

355

245

Proceedings of the I.B.P. Symposium on
Primary Productivity in Aquatic Environments
Pallanza, Italy, April 1965

ECOLOGICAL CORRELATIONS
AND THE RELATIONSHIP BETWEEN PRIMARY
PRODUCTIVITY AND COMMUNITY STRUCTURE

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Mem. Ist. Ital. Idrobiol., 18 Suppl.: 000-000. 1965.

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Abstract

Any expression aiming to give an indirect estimate of primary production on the basis of present properties of an ecosystem, has to include some term reflecting quantitatively the structure of the community (biotic diversity, pigment ratio D_{430}/D_{665}). This is logical, because production has the nature of a derivate relative to time. The expressions of structure, although dimensionless, reflect historic development and thus are related also to time. Accelerations and decelerations in the speed or rate of production are reflected by a decrease or an increase, respectively, of the diversity of the community. Since the pigment ratio D_{430}/D_{665} (or any other analogous ratio) is a good indicator of structural properties of the whole community, it is advisable not to limit analysis of pigment spectra to a single narrow band.

CORRELATIONS AND REGRESSIONS

Information

The data on the properties of the environment and the populations in aquatic ecosystems is growing steadily. A much more rapid increase can be anticipated in the near future, in part perhaps, as a consequence of the International Biological Program. The accumulation of synoptic information, together with the general availability of computer facilities, opens new perspectives and poses new problems in the handling of ecological data.

Programme

We assume that we are in possession of a number of measurements, referred to a set of discrete sampling points, and expressing physical properties of the environment or biological properties of the mixed populations. There are many excellent manuals that tell us how to compute both correlations and regression involving the different variables. To do this may often be useful.

The application of statistical methods requires a sound ecological judgment. Sometimes the data, taken out of their spatio-temporal frame, yield poor statistical correlations. Nevertheless, if such data are plotted, the comparison of cartograms with the distribution of the values of different variables, often discloses significant congruence of patterns. In such instances we need a much more powerful tool than the usual statistical methods, perhaps sequential analysis or methods based on information theory. But, for the moment, we shall be satisfied with ordinary multivariate statistical analysis.

Significant correlations may be found among actual or point values or among their derivatives. Production has the quality of a derivate of biomass relative to time. Production, thus, is likely to be correlated in a more meaningful way with magnitudes that are them-

selves also derivatives. An example of this is depletion of nutrients. Discreteness of samples and movements of water set great difficulties for a generalized usage of derivatives. Here we have another example of the urgent need for methods for rapid and almost continuous sampling.

For the time being we are forced to ignore almost completely the derivatives. All too frequently the proper dimensions of the magnitudes that we relate together in the expression of a regression are disregarded. But we must retain the logical requirement that production should be used in relation with something that conveys the notion of time.

In the working of correlations and regressions, the rough data frequently do not approach a normal distribution. In such cases a transformation is required before further statistical analysis. A logarithmic transformation often proves appropriate for parameters referring to populations (chlorophyll content, production, number of cells) and to environmental factors strongly influenced by organisms (nutrient concentrations). Multiplication and diffusion in a nonuniform environment lead commonly to a type of distribution in which density of populations decreases exponentially with increasing distance from a center of maximum density. If samples are taken with a regular spacing or a regular periodicity, chances are that in any series of samples, not the actual densities, but the logarithms of the densities approach normal distribution. Other variables (temperature, salinity) frequently do not require transformation.

The practice of computing regression equations involving different parameters of the same community, as number of cells, chlorophyll, etc., shows how difficult it is to remain faithful to the so-called «conversion factors». For instance, in marine phytoplankton, number of cells cannot be put simply as a function of the chlorophyll amount, but some other parameter, as the pigment ratio D_{430}/D_{665} must intervene (Herrera and Margalef 1963).

Suppose we want to set the production (P) as a function of several factors, as depth (Z), chlorophyll concentration (C), and the pigment ratio $D_{430}/665$. The first impressions of the results of a study still in progress on marine plankton communities are that we may account for a considerable part of the variation of P by writing,

$$\log P = a + b \log C - c Z - d(D_{430}/665)$$

The author has a weakness for the pigment ratio $D_{430}/665$. It means the ratio of the absorbancies at the stated wavelengths of an acetic extract of pigments, roughly a ratio «yellows»/«greens», that, in addition to other interesting properties, reflects the effect of depletion of nutrients (see further). It seems that in this particular connection the use of said ratio may have advantages over the inclusion in the regression formula of the concentrations of several nutrients, if it happens that not always the same nutrient acts as a limiting factor.

