and F_2 progeny show that the primary structure of the α and β chains of mouse hemoglobins are governed by *Sol* and *Hb* (*10, 11*). The data presented here provide a basis for selecting several different mouse hemoglobins for further studies on: (i) allelomorphism and amino acid sequences, and (ii) molecular structure and biological function.

Additional information on the crossover frequency between *c* and *Hb* and on the position of *Sol* in the mouse genome is also given. Data on the crossover frequency between *c* and *Hb* are presented in Table 1. These values were calculated by the product method (*13*) from F_2 data alone since we obtained comparatively little data on backcrosses in which crossovers between alleles at *c* and *Hb* were phenotypically expressed. Crossover frequencies from different matings varied considerably (Table 1) and ranged from 3.39 to 10.96 percent among relatively small samples. The average recombination value (1459 mice) for the combinations reported here is 0.0647 ± 0.0067, which is slightly higher than the value of 0.0413 ± 0.0061 reported earlier (*3*). Combined analysis of the backcross data (359 mice) gives a crossover value of 0.0947 ± 0.0155, which is somewhat higher. These values were computed from many strains of mice not previously used; for some strains, the recombination frequency between *c* and *Hb* appears to be greater than 5 percent. Since the progeny were classified for coat-color and other visible phenotypic differences, a comparison of such phenotypes with *Sol* types indicates that *Sol* is not sex-linked or closely linked with *p, c, Hb, d, se, W, s, A, Ca, b, Fu, ru, ln, f, Es, fs,* or with the black-eyed white trait of strain C3H.B. Furthermore, no selective survival of mice with any of the *Sol* types was noted.

Inheritance of hemoglobin in mouse and man appears to be similar. Two loci, which segregate independently, control the primary structure of the α- and β-chain polypeptides. In mice with two or more hemoglobins distinguishable by electrophoresis the β-chain locus may be compound, or two loci may be tightly linked as are the β- and δ-chain loci in man. Knowledge of whether the β-chain locus and albinism are linked in man as they are in the mouse would help to determine whether homologous portions of the chromosome have remained intact during evolution. Mating mice of known hemoglobin genotypes makes the mouse useful for investigating some hypotheses concerning the inheritance of hemoglobin.

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Plankton: Optimum Diversity Structure of a Summer Community

Abstract. *The summer plankton community of the York River, Virginia, expends energy to establish and maintain a definite vertical diversity structure in a comparatively unstructured environment. The resultant organization, which involves relationships between diversity, power and efficiency, and stability, is nearly optimal for maximizing profit on the original energy investment.*

How energy balance is achieved in a natural plankton community can be viewed from the standpoint of linear programming (*1*). The community is construed at a given time as having a pool of resources, such as nutrients, growth substances, stocks of organisms with various requirements and properties, and an energy supply. The problem is how to allocate the resources in such a way as to produce an optimum species composition, one which would bring to maximum the community's energy profit under existing conditions in the biotope.

To set this up for linear programming, we might define m as the number of species i in the pool ($i = 1, 2, \ldots, m$); n as the number of resources j ($j = 1, 2, \ldots, n$); a_{ij} as the number of units of resource j required to produce a unit of species i; b_j as the maximum number of units of resource j available; p_i as the energy profit per unit of species i produced; and x_i as the number of units of species i produced. Then, the total amount of the jth resource used is

$$a_{1j}x_1 + a_{2j}x_2 + \ldots + a_{mj}x_m$$

subject to the constraint

$$\sum_{i=1}^{m} a_{ij}x_i \leqq b_j.$$

Since $x_i < 0$ has no meaning, we stipulate $x_i \geqq 0$. The profit derived from producing x_i units of organism i is then $p_i x_i$, giving for a profit function

$$p_1x_1 + p_2x_2 + \ldots + p_mx_m,$$

which is to be maximized. The solution, readily obtained by established procedures, represents the optimum composition (diversity) of the community corresponding to the prescribed conditions of the problem and the profit-maximizing motive.

Although such a formulation would be difficult to apply empirically (for example, trying to provide data for a_{ij} and p_i), as a model it delineates the enormous problem in logistics and communication associated with evolving and maintaining optimum structure in a community. In this context, let us consider the problem of optimum diversity in a particular summer plankton community.

