the forces generated by the gizzards of granivorous birds from several taxonomic groups ranging in body weight from 0.8 to 3.2 kg (*11*) reveal the following linear relationship between a bird's body weight and the force generated by its gizzard:

$$y = 843x + 1210, r = .97$$

where y is the force generated by the gizzard (in kilograms per square meter) and x is the bird's body weight (in kilograms). According to the equation, a 12-kg dodo could have produced forces of about 1.13×10^4 kg/m^2 in its gizzard. Intact nuts of hickory (*Carya ovata*), which fracture under point loads of 152 kg or less, are barely within the crushing capacity of a turkey's (*Meleagris gallapavo*) gizzard, which can generate forces of about 3700 kg/m^2 (*12*). If the dodo had a similar ratio of gizzard force to the maximum load capacity of objects that could be crushed, intact *Calvaria* pits would have been more than strong enough to withstand the forces in a dodo's gizzard. A sample of fresh, intact *Calvaria* pits ($N = 3$) withstood loads averaging 623 kg before fracturing (*13*).

However, if *Calvaria* pits were retained in a dodo's gizzard for extended periods of time, the endocarp could have been progressively abraded until it was thin enough to be crushed. I have estimated that a typical *Calvaria* pit with a maximum diameter of 30 mm would need to be reduced in size by nearly 30 percent before it could be crushed in a dodo's gizzard (*14*). A bird the size of a dodo would almost certainly have passed an object of this size or larger through its intestinal tract. Turkeys readily void through their intestinal tracts uncrushable objects smaller than about 8 mm in diameter (*15*). A dodo would certainly have passed proportionately larger objects, but there is no way to deduce exactly how large.

Perhaps the most convincing evidence that seed-coat dormancy in *Calvaria* can only be overcome naturally by passage through a bird's digestive tract comes from experiments in which I force-fed single, fresh *Calvaria* pits to turkeys. Some of these pits were retained in the turkey's digestive tract for as long as 6 days, and seven of 17 ingested pits were eventually crushed by the bird's gizzard. The remaining ten pits were either regurgitated or passed in the feces after being reduced in size through abrasion in the gizzard. I planted the ten recovered seeds under nursery conditions, and three subsequently germinated. These may well have been the first *Calvaria* seeds to germinate in more than 300 years.

These observations provide empirical support for the hypothesis that the fruits of *Calvaria* had become highly specialized through coevolution with the dodo. After the dodo became extinct, no other animal on Mauritius was capable of ingesting the large pits. As a result, *C. major* has apparently been unable to reproduce for 300 years and nearly became extinct. The findings presented in this report may provide a basis for preserving the species through propagation of artificially abraded seeds.

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13. *Calvaria* pits were subjected to point-loading between two parallel, flat plates of a closed-loop, servo, hydraulic testing machine. A compressive force was applied at a linear rate of loading (226.5 kg/min) until the pits fractured. Loads at fracture were consistent, ranging from 616 to 627 kg.
14. *Calvaria* pits were artificially abraded in a gem tumbler until their maximum diameters were reduced by 10, 20, or 30 percent. They were then subjected to point-loading tests. A 30 percent reduction in diameter reduced the load at fracture by about 50 percent to 310 kg. Extrapolating from the data on turkeys fed hickory nuts, I estimated that any object that fractured under loads of 353 kg or less would have been crushed in a dodo's gizzard.
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16. Supported by grants from the International Council for Bird Preservation, the World Wildlife Fund, and the New York Zoological Society. I thank L. F. Edgerley and the late P. O. Wiehe for pointing out the plight of *Calvaria* and J. W. Dreger for performing point-loading tests.

18 April 1977; revised 16 May 1977

Solar Proton Event: Influence on Stratospheric Ozone

Abstract. *Large-scale reductions in the ozone content of the middle and upper stratosphere over the polar cap regions were associated with the major solar proton event of 4 August 1972. This reduction, which was determined from measurements with the backscattered ultraviolet experiment on the Nimbus 4 satellite, is interpreted as being due to the catalytic destruction of ozone by odd-nitrogen compounds (NO_x) produced by the event.*

It is thought that atmospheric O_3 is destroyed in the stratosphere and mesosphere by catalytic agents and also as a result of reactions with oxygen allotropes. The relative contributions to the destruction of O_3 caused by catalysts are predicted to be altitude-dependent, with odd-hydrogen components (HO_x) dominant in the mesosphere and troposphere and odd-nitrogen compounds (NO_x) and halogens dominant in the stratosphere.