STRUCTURE

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On the other hand, the ratio $D_{430}/_{665}$ gives a measure of « structure ». Present structure is the result of an historical process. Any structure has properties that are quantitatively measurable, as, for instance, diversity. Biotic diversity is any suitable function which has a minimum when all each cells belong to the same species, and a maximum when every individual belongs to a different species. It is practical to measure and express diversity in bits per individual (per cell in the case of phytoplankton), according to the expression

$$D = - \sum p_i \log_2 p_i$$

more
more appropriate

where p_i denotes the participation or probability of occurrence of every species in the total number of individuals ($\sum p_i = 1$). We leave untouched here the point of whether it is ~~non~~ appropriate to speak of diversity without qualifications, or if it is better, as it seems, to refer always to a spectrum of diversity. In any case, eventual interest in diversity should act as a stimulus to not neglect too much a careful taxonomical study of communities.

A pigment diversity could be computed according to the way plant pigments are distributed among different molecular species. It is assumed that the simple pigment ratio $D_{430}/_{665}$ gives a rough estimate of such pigment diversity.

with

The biotic diversity, as bits per individual, or the pigment diversity in the form of a ratio between absorbancies, are simple numbers without dimension. They are well correlated with one another (Table 1) and also with other indices of structure. The last line in Table 1 is interesting, because it suggests that it is possible to use an electronic dimensional particle counter (data were actually obtained with such apparatus) to obtain a useful index of community structure. The correspondance between parameters compared in Table 1 is better than expressed by the correlations, if data are plotted on cartograms.

Table 1. - Statistical correlations between pigment ratio $D_{430}/_{665}$ and other structural properties of plankton populations. Examples from marine environment. Untransformed data.

Area	Property compared with pigment ratio	Pairs of values	Coefficient of correlation
Western Mediterranean	Biotic diversity of net phytoplankton	54	+0.40
Southern Caribbean	Biotic diversity of net phytoplankton	68	+0.30
Tyrrhenean Mediterranean	Per cent of « big » particles in total seston	127	+0.27

Biotic diversity, pigment ratio, particle size ratio, and other indices that could be devised, are expressions of properties concerning organization of the community. As such, they are also expressions of maturity or historical development, and in consequence related to time. For this reason it can be understood why and how they are associated with production, a derivative relative to time.

1/2 understood

PRODUCTION AND PIGMENTS

Observations in sea, freshwater, and in laboratory cultures, both published (Margalef 1963, 1964, in press) and unpublished, substantiate the relationship between carbon uptake and diversity. A high inorganic carbon uptake per unit biomass ~~is~~ always associated with a low biotic diversity or with a low pigment ratio D_{430}/D_{665} .

= is

Let us examine more closely an example concerning fresh water communities (Margalef 1964) that seems to be typical; the more extensive material from marine environments fits the same pattern (or sort of expressions to which we arrive), although the coefficients have different numerical values. Here production means inorganic carbon fixation under constant light conditions, and samples are all surface samples. Thus the approach may be conveniently simplified, because light or depth does not enter into the expressions. The correlation matrix between some parameters of interest is reproduced in Table 2.

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Table 2. - Correlation matrix between several parameters in 4 different freshwater phytoplankton populations (Margalef 1964). Logarithmic transformations, altogether.

- (A) Chlorophyll *a*, mg/m³
- (B) D_{330}/D_{665}
- (C) Diversity, bits/cell
- (D) Carbon uptake, mg C/m³/hour
- (E) Production per unit biomass, mg C/g C/hour

	(A)	(B)	(C)	(D)	(E)
(A)	1	-0.064	+0.057	+0.964	+0.573
(B)		1	+0.796	-0.319	-0.968
(C)			1	-0.107	-0.723
(D)				1	+0.545
(E)					1

There is a strong positive correlation (+ 0.796) between both structural characters, and both are negatively correlated (-0.968 and -0.723) with productivity per unit biomass (turnover). The correlations of production may be worthy of closer examination as concerning the often discussed relationship between production and pigments.

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Production is positively correlated (+ 0.96±) with amount of chlorophyll *a*, as was expected, and negatively correlated with pigment ratio (-0.319) and, more feebly, with biotic diversity.

