

Deadline for Nominations: 15 September 1977

AAAS–Newcomb Cleveland Prize: Contest Year Is Nearly Over

The deadline for nominations of papers for the AAAS–Newcomb Cleveland Prize is fast approaching. Readers are invited to nominate papers published in the Reports section of *Science* from 3 September 1976 to 26 August 1977. The prize of \$5000 and a bronze medal is now given annually to the author of an outstanding paper that is a first-time publication of the author's own research.

Nominations must be typed and the following information provided: the title of the paper, issue in which it was published, author's name, and a brief statement of justification for nomination. Nominations should be submitted to AAAS–Newcomb Cleveland

Prize, AAAS, 1515 Massachusetts Avenue, NW, Washington, D.C. 20005. Final selection will rest with a panel of distinguished scientists appointed by the Board of Directors.

The award will be presented at a session of the annual meeting at which the winner will be invited to present a scientific paper reviewing the field related to the prizewinning research. The review paper will subsequently be published in *Science*. In cases of multiple authorship, the prize will be divided equally between or among the authors; the senior author will be invited to speak at the annual meeting.

Reports

Calcium Carbonate Production of the *Mare Incognitum*, the Upper Windward Reef Slope, at Enewetak Atoll

Abstract. *Corals and algal pavement produce calcium carbonate more slowly on the windward reef slope of Enewetak Atoll than on the reef flat despite the high standing crop of reef-building organisms on the slope. The capacity of reefs to remain at or near sea level is therefore not determined primarily by growth on the seaward slope.*

The windward reef slope of coral atolls abounds with reef-building organisms (Fig. 1, a and b). Ladd considered the windward margin as "the most vital part of a reef" (1, p. 705). He suggested that the slope to depths of 15 m may be biologically the richest region of a coral reef, and he pointed out that on coral atolls of the Marshall Islands this region "is so inaccessible that it has been dubbed the '*mare incognitum*'" (1, p. 706). Recent studies of the growth potential of coral reefs in terms of CaCO_3 production [summarized in (2)] have only hinted at the activity of reef slopes. It is our purpose in this report to consider the role played by the *mare incognitum* in reef growth.

The reduction in the alkalinity of seawater can be used to determine CaCO_3 production rates (2). Seaward reef flats and slightly submerged coral pinnacles produce about 4 kg of CaCO_3 per square meter per year, whereas more

protected lagoonal environments produce about $0.8 \text{ kg m}^{-2} \text{ year}^{-1}$. In order to measure CaCO_3 production by alkalinity reduction on the seaward slope, we have used transparent Plexiglas domes similar to those described by Wells (3) as in situ respirometry chambers (Fig. 1b). We have developed techniques for dome emplacement in packed sediment or irregular limestone terrain (4). During October 1976 we used these techniques to isolate water and measure alkalinity reduction rates by selected components on the windward reef slope of Enewetak (also called Eniwetok) Atoll, Marshall Islands. The primary study site was immediately offshore of Jinimi (Chinimi) Island, near the seaward extension of reef flat transects which have been the subject of earlier studies of community metabolism (5, 6). Incubations were also conducted at selected control sites in shallow water.

Two prominent ecological compo-

nents of the slope were examined: coral heads and algal pavement. Vaseform colonies of *Acropora* (probably *A. hyacinthus*) are the most conspicuous coral on the windward slope (Fig. 1). Wells (7) did not consider this species to be common in the Marshall Islands, but his inability to sample the environment so obviously favored by this coral led to the term *mare incognitum* rather than a zonal name denoting the dominant coral there. Coral cover increases from near 0 percent on the reef crest to about 30 percent at depths of 25 m (the local base near Jinimi of the so-called "ten-fathom" terrace marking the base of this zone) and then decreases to near 0 percent at 50 m. The reef crest is dominated by a pavement of crustose coralline algae (particularly *Porolithon*), and some algal pavement persists to the base of the 25-m terrace. Poorly sorted sand and rubble comprise a third major (but unsampled) component of the slope. Table 1 includes estimates of the vertical distribution of the coral and pavement components near Jinimi. The same general distribution pattern characterizes other areas we have examined on the windward slope of the atoll, although the local distributions differ in detail.

Coral incubations were carried out at depths of 7, 11, 15, and 21 m on the slope. Control incubations were conducted in an abandoned limestone quarry on the reef flat near Enewetak; this quarry supports a rich biota in a protected setting. Corals used for the incubations were vaseform *Acropora* colonies which covered 30 to 80 percent of the bottom area under the domes and displaced 10 to 30 percent of the water volume therein (Fig. 1b). Pavement incubations were carried out on relatively flat areas of 100 percent hard bottom at all but the deepest of the above sites and

at a control site near the reef crest at Enewetak.

