sian region would have encountered the prominent Arnhem Land escarpment on moving inland. Malakunanja II occupies a strategic location along its base and may have been brought into use within a few thousand years of first landfall. Any delay is probably accommodated within the estimates of uncertainty about the TL dates. The absence of artefacts in deposits older than 60 kyr at this key site suggests an upper limit on the time of arrival of modern humans in Australia. □

Received 3 January; accepted 8 March 1990.

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ACKNOWLEDGEMENTS. The Office of the Supervising Scientist granted access to the TL dating and gamma-spectrometry facilities and the assistance of staff at the Alligator Rivers Region Research Institute. The Australian National University Radiocarbon Dating Research Laboratory speedily processed ANU-7006. Bill Neiiji, Gagudju Association, Pancontinental Mining Ltd. and Australian National Parks and Wildlife Service gave permission to enter the sites. A. S. Murray wrote the age calculation program and B. W. Smith supplied the red filter. Both are thanked for valuable discussions. M. J. Aitken, D. J. Huntley, G. C. Nanson, J. R. Prescott and D. M. Price provided additional useful comment. R.G.R. is in receipt of a University Postgraduate Research Award. Table 1 and Figures 2 and 3 are Commonwealth of Australia copyright, reproduced with permission.

# Iron in Antarctic waters

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**WE are testing the hypothesis that Antarctic phytoplankton suffer from iron deficiency[1–3] which prevents them from blooming and using up the luxuriant supplies of major nutrients found in vast areas of the southern ocean. Here we report that highly productive[4] (~3 g C $m^{-2}$ $day^{-1}$), neritic Gerlache Strait waters have an abundance of Fe (7.4 nmol $kg^{-1}$) which facilitates phytoplankton blooming and major nutrient removal, while in low-productivity[4] (~0.1 g C $m^{-2}$ $day^{-1}$), offshore Drake Passage waters, the dissolved Fe levels are so low (0.16 nmol $kg^{-1}$) that the phytoplankton are able to use less than 10% of the major nutrients available to them. The verification of present-day Fe deficiency is of interest as iron-stimulated phytoplankton growth may have contributed to the drawing down of atmospheric $CO_2$ during glacial maxima[2,3]; it is also important because oceanic iron fertilization aimed at the enhancement of phytoplankton production may turn out to be the most feasible method of stimulating the active removal of greenhouse gas $CO_2$ from the atmosphere, if the need arises (J.H.M., manuscript in preparation).**

Seawater samples were collected using Teflon-coated, 30-litre Go-Flo bottles suspended on Kevlar line. After filtering through 0.4 μm Nucleopore filters, metals were pre-concentrated from the water by organic extraction[5] or, in the case of Mn, Chelex-100 ion exchange[6]. Small chunks of floating ice were gathered and placed in acid-cleaned plastic bags. After allowing the outer surfaces to melt away, the remaining ice was rinsed with Milli-Q water; meltwater was then collected in bottles and acidified with 4 ml of 6M HCl $l^{-1}$. As the ice samples were not filtered, the values reported here represent the metals dissolved in the melted water plus the metals that dissolved from particulates when the acid was added and pH lowered to ≈1.9–2.0. Analyses were performed by graphite furnace atomic absorption spectrophotometry. All procedures were carried out using stringent anti-contamination techniques[7].

In the offshore waters of the Drake Passage (Station 2), Fe concentrations in 10 samples ranged from 0.16 nmol $kg^{-1}$ near the surface to 1.55 nmol $kg^{-1}$ at 1,850 m (Table 1). However, when the Fe data were plotted against depth, a 'saw-toothed' profile was observed. It was subsequently determined that in spite of rigorous cleaning, all samples taken from Go-Flo bottle No. 1 had an extra half nmol or so of Fe as well as excess Mn and Co. Nevertheless, the five remaining 'clean' Drake Passage samples are sufficient for initial comparisons of concentrations with those from other offshore waters with an excess of major nutrients, such as the Gulf of Alaska, as well as comparisons with Antarctic neritic waters, such as those from the Gerlache Strait.

