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Forced convection modulates gas exchange in cnidarians

(Anthozoa/boundary layers/respiration rate/convective mass transfer/Sherwood number)

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ABSTRACT **Boundary layer thickness is a potentially important component of the diffusive pathway for gas exchange in aquatic organisms. The soft coral *Alcyonium siderium* (Octocorallia) and sea anemone *Metridium senile* (Actiniaria) exhibit significant increases in respiration with water flow over a range of Reynolds numbers encountered subtidally. A nondimensional mass transfer analysis of the effect of forced convection demonstrates the importance of the state of the organism's boundary layer in regulating metabolism in these invertebrates. Flow-modulated gas exchange may limit secondary productivity in subtidal environments.**

The condition of the boundary layer is the most pervasive physical influence on the biology of many aquatic organisms (1, 2). Through the action of fluid viscosity, boundary layers form over surfaces immersed in moving fluids. Boundary layer thickness is the distance over which fluid speed or dissolved species concentration changes from the value found immediately adjacent to the surface to some constant "mainstream" value found some distance above the surface. All mass transport with the environment occurs through this layer of relatively stagnant water overlying the organism. Although some aquatic invertebrates (3, 4) and vertebrates (5) depend on environmental flows to ventilate their exchange surfaces, the effect of boundary layer thickness has not been examined closely in studies of marine invertebrate respiration. The thickness of the diffusive boundary layer determines the concentration gradient of dissolved species. For example, this layer has been found to modulate bicarbonate diffusion into aquatic plants and, hence, to determine the maximum rate of photosynthesis (6). Similarly, diffusive boundary layer thickness affects gas exchange in symbiotic scleractinian corals (7, 8) and, thus, their growth rates (9).

The bottom momentum boundary layer is usually smooth–turbulent to rough–turbulent in natural flows over benthic organisms (10). The character of the flow around an organism is set by the size and distribution of neighboring roughness elements (other organisms, topographic elements—such as boulders and sand), and the overall shape and the surface roughness or structure of the organism. In a smooth–turbulent flow, a laminar sublayer exists immediately adjacent to the organism surface with a linear profile of flow speed vs. height. In the lower part of this section of the boundary layer, flux of material to an organism occurs by simple diffusion. In a rough–turbulent boundary layer, by definition, the roughness elements are of sufficient height to poke through and disrupt the laminary sublayer (11). Mass transfer increases greatly through the action of turbulent eddies. A final possibility is that the boundary layer over the organism may be transitional between these extremes and laminar sublayers can exist discontinuously in time and space.

The flow past an organism attached to the substrate in a benthic boundary layer can be quite complex, with the thickness of slower moving water changing with spatial location (12, 13). In general, the diffusive boundary layer will behave qualitatively like the momentum boundary layer: boundary layer thickness will increase in a downstream direction and decrease with increased fluid velocity, and increased turbulence will increase the velocity gradient near the surface (1).

Diffusive, boundary layers of appreciable thickness may exist (14), especially if (*i*) the boundary layer flow over the organisms is smooth–turbulent and/or (*ii*) the organism possesses structural features, such as polyps, branches, tentacles, zooids, etc., that redirect flow away from the surface *sensu* Morris (15) or slow it down further through momentum extraction (16). Diffusive boundary layers will be important to an aquatic organism's physiological ecology when other potentially rate-limiting steps in metabolism are small—e.g., the diffusive resistance through the integument is low (5) or, in the case of photosynthetic organisms, there are enough photons for light saturation (17).

In this study, we test the hypothesis that increased water motion can increase aerobic metabolism in subtidal marine invertebrates that rely on integumentary exchange of dissolved species. We describe measurements of gas exchange in two cnidarian species made under controlled conditions of water motion and, hence, boundary layer thickness. We analyze our results using a nondimensional mass transfer analysis [Sherwood number (*Sh*)/Reynolds number (*Re*) plot] that permits size-independent interspecific comparison of the effects of forced convection on metabolism, including analysis of the state of the boundary layer over the organism. Finally, we give evidence that these organisms experience a range of *Re* in the field similar to those used in our laboratory experiments and discuss the implications of our results for the estimation of secondary productivity and the physiological ecology of subtidal invertebrates.

