Table 1. Sessions required for criterion performance. The number of sessions required after ablation shown in parentheses. "Tone" or "Speech" refers to the nature of the stimuli; "Equal" or "Unequal" refers to their intensity.

	Discrimination task			
Subject	Unequal tones	Equal tones	Unequal speech	Equal speech
	Experimental animals			
A	(7)*	4(1)	(10)*	40(>80)
C	15(1)	10(2)	(1)*	49(>98)
D	16(1)		7(2)	38(>76)
	Control animals			
B	26(1)			42(1)
E		28(1)		46(1)

* No training prior to ablation.

tion, transfer took place within 50 trials (approximately 7 minutes' testing time) and was generally apparent after ten trials. Completion of the "female speech" control task was followed by a 2-week rest period, after which the animals were again tested with the "male speech" stimuli (all animals retained the discrimination within the first 50 trials). Bilateral subpial ablations were then made of: the insular-temporal cortex (three animals), the entire cortical auditory receiving areas, AI, AII, and Ep (posterior ectosylvian) (one animal), and portions of AII and Ep not bordering on the insular-temporal cortex (one animal). After a recovery period of at least 2 weeks, the animals were again tested, first on the tone discriminations and next on speech sounds.

Table 1 shows that all animals retained every discrimination except that of speech sounds of equal intensity. This particular task was retained by the two control subjects. The three experimental animals, although retaining their ability to discriminate between simple differences in frequency or intensity, or both, in the three-lever situation, did not retain and were unable to relearn the discrimination between speech sounds of equal intensity in twice as many sessions as had been given before they were operated on.

Operative lesions were confirmed by serial reconstructions; Fig. 1 shows the reconstructed cortical lesions of the experimental animal whose deficit on the critical discrimination was the most striking. For this animal (killed 3 months after surgery), no retrograde thalamic degeneration was evident anywhere in the medial geniculate body. It is generally thought (*2*) that the insular-temporal cortex receives only collaterals from axons projecting from medial geniculate to primary auditory cortex, hence a lesion restricted to this area need not necessarily result in retrograde thalamic degeneration. A recent report (*3*) suggests that the insular cortex receives direct input from AI. Since, in control animal E, all the primary auditory cortex was bilaterally ablated and no performance deficit resulted, transcortical connections from AI to the insular cortex appear unnecessary for the critical task.

Performance on the middle lever (the one through which primary reinforcement was received) reached 95 percent at an early stage in the training before the animals were operated on, and was sustained at this level by all five animals after ablation regardless of the discrimination task. This indicates that the experimental animals could still react appropriately to an immediate change from one speech stimulus to another. When, seemingly by chance, they chose the correct side lever, the [u] (or [i]) was replaced by [a]. The animals showed no deficit in detecting this change and responding to it correctly by pressing the middle lever.

The method described here thus yields data on two facets of discrimination: (i) differential response to one of a class of stimuli, and (ii) single response to stimulus change. The ability of the experimental animals to choose between two alternative responses to a single complex auditory stimulus is materially altered after bilateral ablation of the ventral insular-temporal cortex. This cortical area is thus shown to be implicated in the performance of differential responses to complex auditory signals but not in the performance of differential responses to simple differences in frequency or intensity. The central mechanisms through which this finding may be explained remain obscure.

JAMES H. DEWSON, III

Department of Psychiatry,
Stanford University School of Medicine,
Palo Alto, California

References and Notes

1. R. A. Butler, I. T. Diamond, W. D. Neff, *J. Neurophysiol.* **20**, 108 (1957); I. T. Diamond and W. D. Neff, *ibid.*, p. 300; J. M. Goldberg, I. T. Diamond, W. D. Neff, *Federation Proc.* **16**, 47 (1957); J. M. Goldberg and W. D. Neff, *J. Neurophysiol.* **24**, 119 (1961).
2. J. E. Rose and C. N. Woolsey, in *Biological and Biochemical Bases of Behavior*, H. Harlow and C. N. Woolsey, Eds. (Univ. of Wisconsin Press, Madison, 1958); I. T. Diamond, K. L. Chow, W. D. Neff, *J. Comp. Neurol.* **109**, 349 (1958).
3. Ya. A. Al'tman and A. S. Iontov, *Federation Proc.* **23**, T96 (Translation Suppl.) (1964).
4. Supported by a postdoctoral research fellowship, National Institutes of Health and U.S. Army contract MD-2328 to Karl H. Pribram. This work was reported at the 66th meeting of the Acoustical Society of America. I thank K. H. Pribram and H. H. Schaefer.

