II. An index of fluctuations D_0 connected with diversity and stability of ecosystems : Applications in the Volterra-Lotka model and in an experimental distribution of species

by

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Abstract

Our purpose is to present a practical criterion for the stability of ecosystems.

As the Shannon-Weaver formula is largely used as an index of diversity, we have shown that the average index of diversity of an ecosystem $\overline{H}$ can be written as :

$$\overline{H} = H_0 - \overline{D}_0$$

where H_0 is the diversity of a reference state and $\overline{D}_0$ the average index of fluctuations.

Moreover, the index of fluctuations D_0 can be used as a criterion for the stability of an ecosystem.

The discussion of the time derivative of the index of fluctuations D_0 leads to the non-asymptotic stability of the Volterra-Lotka model for any arbitrary perturbations received from environment.

Finally, the variation of the distribution of *Mysidacea* at a point of the North Sea is discussed. The index of fluctuations appears to be a very attractive measure of the effects on the ecosystem of external perturbations such as tidal effects and turbulence.

Introduction

Ecosystems are subject to the law of conservation of matter and are open systems with respect to energy, usually light energy. Materials must cycle throughout the ecosystem following the general laws of energy transformation. High quality chemical energy degrades to lower quality energy under the influence of catalysts which control the rates of the various processes. We want to review briefly the response of an ecosystem to different variations of materials in the environment, of the conditions affecting the rates of processes and of the transport of energy. Physiological adaptability allows individual organisms to cope with variable conditions affecting the use of energy.

Variations in the activity or size of individuals imply variations in energy transformations and in energy storage. Due to time lag, variations in the number of individuals in the various species cause oscillations in the size of populations; the regrowth of a population may lag behind the reappearance of the energy supply. The ecosystem self-organizes with compensating variations when a decrease in the abundance of some chemical energy may be accomodated by an increase in the abundance of others.

In general, an ecosystem self-organizes as to reduce environmental variations (like Lenz's law in electricity).

A necessary condition for the stability of an ecosystem is the balance condition. An unbalanced system will change until it becomes balanced; the ecosystem must periodically re-establish its own cycle structure in changing its distribution of materials. In certain conditions, the ecosystem can be highly nonlinear and an ecosystem can be very stable even with large fluctuations. Reduction in the oscillation of one species must be compensated by an increase in the fluctuations of some other species. The change in number arising from populations oscillations will be reflected in a corresponding change of energy.

However, this change of energy can be minimized if the organisms of these oscillating populations are simple and can follow the variable energy supply without too much time delay.

Another stabilizing mechanism in an ecosystem is the development of multifunctionality with resultant increase in the number of possible pathways of energy flow in the food chain. The efficiency of an ecosystem increases with multifunctionality (parallel processing) and under these conditions the entire system is more stable because the flow of resources is distributed over a number of different paths.

The problem of stability and its relation to diversity has been discussed by a number of authors [Pielou (1966) measured diversity in different types of biological collections].

In particular, MacArthur (1955) has proposed an index of stability based on the fraction of the energy reaching the top of the web along each distinct pathway q_i of a food chain : his index is highest when q_i is the reciprocal of the number of possible pathways; it may be the same for food webs involving few species with many connections as for those with many species with few connections. Odum (1953) has suggested that stability increases with the amount of choice which the energy has in following the paths up through the food web. But these indexes are not practically utilisable.

Our purpose in this paper is to obtain a practical criterion of the stability of ecosystems which is in agreement with such theoretical model as, for example, the Volterra-Lotka model.

Starting from the Shannon-Weaver formula, Longuet-Higgins (1971) calculated the diversity for several theoretical distributions. He showed that if the distribution of species is a complete log-normal one, then the diversity depends only on the total number of species S and the variance σ_q^2 of the distribution of the species arranged in octaves.

In our paper, we have derived from the Shannon-Weaver formula a very simple relation which depends only on two quantities, the total number of species S and the variance σ^2 of the distribution of species around the mean. If the distribution is arranged in octaves, Longuet-Higgins' formula is rediscovered. (Note that the present derivation has the advantage of making no drastic assumptions about the distribution.)

When the distribution of species differs greatly from a uniform distribution, the derivation is no longer correct. Then, we introduce, for each proportion p_i , the space-time average $\overline{p}_i$ and we call the ensemble of the $\overline{p}_i$'s the "reference state". The diversity may be written as the difference between the diversity of the reference state minus a positive definite function in the sense of Lyapunov : the index of fluctuations D_0 which is the deviation of the distribution from the reference state.