Incubations were conducted between about 1000 and 1400 hours, with samples ordinarily taken at the frequency of one per hour. Alkalinity reduction rates were derived from the slopes of the linear regression lines of alkalinity versus time. The weather face of the atoll is not conducive to nighttime diving or navigation, and so we were unable to acquire information on the complete diurnal calcification cycles.

Alkalinity reduction rates were adjusted for coral displacement volumes under the domes and converted to CaCO_3 production per unit area (Table 1). The rates are expressed in terms of 100 percent cover by each component ["potential production" in the terminology of (8)], then weighted for actual cover, and summed ["gross production" in (8)]. We judged the contributions of calcifying organisms other than *Acropora* or pavement to be quantitatively minor.

The potential production of CaCO_3 by coral is substantially lower on the slope than at the control site and may decrease with depth (Table 1). This apparent decrease is consistent with the virtual dis-

appearance of corals by 50 m. Algal pavement production of CaCO_3 is also considerably lower on the slope than at the control site; the pavement shows no demonstrable production trend with depth. Even pavement production in the shallow and protected quarry is dramatically slower than that of the crest, an environment of extreme turbulence. This localized calcification is consistent with the existence of a localized prominent algal ridge structure on atolls.

Our own unpublished data and those

of Kinsey (9) for other locations suggest that the CaCO_3 production of the sand-rubble component is effectively zero. We may thus approximate the gross CaCO_3 production rate of the slope by summing the contributions of the coral and pavement components alone. The average is $0.16 \text{ g m}^{-2} \text{ hour}^{-1}$. If this rate applies 24 hours per day, it is equivalent to an annual production rate of $1.4 \text{ kg m}^{-2} \text{ year}^{-1}$; 12 hours of daytime production at this rate and no nighttime production yields $0.7 \text{ kg m}^{-2} \text{ year}^{-1}$. There is evi-

Table 1. Production of CaCO_3 as a function of depth, ecological component, and environment.

Depth (m)	Location	Approximate cover (map area) (%)		CaCO_3 production ($\text{g m}^{-2} \text{ hour}^{-1}$)		
		Coral	Pave-ment	Coral*	Pave-ment†	Weighted sum†
0	Reef crest pavement control	0	100		1.85	1.85
1	Quarry coral control	Not estimated		2.30	0.14	
7	Windward slope	10	70	0.76	0.12	0.16
11	Windward slope	15	60	0.88	0.09	0.19
15	Windward slope	20	40	0.47	0.14	0.15
21	Windward slope	25	20	0.46	0.12‡	0.14

*Production per unit map area of cover by these components [= potential production, as defined in (8)]. †Sum of the potential production multiplied by the proportion of cover for coral and pavement [= gross production (8)]. ‡Not measured; assumed to be average of other slope pavement measurements.