A measurement of changes in the mesospheric O_3 content associated with the solar proton event of 2 November 1969 was reported by Weeks *et al.* (*1*). The first of two rockets carrying ultraviolet O_3 photometers was fired into the initial phase of the event at Fort Churchill, Manitoba; the second rocket was launched 2 days later under quieter conditions. The O_3 concentration was lower during the initial phase of the event by a factor of 2 at an altitude of 54 km and by a factor of 4 at 67 km than it was 2 days later. The changes and the rapid recovery are consistent with the HO_x chemistry in the mesosphere.

Experiments that could confirm the catalytic reaction cycles in the stratosphere have been difficult to carry out and analyze. The effects of the gradual introduction of contaminants can be determined only if the natural variations in the O_3 content are known over appropriate time periods. Transient injections with well-defined spatial and temporal signatures, however, remove the ambiguity associated with the natural variability. Attempts to observe the local effects of NO produced as a result of nuclear weapons tests were reported by Miller *et al.* (*2*) and Christie (*3*).

High-energy solar proton events are capable of depositing large amounts of energy into the polar cap regions at all latitudes above 55° in very short time periods. Crutzen *et al.* (*4*) have pointed out that NO can be produced in the stratosphere during intense solar proton events and that such large-scale production of NO (*5*) should be followed by reductions in O_3 concentrations in the affected regions.

We report here the first observations of an O_3 decrease in the stratosphere associated with a solar proton event. That event on 4 August 1972 was the most intense of any recorded in the last 25 years.

The O_3 concentrations were measured with the backscattered ultraviolet (BUV) experiment (*6*) on the Nimbus 4 satellite, which was launched into a sun-synchronous circular orbit with an inclination of 100° in April 1970. This experiment provides vertical O_3 profiles every 200 km along the orbital track from the O_3 maximum (25 mbar) up to 0.4 mbar by mathematical inversion of the earth albedo at selected wavelengths (*7*); the experiment also provides measurements of total O_3 (*8*).

The daily, zonally averaged O_3 concentrations above the 4-mbar pressure surface are shown in Fig. 1 for three geodetic latitude zones during July (days 183 through 213) and August (days 214 through 244) 1972. The zone of highest latitude (75°N to 80°N) is above the geomagnetic cutoff latitude for the energy of the particles associated with the event; the zone at 5°S to 5°N is shielded by the terrestrial magnetic field. The zone at 55°N to 65°N includes a mixture of geomagnetic latitudes; at some longitudes the high-energy particles from the sun penetrate the atmosphere, whereas at others they are deflected.

The event, which occurred late on day 217 (4 August), produced an abrupt O_3 decrease in the zone at 75°N to 80°N of about 0.002 atm-cm above 4 mbar, which apparently persisted throughout the month of August. The effect was first observed in this zone on day 219 (data could not be recovered on day 218 because of high radiation-induced dark currents). The zone at 55°N to 65°N suffered a decrease in the O_3 content on days 219 and 220 but recovered on day 221. Thereafter, a gradual decrease of about 5 percent in 8 days, followed by a return to the values before the event, was observed. This decrease is probably due to the advection of modified air from the source region, which is symmetric in geomagnetic coordinates, by geodetically oriented zonal winds. The succeeding increase is similar to the seasonal changes found in other years in this range of latitudes. For the years 1970, 1971, and 1973 the normal seasonal trend from July through August is one of slowly increasing amounts of O_3 in the zone at 55°N to 65°N, whereas it is essentially constant in the zone at 75°N to 80°N.

In the equatorial zone, 5°S to 5°N, a slow increase occurred during July 1972. In early August a rather steeper decline occurred. These changes differ from the observations made in other years surveyed (1970, 1971, and 1973), when the O_3 content remained remarkably constant. We do not believe that this unusual behavior (the equatorial decrease in O_3 beginning in August 1972) is related uniquely to the proton event. Rather, it is due, at least in part, to an abnormal temperature decrease in July followed by a recovery in August as reported by Labitzke (*9*). The July decrease is associated with a Southern Hemisphere stratospheric warming.