MATERIALS AND METHODS

Recirculating Flow Respirometry. We investigated the effect of flow speed on oxygen consumption in a sea anemone, *Metridium senile*, and a colonial soft coral, *Alcyonium senile*, both abundant on vertical rocky substrates in the New England subtidal zone (18). Both organisms are zooplanktivorous (19, 20), rely largely on direct interception for prey capture (7), and respond to the presence of flow and prey in a synergistic fashion (7, 21). *Alcyonium* is found ≈5–25 m deep (K.P.S., unpublished data), whereas *Metridium* is found from the intertidal zone to as deep as 166 m (22).

Unidirectional recirculating flume respirometers (7) were used to vary the flow past a cnidarian while oxygen concentration, temperature, flow speed, and turbulence in the chamber were measured. Each of three chambers (548, 617, and 1457 ml/sec flow rate) used submersible bilge pumps (Rule, Gloucester, MA; 13.8 V dc) to generate the flow. Each

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Abbreviations: *Sh*, Sherwood number; *Re*, Reynolds number.

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specimen was mounted on a plate that fit flush with the chamber floor. All chambers were fitted with a polarographic oxygen sensor that was pressure/temperature-compensated [Yellow Springs Instruments (Yellow Springs, OH) (YSI) model 5710] installed in the upstream turbulent end of the chamber, connected to a YSI 54ARC oxygen meter. A temperature-compensated flow sensor with a heated thermistor measured flow speed and turbulence intensity 1.0 cm above the uppermost surface of the organism with a frequency response of 4 Hz. Plastic flow straighteners 15.0 cm long removed turbulence of length scales >0.5 cm and suppressed secondary flow generated by the pump and chamber cross-section before the flow encountered the organism. Turbulent kinetic energy (1.9–3.8 cm/sec) normalized to wall shear velocity (1.7–2.4 cm/sec) did not differ greatly between chambers and exhibited a range of values found in the subtidal water near these organisms (M.R.P., unpublished data).

The analog outputs from the sensors were sampled by an 8-bit successive approximation Mountain Computer (Scotts Valley, CA) analog/digital converter. An Apple IIe microcomputer and a Mountain Computer clock sampled data at 20 Hz, polled all sensors once every 4 sec and recorded mean values every 60 sec, and calculated when respirometer flushing should occur. Chambers were flushed after a 10% decrease in oxygen concentration. All experiments were performed at the Marine Science Center, Northeastern University. Both species were collected by scuba diving from nearby subtidal rock walls and were maintained in the laboratory seawater system before use. Seawater used in the chambers was filtered through sand and cotton filters to 100 μm and UV light sterilized, resulting in almost negligible respiration by chamber water. All respirometry runs were made in water 15–17°C, corresponding to summer field temperatures measured in the top 10 m of water near the habitat occupied by these species (23).

Mass Transfer Calculations. After the runs, the specimens were blotted dry, dried for 72 hr at 70°C, and weighed (0.001 g precision). Surface area available for gas exchange in *Alcyonium* was calculated from morphometric measurements assuming the colonies to be an ellipsoid. In *Metridium*, the polyp column was modeled as a tapered cylinder, whereas the tentacular surface area was approximated using the regression in Sebens (20). Least-squares linear regression of oxygen concentration vs. time in the chamber estimated respiration rates ($r^2 > 0.95$ in all cases) after subtraction of respiration rate of the chamber water (no cnidarian present).

Additionally, the effects of forced convection on mass transfer were analyzed in dimensionless form to allow prediction of gas exchange for flow conditions and organism sizes not used in our protocol. *Sh* is the ratio of the measured mass flux per unit area assisted by forced convection to the flux that would occur if diffusion through a completely stagnant boundary layer (scaled in proportion to organism size) was the sole mechanism for mass transport (24). *Sh* ($Sh = h_m l/D$) was calculated using the mass transfer coefficient (h_m; ref. 24), which was determined empirically from the ratio (of the mass flux to the concentration difference between the chamber and the site of oxidative metabolism), the characteristic dimension of the organism [(l) greatest horizontal dimension of *Alcyonium* colonies, polypal diameter of *Metridium*], and the diffusion coefficient for oxygen (D). For *Sh* calculations, oxygen concentrations were assumed to be very close to zero internally in respiring cell layers of ectoderm and endoderm, which seems a valid assumption in cnidarians for which oxygen microelectrode data exist (ref. 25; M.R.P., unpublished data). To characterize the nature of the forced convection regime around the organisms, we used *Re*, calculated from the flow speed, organism size, and momentum diffusivity (kinematic viscosity) of the fluid. *Re* is the ratio of inertial to viscous forces acting on parcels of moving fluid and, hence, an index of the gross character of the flow past the organism (2).

