Physiol. **121**, 533 (1984); H. S. Oettgen, C. Terhorst, L. C. Cantley, P. M. Rosoff, *Cell* **40**, 583 (1985).

16. Y. N. Jan, L. Y. Jan, M. J. Dennis, *Proc. Roy. Soc. London Ser. B* **198**, 87 (1977); M. A. Tanouye, A. Ferrus, S. C. Fujita, *Proc. Natl. Acad. Sci. U.S.A.* **78**, 6548 (1981); L. Salkoff and R. Wyman, *Nature (London)* **293**, 228 (1981); L. Y. Jan *et al.*, *Cold Spring Harbor Symp. Quant. Biol.* **48**, 233 (1983); L. Salkoff, *Nature (London)* **302**, 249 (1983); C. H. Wu and B. Ganetzky, *Biophys. J.* **45**, 77 (1984).
17. We thank M. Thornton for technical assistance. Diltiazem and verapamil were generously provided by R. W. Tsien (Yale University, New Haven, CT). The 9F3 antibody was generously provided by F. J. Dumont (Merck, Sharp, and Dohme Research Laboratories, Rahway, NJ), and the 7D4 antibody (anti–IL-2 receptor) by E. Shevach (NIH, Bethesda, MD). Supported by a Research Career Development Award (M.D.C.), the American Diabetes Association, Southern California Affiliate (K.G.C.), and USPHS grants NS-14609, AI-21808, AI-20717, and AG-04361.

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High Nitrite Levels off Northern Peru: A Signal of Instability in the Marine Denitrification Rate

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During February and March 1985, nitrite levels along the northern (approximately 7° to 10°S) Peruvian coast were unusually high. These accumulations occurred in oxygen-deficient waters, suggesting intensified denitrification. In a shallow offshore nitrite maximum, concentrations were as high as 23 micromoles per liter (a record high). Causes for the unusual conditions may include a cold anomaly that followed the 1982–83 El Niño. The removal of combined nitrogen (approximately 3 to 10 trillion grams of nitrogen per year) within zones of new or enhanced denitrification observed between 7° to 16°S suggests a significant increase in oceanic denitrification.

THEORETICAL CONSIDERATIONS SUGGEST that the loss of combined nitrogen from the sea by denitrification may be highly variable (*1*). Observations off Peru and Chile support this assertion. Investigators have consistently encountered oxygen-deficient (O_2 less than ~0.05 ml of oxygen per liter) waters with embedded nitrite maxima, and have shown that denitrification is a major process in these zones (*2–5*). These features are, however, highly variable. For example, after the 1972 El Niño and the collapse of the anchoveta stocks, denitrification may have increased by $\sim 10 \times 10^{12}$ g of nitrogen per year (*2*) to a rate of $\sim 25 \times 10^{12}$ g/year. This value is 20 to 60% of the total marine denitrification rate (*4, 6*) and ~20% of the largest estimate for the removal rate of fixed nitrogen from the ocean by all processes (*6*).

From 1 February to 5 March 1985, observations (*7*) off Peru (Fig. 1) suggested another increase in denitrification. Between 7° and 10°S, nitrite levels in oxygen-deficient waters (Figs. 2 and 3) were unusually high (*8*). High nitrite concentrations occurred (i) in a maximum centered at depths of 200 to 300 m, (ii) in a shallow offshore maximum where extreme values were observed (maximum value of 23 μ*M* at 24 m at station 16), and (iii) over the shelf. High concentrations have occurred over the shelf (*9*), but a maximum at 200 to 300 m is rare at this latitude, and the nitrite concentrations in the shallow offshore maximum appear to be the highest ever observed in the open ocean. Maximum nitrous oxide concentrations (Fig. 2) were also high, and the wide range of values (0 to 8.6 μg/liter) implied rapid turnover (*6*).

Observations from northern Peru similar to ours were taken from February to March 1974 and February to May 1975 (*10, 11*) during cold anomalies as indicated by temperatures measured at 7°43′S (*12*). During 1974, a nitrite concentration of ~11 μ*M* was observed offshore at a depth of 50 m, and a zone of complete nitrate removal and sulfide accumulation occurred over the shelf. During 1975, suggestions of the initial stages of shallow offshore nitrite maxima and maxima below 100 m were encountered.