No significant change was observed in the global O_3 fields which could be associated with major optical solar flares,

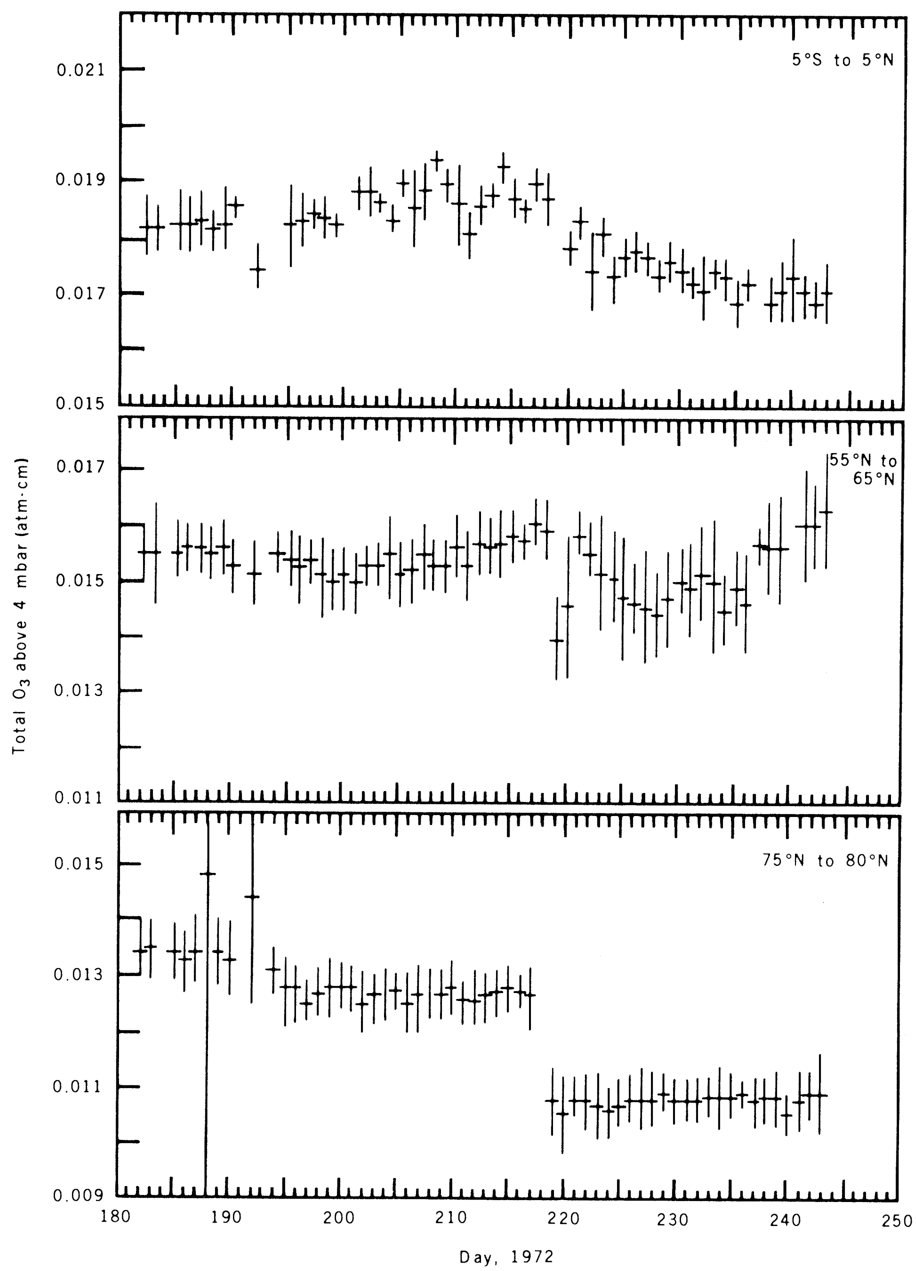

Fig. 1. Zonally averaged total O_3 above the 4-mbar pressure surface for equatorial (top), middle (middle), and high latitudes (bottom) during July and August 1972. The solar proton event occurred on 4 August (day 217).

which also occurred during the August 1972 period of intense solar activity. Indications of the event have been unsuccessfully sought in other sources of O_3 data. The Dobson O_3 spectrophotometer station at Resolute, Northwest Territories, is ideally located within the polar cap. Although there were changes in the total O_3 content during August 1972, they are not distinguishable from the normal variations.