Very similar Fe depth distributions were observed in the Drake Passage and the Gulf of Alaska (Ocean Station 'PAPA'; 50° N; 145° W), that is, very low (≈0.10–0.16 nmol $kg^{-1}$) surface values and increasing concentrations with depth (Fig. 1). As was the case with the Alaska data, increasing Fe values in Drake Passage more or less go along with increasing major nutrient concentrations and decreasing oxygen levels (Table 1); there are not enough data for meaningful regression analysis, however.

Surface Co concentrations (≈25 pmol $kg^{-1}$) were about the same in both regions; however, the subsurface maximum found in Alaska was not observed here. The Mn maximum commonly found in association with northeast Pacific oxygen minima was also missing (Fig. 1), as would be expected, as subsurface Drake Passage oxygen concentrations do not fall below 180 μmol $kg^{-1}$. The surface Mn concentration, 0.08 nmol $kg^{-1}$, is markedly lower than that observed at 'PAPA' (0.52 nmol Mn $kg^{-1}$). Depth profiles of other elements such as Cu, Cd and Zn (Table 1) were similar to those observed in the northeast Pacific.

Neritic Gerlache Strait concentrations of Fe and Mn were 50–60 times higher than those measured in the open-ocean waters of the Drake Passage (Table 1, Fig. 2). Assuming that the Fe requirement of phytoplankton in relation to nitrogen is about 5000N:1Fe (ref. 2), the 7.4 nmol Fe $kg^{-1}$ is more than enough to support the removal of the ≈24 μmol $NO_3$ $kg^{-1}$ occurring in the Gerlache. Clearly, there is no Fe limitation, a fact that we believe helps to explain the very high productivity rates reported here (3 g C $m^{-2}$ $day^{-1}$) (ref. 4) and in other shallow southern ocean coastal regions that should be equally rich in Fe (for example, South Georgia[8] and Deception Island[4]).

In contrast to Fe-rich, shallow, inshore waters, it is apparent that very little Fe is available in offshore Drake Passage waters. For example, if we use an upwelling rate of 0.25 m $day^{-1}$ (ref. 9), the $NO_3$ upwelling to the surface each day (25 mmol $NO_3$ $m^{-3}$ × 0.25 m $day^{-1}$ = 6.25 mmol $m^{-2}$ $day^{-1}$) would be enough to support rates of new phytoplankton productivity of the order of 40 mmol C $m^{-2}$ $day^{-1}$ (6.25 mmol $NO_3$ × C:N Redfield ratio of 6.6). With the same upwelling rate, and assuming a phytoplankton C:Fe demand ratio of 33,000:1 (ref. 2), the ≈0.10 μmol Fe $m^{-3}$ upwelling with the $NO_3$ would support only about 1 mmol C $m^{-2}$ $day^{-1}$. Even using the highest C:Fe ratio[10] for iron-starved phytoplankton (100,000:1) would result in little more than 3 mmol C $m^{-2}$ $day^{-1}$; that is, less than 10% of the carbon that could be fixed with the upwelled nitrogen.

Clearly, insufficient Fe is introduced by upwelling; and as this station is well offshore (230 km from the Antartic Peninsula), the Fe necessary for phytoplankton growth would have to come from an alternative source such as fallout of atmospheric dust. But, this region is known for having the lowest atmospheric dust loads in the world: Prospero[11] reports only 0.5 ng Fe for the South Pole in comparison to 9 and 90 ng Fe $m^{-3}$ for offshore islands such as Oahu and Bermuda.