Since the index D_0 is a positive definite function which is zero at the reference state, the time derivative of D_0 can be used as a criterion of stability of the ecosystem, in the sense of Lyapunov.

In order to test this index D_0 by studying the stability of a theoretical model, we discuss briefly the properties of the Volterra-Lotka model.

The Volterra-Lotka equations describe the dynamics of a predator-prey population. Considering the non-trivial case, any set of initial populations yields periodic population variations which are represented by a closed curve about the steady state. There is a whole family of these curves depending upon the initial conditions. Moreover, the time averages of populations during a cycle correspond to the populations at the steady state.

We adapt the index of fluctuations to the fluctuations of populations rather than to probability distributions. An integration over the whole cycle with period T is made to take into account all the different accessible states of the system. A simple relation between the mean diversity of an ecosystem and the mean index of fluctuations is presented. Moreover, another positive definite function $D_0^{(2)}$ is constructed symetrically to D_0 . A surprising property of $D_0^{(2)}$ is it differs from D_0 only beyond the second order. From these functions D_0 and $D_0^{(2)}$, the stability of the Volterra-Lotka model is discussed. In the case of small fluctuations of the system around the stationary state, the index of fluctuations D_0 is a constant of motion and the system possesses non-asymptotic stability. Moreover, the function $D_0^{(2)}$ is surprisingly a constant of a motion of the system for arbitrary fluctuations and the non-asymptotic stability is valid for any perturbation received from environment.

Finally, a comparison of all these indexes is made on an experimental example; the variation of the distribution of *Mysidacea* at a point of the North Sea over a period of 72 hours. The index of fluctuations appears to be a very attractive measure of the effects on the ecosystem of external perturbations, such as tidal effects and turbulence.

1.- Diversity of a log-normal distribution

The Shannon-Weaver formula is widely used as a measure of the diversity of ecological systems [Margalef (1958)]. If p_i is the proportion of the i^{th} species, the diversity is written :

(1) $$H = - \sum_{i=1}^{S} p_i \ln p_i$$

with the normalisation condition

(2) $$\sum_{i=1}^{S} p_i = 1$$

where S is the total number of species.

Longuet-Higgins (1971) proposed to arrange the numbers of species in octaves. Writing

(3) $$q \equiv \ln p$$

he supposed that, within some range of q ,

(4) $$- \frac{dn}{dq} = f(q)$$

where $f(q)$ is a universal function, characteristic of the parent population. To determine H , he has the following relations :

(5a) $$S = \int_{\epsilon}^{S} dn \qquad (\varepsilon \ll 1) ,$$

(5b) $$1 = \int_{\epsilon}^{S} p \, dn$$

and

(5c) $$H = - \int_{\epsilon}^{S} p \ln p \, dn .$$

Starting from the complete log-normal distribution :

(6) $$f(q) = \frac{c}{\sigma_q \sqrt{2\pi}} \exp[- \frac{(q - \mu)^2}{2 \sigma_q^2}]$$

where μ and σ_q denote the mean and the standard deviation respectively, and c is a normalising constant, Longuet-Higgins obtained

(7) $$H = \ln S - \frac{1}{2} \sigma_q^2 .$$

This very simple relation depends only on two quantities, the total number of species S and standard deviation σ_q .

As the first term of equation (7) is the maximum of the diversity, *i.e.*,

(8) $$H_{max} = \ln S$$

which occurs when all the p_i 's are equal to the mean $\overline{p} = \frac{1}{S}$, we want to compare Longuet-Higgins formula with a series expansion around the mean $\overline{p}$.