Energy flow in the community at a station in the lower York River, Virginia, was studied during the summer of 1960 by means of dark and light bottle microcosms (*2*); the primary variables measured were gross production (π) and respiration (ρ) of the enclosed samples. Ten 24-hour experiments were conducted. The depths investigated were 2, 6, and 10 feet. Since the mean 24-hour compensation depth (the depth at which $\pi = \rho$) was 6.5 feet, the samples from 2 feet were naturally in positive energy balance ($\pi - \rho > 0$), those from 6 feet were approximately in steady state ($\pi - \rho \approx 0$), and those from 10 feet were in negative balance ($\pi - \rho < 0$). In the field, water samples were enclosed in paired dark and light BOD bottles and resuspended in the water column. The dark bottles were suspended at the same depths from which the samples they contained had been collected, whereas the light bottles were suspended at all combinations of collection depths. Dissolved oxygen was determined by the unmodified Winkler method. On the assumption that $PQ = RQ = 1$, conversion was made from milligrams of oxygen per liter to gram calories per square centimeter (based on a 20-foot water column, volume 0.61 liter per square centimeter). Incident solar radiation I was measured in gram calories per square centimeter by an Eppley 10-junction pyrheliometer installed a few hundred yards from the station. Extinction coefficients were calculated from optical densities determined colorimetrically with a neutral filter on samples obtained at the beginning and end of each experiment. Mean values for the upper water column were then used to estimate illumination at specific depths during each experiment. Duplicates of the suspended water samples were examined to determine the initial concentration (x_i) of the ith phytoplankton species identified. Initial diversity per milliliter was then computed from the relationship

$$D \text{ (bits)} = -\sum_{i=1}^{m} x_i \log_2 (x_i/X),$$

where D is sample diversity and (3)

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

Although significance tests were not performed, variability in all data was assessed by means of the coefficient of variation before inferences were made.

Table 1. Phytoplankton taxa and concentrations at various depths in units (cells, colonies, or chains) per milliliter at the beginning of one experiment (6 July) of the ten reported.

Surface	2 ft	6 ft	10 ft	Bottom
Massartia rotundata (Lohmann) Schiller				
3828	1508	139	—	139
Chilomonas (?) sp. Ehrenberg				
928	928	—	—	70
Gyrodinium aureum (?) (Conrad) Schiller				
348	1276	417	695	70
Eutreptia sp. Perty				
348	464	556	139	70
Leptocylindrus danicus Cleve				
232	232	209	348	209
Amphidinium fusiforme Martin				
232	232	209	139	139
Gymnodinium nelsoni Martin				
232	—	—	—	—
Cryptomonas sp. Ehrenberg				
116	580	—	—	209
Unidentified dinoflagellate				
116	—	—	—	—
Peridinium trochoideum (Stein) Lemmermann				
12	116	70	—	70
Skeletonema costatum (Greville) Cleve				
12	12	—	7	139
Thalassiosira gravida Cleve				
12	12	70	70	70
Dunaliella (?) sp. Teodoresco				
12	—	—	—	70
Prorocentrum micans Ehrenberg				
12	—	—	—	—
Pyramimonas sp. Schmarda				
—	232	209	417	139
Nitzschia closterium (Ehrenberg) Smith				
—	232	—	—	—
Unidentified diatom				
—	116	—	—	—
Prorocentrum triangulatum Martin				
—	12	7	—	—
Unidentified chlorophyte I				
—	116	70	—	—
Dinophysis sp. Ehrenberg				
—	—	—	7	—
Unidentified chlorophyte II				
—	—	—	—	70
Thallassionema nitzschioides Grunow				
—	—	—	—	70
Total species (m)				
14	15	10	8	14
Total cells (X)				
6440	6068	1956	1892	1534

Mean diversity in the ten experiments is graphed as a function of depth (Fig. 1). Pronounced stratification of organisms above the compensation depth (broken line) is indicated, and the graph in fact bears a close resemblance to the usual form of photosynthesis profiles (4). Let us investigate whether the vertical organization depicted represents an optimum for maximum energy profit under the prevailing conditions.

Mean photosynthesis for the ten experiments may be plotted as a function of collection and suspension depths (Fig. 2). The surface shown indicates clearly greater capacity for photosynthesis in the 2-foot populations: From left to right (π as a function of collection depth), Fig. 2 shows that the high diversity 2-foot samples always photosynthesized more than those from 6 and 10 feet irrespective of suspension depth. Thus, high productive capacity in this community appears to be associated with high diversity, and the observed pattern of diversity concentration in a zone of high illumination seems consistent with an energy maximization criterion.