An estimation of the change in total O_3 due to the event can be made from BUV data. The average integral O_3 content above the 10-mbar surface in the zone at 75°N to 80°N before the event (days 211 through 217) was 0.0346 atm-cm. After the event (days 222 through 225 and 227 through 229), the average was 0.0305 atm-cm, a decrease of 0.0041 atm-cm. The change is greater by a factor of 4 than the standard deviation of the data in the two time intervals. The total O_3 determined from the BUV for the same zone during the period including the event (days 211 through 229) was 0.303 atm-cm with a standard deviation of 0.019 atm-cm. The change above 10 mbar is 1.3 percent of the total and is only one-fifth of the total O_3 variability. Thus detection of this event in total O_3 data is not likely.

The production and deposition of NO at high geomagnetic latitudes during this event have been estimated by Reagan *et al.* (*10*), using solar proton flux and energy data obtained from satellites. We calculated the effect of this pulse of NO input on stratospheric O_3 concentrations, using a time-dependent, two-dimensional model which simulates the most important photochemical reactions and zonally averaged transport in the stratosphere (*11*). A vertical profile showing the calculated reduction in O_3 concentrations resulting from NO catalysis for 1 September 1972 (4 weeks after the solar proton event of 4 August) at 75°N to 80°N is given in Fig. 2 (*12*).

The observed reductions in the partial pressure of O_3 as a function of air pressure for the zone at 75°N to 80°N are also shown in Fig. 2. The data are derived from the average for the 7 days preceding the event (days 211 through 217) compared with 7-day averages centered on 8 and 19 days after the event (*13*). The observed and predicted O_3 changes are in reasonable agreement with respect to the pressure level of maximum change (2 mbar). The calculated decrease of 16 percent is about 30 percent less than the observed reductions (*14*). On the other hand, the model calculations also showed reductions of the O_3 concentration down to the latitude circle from 30°

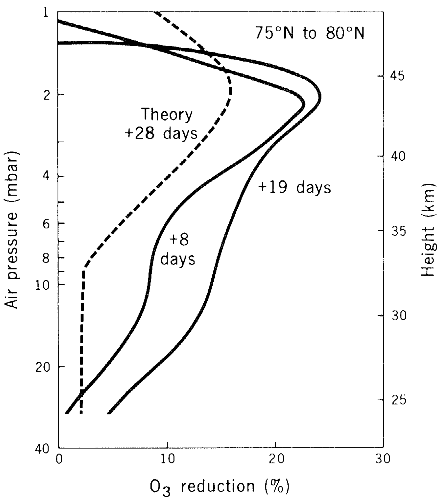

Fig. 2. Percentage decrease of the O_3 partial pressure versus air pressure derived from the average of the 7 days before 4 August 1972 and 7-day periods centered on 8 and 19 days after the solar proton event (solid lines). (Data for 7 days before the event are used as the base line for the two solid-line curves.) The dashed line is a calculation of the O_3 reduction for 1 September 1972, due to the catalytic effect of solar proton–produced NO.

to 40° (not shown here), which were not observed from the satellite. It is therefore clear that horizontal mixing in the region from 35 to 45 km was overestimated in the model. Another interesting feature shown in Fig. 2 which requires explanation is the apparent relative increase in O_3 reduction in the stratosphere from day 8 to day 19 after the event. These examples indicate the superiority of continued analysis of the observed O_3 distributions by satellite observations as compared with rocket observations in supplying essential new information on badly known mixing and on photochemical processes in the stratosphere.

If our current understanding of stratospheric transport and photochemistry is correct, in the summer season above 10 mbar the O_3 concentrations should be determined mainly by the effect of the photochemical reactions, especially those of NO and NO_2 occurring below 1 mbar. The production rates of NO below the 4-mbar surface are somewhat uncertain because of inadequate knowledge of the proton fluxes at high energies. However, almost all the NO produced by the solar proton event was injected into the stratosphere above 10 mbar. The uncertainties in the deposition profile and in atmospheric transport are likely to be responsible for the differences between the model calculations and the observations in the 10-mbar region.