2.- Diversity around the mean

Using Taylor's formula, the expansion of the Shannon-Weaver index of diversity [equation (1)] around its maximum [equation (8)]

$$\overline{p} = \frac{1}{S}$$

is then written to the second order

(9) $$H = \sum_{i=1}^{S} \{- \frac{1}{S} \ln \frac{1}{S} + (- \ln \frac{1}{S} - 1)(p_i - \frac{1}{S}) + \frac{1}{2} (- S)(p_i - \frac{1}{S})^2 + O[(p_i - \frac{1}{S})^3]\}$$

which becomes with equation (2) :

(10) $$H = \ln S - \frac{1}{2} S \sum_{i=1}^{S} (p_i - \frac{1}{S})^2 + O[(p_i - \frac{1}{S})^3] .$$

Neglecting the third term of equation (10), we define the index of diversity D_1 as

(11) $$D_1 = \ln S - \frac{1}{2} S^2 \sigma^2$$

with

(12) $$\sigma^2 \equiv \frac{1}{S} \sum_{i=1}^{S} (p_i - \frac{1}{S})^2$$

which includes only the total number of species S and the variance σ^2 of the distribution of species around its mean $\overline{p} = \frac{1}{S}$.

Writing

(13) $$q_i \equiv \ln p_i$$

(14) $$q_0 \equiv \ln \overline{p} = \ln \frac{1}{S} ,$$

we have

(15) $$q_i - q_0 = \ln[\frac{1}{S} + (p_i - \frac{1}{S})] - \ln \frac{1}{S}$$

$$= \ln[1 + S(p_i - \frac{1}{S})] \quad .$$

Hence, to the second order,

(16) $$q_i - q_0 = S(p_i - \frac{1}{S}) + O[(p_i - \frac{1}{S})^2] \quad .$$

From equations (12) and (16), we get

$$\sigma^2 \equiv \frac{1}{S} \sum_{i=1}^{S} (p_i - \frac{1}{S})^2$$

$$= \frac{1}{S^3} \sum_{i=1}^{S} (q_i - q_0)^2$$

(17) $$\sigma^2 = \frac{\sigma_q^2}{S^2}$$

and equation (11) becomes

(18) $$D_1 = \ln S - \frac{1}{2} \sigma_q^2$$

which is similar to Longuet-Higgin's result.

The diversity D_1 is fairly general but its validity is reduced to distributions of species not too far from the mean (uniform distribution). So, for very non uniform distribution, it is necessary to define mean values of each of the proportions $\overline{p}_i$. This will be done in the next section.

3.- Space-time averages and reference state

In a general way, the proportion of species is a function of the space and of the time, *i.e.*,

$$p_i = p_i(\mathbf{r},t) \tag{19}$$

where $\mathbf{r}$ is the position vector and t the time.

To obtain some information on the diversity and the stability of ecosystems, it may be interesting to define a sort of local equilibrium of the ecosystem.

We shall call the reference state the local space-time averaged proportions $\overline{p}_i$ defined by

$$\overline{p}_i = \frac{\iiint_{\delta V} \int_{\delta T} p_i(\mathbf{r},t)\ dV\ dt}{\iiint_{\delta V} \int_{\delta T} dV\ dt} \tag{20}$$

where δV is the neighbourhood of the local domain we want to study and δT a time sufficiently long with respect to the relaxation time of all phenomena.

It may be noted that equation (2) is always applicable, *i.e.*,

$$\sum_{i=1}^{S} \overline{p}_i = 1 \tag{21}$$

The state of the ecosystem will be found from its deviation from the reference state. In the next section, the diversity is given around the reference state.

4.- Diversity around the reference state

Using Taylor's formula, we expand the diversity [equation (1)] around the reference state of the ecosystem [equation (20)], *i.e.*,

$$(22)\quad H = \sum_{i=1}^{S} \{-\bar{p}_i \ln \bar{p}_i - (\ln \bar{p}_i)(p_i - \bar{p}_i) - (p_i - \bar{p}_i) + \frac{1}{2}\left(-\frac{1}{\bar{p}_i}\right)(p_i - \bar{p}_i)^2 + O[(p_i - \bar{p}_i)^3]\}$$

which is written with equations (2) and (21)

$$(23)\qquad H = \sum_{i=1}^{S} \{p_i \ln \frac{1}{\bar{p}_i} - \frac{1}{2}\,\frac{1}{\bar{p}_i}(p_i - \bar{p}_i)^2 + O[(p_i - \bar{p}_i)^3]\} \ .$$

Neglecting the third term of equation (23), we define the index of diversity D_2 by

$$(24)\qquad D_2 = \sum_{i=1}^{S} \left(p_i \ln \frac{1}{\bar{p}_i} - \frac{1}{2}\,\frac{\sigma_i^2}{\bar{p}_i}\right)$$

with

$$(25)\qquad \sigma_i^2 \equiv (p_i - \bar{p}_i)^2 \ .$$

As the second term of equation (24) is positive definite and has only one zero at the point

$$p_i = \bar{p}_i \qquad (i = 1,2,\ldots,S) \ ,$$

we introduce an index D_0^* defined by

$$(26)\qquad D_0^* = \frac{1}{2} \sum_{i=1}^{S} \frac{\sigma_i^2}{\bar{p}_i} \ .$$

We see that D_0^* is large when the ecosystem is far from its reference state. It may be a measure of its deviation from the reference state.