6 January 1964

The Plankton Community

The report on "Plankton: Optimum diversity structure of a summer community" [*Science* **140**, 894 (24 May 1963)] is open to several criticisms. B. C. Patten, the author, presents a linear programming model of a plankton community which requires that the available resources be allocated in a specific manner to give what he terms the optimum composition (diversity) of the community. From the solution of the author's model this optimum composition represents the standing crop at that point in time when at least one of the essential resources has been depleted.

As a consequence no materials will be available for further growth. This means that there can be no net community production. For this reason the model is not applicable to actively growing plankton populations or those undergoing species succession since only the final composition is specified and not the intermediate stages or the rates at which this optimum is attained. Since the York River plankton community had positive rates of net production, it is not really appropriate to discuss it in the context of the model presented.

The fact that some of the author's terms have one meaning in the model and another in the discussion of the York River is rather confusing to the reader. For example, in the model, *diversity* refers to both the qualitative and quantitative composition of the community. The numerical measure of diversity used for the York River plankton as expressed in bits per milliliter is a function of both the distribution of cells between the species present and the density of cells in the samples. One property of this function is that if the relative proportion of cells representing the various species in a sample is held constant, the diversity measure becomes a linear function of the population size. Thus when the author compares populations with high and low diversities, it may only reflect differences in cell density and not qualitative composition. The association of high productive capacity with high diversity may simply be a reflection of greater cell densities.

In considering how diversity adjustments may be adaptive at different depths, the author lets a given diversity change alter respiration by a factor k_1 and gross production by a factor k_2 and then states that the case $k_1 = k_2$ is so unlikely that it can be disregarded. This conclusion appears to be incorrect. For example, if the population density of all species in a plankton community were doubled, his diversity measure would also be doubled. If at the same time the rates of respiration and gross photosynthesis per cell remained the same, then the community respiration would be increased by a factor of 2 and the gross photosynthesis would also be increased by a factor of 2. The case $k_1 = k_2$ does not seem to be at all unlikely. For the same reason it is difficult to understand the author's statements that in the trophogenic zone $k_1 < k_2$ would be most probable, and that in the tropholytic zone diversity increases can only result in $k_1 > k_2$.

Lastly, in an attempt to show that the vertical distribution of species in the York River is adaptive with respect to the prevailing light conditions, the author cites data from culture experiments reported in the literature to show that the species of dinoflagellates found at 2 feet typically have photosynthetic maxima at high light intensities, while two of the dominant groups found at 10 feet have their maxima at low or moderate light intensities. His own data, however, would indicate that all of the populations have their maxima at the light intensities found near 2 feet.

An examination of the values for gross photosynthesis in Fig. 2 shows that in moving from a suspension depth of 6 feet to a suspension depth of 2 feet the gross photosynthetic rate of the population at 2 feet increased by a factor of 1.81, the population at 6 feet by a factor of 1.92, and the population at 10 feet by 1.81. From these comparisons there is no evidence that the vertical distribution of plankton species in the York River is related to their light intensities for maximum photosynthesis.

In conclusion, I feel that by introducing a theoretical model inappropriate to the community under study, Patten has hindered rather than helped the reader's understanding of the material presented. The main conclusion of the paper (that by expending energy to maintain a large proportion of the photosynthetic algae in a well illuminated zone, the community acts to maximize its rate of production) could be demonstrated much more clearly and concisely without it.

ROGER W. BACHMANN
Department of Zoology,
University of California, Davis

18 September 1963

The linear programming model is of course static and not dynamic. This is true of all linear programming, but the methods are nevertheless routinely applied to dynamic systems in, for example, economics, operations research, and management science, in order to specify an optimum final state when initial conditions are known. It is clear that as soon as any real system begins to undergo time-related state transformations, the model parameters change instantaneously and the optimum solution itself becomes subject to dynamic behavior unless the system is a priori completely determined, as few natural systems are. Since the concept of optimality is basic to that of adaptation, I do not agree with Bachmann that the linear programming formulation is inappropriate; it was used only to provide a conceptual framework—that is, to state an ecological adaptation problem (resource allocation) in an optimization context. The difficulties of actually applying even this static model were mentioned.

With regard to my usage of the term *diversity*, I cannot argue the validity of the duality charge since the distinction between "qualitative" and "quantitative" composition is unclear to me. The former concept I find particularly elusive, and I question whether it would bear up under critical examination. My use of "diversity" was unambiguous, namely

$$D\ [\text{bits ml}^{-1}] = -\sum_{i=1}^{m}\left[x_i \log_2 \frac{x_i}{X}\right], \qquad (i = 1, 2, \ldots, m)$$

when m is the number of species, x_i is the number of individuals of i'th kind, and

$$X = \sum_{i=1}^{m} x_i.$$

Since I agree substantially with the analysis of this function's properties as given in the last half of Bachmann's second paragraph, I am uncertain whether he is objecting or merely clarifying. There is some basis for confusion in that diversity theory in ecology has largely concerned the relationships between numbers of species and numbers of individuals, per se, and has consequently employed intensive measures —indices independent of X. The simple index m/X, for example, is invariant so long as m and X are in the same proportion, regardless of the value of X.