An appropriate estimate of production was

equal to $\log P = 1.047 + 0.728 \log C - 0.615 \log (D_{430}/D_{665})$

$P = 11.1 C^{0.728} / (D_{430}/D_{665})^{0.615}$

0.728 *line*

Since C is approximately proportional to D₆₆₅, we could equally well write

$P = 67.7 (D_{665})^{1.343} / (D_{430})^{0.615}$

Fig.

In Figure 1 this expression is compared with the often held assumption that production is proportional to the amount of chlorophyll *a*. The study of more extensive material will afford an estimate of the variability of the « constants » involved in our expression, and whether it is worthwhile after all to retain such expression in the proposed form.

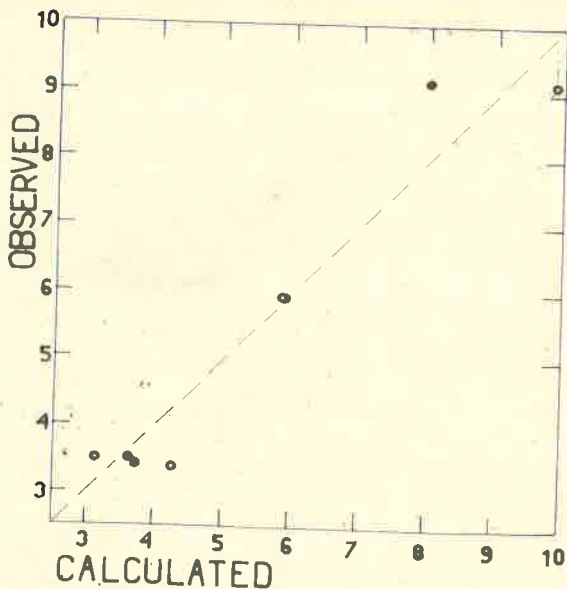


Fig. 1. - Dams in NE Spain (Margalef 1964), surface phytoplankton. Comparison between the observed values of inorganic carbon uptake, in mg C/m³/hour, and the calculated values using the expressions

$P = 11.1 C^{0.728} / (D_{430}/D_{665})^{0.62}$, black circles

$P = 3.7 C$, white circles

Note that in the center of the figure a black and a white circle are almost superposed.

As a result of previous work on marine plankton (Margalef 1960) and laboratory cultures (Margalef 1963), the biomass (B) was expressed as a function of the absorbancy of pigment extracts at two wavelengths, F being a convenient factor:

$$B = F (D_{430})^3 / (D_{665})^2$$

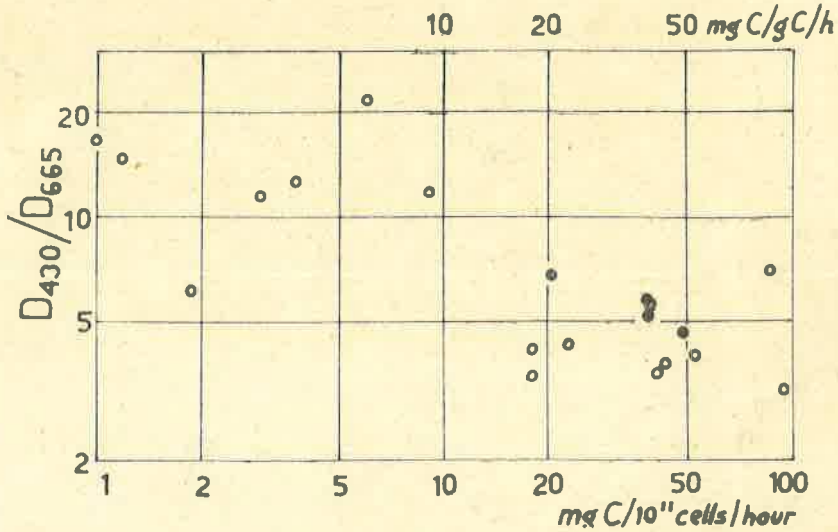


Fig. 2. - Comparison of the pigment ratio D_{430}/D_{665} with the production per unit biomass. Black circles, surface phytoplankton of dams in NE Spain; productivity in mg C/g C/hour; $T = 20^{\circ}\text{C}$, $L = 5000$ lux. White circles, laboratory cultures in sea water; productivity in mg C/10¹¹ cells/hour; $T = 16^{\circ}\text{C}$, $L = 5000$ lux.