During 1985, nitrite concentrations greater than 1 μ*M* were found everywhere in the oxygen-deficient waters of our study region (Fig. 2) except near 11°S where an onshore flow of low-nitrite waters separated the nitrite maxima. The onshore flow occurred near the typical northern boundary of the main secondary nitrite maximum normally found between ~100 and 400 m and between 10° and 25°S (*2*), suggesting that the deep maximum found in the north is not an expansion of this feature. We have omitted the section taken at 15°S (Fig. 1), but intense denitrification was indicated by high nitrate deficits (*13*) at shallow depths. In addition, the only site of complete denitrification (total consumption of nitrate and nitrite and the presence of hydrogen sulfide) that we found was in the bottom 50 m at station 107 (Fig. 1).

Resolving the seasonal variability in the ocean off Peru is difficult even for temperature alone (*14*). Consequently, some of the seemingly unusual conditions may have resulted from seasonal variability. For example, intensified denitrification over the shelf might be largely associated with seasonal changes, since episodes of complete denitrification have been observed in other years between February and April (*8, 10, 15*). Seasonal changes may also be partly responsible for the development of the intense offshore nitrite maximum (Figs. 2 and 3). This feature was associated with a seasonal shoaling of a density isopleth (σ_t = 26.0). It is difficult, however, to attribute all of the changes to the seasonal cycle. For example, the 26.0 σ_t surface in the region of the intense nitrite maximum was at the shallowest level ever observed (*8*), with a mean depth of 39 m; the historical average is 90 m. In addition, the deeper nitrite maximum found between 7° and 10°S has its only known antecedent in the 1975 data.

It is tempting to examine the hypothesis that a significant acceleration in the marine denitrification rate took place off Peru in 1985. The most detailed estimate (*2*) of the rate in the eastern tropical South Pacific suggested a total rate of 25×10^{12} g/year in an oxygen-deficient volume of 150×10^{12} m^3. We assumed a volume of 12×10^{12} m^3 for the deep nitrite maximum observed between 7° and 10°S. We used an average denitrification rate of 0.175 g of nitrogen per cubic meter per year, based on 25 observations of the activity of the respiratory electron transport system (ETS) and assumptions made in the past (*2, 16*) to arrive at a denitrification rate for this feature of 2×10^{12} g/year. Estimating denitrification rates in the shallower sites of intensified denitrification is more difficult because (i) a significant fraction of the ETS activity may arise from organisms that are not involved in

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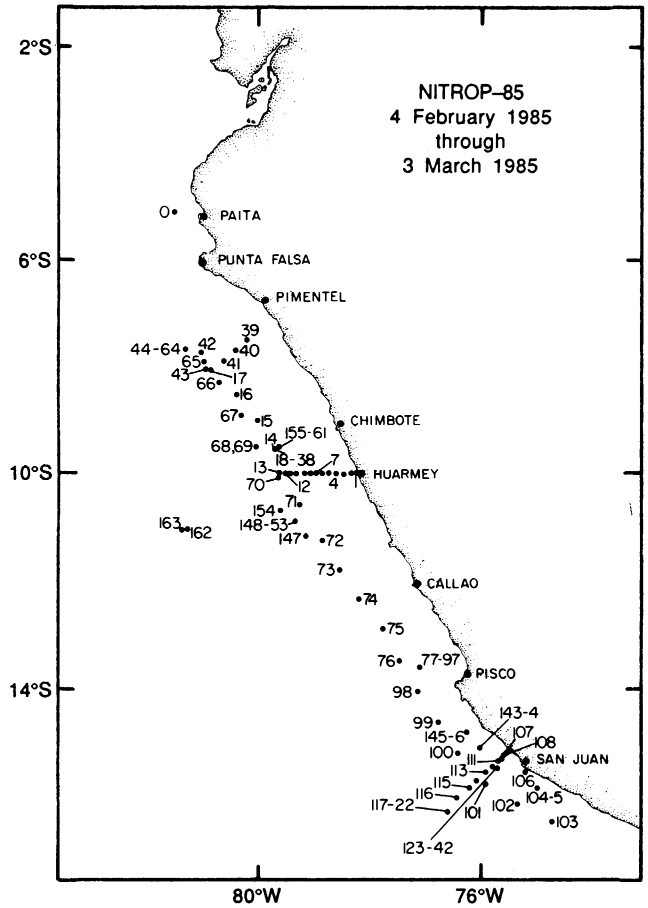