The low rates of atmospheric dust input are exemplified by the surface Mn concentration observed at this station,

TABLE 1 Hydrographic, nutrient and trace metal data from the March/April 1989 *Polar Duke* cruise

| Depth (m) | Potential temperature (°C) | Salinity (‰) | $\sigma\theta$ (g l$^{-1}$) | $O_2$ | $NO_3$ | $PO_4$ | $SiO_3$ | Fe | Mn | Co | Cu | Cd | Zn |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Station 1, 56°38'S; 65°20'W, 27 March 1989, North Drake Passage | | | | | | | | | | | | | |
| 50 | 6.54 | 34.035 | 26.72 | 274 | 23.0 | 1.60 | 2.0 | 0.16 | 0.26 | 27.1 | 0.71 | 0.26 | 0.24 |
| Station 2, 60°46'S; 63°26'W, 28 March 1989, South Drake Passage | | | | | | | | | | | | | |
| 30 | 2.97 | 33.798 | 26.93 | 314 | 24.8 | 1.78 | 8.8 | 0.16 | 0.08 | 25.4 | 0.97 | 0.28 | 0.63 |
| 60 | 2.96 | 33.802 | 26.93 | 315 | 25.5 | 1.76 | 12.3 | (0.52) | (0.20) | (43.3) | 1.05 | 0.28 | 0.30 |
| 110 | −0.34 | 33.928 | 27.26 | 341 | 29.3 | 2.12 | 25.7 | 0.10 | 0.21 | 25.8 | 1.12 | 0.56 | 1.49 |
| 200 | 1.51 | 34.250 | 27.41 | 300* | 33.9 | 2.39 | 51.7 | (0.85) | (0.45) | (56.3) | 1.46 | 0.75 | 3.86 |
| 300 | 1.89 | 34.399 | 27.50 | 225* | 35.1 | 2.54 | 64.7 | 0.26 | 0.25 | 28.6 | 1.52 | 0.81 | 4.74 |
| 400 | 2.05 | 34.491 | 27.56 | 200* | 35.5 | 2.56 | 70.2 | (0.88) | (0.48) | (47.8) | 1.71 | 0.80 | 5.10 |
| 550 | 2.11 | 34.588 | 27.63 | 180* | 35.4 | 2.55 | 89.8 | 0.40 | 0.29 | 27.4 | 1.68 | 0.77 | 5.25 |
| 1000 | 1.92 | 34.703 | 27.74 | 180* | 33.3 | 2.42 | 96.0 | (0.88) | (0.49) | (40.1) | 1.90 | 0.70 | 5.46 |
| 1420 | 1.56 | 34.723 | 27.78 | 185* | 30.3 | 2.28 | 101.0 | 0.76 | 0.31 | 21.1 | 2.07 | 0.66 | 5.67 |
| 1850 | 0.80* | 34.713* | 27.86* | 205* | 31.6 | 2.40 | 108.0 | (1.55) | (0.77) | (63.8) | 2.38 | 0.66 | 6.34 |
| Station 3, 64°55'S; 63°19'W, 1 April 1989, Gerlache Strait | | | | | | | | | | | | | |
| 15 | 0.92 | 33.641 | 26.95 | 317 | 23.8 | 2.19 | 74.3 | 7.40 | 5.05 | 82.0 | 2.24 | 0.56 | 4.90 |
| 50 | 1.05 | 33.865 | 27.13 | 310 | 22.9 | 2.29 | 81.5 | 4.70 | 4.19 | 58.7 | 2.09 | 0.60 | 5.10 |
| 200 | 0.31 | 34.389 | 27.60 | 272 | 30.7 | 2.65 | 94.0 | 6.85 | 3.86 | 82.0 | 2.16 | 0.70 | 5.90 |
| ice | — | — | — | — | — | — | — | 25.9† | — | 56.6 | 0.02 | 0.02 | — |

Values for $O_2$, $NO_3$, $PO_4$, $SiO_3$ are given in $\mu$mol kg$^{-1}$, Fe, Mn, Cu, Cd, Zn in nmol kg$^{-1}$, Co in pmol kg$^{-1}$.
* Data estimated from GEOSECS Station 78, 61°3'S; 62°58'W, 3 January 1973 (ref. 20). † Total dissolvable Fe. ( ) Contaminated; all taken from Go-Flo No. 1. $\sigma\theta$ is the density of sea water in g l$^{-1}$ based on salinity and potential temperature.