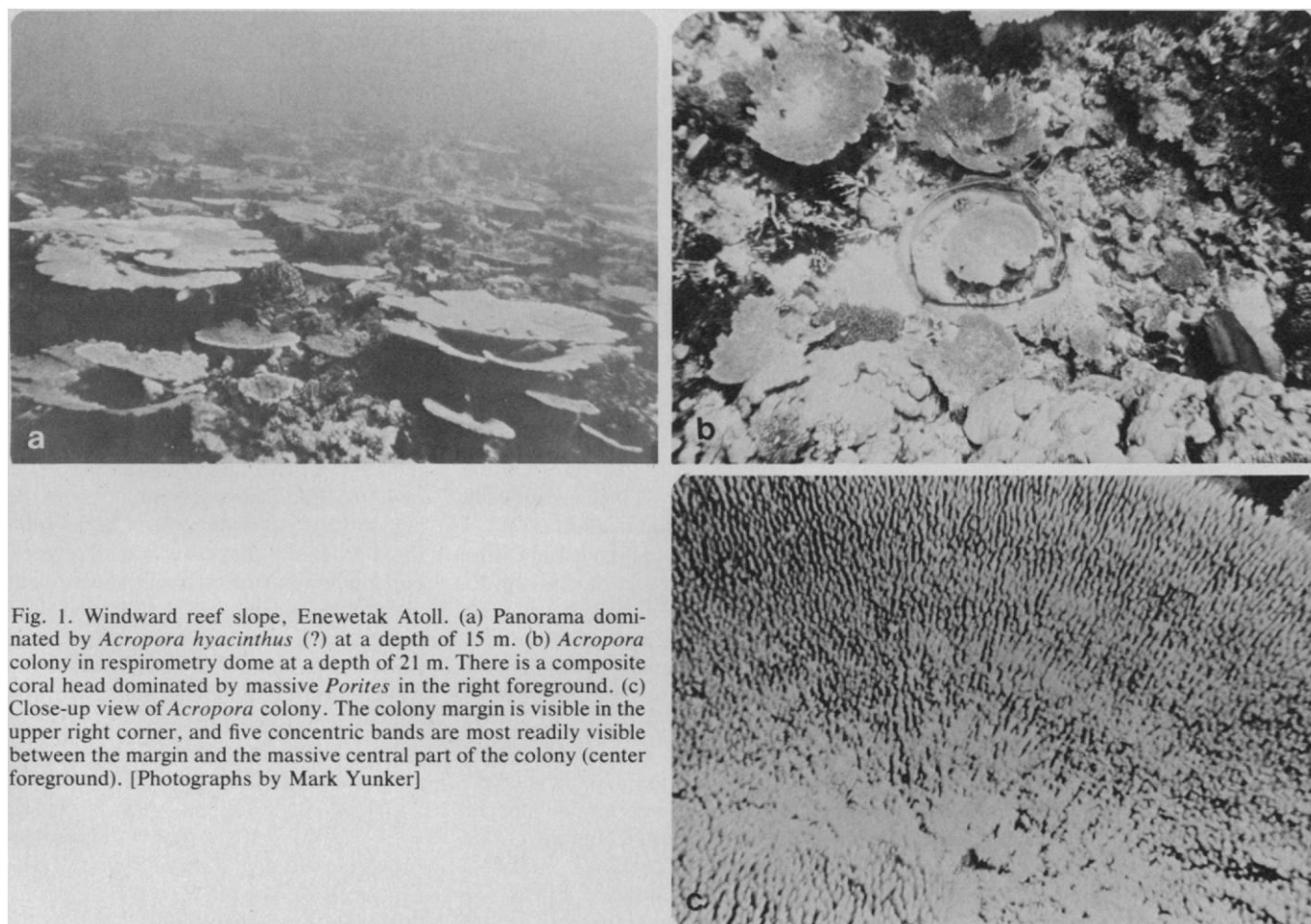


Fig. 1. Windward reef slope, Enewetak Atoll. (a) Panorama dominated by *Acropora hyacinthus* (?) at a depth of 15 m. (b) *Acropora* colony in respirometry dome at a depth of 21 m. There is a composite coral head dominated by massive *Porites* in the right foreground. (c) Close-up view of *Acropora* colony. The colony margin is visible in the upper right corner, and five concentric bands are most readily visible between the margin and the massive central part of the colony (center foreground). [Photographs by Mark Yunker]

dence for diel variation in the CaCO_3 production rate of reef organisms (10) and communities (11) at other locations, although studies on the reef flat at Enewetak (6) have not demonstrated such variation there.

Topographic irregularities in the *mare incognitum* (especially the groove and spur structures) and the slope of the sea floor increase the effective surface area available for calcification by as much as 50 percent above the map area of the slope. Thus the actual production rate of the *mare incognitum* may be as high as 1 to 2 $\text{kg m}^{-2} \text{ year}^{-1}$. Areas with total coral cover might produce 3 to 6 $\text{kg m}^{-2} \text{ year}^{-1}$. Virtually total coral cover occurs locally but is not a regionally significant feature. The windward slope between 15 and 25 m gives the initial casual (and incorrect) visual impression of nearly total coral cover (Fig. 1a and Table 1).

By comparison, a reef flat with 10 percent *Acropora* and 30 percent algal pavement [about the composition at the site of studies of reef flat metabolism (5, 6)] and producing CaCO_3 at the control site rates listed in Table 1 yields a gross production rate of 3 or 6 $\text{kg m}^{-2} \text{ year}^{-1}$ (12- or 24-hour "production day"). This crude estimate is in substantial agreement with production rates determined directly for that community by flow respirometry [4 $\text{kg m}^{-2} \text{ year}^{-1}$ (6)] and suggests that the domes do not greatly bias results by temporarily altering water chemistry, temperature, or motion. The windward slope produces substantially less CaCO_3 than the reef flat.