Inherent in the diversity structure in Fig. 1 is a capability for dark adaptation. This is shown in Fig. 3 where mean photosynthetic efficiency (πI^{-1}) is graphed as a function of collection and suspension depths. From back to front, efficiency is indicated to increase with suspension depth regardless of depth of origination. The 2-foot samples generally performed better than those from the other depths, with the notable exception of the 10-foot samples suspended at 10 feet. Since the latter populations were markedly less diverse than those from 2 feet (Fig. 1), a basic adjustment is indicated.

In the linear programming formulation, the question was posed: How many organisms of type i should be produced with the limited resources of the system? It was acknowledged that each species had different propensities and requirements. The relationships shown in Fig. 3 suggest that populations down to the compensation depth are geared for production at low efficiency and high power output (5), whereas those in the tropholytic zone beneath function at considerably higher efficiencies (44.7 gcal/kcal at 10 feet, compared to 19.5 at 6 feet and 18.5 at 2 feet) although with reduced overall throughput (Fig. 2: 0.85 gcal/cm^2 per day at 10 feet versus 1.46 at 6 feet and 4.61 at 2 feet). Thus in this community diversity appears arrayed in space so that high diversity corresponds to relatively low efficiency and high output, while lower diversity corresponds to somewhat higher efficiencies and

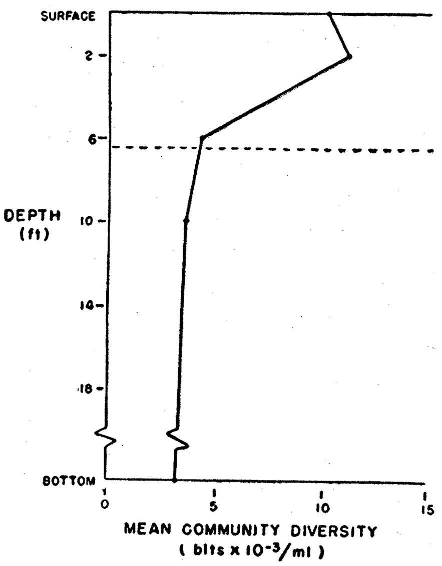

Fig. 1. Mean community diversity, $D = -\sum_{i=1}^{m} x_i \log_2 (x_i/X)$, in the ten experiments at various depths; x_i is the concentration of organisms of ith kind ($i = 1, 2, \ldots, m$), and X is the concentration of organisms of all kinds.

lower outputs. If we consider the light conditions at the different depths, both modes would seem adaptive in respect to energy maximization. Examination of the species lists indicates that the modes are indeed dependent upon composition.

Table 1 shows that in a typical experiment two flagellates, *Massartia* and *Chilomonas,* were the dominant forms at the surface but at a depth of 2 feet *Massartia, Gyrodinium,* and *Chilomonas* dominated in that order. These organisms, all dinoflagellates, typically exhibit photosynthetic maxima at the higher light intensities (*6*). At 6 feet, with diversity markedly reduced (Fig. 1), the surface forms were no longer significant; dominants were *Eutreptia* and *Gyrodinium.* At 10 feet, where diversity is still further reduced, the surface forms were not represented at all; *Eutreptia, Pyramimonas* and *Leptocylindrus* were dominant in that order. *Eutreptia* is a euglenoid, *Pyramimonas* a flagellated chlorophyte, and *Leptocylindrus* an immotile diatom. The latter two groups typically have photosynthetic maxima at low or moderate light intensities (*6*). Thus, inherent in the vertical diversity structure of the community is a more or less continuous compositional adjustment which tends to produce optimum relationships of power to efficiency for the prevailing conditions of illumination at each level. It is pertinent to inquire whether such organization is purely fortuitous, or whether it requires energy expenditure by the community to bring it about.

The mean temperature difference from surface to bottom in the ten experiments was only 0.29°C, and the mean chlorinity difference (tidal stage random) only 0.75 parts per thousand. The diversity structure of Fig. 1 could hardly have resulted, therefore, from hydrographic stratification since too much vertical mixing is indicated. This implies that flotation mechanisms (motility primarily) were involved. Since all such mechanisms use energy, they would appear incompatible with the energy maximization postulate, unless of course they resulted in more energy gained back than was originally expended.