5.- An index of fluctuations D_0

Let us define a quantity D_0 by the following equation

$$(27)\qquad H = \sum_{i=1}^{S} p_i \ln \frac{1}{\bar{p}_i} - D_0 \ .$$

The first term of equation (27) is identical with the first term of equation (24). So D_0 represents all the terms of the expansion in series of H beyond the first order.

From equations (1) and (27), the expression of D_0 is

(28) $$D_0 = \sum_{i=1}^{S} p_i \ln \frac{p_i}{\overline{p}_i}$$

expansion of which gives

(29) $$D_0 = D_0^* + O[(p_i - \overline{p}_i)^3] \quad .$$

Remarkably, the function D_0 is definite positive (in the sense of Lyapunov) and is zero only at the singularity $[p_i = \overline{p}_i \ . \ (i = 1,2,\ldots,S)]$. As the first term of the expansion of D_0 is D_0^* [equation (29)] we suggest calling D_0 the index of fluctuations.

With a view of applying this index D_0 to a theoretical model, we discuss briefly the Volterra-Lotka model.

6.- The Volterra-Lotka equations

Let us consider the kinetic equations describing the predator-prey model of Volterra (1931) and Lotka (1956) :

(30a) $$\frac{dN_1}{dt} = \alpha_1 N_1 - \lambda_1 N_1 N_2$$

(30b) $$\frac{dN_2}{dt} = \lambda_1 N_1 N_2 - \alpha_2 N_2$$

where N_i $(i = 1,2)$ is the population of species i and α_1 , α_2 and λ_i are positive constants.

The steady state is characterized by a set of populations $\{N_{j0}\}$ for which

$$\frac{dN_j}{dt} = 0$$

for $j = 1,2$.

The quantities N_{j0} $(j = 1,2)$ are the values of N_j satisfying the following equations :

(31a) $$N_{10}(\alpha_1 - \lambda_1 N_{20}) = 0$$

(31b) $$N_{20}(\lambda_1 N_{10} - \alpha_2) = 0 \ .$$

When none of the N_{i0} 's vanish, they satisfy :

(32a) $$N_{20} = \frac{\alpha_1}{\lambda_1}$$

(32b) $$N_{10} = \frac{\alpha_2}{\lambda_1} \quad .$$

Volterra (1931) has shown that there is a constant of motion which depends on the $\{N_{i0}\}$. One defines :

$$v_j = \ln \frac{N_j}{N_{j0}}$$

or

(33) $$N_j = N_{j0}\, e^{v_j}$$

and we see that, as $N_j \to N_{j0}$, $v_j \to 0$ so that v_j is a measure of the deviation of N_j from the steady state.

The equations (30a), (30b) are expressed in terms of the v_j by :

(34a) $$\frac{dv_1}{dt} = \alpha_1(1 - e^{v_2})$$

(34b) $$\frac{dv_2}{dt} = \alpha_2(e^{v_1} - 1)$$

using equations (32a) and (32b).

Dividing (34a) by (34b), one obtains, after integration :

(35) $$N_{10}(e^{v_1} - v_1) + N_{20}(e^{v_2} - v_2) = C^{nt} = K_1$$

which is the constant of motion. Each individual term in equation (35) is positive : $v_j > 0$ implies $e^{v_j} > v_j$ and $v_j < 0$, $- v_j > 0$ and e^{v_j} is positive.

Hence we have $K_1 > 0$.

Any set of initial populations yields periodic population variations which are represented by a closed curve about the steady state. There is a whole family of these curves depending upon the initial conditions.