We did not consider the effect of increased production of HO_x in the mesosphere in the model (*15*). The recovery is slow below 1 mbar (Figs. 1 and 2). This finding is compatible with the expected long chemical removal time of NO_x in the stratosphere and with the relatively slow transport of NO_x out of the source region.

The good agreement between observed and calculated O_3 reductions at high latitudes and altitudes in the Northern Hemisphere after the August 1972 solar proton event constitutes a unique confirmation of the presently accepted photochemical theory of stratospheric O_3 above 30 km. These global-scale observations from a satellite of the changes in stratospheric O_3 associated with a major solar proton event greatly extend one's capability in space and time for making comparisons between theory and observations that are so necessary for understanding stratospheric processes.

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11. Included in the model are the most important photochemical reactions which determine the concentrations of O, O_3, N_2O, N, NO, NO_2, NO_3, N_2O_5, HNO_3, CH_4, CO, H_2, H, OH, HO_2, and H_2O_2. Rate coefficients for the reactions were those recommended by D. Garvin and R. F. Hampson, Eds., *Chemical Kinetics Data Survey* (Report NBSIR 74-430, National Bureau of Standards, Washington, D.C., 1974). Temperature and density data were adopted from *CIRA 1965* (Committee on Space Research Working Group 4, COSPAR International Reference Atmosphere, North-Holland, Amsterdam, 1965) and from A. H. Oort and E. M. Rasmusson (*Atmospheric Circulation Statistics*, National Oceanic and Atmospheric Administration Professional Paper, U.S. Department of Commerce, Rockville, Md., September 1971). The model extends from ground level to approximately 55 km and from the South Pole to the North Pole. Production of NO above 55 km could not be taken into account in this model; that is, the downward flux of NO through the upper boundary was neglected. This neglect is

not expected to affect critically calculated O_3 concentrations during the first 3 weeks after the solar proton event, as NO and NO_2 do not affect O_3 concentrations significantly above about 45 km. Zonally averaged concentrations of chemical compounds were calculated on the basis of mean meridional circulation data [J. F. Louis, thesis, University of Colorado (1974)] and empirically determined time-dependent eddy diffusion coefficients (P. J. Crutzen, paper presented at the 4th Climatic Impact Assessment Program Conference, Cambridge, Mass., February 1974).
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13. Days 222 through 225 and 227 through 229 are used for the mean 8 days after the event. Day 226 was excluded because of a small sample size. Days 233 through 239 are used for the average 19 days after the event. Theoretical calculations were made for day 244 (1 September 1972).
14. The observations may be an underestimate of the depletion. Artifacts in the data due to spacecraft pitch errors show positive biases increasing with time at the upper levels. As a result, the O_3 content appears to increase above 1.1 mbar at 8 days and above 1.3 mbar at 19 days.
15. The O_3 content above 1 mbar exhibited a perturbation which disappeared a few days after the event, in accordance with a short photochemical removal time for an HO_x deposition.
16. The National Center for Atmospheric Research is sponsored by the National Science Foundation.
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19 July 1976; revised 27 June 1977

Venous Gas Bubbles: Production by Transient, Deep Isobaric Counterdiffusion of Helium Against Nitrogen

Abstract. *When awake goats were subjected to isobaric gas switching from saturation (17 hours) on 4.7 atmospheres of nitrogen (0.3 atmosphere of oxygen) to 4.7 atmospheres of helium (0.3 atmosphere of oxygen), bubbles detected by 5-megahertz Doppler ultrasound in the posterior vena cava 20 to 60 minutes after the switch continued for 4 hours. Similar experiments carried out at 6.7 atmospheres of inert gas and 0.3 atmosphere of oxygen produced more bubbles for as long as 12 hours after the gas switch. This is believed to be the first objective demonstration of the phenomenon of deep isobaric supersaturation under transient operational diving conditions at relatively shallow diving depths. Detection of bubbles by Doppler ultrasound confirms the potential importance of the phenomenon to shallow saturation diving and holds promise for better quantification of its effects as well as those of its counterpart, isobaric undersaturation, which can confer a decompression advantage.*

