover and M. E. Huntley, *J. Mar. Systems*, in press.
24. R. E. Eppley and B. J. Peterson, *Nature* 282, 677 (1979).
25. W. O. Smith, Jr., and D. M. Nelson, *Limnol. Oceanogr.* 35, 809 (1990).
26. D. M. Karl, B. Tilbrook, G. Tien, *Deep-Sea Res.*, in press.
27. P. P. Tans, I. Y. Fung, T. Takahashi, *Science* 247, 1431 (1990).
28. A. C. Redfield, B. H. Ketchum, F. A. Richards, in *The Sea*, M. N. Hill, Ed. (Wiley-Interscience, New York, 1963), vol. 2, pp. 26–77.
29. A. F. Vézina and T. Platt, *Mar. Ecol. Prog. Ser.* 42, 269 (1989).
30. R. J. Conover, in *Marine Ecology*, vol. 4, *Dynamics*, O. Kinne, Ed. (Wiley, New York, 1978), pp. 221–499.
31. R. E. Ricklefs, *Ecology* (Chiron, Portland, OR 1973).
32. I. Everson, in *Antarctic Ecology*, R. M. Laws, Ed. (Academic Press, London, 1984), vol. 2, pp. 783–819.
33. M. E. Huntley and E. Brinton, *Deep-Sea Res.*, in press.
34. W. F. Humphreys, *J. Anim. Ecol.* 48, 427 (1979).
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Evolution of Pollen Morphology

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Over evolutionary time, the morphology of angiosperm pollen has evolved toward an increasing number of apertures, among other things. From a neo-Darwinian point of view, this means that (i) some polymorphism for aperture number must exist and (ii) there must be some fitness increase associated with increasing the aperture number. Pollen types with different aperture numbers often occur in the same species. Such is the case in *Viola diversifolia*. Comparison of pollen with three and four apertures in this species showed that four-apertured grains germinated faster than three-apertured ones but that the four-apertured ones experienced other disadvantages. These results obtained on the gametophyte can be interpreted in terms of strategies of the sporophyte.

THE REDUCTION OF THE HAPLOID phase is one of the most striking characteristics of the evolution of animals and plants. Unlike animals, plants still produce multicellular haploid life stages, the gametophytes. In higher plants, the male gametophyte is the pollen grain. The evolution of pollen has been studied both from a morphological and a physiological point of view. The morphological analyses have been mainly (if not exclusively) devoted to systematics and used in stratigraphic applications. (The exine of pollen is extraordinarily resistant and can easily be extracted from sediments.) This approach relied on the implicit assumption that pollen morphology is constant within a species or a group of species. The view of pollen morphology has thus been very typological. More consideration must be given to the importance of pollen variation within species. Three main features of pollen evolution have been described; only the first two have been studied.

First, there has been an increase through evolutionary time in the speed of pollen tube growth (1, 2). For example, from gymnosperms to angiosperms the rate of pollen tube growth has increased by a factor of 2000 (from 10 to 20,000 μm/hour) (3). These increases in germination and growth rates of pollen tubes have been interpreted as adaptive responses to enhance pollen competitive ability in the style (4). Such competition can play a very important role in the structure and quality of the next sporophytic generation (5–7): pollen grains that have fast growing pollen tubes will be the first to fertilize and thus will transmit more of their genes to the next generation than will slower growing types.

Second, there has been a decrease through evolutionary time in the life expectancy of pollen grains: generally, "primitive" pollen grains are long-lived, whereas "highly

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