P/B

Table

By division of the two last expressions, we would expect their ratio (P/B = production per unit biomass) to be approximately proportional to a power (near the cube) of the inverse of pigment ratio D_{430}/D_{665} (fig. 2). This fits well with the high negative correlation found between production per unit biomass and pigment ratio (Table 2). In a series of laboratory cultures (Margalef, in press; 17 pairs of values, data not transformed), the correlation between production per unit biomass and pigment ratio was found to be -0.588 ; these data have been plotted also in figure 2.

approximate

Fig

I am insisting deliberately on the interest of the pigment ratio D_{430}/D_{665} , or of any other descriptive of the general form of the absorption spectrum. Almost everybody agrees that proposed expressions for computation of the concentration of pigments other than from chlorophyll a , from spectra of acetonic extracts, are unreliable. But we must think twice before limiting analysis to the measure of a narrow band of the spectrum, and expression of pigments to

concentration of chlorophyll *a*. In so doing, we lose irretrievable information about «structure» of the photosynthesizing equipment of phytoplankton. An empirical approach to the problem would be to run complete spectra of a great number of extracts of phytoplankton of different types (as production, species composition, etc.) and to look successively for 1, 2, 3 ... wavelengths permitting the best discrimination between spectra. This could be done by purely statistical methods, and *a posteriori* a biochemical interpretation of the selected points with high indicator value would follow.

STRUCTURE AND FUNCTION

To return to the main subject, we are led to expressions similar to the ones discussed if we introduce biotic diversity in lieu of the pigment ratio. This latter ratio has been preferred here for obvious reasons connected with the extensive use of plant pigment analysis in ecological research. In any case, study of multiple regressions indicates that production is a function, in the mathematical sense, of the structure of the community too, and not only of a simple expression of biomass or total chlorophyll. In a biological sense, production is a genuine function of structure. If the structure of the community remains the same, its function, that is, production per unit biomass, remains also constant. Any change of the community structure, in space or time, is linked to a change in the rate of production.

The correlations between inorganic carbon uptake and structural properties of the community can be easily clarified with a dynamic model. Suppose that the supporting capacity of the environment increases: immediately the ratio primary production/total biomass increases. As the cells of the different species multiply relatively free of impediment, the differences in their respective potential rates of increase and in the speed at which rates of increase can be modified, manifest themselves. The consequence is that the representation of the different species (p_i) becomes more and more unequal and the value $-\sum p_i \log_2 p_i$ drops. The process can continue up to the final dominance of one or a few species, usually of small cells.

As for the pigments, those having a key position or synthesising and decaying more rapidly than others, as chlorophyll *a*, are comparable to the species endowed with a high potential rate of increase. They are simply parts of the system allowing a higher flow of energy through them. Undoubtedly, the rearrangement of the pigment composition is a complex process, as is easily evidenced in thin layer chromatograms; but the bursts of production are always associated with a more rapid increase of the «greens» than of the «yellows», and there is a drop in the pigment ratio D_{430}/D_{665} . Changes in this ratio reflect changes not only in the species composition of the community, but also in the physiological state of unispecific popu-

tations. The sensitivity of the pigment ratio to nutrient depletion and supply makes its response useful in the assessment of elements limiting growth (Castellví 1964).

From the preceding it can be understood why, under similar conditions of light, production per unit biomass is strongly correlated to pigment ratio D_{430}/D_{665} . We may anticipate that this ratio is subjected to a daily rhythm, but further work is necessary to ascertain its generality, importance and meaning. It changes easily under different environmental influences. Although the physiological adaptation of plankton algae to different environmental conditions has been often studied and discussed, insufficient attention has been paid to the eventual reflection of the changes on the pigment composition.

When environmental conditions remain stable and biomass increases, production per unit biomass drops, the population diversifies, dominance disappears, and pigment ratio increases. In short, rate of change of quantitative expressions of structural properties of communities is always linked to accelerations or decelerations in the speed of production.

The author would of course prefer a more elegant and general way of harmonizing these findings in an interpretation of the ecosystem as a cybernetic system, but such a way of reasoning seems not to be acceptable yet to a great number of workers. This is irrelevant here, since the purpose of this paper was to stress only that if we want to make indirect estimates of production, based on environmental factors (light, nutrients) and on organisms, then structural properties of phytoplankton populations probably need to be taken into account, in addition to non structural properties taken separately, such as biomass, number of cells, or amount of chlorophyll *a*.

(addition)

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