The vasiform *Acropora* colonies have concentric bands approximately 7 cm apart (Fig. 1c). Ma suggested that these bands are annual growth lines (12), and they may be similar in origin to the annual density bands in massive corals (13). Plates from the deepwater vasiform *Acropora* colonies weigh approximately 10 kg m^{-2} , whereas shallow-water specimens weigh about 20 kg m^{-2} . If all of the mass increase represented by the coral calcification rates goes into radial extension, it is sufficient for a radial extension of about 5 or 10 cm year^{-1} on a 1- m^2 coral (12- or 24-hour production day). Growth form (largely colony robustness or bushiness) rather than the amount of radial extension between bands (apparent years) seems to be the morphological response most closely related to variable calcification rate.

Corals with up to 13 bands (colonies nearly 2 m in diameter) are common at depths of 15 to 25 m; larger colonies are absent. At shallower depths, few colonies exceed 1 m in diameter. There are large, composite colonies of massive

corals which may be substantially older than this (Fig. 1b). The existence of an upper size limit for the *Acropora* colonies suggests either that these corals cannot exceed this size or that something disrupted corals on the windward slope during or shortly before 1963. A typhoon which devastated Guam in November 1962 generated waves which caused considerable onshore damage at Enewetak (14) and perhaps also disrupted deeper portions of the windward slope. On at least three occasions over the past 5 years (the period during which S.V.S. has conducted research at Enewetak) severe waves have disrupted portions of the reef flat and perhaps the uppermost part of the slope, apparently without inflicting damage on the deeper portions of the windward reef slope. Although it can by no means be proven that the 1962 typhoon accounts for the observed size limit of the corals, these observations are consistent with the view that there has been no such damage on the windward slope below 15 m at least since the time of that event. On Funafuti Atoll, waves generated by a typhoon disrupted the reef community to a depth of 20 m (15).

Goreau *et al.* (16, p. 123) observed: "For reasons that are not yet understood, many coral communities, some of them very extensive, never reach the stage of framework construction." One explanation may be that destructive events periodically reduce incipient reef frame to unconsolidated debris before that framework achieves some minimal degree of structural integrity.

If sea level rises more rapidly than the shallow reef grows upward, then submergence will eventually lower the capacity of the community to produce CaCO_3 . The most actively calcifying portion of an atoll is very near sea level even though the standing crop may be lower on the reef flat than on the seaward slope, and sediment retention is lower on the flat than on the lagoonward slope. This interpretation is generally consistent with geological evidence from accumulation rates [summarized in (17)].

The abrupt vertical transition from rapid CaCO_3 production on the reef flat to slow production on the slope suggests that factors controlling CaCO_3 production show a similar change with depth on the slope; light and water motion are the two most obvious candidates (2, 10, 11, 13). At least in the case of the slower pavement calcification rate in shallow, protected water, water motion appears important. The eventual lagoonward degeneration of well-developed coral communities on the windward flat is also consistent with the hypothesis that water

motion exerts major influence on reef calcification.

Optimum environments for the development of reef frameworks are probably broad shoal areas only a few meters deep and generally open to oceanic swell. Such a configuration would break the destructive force of the waves and at the same time retain sufficient water motion or receive sufficient light for optimum CaCO_3 production, or both. There would also be "room" for some upward growth, as long as rising sea level offsets vertical infilling. Such an optimum environment is apparently uncommon on Pacific atolls today, probably at least in part because sea level has been relatively constant over the past few thousand years and reef growth on most shoal platforms has had an opportunity to catch up with sea level. Davies and Kinsey (18) present such a scenario for just such platform infilling at One Tree reef on the Australian Great Barrier Reef, as sea level has risen and then stabilized during the Holocene.

Much of the shoal area of Johnston Atoll may represent an environment with nearly optimum reef growth potential (19). There is an extensive area with elaborate corrugation of reef structures extending from slightly below sea level to depths of up to 10 m, with high coral cover and large corals across much of this area. Except in the deeper troughs between the reefs, water motion is relatively strong. We are not familiar with other similar atoll environments of comparable areal extent, although the proliferation of patch reefs near lagoon passes (20) probably represents much the same phenomenon of optimal reef growth in relatively protected shoal areas with high water motion.