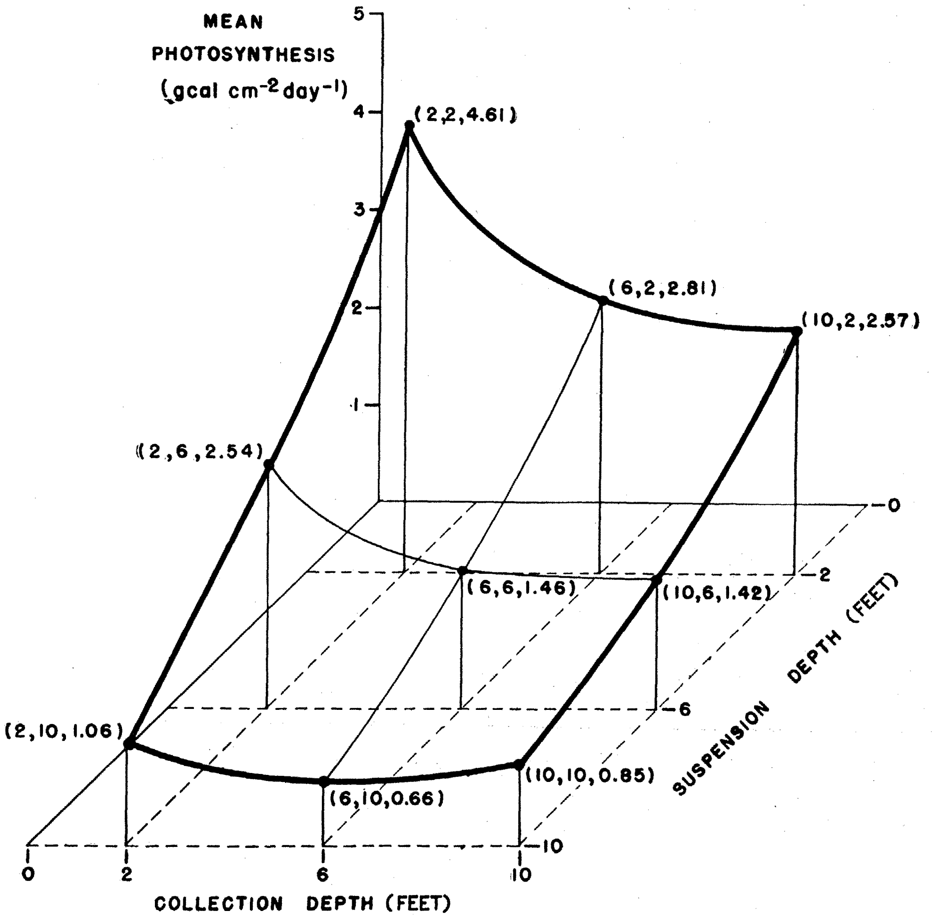

Fig. 2. Photosynthesis as a function of sample collection and suspension depths (means for ten experiments).

Mean cost ($\rho\pi^{-1}$) is plotted as a function of collection and suspension depths (Fig. 4). To provide a better perspective the graph has been rotated 90° clockwise around the vertical axis (compared with Figs. 2 and 3). The surface is saddle-shaped: convex upward from back to front, and concave upward from right to left. Viewing from right to left, one sees cost increase with suspension depth because of reduced π as light becomes dimmer. Although this tends to be moderated by dark-adaptation (Fig. 3), it is not prevented altogether. From Fig. 4, then, it is apparent that one way to reduce cost effectively is to distribute organisms higher in the water column. It is clear from comparison of the points (10,10,2.99), (6,6,1.35) and (2,2,0.34) in the figure that the energy expense of flotation mechanisms needed to accomplish this is justified by increased profit to the community.

The ribbon-shaped surface in the center of Fig. 4 denotes loci where cost is unity, which signifies an exact 24-hour balance between inputs and expenditures. For a given collection depth, this ribbon indicates the suspension required for steady state. This becomes shallower as collection depth is increased, which indicates that a narrower range of cost is maintained by the 2-foot samples when suspended between 2 and 10 feet than by the 6- and 10-foot samples. Specifically, costs ranged from 0.75 to 2.99 for the 10-foot samples, 0.74 to 2.67 for those from 6 feet, but only 0.34 to 1.58 for those from 2 feet. Since the 2-foot samples are the more diverse, stability and diversity are directly related in this community, which is in accordance with ecological theory (*7*).