My approach to the diversity problem has been in the context of limited environments, where number of species is a function of number of individuals, and conversely. Therefore it is appropriate to employ an extensive index which takes into consideration both the "richness" of the environment and the "quality" of the organisms which occupy it. That the index D does this I previously attempted to demonstrate (*1*), but the derivation contained some mathematical errors which rendered the result invalid (*2*). Since this is important, and since it is apropos of Bachmann's comments, it seems expedient to make the correction now.

The best intensive diversity index available is the Shannon-Wiener formula from information theory:

$$\bar{D}\ [\text{bits}] = -\sum_{i=1}^{m}\left[\frac{x_i}{X}\log_2\frac{x_i}{X}\right]. \qquad (i = 1, 2, \ldots, m)$$

If, as in my earlier paper (*1*), β represents a phase space which is the biotope, and $\Delta_i\beta$ is the specific biotope (*3*) of species i (the fraction of β occupied by one individual), then it is desired to show that D is directly proportional to β and inversely proportional to $\Delta_i\beta$ whereas $\bar{D}$ is unrelated to β. This will establish D as a preferred index in an ecosystem context since, intuitively, the "diversity of species" in an equilibrium community is related directly to the "quality" of the biotope and inversely to the "quality" of the inhabitants since resources are in limited supply.

Species "quality" may be represented

abstractly as the quantity $\Delta_j\beta$, the part of the biotope occupied by a member of species j. The total occupancy by the species is then $x_j\ \Delta_j\beta$. At equilibrium, when the biotope space has (ideally) been completely partitioned among the species, we have

$$\beta = \sum_{j=1}^{m} x_j\ \Delta_j\beta. \qquad (j = 1, 2, \ldots, i, \ldots, m)$$

Solving for the number of individuals in the i'th species:

$$x_i = \frac{\beta - \sum_{j=1}^{i-1} x_j\ \Delta_j\beta - \sum_{j=i+1}^{m} x_j\ \Delta_j\beta}{\Delta_i\beta}. \qquad (1)$$

$$\left(\sum_{j=a}^{b} x_j\ \Delta_j\beta = 0 \text{ when } a > b\right)$$

The expression for the total individuals in the community is then

$$X = \sum_{i=1}^{m} \frac{1}{\Delta_i\beta} \left[\beta - \sum_{j=1}^{i-1} x_j\ \Delta_j\ \beta - \sum_{j=i+1}^{m} x_j\ \Delta_j\beta\right],$$

$$\left(\sum_{j=a}^{b} x_j\ \Delta_j\beta = 0 \text{ when } a > b\right)$$

so that the probability of species i is

$$\frac{x_i}{X} = \left[\Delta_i\beta \sum_{i=1}^{m} \frac{1}{\Delta_i\beta}\right]^{-1} \qquad (2)$$

The equation for $\bar{D}$ may now be expressed in terms of Eq. 2,

$$\bar{D} = -\sum_{i=1}^{m} \left[\left(\Delta_i\beta \sum_{i=1}^{m} \frac{1}{\Delta_i\beta}\right)^{-1} \log_2 \left(\Delta_i\beta \sum_{i=1}^{m} \frac{1}{\Delta_i\beta}\right)^{-1}\right],$$

showing that $\bar{D}$ is directly proportional to the summation of specific biotopes and inversely related to the size of the specific biotopes, but unrelated to β. The expression for D in terms of Eqs. 1 and 2 is

$$D = -\sum_{i=1}^{m} \left[\left(\frac{\beta - \sum_{j=1}^{i-1} x_j\ \Delta_j\beta - \sum_{j=i+1}^{m} x_j\ \Delta_j\beta}{\Delta_i\beta}\right) \times \log_2\left(\Delta_i\beta \sum_{i=1}^{m} \frac{1}{\Delta_i\beta}\right)^{-1}\right],$$

$$\left(\sum_{j=a}^{b} x_j\ \Delta_j\beta = 0 \text{ when } a > b\right)$$

which displays a strong direct proportionality with β and is generally inversely proportional to the specific biotopes, although the relationships here are quite complicated. This equation supersedes Eq. 14 of my previous paper (*1*). It should be noted in passing that nonequilibrium expressions for $\bar{D}$ and D can be obtained essentially in the same manner as the above from

$$\beta > \sum_{j=1}^{m} x_j\ \Delta_j\beta$$

or

$$\beta < \sum_{j=1}^{m} x_j\ \Delta_j\beta,$$

as appropriate.