To permit comparisons between our laboratory experiments and natural conditions of forced convection, we measured flow in the field using a submersible thermistor flow meter (26) at three locations where the soft coral coexists with the sea anemone. Flow was measured at a height of 1.0 cm above the organisms. The range of *Re* experienced by a cnidarian 10 cm in greatest linear dimension was calculated.

RESULTS AND DISCUSSION

The Effect of Water Motion on Gas Exchange. Flow speed has a strong effect on oxygen transport in the two cnidarians (Fig. 1*A*). Although the number of flow speeds obtained was constrained by the available chamber pump sizes, the data for the soft coral exhibit asymptotic behavior also seen in gas-exchange studies in marine algae (6, 27, 28) and freshwater insects (29). The nondimensional analysis of the effect of forced convection on the dissolved gas transfer is shown in Fig. 1*B*. At all *Re*, the sea anemone had a much higher *Sh* than the soft coral.

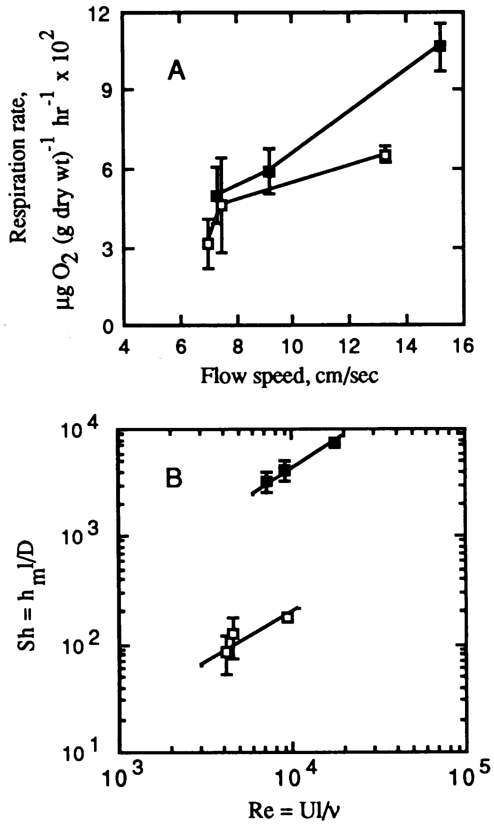

FIG. 1. (*A*) The effect of flow speed in a recirculating flow respirometer on respiration rate in the octocoral *Alcyonium siderium* (□, $n = 9$ runs, three specimens) and the sea anemone *Metridium senile* (■, $n = 16$ runs, three specimens). Flow speeds were measured 1.0 cm above the highest point on the organisms. Bars represent 95% confidence intervals. (*B*) Nondimensional plot of *A*, illustrating the convective mass transfer characteristics of the two species. The least-squares regression lines are as follows: *Sh*, 0.04 $(Re)^{0.92}$ for *Alcyonium* (□, $r = 0.55$, $P < 0.005$) and *Sh*, 0.28 $(Re)^{1.04}$ for *Metridium* (■, $r = 0.73$, $P < 0.001$). h_m, mass transfer coefficient (cm/sec); l, characteristic dimension of the specimen (cm); D, diffusion coefficient for oxygen (2×10^{-5} cm^2·sec^{-1}); U, flow speed (cm·sec^{-1}); and v, kinematic viscosity of seawater (1.04×10^{-2} cm^2·sec^{-1}). Bars represent 95% confidence intervals.

Factors Affecting *Sh*/*Re* Relationships. The convection-enhanced mass transport is related to the gross morphology of the organisms. The soft coral colonies used in these experiments were globose to ellipsoidal in shape (30); the surface of the colony is studded with small feeding structures, the polyps <1 cm in height, that greatly retard flow near the polyp columns and surface of the colony (12). In contrast, the sea anemone has a finely divided tentacular crown located at the maximum possible height above the substrate, and the smooth cylindrical polypal column is an important site for gas exchange (31). The slope of the logarithmic regression of *Sh* on *Re* for *Metridium* is significantly different from 0.5 (Student's *t* test; $P < 0.05$), indicating that mass transfer is governed by a turbulent boundary layer with the size of the wake and the location of the separation point important in determining the mass transfer (32, 33). In contrast, exchange of gas in *Alcyonium* conforms with laminar-boundary layer theory; the reduced flow in the layer of water flowing in and around the polyps results in a functionally thicker diffusive boundary layer than in *Metridium* for similar *Re*. However, for both species the calculated slopes were higher than slopes measured empirically for the analogous property of heat transfer in similar geometric shapes (32). It remains to be seen whether this property is inherent to biological exchange surfaces in a wide variety of macroinvertebrates relying on integumentary exchange or is simply an artifact of dissimilar turbulence intensities used in these different types of transport experiments.