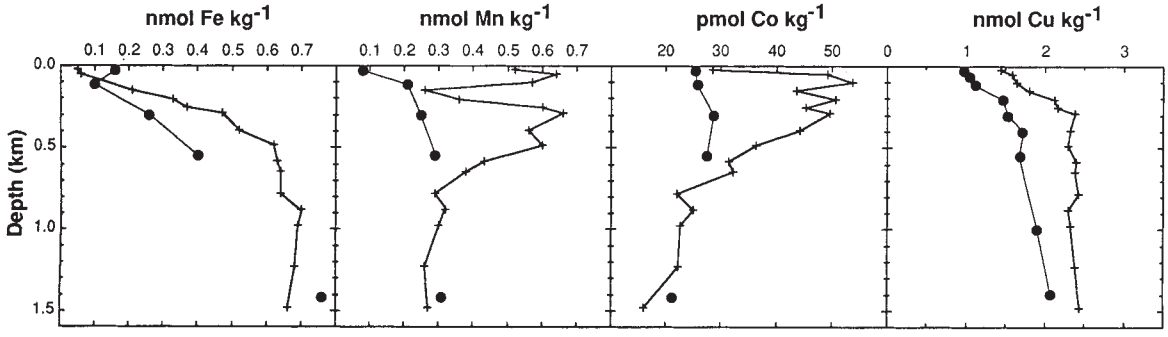


FIG. 1 Drake Passage (Station 2) dissolved Fe, Mn, Co and Cu concentrations (●) compared with those from the Gulf of Alaska (+) Station 'PAPA' (ref. 2).

0.08 nmol kg$^{-1}$. In their comprehensive study of Mn in Pacific Ocean surface waters, Klinkhammer and Bender[12] noted that the correlation between Mn and $^{210}$Pb suggested aeolian control of surface ocean Mn. They also reported that Mn concentrations were lowest in the Southern hemisphere: 0.3 nmol kg$^{-1}$, a value that is about four times higher than the 0.08 nmol we measured in the Drake Passage. To our knowledge, this Mn concentration is the lowest yet reported for surface water in the world ocean; it suggests that Mn deficiency may also be a factor contributing to the limitation of phytoplankton growth in the southern ocean.

In addition to the input from Fe-rich sediments in shallow waters and atmospheric dust in offshore waters, a third Fe supply mechanism exists in the southern ocean—Fe released from melting sea ice. On the basis of the amounts of Fe measured in shallow snow pits (0.02 nmol Fe g$^{-1}$) (ref. 13) and Holocene ice cores (0.03 nmol Fe g$^{-1}$) (ref. 14), Martin[3] estimated that the phytoplankton could fix about 150 mmol C m$^{-2}$ with the Fe made available as sea ice melts during the austral spring and summer (estimates based on 10% available Fe and a C:Fe ratio of 33,000:1). We report here an initial ice Fe concentration of 0.026 nmol g$^{-1}$ (Table 1), an amount that agrees well with the values mentioned above. This was glacial ice of unknown age, however, not annual sea ice. Determining the Fe content of annual sea ice is important in view of the amounts of ice involved: Munk[15], for example estimates that $2.1 \times 10^{19}$ g of ice forms and melts back each year. Obviously, the biological availability as well as the Fe content of the annual ice will need to be known if accurate estimates are to be made of new phytoplankton productivity that could be supported by this potentially important Fe input mechanism.