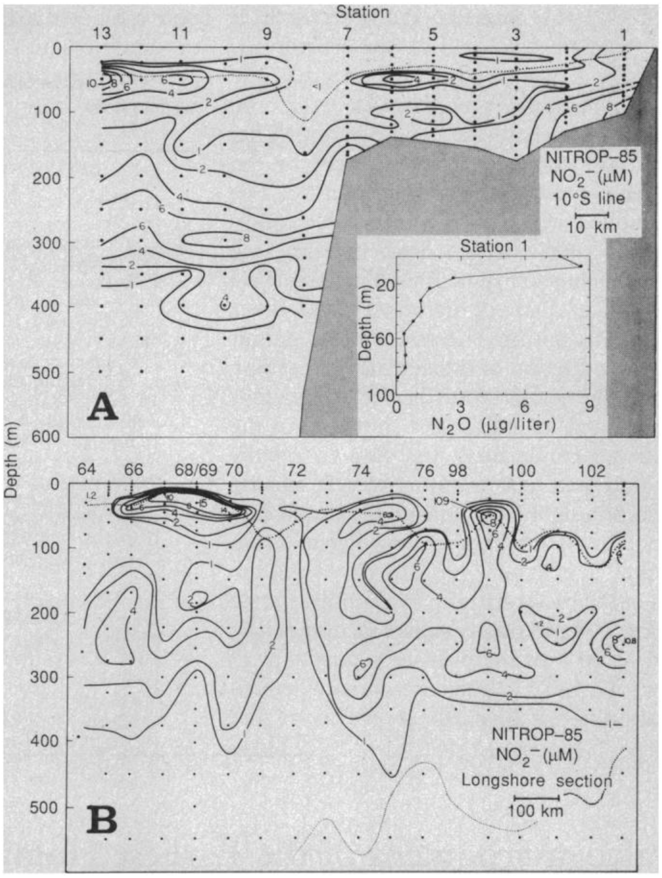

Fig. 1 (left). Location chart for the stations taken during the Nitrogen Transformations off Peru Experiment (NITROP-85). Fig. 2 (right). Nitrite distributions in sections taken along 10°S (A) and in a longshore section (B). The dotted lines are the 0.2 ml/liter dissolved oxygen isopleth as determined by Carpenter's technique (*7*, p. 21). The true concentrations corresponding to the dotted lines are probably about 0.1 ml/liter or less (*6*). The insert in (A) shows the N_2O distribution at station 1.

denitrification, (ii) a significant loss of nitrite is likely before further reduction occurs (*6, 17*), and (iii) a significant fraction of the bacteria may be in log-phase growth rather than the senescent phase conditions normally assumed. Under (i) and (ii) the estimates are too high, whereas under (iii) they are too low (*18*). Nevertheless, the ETS activities observed in the shallow offshore maximum and in the bottom waters over the shelf with intensified denitrification were approximately five times those in the deeper maximum. These waters had a volume of about 5×10^{12} m^3. Furthermore, enhancement of nitrate deficits was on the order of 10 μM, and the residence times of the waters in these zones are on the order of a month to less than a year (*2, 6, 14, 19*). Under the standard assumptions (*2*), the ETS-based denitrification rate for the enhanced shallow zones would be 5×10^{12} g/year. On the basis of the residence times and enhanced nitrate deficits, the rate would range from 1×10^{12} to 8×10^{12} g/year.

These considerations suggest that an increase in the regional denitrification rate of 3×10^{12} to 10×10^{12} g/year may be associated with the conditions we observed. This rate represents a 2 to 25% increase in the total marine denitrification rate (*4, 6*). The 1985 observations also suggest that denitrification is not necessarily weaker during the season of weak coastal upwelling. Our evidence for a variable marine denitrification rate tends to support those who suggest that changes in the marine combined nitrogen budget may contribute to climatic variability (*20*).

The changes observed in 1985 may be partly related to the shallowness of the 26.0 σ_t surface in the extreme offshore nitrite maximum and over the shelf at 10°S. This density level is characterized by low oxygen and high nitrate concentrations ($\sim$30 μM before denitrification), and its shoaling provided nutrients to the photic zone, thereby encouraging high primary production. It also placed waters low in oxygen and with initially high nitrate levels close to the source of organic material (the photic zone) and in proximity to the sediments over the shelf and slope, where high metabolic rates are to be expected (*2*). Since local winds were weak (average speed, <4 m/sec), the shoaling may have been related to a larger-scale seasonal response that was intensified by dynamic events that followed the 1982–83 El Niño. Temperature records from Peru (*12*) and theoretical studies (*21*) suggest that El Niños are often followed by cold anomalies.