We predict that organisms with a general architecture similar to *Metridium* (right circular cylinder with attached disk) will be more sensitive to flow-modulated metabolic changes because the thickness and even existence of the laminar sublayer will be easily affected by changes in *Re*. In contrast, the closely packed polyps on the *Alcyonium* colonies retard laminar sublayer disruption as flow speed increases; colonial cnidarians covered with a dense layer of polyps are predicted to show less metabolic sensitivity to forced convection.

Relation Between Convection Chamber Experiments and Field Conditions. Are the measurements made in the flow respirometer comparable to flow over these cnidarians in the field? In a strictly quantitative sense, they are not. The flow in the chamber is best described as growing, uniform, steady flow. The boundary layer thickness (and shear velocity) on the walls in the respirometer depends on downstream position in the flume. The eddy sizes in the flume (<10 cm) differed from those encountered in flow near boundaries in nature (34) by up to an order of magnitude, and did not show a linear increase with height above the floor of the chamber, a situation that occurs in nature (35). Shear velocity in an unoccupied respirometer is about equal to that seen in the field. But introduction of a cnidarian alters the flow in the chamber because "blockage effects" occur; the three-dimensional nature of the flow around the organism is affected by the nonequilibrium wall boundary layers and by the acceleration of water in the gap between organism and wall. Finally, in habitats shallower than one-half wavelength of the dominant swell, the flow will be bidirectional with a phase shift in maximum velocity relative to that of the overlying water occurring at some distance from the bottom (11), a situation not easily replicated in a closed system.

Despite these largely unavoidable limitations, we believe our results allow a useful comparison with field conditions of forced convection (Fig. 2). The distribution of *Re* at the left of the figure is typical for flow on calm days at several subtidal sites densely populated by the two species and indicates the potential importance of flow-modulated gas exchange for these animals in the field. The data forming the distribution at the right of the figure were collected under much rougher conditions; based on our laboratory data, strong flow modulation of gas exchange at these speeds is less important. For planar organisms flush with the substrate or respiring sediments, the shear velocity is the most important predictor of whether a diffusive Fickian sublayer exists and is important for mass transfer (10). Recently, there has been a renewal of interest in modeling interfacial mass transfer in terms of random eddy-surface renewal (32). How often eddies scrub through the viscous sublayer over sessile aquatic organisms is very habitat dependent and is unknown at present.

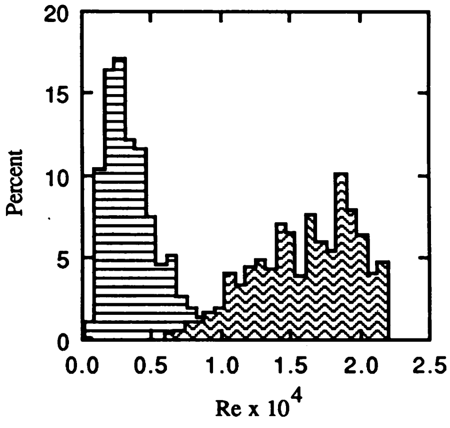

FIG. 2. Histograms of flow 1.0 cm above a mixed population of the two species at a field site (Dive Beach, MA) expressed as *Re* for flow past a cnidarian 10 cm in greatest linear dimension (*l*). Horizontally hatched columns, flow under calm surface conditions (mean = 3,562, SD = 2,405); wavy columns, flow under rough surface conditions (mean = 17,442, SD = 4,657). This shift in *Re* is typically seen at this site and two other sites in Massachusetts; all sites are described in Sebens (36). Data are derived from thermistor flowmeter recordings (30 min, $n = 900$).