By contrast, the Enewetak windward reef flat in the vicinity of our study area has lacked "room" for significant vertical accumulation of sedimentary materials over the last 3000 years (21), even though the production rate on that flat is rapid (6). Sediments accumulating on the lagoonward slope have been largely derived from the flat. The abundant reef-building organisms on much of the windward margin represent a slow and temporary buildup rather than either rapid CaCO_3 production or effective framework construction. The *mare incognitum* of windward Enewetak Atoll plays only a small part in the CaCO_3 mass balance of that atoll.

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References and Notes

1. H. S. Ladd, *Science* **134**, 703 (1961).
2. S. V. Smith and D. W. Kinsey, *ibid.* **194**, 937 (1976).
3. J. M. Wells, *Mar. Technol. Soc. J.* **8**, 9 (1974).
4. The domes are hemispheres 1 m in diameter. They isolate a "map" area of approximately 0.785 m² and a water volume of approximately 0.262 m³. The domes have a flange 5 cm wide about the rim. We achieved a satisfactory seal between the dome edge and the seafloor by gluing a strip of low-density foam rubber (10 cm thick) to the flange, loading it with three to eight 12-kg lead bricks (ordinarily four), and stuffing extra foam into any leaks. For one incubation on the reef crest, the dome was further secured with rock bolts. We evaluated the leakage by watching sediment movement within the domes during the incubations or, after the incubations, by injecting dye and then taking serial samples. In all but one experiment, leakage was judged to be negligible; results from that single experiment were discarded. Water samples were extracted with syringes through a serum cap port at the dome apex.
5. H. T. Odum and E. P. Odum, *Ecol. Monogr.* **25**, 291 (1955); R. E. Johannes *et al.*, *BioScience* **22**, 541 (1972).
6. S. V. Smith, *Limnol. Oceanogr.* **18**, 106 (1973).
7. J. W. Wells, *U.S. Geol. Surv. Prof. Pap.* 260-I (1954).
8. K. E. Chave *et al.*, *Mar. Geol.* **12**, 123 (1972).
9. D. W. Kinsey, personal communication.
10. T. F. Goreau, in *Biology of Hydra and Other Invertebrates*, H. M. Lenhoff and W. F. Loomis, Eds. (Univ. of Miami Press, Miami, 1961), p. 269.
11. D. W. Kinsey, *Proc. Symp. Corals Coral Reefs (Mar. Biol. Assoc. India)* (1972), p. 13.
12. T. Y. H. Ma, *The Relation of Growth Rate of Reef Corals to Surface Temperature of Sea Water as Basis for Study of Causes of Diastrophism Instigating Evolution of Life* (World Book, Taipei, 1958).
13. D. W. Knutson, R. W. Buddemeier, S. V. Smith, *Science* **177**, 270 (1972).
14. S. Price (Honolulu office, National Weather Service) has informed us that Typhoon Karen, with winds in excess of 70 m/sec, struck Guam in November 1962. The 1962-1963 annual report of the Eniwetok Marine Biological Laboratory (EMBL), University of Hawaii, states: "Storm damage during the typhoon which devastated Guam was considerable at EMBL. . . . Annual reports for several years before and after 1963 allude to no other such major storm damage at Eniwetok. Professor C. Ramage (University of Hawaii Meteorology Department) has observed that the November 1962 weather records for Eniwetok Atoll showed no unusual conditions, and so the reported damage must have been caused by sea conditions, even though the typhoon storm track missed Eniwetok."
15. J. E. Maragos, G. B. K. Baines, P. J. Beveridge, *Science* **181**, 1161 (1973).
16. T. F. Goreau, J. C. Lang, E. A. Graham, P. D. Goreau, *Bull. Mar. Sci.* **22**, 113 (1972).
17. I. G. Macintyre and P. W. Glynn, *Am. Assoc. Petrol. Geol. Bull.* **60**, 1054 (1976).
18. P. J. Davies and D. W. Kinsey, *Mar. Geol.*, in press.
19. K. O. Emery, *Geol. Soc. Am. Bull.* **67**, 1505 (1956); A. B. Amerson, Jr., and P. C. Shelton, *Atoll Res. Bull.* **192**, 1 (1976).
20. H. J. Wiens, *Atoll Environment and Ecology* (Yale Univ. Press, New Haven, Conn., 1962), pp. 35-39.
21. R. W. Buddemeier, S. V. Smith, R. A. Kinzie III, *Geol. Soc. Am. Bull.* **86**, 1581 (1975).
22. We thank R. W. Buddemeier, P. L. Jokiel, D. W. Kinsey, and R. A. Kinzie III for critical comments on various drafts of this report. The research was supported by U.S. Energy Research and Development Administration contract EY-76-C-08-0703, for the operation of the Mid-Pacific Marine Laboratory. Contribution No. 523 of the Hawaii Institute of Marine Biology.