Isobaric supersaturation (*1, 2*) and the resulting production of cutaneous and deep-tissue bubbles by counterdiffusion at constant pressure of two or more gases with unequal permeation rates has been identified in man (*1, 2*) and demonstrated in animals (*3–5*) both in vitro and in vivo (*6*); it is generally considered to explain certain abnormalities that can be encountered in relatively deep (greater than 100 m) saturation diving (*6*). Two interrelated forms have been distinguished: (i) "superficial isobaric counterdiffusion" through skin and other tissues in direct contact with the ambient atmosphere, and (ii) "deep isobaric counterdiffusion" between tissue fluids and capillary circulation (*6*). Each is capable of supersaturating tissue, and the superficial form has been shown to produce not only gas lesions in man (*7*), but also continuous gas embolism in animals (*3–5*) under steady-state conditions. However, the probability of risk from the phenomenon in "deep" tissues in shallow-water diving involving transient gas switching rather than steady-state experimental situations is not known (*8*).

We now report the in vivo production of bubbles detected with Doppler ultrasound (*9*) in awake goats after a rapid isobaric switch of the inert gas in the chamber from nitrogen to helium at 40.2 m (132 feet) and 60.35 m (198 feet) of seawater (7 atm absolute) (all measures are expressed in terms of meters of seawater). These are the shallowest depths at which this phenomenon has been demonstrated. Further, the fact that it was produced by transient rather than steady-state conditions is of both practical and theoretical importance to the physiology and medicine of diving, particularly in reference to projected submarine rescue procedures requiring successive exposure to different inert gas atmospheres at these pressures.

Use of continuous-wave Doppler ultrasound for detection of vascular bubbles has become an accepted technique in hyperbaric physiology; the system and counter in use in our laboratory are theoretically capable of detecting bubbles 1 μm in diameter and have been experimentally demonstrated to detect 10-μm bubbles (*9*).

Eight adult goats weighing between 40 and 70 kg had Doppler ultrasonic transducer cuffs surgically implanted around the posterior vena cava (*9*). Animals were exposed in pairs to one of two different regimens. The first consisted of saturation to 40.2 m of seawater in normoxic nitrogen. Compression was at the rate of approximately 4.6 m/min, varied slightly as required to minimize noise-induced anxiety in the animals. The animals were held for 17 hours at 40.2 m at an O_2 pressure of 0.3 atm [the remainder was N_2 (CO_2 less than 0.09 percent)], after which it was assumed that saturation was virtually complete.

Isobaric gas flushing of the N_2-O_2 environment with He-O_2 was accomplished within 5 minutes at a flow rate of approximately 17 m^3/min [600 standard cubic feet per minute (SCFM)] for the 40.2-m dives, and 19.8 m^3/min (700 SCFM) for the 60.35-m dives. After the gas exchange, the residual chamber N_2 percentage varied from 0.3 to 5 percent as a maximum. These kinetics allow mathematical treatment of the gas switch as essentially a step function for all but the fastest tissues.

Ultrasonic Doppler monitoring and recording of bubble signals began 5 minutes before switching gases and continued for the duration of the isobaric phase of the dive and at regular intervals during the subsequent decompression. The earliest bubbles were detected 20 minutes after the first 40.2-m gas switch and continued to be detected in varying numbers for 4 hours. Two more 40.2-m dives were carried out with very few bubbles detected both in the same two animals and in another pair (*10*). The isobaric switch from saturation at 60.35 m produced bubbles in every case, which suggests that a threshold may exist near 40.2 m for isobaric bubble formation. After the switch from the 60.35-m saturation, bubbles were detected as early as 30 minutes, lasted several hours, and were detected for as long as 10 or 11 hours under isobaric conditions. No serious skin lesions were observed in this study; however, it is not possible to exclude such results because of the greater difficulty in perceiving skin discoloration in these animals.

Figure 1 shows a combined plot of Doppler bubble signal counts after an isobaric gas switch at 60.35 m and calculated curves showing the fractional saturation of N_2 and He and the total supersaturation ratio (N_2 + He) (Fig. 1A) and the total excess inert gas concentration after the isobaric switch for three pairs of N_2 + He half-times, corresponding to 13 + 5, 93 + 41, and 139 + 63 minutes, respectively (Fig. 1B) (*11*). The long period over which bubble signals were heard is striking. This immediately identifies bubbles with the so-called "slower" tissues. Although the approximately unimodal distribution of bubbles with time (Fig. 1A) may suggest the importance of a particular half-time (*12*), other experiments show either fairly constant rates of bubble production or bimodal