The results of this study are in qualitative agreement with work done on gas exchange in terrestrial plants (18), insect larvae (37), freshwater algae (38), and marine algae (6, 28). In all cases, fluid speed was shown to increase the rate of gas exchange markedly. In aquatic systems, the diffusive boundary layer over bottom sediments can be on the order of 0.2–1.0 mm for calm conditions, with equilibration times ranging from ≈1 to 9 min (14). Diffusive-boundary layer thickness is a reasonable mechanism for modulating gas-exchange rates in invertebrates; but do rates of gas exchange scale with increasing flow speed, as boundary layer mechanics would predict? By and large, the evidence is scanty; we calculated a geometric regression using data from a study of gas exchange in caddisflies (29) and found that the mass transport was proportional to (flow speed)$^{0.38}$. This exponent was not significantly different from the exponent (0.5) predicted by laminar-boundary layer theory (39). We obtained similar results by fitting a curve to the data for oxygen concentrations just below the threshold for survival of a mayfly larva at various current speeds (29). As our study indicates, the state of the boundary layer and, hence, the slope of the function relating mass transfer to flow rate depends on the interaction between flow regime and organism structure.

CONCLUSION

Our results are in quantitative agreement with a model that assumes the boundary layer thickness is an appreciable resistance to the diffusion of gases. Shortening of the diffusive path for gas exchange by decreasing the boundary layer thickness will (*i*) increase the gas flux by linearly increasing the concentration gradient (Fick's first law), and (*ii*) parabolically decrease the time needed to equilibrate changes in gas concentration (Fick's second law) resulting from the action of the environment or the organism (40). Because of the inverse power relation between boundary layer thickness and flow speed, flow-modulated gas exchange will be most important for those organisms living in habitats where the flow regime changes from relatively stagnant to faster moving. It may also be important to aquatic organisms in higher energy flow regimes, where part of the gas-exchange structure is protected from flow—e.g., the fronds of many branching reef corals often are in greatly reduced flow toward the center of the colony (41).

The importance of the boundary layer has been discussed rarely with respect to respiration in invertebrates, although the importance of wave-generated mixing in enhancing intertidal productivity has recently been recognized (42). In most previous work on gas exchange in cnidarians the respirometry chambers were vigorously stirred and flushed, usually to ensure adequate mixing around the oxygen probe (36, 43, 44), but flow effects on respiration *per se* were not addressed. Estimates of community production often rely on gas-exchange studies made in enclosed respirometers (45) with various, and often unknown, mixing regimes. Field and laboratory respirometry work with aquatic organisms should characterize the flow regime of the chamber, especially in studies intended for calculations of secondary production. Organism size can alter flow patterns experienced in a given chamber with attendant effects on mass transfer. To deal with this forced convection variation, *Sh–Re* plots are useful to compare mass-transfer properties of organisms of different size and geometry exposed to different flows. More attention needs to be given to the proper field measurement and characterization of benthic flow environments, so the generality and importance of flow-modulated community metabolism can be assessed.