Moreover, it must be remarked that the time averages of N_1 and N_2 during a cycle of period T give, from equations (34a) and (34b), the relations :

(36) $$\frac{1}{T}\int_0^T \frac{dv_1}{dt}\,dt = 0 = \alpha_1 - \alpha_1\,\frac{1}{T}\int_0^T e^{v_2}\,dt$$

or

(37a) $$\overline{N}_2 = \frac{1}{T}\int_0^T N_2\,dt = N_{20}\ .$$

Similarly

(37b) $$\overline{N}_1 = N_{10}\ .$$

The time averages of N_1 and N_2 calculated during a cycle correspond to the values of N_1 and N_2 at the steady state, N_{10} and N_{20} .

In order to apply the index of fluctuations to this model, the natural definition of proportions p_i is

(38) $$p_i = \frac{N_i}{\sum_{i=1}^{2} N_i} \qquad (i = 1,2)$$

but this definition causes mathematical difficulties, due to the fact that $N_1 + N_2$ is different of a constant. Indeed, equations (30a) and (30b) give :

(39) $$\frac{d}{dt}(N_1 + N_2) = \alpha_1 N_1 - \alpha_2 N_2$$

which is zero only at the stationary state.

It is convenient to take the following definitions of proportions p_i :

(40a) $$p_i = \frac{N_i}{N_0} \qquad (i = 1,2)$$

and

(40b) $$\overline{p}_i = \frac{\overline{N}_i}{N_0} = \frac{N_{i0}}{N_0} \qquad (i = 1,2)$$

with

(41) $$N_0 = \sum_{i=1}^{2} \frac{1}{T}\int_0^T dt\, N_i = \sum_{i=1}^{2} \overline{N}_i = \sum_{i=1}^{2} N_{i0}\ .$$

These definitions involve some rather delicate changes : in integrating equations (1) and (2) with respect to all the different accessible states of the system, we obtain :

(42) $$\overline{H} = -\frac{1}{T}\int_0^T dt \sum_{i=1}^{2} p_i \ln p_i$$

with

(43) $$\frac{1}{T}\int_0^T dt \sum_{i=1}^{2} p_i = 1 \quad .$$

However, there is no mathematical necessity to work in terms of cycle averages but it is only mathematically convenient.

With these new definitions, let us calculate the index of fluctuations D_0 .

Starting from

(44) $$H = -\sum_{i=1}^{S} \frac{N_i}{N_0} \ln \frac{N_i}{N_0}$$

let us expand it in series around $\frac{\overline{N_i}}{N_0}$ up to second order

(45) $$H = \frac{1}{N_0}\sum_{i=1}^{S} \{N_i \ln \frac{N_0}{\overline{N_i}} - (N_i - \overline{N_i}) - \frac{1}{2}\frac{(N_i - \overline{N_i})^2}{\overline{N_i}} + O[(N_i - \overline{N_i})^3]\} \quad .$$

Defining D_0 by the relation

(46) $$H = \frac{1}{N_0}\sum_{i=1}^{S} [N_i \ln \frac{N_0}{\overline{N_i}} - (N_i - \overline{N_i})] - D_0$$

we obtain immediately :

(47) $$D_0 = \frac{1}{N_0}\sum_{i=1}^{S} (N_i \ln \frac{N_i}{\overline{N_i}} + \overline{N_i} - N_i) \quad .$$

D_0 is a positive definite function (in the sense of Lyapunov) which is zero for $N_i = \overline{N_i}$ $(i = 1,2,\ldots,S)$. For small deviations of N_i from $\overline{N_i}$ $(i = 1,2,\ldots,S)$ D_0 reduces to

(48) $$D_0^* = \frac{1}{N_0}\,\frac{1}{2}\sum_{i=1}^{S} \frac{(N_i - \overline{N_i})^2}{\overline{N_i}} \quad .$$

The average of D_0 on a cycle of period T is

$$\overline{D_0} = \frac{1}{T}\int_0^T dt\ D_0$$

$$= \sum_{i=1}^{S} \frac{1}{T}\int_0^T dt\ \frac{N_i}{N_0} \ln \frac{(\frac{N_i}{N_0})}{(\frac{\overline{N_i}}{N_0})}$$

$$(49) \qquad \overline{D_0} = \sum_{i=1}^{S} \frac{1}{T}\int_0^T dt\ p_i \ln \frac{p_i}{\overline{p_i}}$$

which reduces to the average of function D_0 [equation (28)] given before.