With regard to my discussion of the effects of diversity changes on respiration and gross production in the York River summer plankton, while it is true that $k_1 = k_2$ may be possible in some environments over a limited diversity range, this would not hold generally unless the two functions $\pi_z(D_z)$ and $\rho_z(D_z)$ were identical. Since π and ρ are determined differently by environmental factors, light and temperature, for example, $\pi_z(D_z)$ and $\rho_z(D_z)$ are never the same. To select an obvious example, a diversity increase under dark conditions would be accompanied by an increase in respiration but not in photosynthesis; therefore $k_1 > k_2$. In the light, $k_1 < k_2$ is at least permissible, and becomes more probable as optimum intensity is approached. This is generally above the compensation depth.

Concerning Bachmann's final point, I concede that bringing the subject of light optima into the discussion was inappropriate in view of the relationships exhibited in Fig. 2 (*4*). The adaptiveness of compositional changes with depth is nonetheless a reality, however, as the following observations will serve to reemphasize.

In my paper I postulated that power considerations were the primary determinants of community structure in the upper water column where photons are abundant, whereas efficiency criteria are more important further down. Let us examine some relationships of power and efficiency to diversity at different depths.

The average diversity of the populations at 2, 6, and 10 feet was 1.12×10^7, 4.41×10^6, and 3.62×10^6 [bits ml^{-1}] (Fig. 1). In terms of area, these values correspond to 6.83×10^9, 2.69×10^9, and 2.21×10^9 [bits cm^{-2}], since the volume of water under an area of 1 cm^2 in a 20-foot water column is 610 ml. The efficiency of photosynthesis per unit diversity, $\pi I^{-1}D^{-1}$, can be calculated in the units [gcal kcal^{-1} cm^2 bits^{-1}] by dividing the efficiencies in Fig. 3, [gcal kcal^{-1}], by diversity [bits cm^{-2}]. Similarly, cost per unit diversity, $\rho\pi^{-1}D^{-1}$, is the quotient of the data given in Fig. 4 and diversity, and has the units [gcal gcal^{-1} cm^2 bits^{-1}]. Net production [gcal cm^{-2} day^{-1}] per unit diversity is $(\pi - \rho)D^{-1}$, in [gcal day^{-1} bits^{-1}].

At the 10-foot suspension depth the values of $\pi I^{-1}D^{-1}$, respectively, for the populations from 2, 6, and 10 feet, were 7.77×10^{-9}, 1.29×10^{-8}, and 2.02×10^{-8} [gcal kcal^{-1} cm^2 bits^{-1}], demonstrating that the naturally occurring populations at 10 feet were nearly twice as efficient per diversity unit as those from 6 feet, and almost three times more efficient per diversity unit than those from 2 feet.

At the 2-foot suspension the values for $(\pi - \rho)D^{-1}$, in the same sequence of collection depths, were 4.42×10^{-10}, 4.31×10^{-10}, and 3.94×10^{-10} [gcal day^{-1} bits^{-1}], indicating little differentiation between the populations from 2 and 6 feet in terms of unit capacity for power throughput, but significantly less net production per unit diversity in the populations from 10 feet. The total net production of each sample when suspended at 2 feet averaged 3.03, 1.16, and 0.87 [gcal cm^{-2} day^{-1}], respectively, for samples collected from 2, 6, and 10 feet, which emphasizes the advantage of the vertical diversity pattern shown in Fig. 1. A final point is that the cost of maintaining the populations at 2-foot suspension increased with collection depth (Fig. 4). On a unit diversity basis, $\rho\pi^{-1}D^{-1}$ values were 4.98×10^{-11}, 2.75×10^{-10}, and 3.39×10^{-10} [gcal gcal^{-1} cm^2 bits^{-1}], showing that the maintenance cost of a diversity unit was almost a full order of magnitude less for the populations from 2 feet than for those from 6 and 10 feet.

In view of these results, there can be little question that the populations were adapted to the depths from which they were drawn, in a manner consistent with the hypothesis, and that the observed differences in species composition must to some extent be responsible.

BERNARD C. PATTEN

Radiation Ecology Section, Health Physics Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee*

References and Notes

1. B. C. Patten, *J. Marine Res.* **20**, 57 (1962).
2. J. H. Connell, personal communication.
3. G. E. Hutchinson, *Cold Spring Harbor Symp. Quant. Biol.* **22**, 415 (1957).
4. All figures mentioned in this report are from *Science* **140**, 894 (1963).

* Operated by Union Carbide Corporation for the U.S. Atomic Energy Commission.

9 December 1963