A functional relationship between diversity and energetics was implied earlier in the profit function of the linear programming model since energy profits become part of the resource pool to be utilized in creating new diversity. Consequently, at any depth z in the ecosystem, diversity is expressible as a function of energy gain and loss components,

$$D_z = D_z(\pi_z, \rho_z),$$

and alternatively, the components are expressible as functions of the available diversity,

$$\pi_z = \pi_z(D_z);\ \rho_z = \rho_z(D_z),$$

where π_z and ρ_z are monotonic increasing functions of D_z, not necessarily the

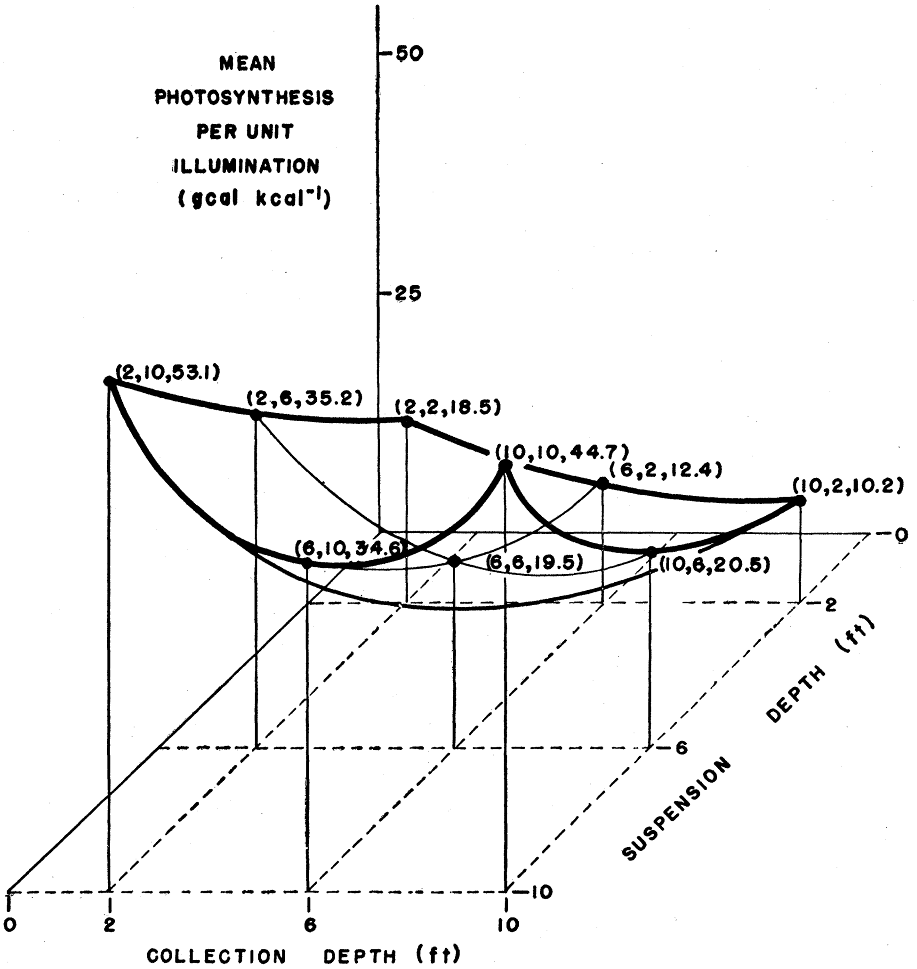

Fig. 3. Photosynthesis per unit light intensity as a function of sample collection and suspension depths (means for ten experiments).