Moreover, starting from equations (42) and (49), the relation (46) is written :

$$(50) \qquad \overline{H} = H_0 - \overline{D_0}$$

with

$$(51) \qquad H_0 = - \sum_{i=1}^{S} \frac{\overline{N_i}}{N_0} \ln \frac{\overline{N_i}}{N_0}$$

where H_0 is the value of H at the reference state. This relation shows that the mean diversity of an ecosystem $\overline{H}$ is equal to the diversity of the reference state H_0 minus the mean index of fluctuations $\overline{D_0}$. Thus, only two parameters can define the diversity $\overline{H}$ of an ecosystem : the first H_0 is the diversity of the reference state and the second $\overline{D_0}$ characterizes the fluctuations of the system about the reference state.

Remark

It is possible to define the function $D_0^{(2)}$ symetrically to D_0 by the following relation

$$(52) \qquad D_0^{(2)} = \frac{1}{N_0} \sum_{i=1}^{S} (\overline{N_i} \ln \frac{\overline{N_i}}{N_i} + N_i - \overline{N_i})$$

which is also positive definite and zero at

$$N_i = \overline{N_i} \qquad (i = 1,2,\ldots,S) .$$

Expansion of function $D_0^{(2)}$ around $\overline{N_i}$ until the second order can be written :

$$D_0^{(2)} \sim D_0^* = \frac{1}{N_0} \frac{1}{2} \sum_{i=1}^{s} \frac{(N_i - \overline{N_i})^2}{\overline{N_i}} . \tag{53}$$

Thus the two functions D_0 and $D_0^{(2)}$ are different only beyond the second order.

Now let us apply the index of fluctuations D_0 to the study of the stability of the Volterra-Lotka model.

7.- Application of the index D_0 in the Volterra-Lotka model

Following Lyapunov, a perturbed system is stable if it is possible to find a function L which is positive definite and the time derivative of which is

$$\frac{dL}{dt} \leq 0 . \tag{54}$$

The equality characterizes a weakly stable system, *i.e.* a non-asymptotic stability. Under these conditions, fluctuations of the perturbed system do not decay with time; thus, the system remembers indefinitely perturbations received from its environment.

As we have defined two positive definite functions D_0 and $D_0^{(2)}$, in the sense of Lyapunov, which reduce to D_0^* for small fluctuations, let us apply these functions to study the stability of the Volterra-Lotka model.

Equation (47) is written, using equation (33) :

$$D_0 = \frac{N_{10}}{N_0} e^{v_2} (v_1 - 1) + \frac{N_{20}}{N_0} e^{v_2} (v_2 - 1) + 1 . \tag{55}$$

For small fluctuations around the stationary state, D_0 reduces to

$$D_0^* = \frac{N_{10}}{N_0} v_1^2 + \frac{N_{20}}{N_0} v_2^2 = \frac{K_1}{N_0} - 1 = K_2 = C^{nt} \geq 0 \tag{56}$$

expanding equation (35) up to second order.

Thus, the index D_0^* is a constant of motion of the Volterra-Lotka model and the stability of this system is non-asymptotic according to Lyapunov. As D_0^* is equal to K_2 in the case of small fluctuations, in the Volterra-Lotka model, equation (50) is written :

$$\overline{H} = H_0 - K_2 \tag{57}$$

where H_0 is the diversity of the reference state and K_2 the constant of motion.

We can conclude that, in the case of small fluctuations, the mean diversity of the Volterra-Lotka model is equal to the diversity of the stationary state H_0 minus the constant of motion K_2 .

Moreover, using equation (33), equation (52) is written :

$$D_0^{(2)} = \frac{N_{10}}{N_0} (e^{v_1} - v_1) + \frac{N_{20}}{N_0} (e^{v_2} - v_2) - 1 \tag{58}$$

which can be compared to equation (35) :

$$K_1 = N_{10} \; (e^{v_1} - v_1) + N_{20} \; (e^{v_2} - v_2) \geq N_0 \tag{59}$$

and we have

$$D_0^{(2)} = \frac{K_1}{N_0} - 1 = C^{nt} \geq 0 \; . \tag{60}$$

Thus, the index $D_0^{(2)}$ is surprisingly a constant of motion of the Volterra-Lotka model and we can conclude that the stability of this system is non-asymptotic for any arbitrary perturbation received from environment.

Now, let us apply this index of fluctuations in an experimental distribution of species in the North Sea.