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Inducibility of Transferrin Receptors on Friend Erythroleukemic Cells

Abstract. *The ability of Friend erythroleukemic cells to bind transferrin and take up its iron increases substantially as a result of dimethyl sulfoxide-stimulated differentiation. Although transferrin-binding activity is also demonstrable in another mouse cell line of hematopoietic origin, the lymphoma cell, it does not increase on exposure to dimethyl sulfoxide. Gel filtration studies corroborate that the binding of transferrin to the erythroleukemic cells is due to the formation of a specific complex of transferrin and a membrane receptor. Thus, the specific interaction of transferrin with its receptor is another expression of dimethyl sulfoxide-induced differentiation in the Friend cell.*

Certain murine erythroleukemic cell lines, first isolated by Friend and co-workers (1), appear to behave like transformed erythroid precursor cells that are arrested at an intermediate stage of development. In culture, the cells resemble proerythroblasts and exhibit several macromolecules that are characteristic of erythroid cells. Among these are globin messenger RNA's (2), heme biosynthetic enzymes (3), carbonic anhydrase (4), and erythrocyte-specific membrane proteins (5). When grown in media supplemented with dimethyl sulfoxide (6) or various other chemical agents (7), the cells differentiate into forms that resemble orthochromatic erythroblasts and the amounts or activities of the characteristic erythrocytic macromolecules increase (2, 5, 6), hemoglobin becomes readily detectable (6, 8), and iron accu-

mulates within the cells (6). Since transferrin is the major and perhaps the only source of iron for the biosynthesis of heme by erythroid cells (9), and the first stage in the interaction of transferrin with cells involves the binding of the protein to specific receptors on the cell surface (9, 10), we have studied the effects of growth in dimethyl sulfoxide on the capacity of erythroleukemic cells to bind transferrin. Although our measurements indicate that Friend cells have a significant number of receptors for transferrin prior to dimethyl sulfoxide treatment and hemoglobin accumulation, the capacity of the cells to bind transferrin and take up its iron is substantially increased during dimethyl sulfoxide-stimulated differentiation.

Studies with reticulocytes have shown that the binding of iron transferrin to its

receptors is a time-, temperature-, and energy-dependent process (10, 12). A small amount of transferrin is adsorbed nonspecifically to reticulocytes at 4°C (13), but upon incubation at 37°C there is a progressive uptake of transferrin until a steady state is reached at 10 to 20 minutes (10, 12). This state is characterized by continued iron incorporation, but the amount of transferrin bound to the cell remains relatively constant. Thus, in the steady state the rate of binding of iron transferrin and the rate of release of iron-depleted transferrin are approximately equal. Mature erythrocytes appear to lack specific transferrin receptors as they exhibit only the nonspecific adsorption that occurs at 4°C (14).

In order to measure their transferrin-binding capacity erythroleukemic cells grown under various conditions were extensively washed with serum-free solutions and then incubated at 37°C in buffered saline containing glucose, bovine serum albumin (to minimize nonspecific adsorption of transferrin to cell membranes), and transferrin labeled with ¹²⁵I. Transferrin-binding capacity of the cells was studied with iron-saturated transferrin in order to maximize the binding to specific receptors (11). Attempts to study iron uptake with iron-saturated transferrin gave variable results, which we attribute to the presence of small amounts of iron nonspecifically bound to protein. In order to minimize this error, 60 percent saturated [⁵⁹Fe]-transferrin (15) was used to study iron uptake. In these experiments the size of the cells varied depending on the growth state of the culture and whether or not the growth medium was supplemented with dimethyl sulfoxide. Cultures approaching a stationary growth phase contained cells with a smaller average size than those growing exponentially. Likewise, cells grown in the presence of dimethyl sulfoxide for several days were smaller than cells grown in its absence. To correct for these effects, in each experiment a cell sample was taken for measuring the cell number and size (a Coulter model F counter calibrated with latex beads was used). Transferrin binding and iron uptake were expressed as micrograms bound per milliliter of cells.

The kinetics of transferrin binding to Friend erythroleukemic cells (clone 745) grown in the absence of or presence of dimethyl sulfoxide for 3 and 5 days is shown in Fig. 1. The time course of transferrin uptake by these cells is similar to that observed with reticulocytes, although the time required to reach a steady state is somewhat longer. Values obtained for transferrin binding to Friend