It is tempting to speculate on the persistence of the shallow nitrite maximum associ-

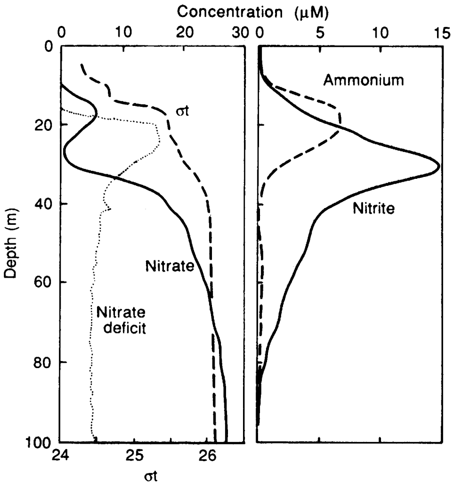

Fig. 3. Vertical profiles in the shallow and intense offshore nitrite maximum (station 26) taken with our pumping system (*7*).

ated with this anomaly. We observed it at the beginning and end of our experiment, and the historical data suggest that the circulation features with which it may be associated persist for a few months. Its longevity may have been increased by the extreme conditions that we observed. For example, one can posit a metastable condition in which oxygen deficiency near the surface tends to maintain itself by restricting the living space of herbivores and other higher organisms. This stress would permit a higher fraction of organic material to sink from the photic zone before being consumed and would favor a shift toward the sinking of individual cells vis-à-vis rapidly sinking fecal pellets. More slowly sinking particles might favor enhanced bacterial metabolism within the shallow nitrite maximum.

On the basis of a primary production rate of 0.5 g of carbon per square meter per day, only ~10% of the primary production off Peru and Chile is required to drive a denitrification rate of 20×10^{12} g/year (*2*), so that only a modest redistribution of the carbon produced by our estimated average primary production rate of 2 g m^{-2} day^{-1} would be required to cause the observed changes.

REFERENCES AND NOTES

1. D. Z. Piper and L. A. Codispoti, *Science* **188**, 15 (1979).
2. L. A. Codispoti and T. T. Packard, *J. Mar. Res.* **38**, 453 (1980).
3. T. T. Packard, R. C. Dugdale, J. J. Goering, R. T. Barber, *ibid.* **36**, 59 (1978).
4. K. K. Liu and I. R. Kaplan, *Earth Planet. Sci. Lett.* **68**, 88 (1984).
5. J. W. Elkins, thesis, Harvard University (1978).
6. L. A. Codispoti and J. P. Christensen, *Mar. Chem.* **16**, 277 (1985).
7. Data and methods are in *Bigelow Laboratory Technical Report 59* (1985).
8. Based on the historical data examined in (*2*) plus results reported by R. T. Barber and A. Huyer [*Geophys. Res. Lett.* **6**, 409 (1979)]; R. B. Gagosian *et al.*, [*Woods Hole Oceanographic Inst. Tech. Rep. WHOI-80-1* (1980)]; and R. B. Gagosian, T. Loder, G. Nigrelli, and J. Love [*ibid.*, *WHOI-83-5* (1983)].
9. See, for example, L. A. E. Doe [*Project ICANE* (Rep. Ser./B1-R-78-6, Bedford Institute of Oceanography, Halifax, Nova Scotia, 1978)].
10. Yu. I. Sorokin, *Oceanology* **18**, 62 (1978).
11. W. C. Patzert, T. J. Cowles, C. S. Ramage, *El Niño Watch Atlas* (Ref. Ser. 78-7, Scripps Institution of Oceanography, La Jolla, CA, 1978).
12. O. G. Guillen and R. Z. Calienes, in *Resource Management and Environmental Uncertainty*, M. H. Glantz and J. D. Thompson, Eds. (Wiley-Interscience, New York, 1981), pp. 255–282.
13. Nitrate deficits estimate the free nitrogen produced by denitrification. We used Elkins's method (*5*).
14. D. B. Enfield, in *Resource Management and Environmental Uncertainty*, M. H. Glantz and J. D. Thompson, Eds. (Wiley-Interscience, New York, 1981), pp. 213–254.
15. R. C. Dugdale, J. J. Goering, R. T. Barber, R. L. Smith, T. T. Packard, *Deep-Sea Res.* **24**, 601 (1977).
16. The 1977 ETS method [T. T. Packard, A. Devol, F. D. King, *ibid.* **22**, 237 (1975)] is less sensitive than that used in 1985, so the latter results were multiplied by 0.635 to be comparable.
17. J. J. Anderson, A. Okubo, A. S. Robbins, F. A. Richards, *ibid.* **29**, 1112 (1982).
18. J. P. Christensen, R. G. Owens, A. H. Devol, T. T. Packard, *Mar. Biol.* **55**, 267 (1980).
19. L. A. Codispoti, in *Nitrogen in the Marine Environment*, E. J. Carpenter and D. G. Capone, Eds. (Academic Press, New York, 1983), pp. 513–564.
20. M. B. McElroy, *Nature (London)* **302**, 328 (1983); F. Knox and M. B. McElroy, *J. Geophys. Res.* **89**, **D3**, 4629 (1984).
21. M. A. Cane and S. E. Zebiak, *Science* **228**, 1085 (1985).