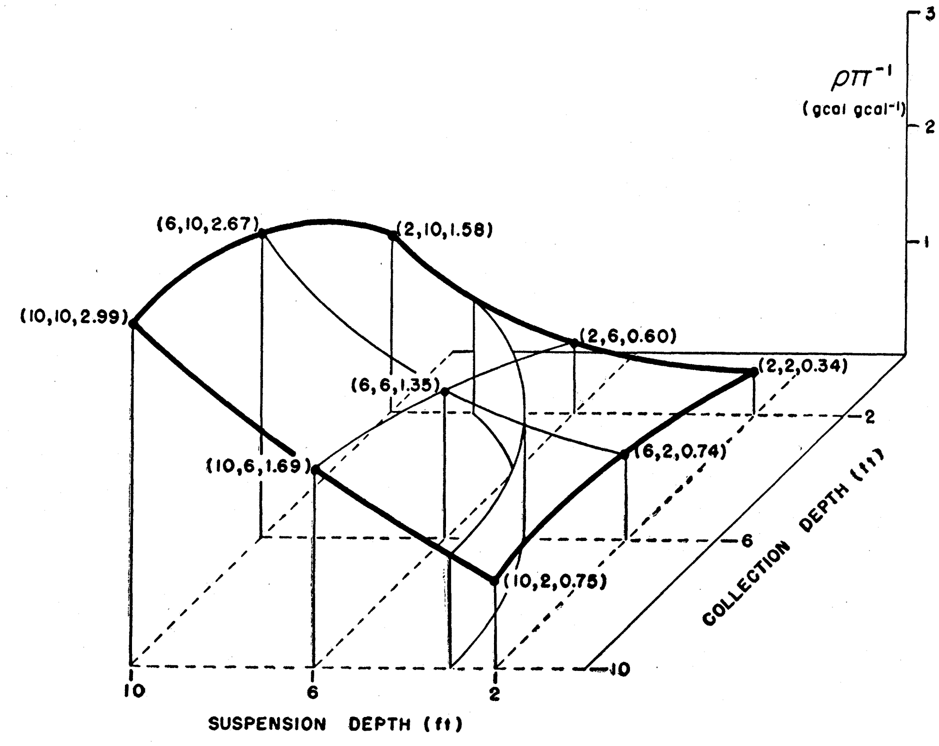

Fig. 4. Cost as a function of collection and suspension depths (means for ten experiments).

same for all depths z. With these relationships in mind, let us consider broadly how diversity adjustments may be energetically adaptive at different depths.

In the zone above the compensation depth the conditions $\rho_z/\pi_z < 1$ and $\pi_z - \rho_z > 0$ prevail at all depths, z. A diversity change will produce new values for cost and net production:

$$k_1\rho_z/k_2\pi_z \ ; \ k_2\pi_z - k_1\rho_z .$$

If $k_1 < k_2$, then cost will be reduced and net production increased:

$$k_1\rho_z/k_2\pi_z < \rho_z/\pi_z;$$

$$k_2\pi_z - k_1\rho_z > \pi_z - \rho_z .$$

Similarly, if $k_1 > k_2$, cost is increased and net production diminished:

$$k_1\rho_z/k_2\pi_z > \rho_z/\pi_z;$$

$$k_2\pi_z - k_1\rho_z < \pi_z - \rho_z .$$

Finally, if $k_1 = k_2$, then

$$k_1\rho_z/k_2\pi_z = \rho_z/\pi_z;$$

$$k_2\pi_z - k_1\rho_z = k(\pi_z - \rho_z) ;$$

cost is unchanged and net production is augmented or reduced by the factor k. Since it is unlikely that π_z and ρ_z would behave so similarly over a given range of diversity as to produce $k_1 = k_2$, this last case can be disregarded.

In the trophogenic zone, the case $k_1 < k_2$ would be most probable in the region of optimum illumination. It is here, therefore, that high diversity should be maintained in the community since net production is assumed to increase proportionally. The observed maximum diversity at 2 feet (Fig. 1) is consistent with this reasoning. Outside the optimum light zone, that is, near the surface where high light inhibits photosynthesis and lower down where the process is limited by dim light, the condition $k_1 > k_2$ is likely to prevail. Since this results in decreased net production, diversity should be reduced in these regions to levels which maximize $\pi_z - \rho_z$. Our data show that diversity is indeed less at the surface and 6 feet than at 2 feet (Fig. 1).

In the tropholytic region beneath the compensation depth, the relationships $\rho_z/\pi_z > 1$ and $\pi_z - \rho_z < 0$ prevail at all levels. Diversity increase here can only result in $k_1 > k_2$ because of low light, thus aggravating energy loss by the community. The imperative is to reduce diversity below the compensation depth, and Fig. 1 depicts an appropriate response.

It is concluded that the pattern of diversity stratification observed in the York River summer plankton community is consistent with a profit motive and, since energy is required to establish and maintain it, that the community acts to optimize its structure in the prevailing hydrography for maximum energy gain (*8*).