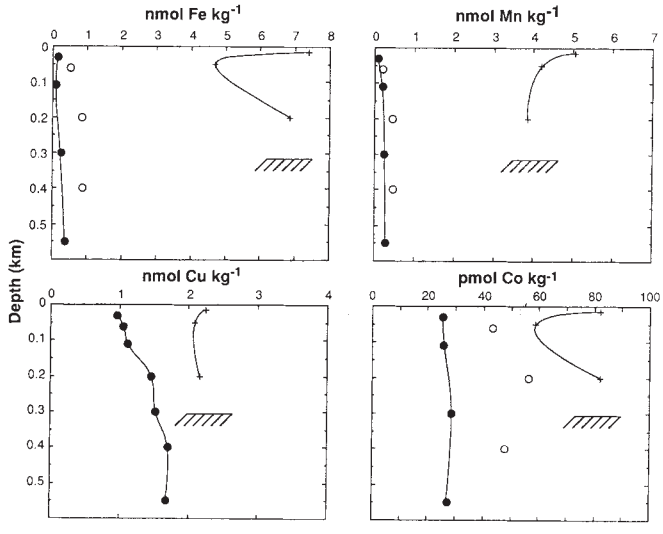


FIG. 2 Drake Passage Fe, Mn, Co and Cu concentrations (●) compared with those (+) from the Gerlache Strait (Station 3). Open circles are contaminated samples collected via Go-Flo No. 1.

In conclusion, the results presented here clearly support the observations of the 1925–27 *Discovery* Expedition scientists—that the neritic areas probably were (and are) rich in phytoplankton because of Fe introduced from land[8,16,17]. The very low dissolved Fe (and Mn) levels in the Drake Passage provide support for our argument[2,3] that present-day plant productivity is limited in offshore waters of the Antarctic because of Fe deficiency. Judging by the unused excess of major plant nutrients, this lack of essential Fe (ref. 18) seems to be severely limiting the power of the 'biological pump' and thus contributing to the raised atmospheric $CO_2$ concentrations typical of previous and present interglacial periods (preindustrial ≈280 p.p.m.) (ref. 19). In contrast, greatly enhanced Fe input from atmospheric dust[2,3,14] may have stimulated phytoplankton growth and increased the power and efficiency of the biological pump, thus contributing to the drawing down of atmospheric $CO_2$ during glacial maxima[19].

*Note added in proof.* We have since shown in experiments in the Ross Sea that Fe will indeed stimulate plankton productivity in the austral spring and summer in amounts that may be relevant to the removal of excess $CO_2$ from the atmosphere. Further details will be published elsewhere. □

Received 19 December 1989; accepted 12 January 1990.

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ACKNOWLEDGEMENTS. We thank Bill Broenkow and Mark Yarbrough for the CTOD data and Sara Tanner for the nutrient analyses. This research was supported by grants from the Biology and Medicine Section of NSF Polar Programs, the ONR Ocean Chemistry Program, and the NSF Marine Chemistry Program.

# Glucagon stimulates the cardiac $Ca^{2+}$ current by activation of adenylyl cyclase and inhibition of phosphodiesterase

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**GLUCAGON exerts positive inotropic and chronotropic effects in the heart[1,2]. Like its glycogenolytic effect in liver cells[3], the cardiac effects of glucagon are often correlated with adenylyl cyclase stimulation[2,4–7]. Therefore, cyclic AMP-dependent phosphorylation of L-type $Ca^{2+}$ channels[8–10] might be involved in the inotropic effect of glucagon. There have been no reports, however, of the effects of glucagon on the cardiac $Ca^{2+}$ current ($I_{Ca}$). Also, the physiological effects of glucagon could involve mechanisms other than stimulation of adenylyl cyclase[11,12]. Here we show that glucagon enhances $I_{Ca}$ in frog and rat ventricular myocytes. The effect of glucagon in rats resulted from a stimulation of adenylyl cyclase. In frogs, however, the effect of glucagon on $I_{Ca}$ was smaller and occurred at a concentration tenfold lower than in rats, and adenylyl cyclase was not modified. In addition, cAMP potentiated the effect of glucagon on $I_{Ca}$ in frog ventricle, which correlated with the observed inhibition by glucagon of low-$K_m$ cAMP phosphodiesterase activity. Therefore, this is an example of a hormone that affects cardiac function in a similar way to a variety of synthetic cardiotonic compounds, such as milrinone and Ro-20-1724 (ref. 13). Inhibition of phosphodiesterase activity by glucagon may be essential in animals in which glucagon increases cardiac contractility but does not effectively stimulate adenylyl cyclase[7,14,15].**