22. We thank M. Campbell, L. Kerkoff, J. Kogelschatz, G. Kullenberg, A. Levin, A. Smith, M. Rodier, the crew of R/V *Wecoma*, P. Boisvert, M. Colby, and J. Rollins for their assistance. Supported by NSF grants OCE-83-16607, -16608, -16609, -16610, -16011, and OCE-81-10702.

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Paleoenvironment of the Earliest Hominoids: New Evidence from the Oligocene Avifauna of Egypt

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Analysis of fossil birds from the Oligocene Jebel Qatrani Formation in the Fayum depression of Egypt, site of the oldest known hominoid primates, allows precise paleoenvironmental reconstruction of the climatic and biotic conditions that influenced some of the earliest stages of hominoid evolution. Unlike the fossil mammals of the Fayum, which belong largely to extinct groups, most of the birds are referable to living families, with some being close to modern genera. The avifauna consists mainly of aquatic species, with such forms as jacanas (Jacanidae) and shoebilled storks (Balaenicipitidae) indicating expanses of freshwater with dense floating vegetation. An avifauna closely analogous to that of the Fayum is found today only in a limited area of Uganda, north and west of Lake Victoria, a region of swampland bordered by forest and grasslands that presents marked faunal similarities to the environment inferred for the Egyptian Oligocene.

THE EARLY OLIGOCENE FOSSIL DEPOSITS of the Fayum depression in Egypt are renowned for having produced remains of the earliest known hominoid primates (*1–4*). The importance of these fossils to understanding evolution in the lineage thought to have given rise to *Homo sapiens* has focused interest on the nature of the environment in which these early primates lived, and the deposits have been subject to intensive modern paleontological collecting. Fossils come mainly from two intervals in the Jebel Qatrani Formation known as the upper and lower sequences that are probably early Oligocene in age (*5*, *6*). Two of the Fayum primate genera, *Aegyptopithecus* and *Propliopithecus*, are hominoids possibly ancestral to *Homo* and the modern great apes. The Fayum is the only place yet known where this stage in human ancestry is preserved, and a complete understanding of the Fayum paleoenvironment is thus essential to interpreting the adaptations of these earliest apes.

Controversy has surrounded the nature of the paleoenvironment of the Fayum deposits and its implications for the adaptations of the primates that lived there. Kortlandt (*7*), in attempting to counter the belief that the area was forested and the primates arboreally adapted, argued that the environment consisted of semiarid, almost treeless scrubland, for which reason the Fayum primates must have been terrestrial. These arguments were vitiated by Bown *et al.* (*8*) based on evidence from lithology, sedimentology, fossils of plants, vertebrates, and invertebrates, and finally from the structural adaptations of the primates themselves. They concluded that the Jebel Qatrani Formation was deposited near the coastline of the Tethyian seaway with interdigitating habitats of estuarine mangroves, fresh and brackish fluviatile swamps, and forested floodplains flourishing in a climate "typified by adequate, though probably seasonal rainfall" (*8*).

Fossil birds have hitherto played little part in the reconstruction of the paleoenvironment of the Fayum as only four taxa were recorded in the early collections. Among the modern collections is a greater variety of fossil birds that have recently been studied and identified (*9*). Although the total number of diagnostic avian specimens is only 30, a minute fraction of the total number of vertebrate fossils obtained, some 17 to 19 species are represented, indicating great diversity in the avifauna considering the small sample size. The significance of these specimens for paleoecological studies is greater than their scarcity would imply because

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