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Erosion and Deposition of Italian Stream Valleys During Historic Time

Abstract. *The recent geologic history of small streams in east-central Sicily and southern Etruria has been dated archeologically. In Sicily a period of deposition began post 8th century* B.C. *and had ended by 325* B.C. *After a period of erosion, another, less extensive, alluviation took place, probably in medieval time. North of Rome in southern Etruria an alluviation that began no earlier than the late Roman empire probably continued into medieval time.*

Silting of river mouths along the Mediterranean coast has occurred in many places since classical times. For example, Ostia Antica, Rome's ancient seaport, is buried by Tiber River sediments and the fabled town of Sybaris still lies lost beneath the silts of the Crathis River, along the instep of the Italian boot. Farther east, the rivers of western Turkey have carried so much silt to the coast that the Meander River, for example, has pushed back the sea about 8 km during the last 2000 years. Deposition at the mouth of the Nile was talked of even before Herodotus (484–425 B.C.)

This report deals with silting and erosion along certain small inland valleys in Italy. These small valleys, wherever they contain a well-developed stream channel, also exhibit a flat-bottomed valley, which is the result of alluviation. The nature, extent, and date of this alluviation form the subject of this report. It deals specifically with archeologic and geologic studies along streams in east-central Sicily and southern Etruria (*1*).

The Gornalunga Valley heads on the eastern margin of the high plateaus of Sicily and flows eastward toward Catania and the Ionian Sea. In the upper reaches of this valley, 60 km from Catania, geologic and archeologic studies demonstrate a sequence of alluviation and erosion during historic time.

The local bedrock includes clay, limestone, and standstone of Tertiary age, and forms hills on either side of the valley. The stream here drains an area of about 90 km^2. The valley bottom itself is terraced with a series of broad flat surfaces separated by steep risers. These terraces are underlain by the sands, gravels, and silts deposited by the modern stream and by streams of the immediate geologic past. Four stream terraces can be recognized easily. Several higher gravel patches may also represent former terraces, but their significance and continuity have not been established. The surface of the highest terrace stands between 17 and 20 m above the modern stream; the next highest is between 8 and 10 m above the stream; a small terrace between 4 and 5 m is still lower; and the lowest terrace (the present flood plain) is at approximately 2 m (see Fig. 1). The two higher terraces are wide and form the bulk of the valley bottom. The two lower terraces are only narrow benches.

The 17- to 20-m terrace is the highest in the area that still retains an original upper surface. The single good exposure of its sediments is at kilometer 30.65 on the Aidone-Catania road, where the road is built on the terrace surface.

In a small draw leading toward the main Gornalunga drainage, a section approximately 3 m thick exposes dark gray clayey alluvium, which contains fragments of limestone from adjacent slopes. The alluvium is compact and has prismatic jointing. Locally there is staining by limonite, and some oxides of manganese stain the joint planes. Manganese oxide also forms nodules up to ½ cm in diameter. The gray color probably was derived from black soil on the slopes of the valley at this place. No archeological material has been discovered.

The sediments of the 8- to 10-m terrace reach to stream level in many places. In other places they are seen to be 5 to 6 m thick over bedrock. Coarse gravel, with fragments up to ½ m in size, forms the lowest 1 to 2 m of the deposit. This gravel is overlain by alluvial sand and silt that varies in color from gray-brown to yellow-brown.

Near the base of the 8 to 10-m terrace, in fine-textured facies of the basal gravel, have been found some 30 pieces of pottery and tile. None could definitely be identified as younger than the 8th century B.C. No definitely demonstrable Roman, medieval (*2*), or modern material was discovered. In the uppermost deposits of this terrace Greek burials of 325 B.C. have been discovered (*3*), and these provide an *ante quem* date for the end of deposition.

The 4- to 5-m terrace occupies narrow bands along the modern stream. It consists of sandy alluvium, buff in color, which overlies approximately 1 m of coarse basal gravel. A number of terra cotta fragments have been found in the deposits, and all of them have been identified as either ancient or medieval.

The 2-m terrace also occupies restricted positions along the modern stream. It is made up of a light, sandy, buff-colored alluvium, overlying a meter or so of coarse basal gravel, and is thus lithologically similar to the 4- to 5-m terrace. Fragments of ancient, medieval, and modern tile are present in the deposits. Hence, these terrace deposits are presumably the present flood-plain deposits and are being moved with each high-water stage.

In southern Etruria, immediately north of Rome, small stream valleys are characterized by broad, flat floors, trenched by narrow stream channels from 3 to 8 m deep. Flood plains within these trenches are 1 to 2 m high, and are restricted by the narrowness of the trenches.

The valley deposits older than the modern flood plain seem to represent a single stage of alluviation. The deposits are 3 to 8 m thick. They are characterized by basal deposits of