The effects of 1 and 10 μM glucagon on $I_{Ca}$ were recorded from a frog (Fig. 1*a*) and rat (Fig. 1*b*) ventricular cell using the whole-cell patch-clamp technique. Glucagon increased $I_{Ca}$ in both preparations in a dose-dependent and reversible way. Significant differences were found, however, between the two species. In frog, glucagon increased $I_{Ca}$ with a 50% stimulatory concentration ($EC_{50}$) of 41 nM (Fig. 1*c*), whereas in rat, the $EC_{50}$ was more than 10 times this value and the maximal stimulation of $I_{Ca}$ was more than three times that in frog (Fig. 1*d*). Furthermore, not all the frog cells responded to glucagon, whereas every rat ventricular cell did. The lack of responsiveness to glucagon in some of the frog cells was probably due to a notably low level of cAMP (see below).

The effects of glucagon in rat quantitatively resembled the effects of isoprenaline, a β-adrenergic agonist. Furthermore, maximal concentrations of isoprenaline and glucagon did not have an additive effect on $I_{Ca}$ (data not shown), and the effects of glucagon on $I_{Ca}$, like those of isoprenaline, were strongly antagonized by acetylcholine (ACh) (Fig. 2*a*). This indicates that glucagon and isoprenaline act through similar mechanisms in the rat. As β-adrenergic stimulation of $I_{Ca}$ is essentially due to activation of adenylyl cyclase[8–10], we investigated the effects of glucagon on the activity of this enzyme in rat ventricle. As reported previously[2,4–7], glucagon increased adenylyl cyclase activity in a dose-dependent way (Fig. 2*b*), and its effects were antagonized by ACh[16].

In frog, the stimulatory effect of glucagon on $I_{Ca}$ was not reduced by ACh (Fig. 2*c*), in contrast to the activation of $I_{Ca}$ by isoprenaline[10]. Moreover, maximal activation of $I_{Ca}$ by glucagon was about 15 times smaller than that evoked by isoprenaline (Fig. 2*c*). Finally, whereas isoprenaline enhanced adenylyl cyclase activity in a dose-dependent way in frog ventricle, glucagon was unable to modify either basal or isoprenaline-stimulated adenylyl cyclase activity in this preparation (Fig. 2*d*). Therefore, we concluded that the stimulatory effect of glucagon on $I_{Ca}$ in frog cardiac cells was not mediated by enhanced cAMP production.

Cyclic AMP, however, did seem to be involved in $I_{Ca}$ stimulation by glucagon in frog cells. This was suggested by a comparison of the effect of a first application of glucagon to a cell under basal conditions with a subsequent application of the peptide after $I_{Ca}$ had been stimulated by isoprenaline or cAMP. In nine cells in which the basal $I_{Ca}$ was 169.7 ± 22.2 pA (mean ± s.e.m.), an initial application of 3 μM glucagon for 5–6 min increased $I_{Ca}$ by only 7.6 ± 7.2% on average, because five of these nine cells did not respond to the peptide (Fig. 3). After the peptide was washed out, application of submaximal concentrations of isoprenaline (0.1 or 1 μM) or perfusion of the patch pipette[17,18] with cAMP (1 or 3 μM) enhanced $I_{Ca}$ to 969.2 ± 237.1 pA. A subsequent application of glucagon further increased $I_{Ca}$ by 36.4 ± 8.8% (Fig. 3). Also, glucagon increased $I_{Ca}$ more consistently in frog cells under stimulated conditions

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