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1. Gates, D. M. (1980) in *Biophysical Ecology* (Springer, New York), pp. 271–275.
2. Vogel, S. (1983) in *Life in Moving Fluids* (Princeton Univ. Press, Princeton, NJ), pp. 127–162.
3. Knight, A. W. & Gaufin, A. R. (1963) *Proc. Utah Acad. Sci.* **40,** 175–184.
4. Strathmann, R. C. & Chaffee, C. (1984) *J. Exp. Mar. Biol. Ecol.* **84,** 85–93.
5. Feder, M. E. & Burggren, W. W. (1985) *Biol. Rev.* **60,** 1–45.
6. Wheeler, W. N. (1980) *Mar. Biol.* **56,** 103–110.
7. Patterson, M. R. (1985) Ph.D. Dissertation (Harvard Univ., Cambridge, MA).
8. Dennison, W. C. & Barnes, D. J. (1988) *J. Exp. Mar. Biol. Ecol.* **115,** 67–77.
9. Jokiel, P. L. (1978) *J. Exp. Mar. Biol. Ecol.* **35,** 87–97.
10. Nowell, A. R. M. & Jumars, P. A. (1984) *Annu. Rev. Ecol. Syst.* **15,** 303–328.
11. Denny, M. (1988) in *Biology and Mechanics of the Wave-Swept Environment* (Princeton Univ. Press, Princeton, NJ), pp. 122–129.
12. Patterson, M. R. (1984) *Biol. Bull.* **167,** 613–629.
13. Carey, D. (1983) *Can. J. Fish. Aquat. Sci.* **40,** 301–308.
14. Jørgensen, B. B. & Revsbech, N. P. (1985) *Limnol. Oceanogr.* **30,** 111–122.
15. Morris, H. M. (1955) *Trans. Am. Soc. Civ. Eng.* **120,** 373–398.
16. Anderson, S. M. & Charters, A. C. (1982) *Limnol. Oceanogr.* **27,** 399–412.
17. Nobel, P. S. (1983) in *Biophysical Plant Physiology and Ecology* (Freeman, San Francisco), pp. 268–270.
18. Sebens, K. P. (1985) in *The Ecology of Rocky Coasts*, eds. Moore, P. G. & Seed, R. (Hodder and Stoughton, Kent, England), pp. 346–371.
19. Sebens, K. P. & Koehl, M. A. R. (1984) *Mar. Biol.* **81,** 255–271.
20. Sebens, K. P. (1981) *Biol. Bull.* **161,** 152–171.
21. Robbins, R. E. & Shick, J. M. (1980) in *Nutrition in the Lower Metazoa*, eds. Smith, D. C. & Tiffon, Y. (Pergamon, New York), pp. 101–116.
22. Widersten, B. (1976) *Fish. Bull.* **74,** 857–878.
23. Smith, D. A. & Sebens, K. P. (1983) *J. Exp. Mar. Biol. Ecol.* **72,** 287–304.
24. Campbell, G. S. (1977) in *An Introduction to Biophysical Ecology* (Springer, New York), p. 65.
25. Revsbech, N. P. & Jørgensen, B. B. (1986) in *Advances in Microbial Ecology*, ed. Marshall, K. C. (Plenum, New York), Vol. 9, pp. 293–352.
26. LaBarbera, M. & Vogel, S. (1976) *Limnol. Oceanogr.* **21,** 750–756.
27. Dromgoole, F. I. (1978) *Aquat. Bot.* **4,** 281–297.
28. Koehl, M. A. R. & Alberte, R. S. (1988) *Mar. Biol.* **99,** 435–444.
29. Jaag, O. & Ambuhl, H. (1964) in *International Conference on Water Pollution Research London* (Pergamon, Oxford), pp. 31–49.
30. Patterson, M. R. (1980) in *Biofluid Mechanics 2,* ed. Schneck, D. J. (Plenum, New York), pp. 183–201.
31. Sassaman, C. & Magnum, C. P. (1972) *Biol. Bull.* **143,** 657–678.
32. Rosner, D. E. (1986) in *Transport Processes in Chemically Reacting Flow Systems* (Butterworth, Boston), pp. 246–261, 342–344, 375.
33. Zukauskas, A. & Ziugzda, J. (1985) in *Heat Transfer of a Cylinder in Crossflow* (Hemisphere, Washington), pp. 97–127.
34. Okubo, A. (1980) *Diffusion and Ecological Problems: Mathematical Models* (Springer, Berlin), pp. 12–14.
35. Mitchell, J. W. (1976) *Biophys. J.* **16,** 561–569.
36. Sebens, K. P. (1983) *J. Exp. Mar. Biol. Ecol.* **72,** 263–285.
37. Feldmeth, C. R. (1970) *Comp. Biochem. Physiol.* **32,** 193–202.
38. Hynes, H. B. N. (1970) in *The Ecology of Running Waters* (Univ. Toronto Press, Toronto), pp. 63–65.
39. Schlichting, H. (1979) in *Boundary Layer Theory* (McGraw-Hill, New York), pp. 135–141.
40. Berg, H. C. (1983) in *Random Walks in Biology* (Princeton Univ. Press, Princeton, NJ), pp. 17–36.
41. Chamberlain, J. A., Jr., & Graus, R. R. (1975) *Bull. Mar. Sci.* **25,** 112–125.
42. Leigh, E. G., Jr., Paine, R. T., Quinn, J. F. & Suchanek, T. H. (1987) *Proc. Natl. Acad. Sci. USA* **84,** 1314–1318.
43. Porter, J. W. (1980) in *Primary Productivity in the Sea*, ed. Falkowski, P. G. (Plenum, New York), pp. 403–410.
44. McCloskey, L. R., Wethey, D. S. & Porter, J. W. (1978) in *Coral Reefs: Research Methods*, eds. Stoddart, D. R. & Johannes, R. E. (UNESCO, Paris), pp. 361–378.
45. Svoboda, A. & Ott, J. (1983) in *Polarographic Oxygen Sensors*, eds. Gnaiger, E. & Forstner, H. (Springer, Berlin), pp. 285–297.