8.- Application of the index D_0 in an experimental distribution of species

Hecq and Heyden (1971) have obtained experimental data on the variation of the proportions of five species of *Mysidacea* during 72 hours, between 4th and 9th December 1971, at Station M06 (58°28'25" N,

Table 7.3

Proportions of five species of Mysidacea

sp 1 Schistomsis spiritus
sp 2 Schistomsis kervillei
sp 3 Mesopodopsis stelleri
sp 4 Gastrosaocus sanctus
sp 5 Gastrosaocus spinifer

Date	Hour	Sampling number	$P_1(t)$ %	$P_2(t)$ %	$P_3(t)$ %	$P_4(t)$ %	$P_5(t)$ %
6/12/71	17h20	1	47.2	31.5	4.6	4.6	12
	20h23	2	18.9	75.8	0.2	2.7	2.3
	23h23	3	31.6	54.16	6.6	6.6	1.04
7/12/71	2h35	4	23.2	49.1	2.1	16.1	10.7
	5h15	5	36	23.7	13.4	15.4	11.3
	8h55	6	10.3	87.4	0.2	1.5	0.6
	12h05	7	47.8	31.1	2.1	0	10.8
	15h00	8	43.3	36.6	3.3	3.3	13.3
	18h55	9	18.5	65.5	3.7	0	9.2
	21h30	10	8.9	87.9	0.3	1.1	1.7
8/12/71	0h15	11	18.28	70.91	0	8	2.7
	3h15	12	28.67	38.97	0	25.73	6.61
	6h30	13	33.3	33.3	13.3	10	10
	9h20	14	49.3	30.6	8	0	12
	13h05	15	69	25.3	1.4	0	9.1
	15h30	16	45.2	28.5	21.4	0	4.76
	18h30	17	49.3	23.9	16.9	0	9.8
	21h50	18	20.68	72.4	0	1.72	5.17
9/12/71	1h25	19	27.8	63	0.5	4.4	4.1
	4h30	20	25.39	43.65	0.79	30.95	7.14
	7h20	21	23.4	62.06	2.06	9.65	2.75
	10h15	22	40.62	53.12	6.25	0	0
	13h35	23	86.3	0	9	0	4.54
	16h54	24	23.68	71.57	0	4.2	0.5

Table 7.4

Mean proportions of the five species of Mysidacea

$\overline{P}_1$	$\overline{P}_2$	$\overline{P}_3$	$\overline{P}_4$	$\overline{P}_5$
0.3444	0.4833	0.0483	0.0608	0.0632

03°09'15" E), close to the Westerschelde Estuary in the North Sea. These haults were taken in the surface layer every three hours, so that four samplings were made by tidal period. Results are given in Table 7.3. The five species of studied *Mysidacea* are the following : *Schistomsis spiritus, Schistomsis kervillei, Mesopodopsis stelleri, Gastrosaocus sanctus, Gastrosaocus spinifer*. The first two species are in great abundance and the other three less numerous.

Let us say that the sea, relatively quiet during the first three tidal periods, became agitated, so that we have two distinct intervals from the point of view of turbulence of the sea.

In Table 7.4 we give the time averaged proportions of each species during the 72 hours. The first two species are the most abundant, whereas the last three are in small number.

Table 7.5 gives the time variations of the three indexes of diversity : H given by equation (1), D_1 by equation (11) and D_2 by equation (24). The indexes of fluctuations D_0 , equation (28), and D_0^* , equation (29) and the variance σ^2 , equation (17), are also given. The binary units (bit) were used, *i.e.* the indexes are expressed in terms of a logarithmic scale to the base 2 . The conversion formula is given by

$$\log_2 = (\ln 2)^{-1} \ln = 1.443 \ln \quad .$$

The comparison between the index D_2 with the exact H shows a very good agreement whereas the index D_1 is only applicable when the diversity is sufficiently large; for small diversity D_1 can be negative. An interesting fact is that the minima and the maxima of all the three indexes occur at the same time. Thus, qualitatively, the three indexes give identical information.

The index D_0 is in good agreement with D_0^* but the variance σ^2 is very bad. The variance σ^2 cannot be used as a measure of the intensity of the fluctuations of the ecosystem.

Figure 7.24 gives the evolution of the three indices H , D_1 and D_2 with time (sampling number). At first sight, it is seen that the diversity oscillates with a period in close relation with the tidal period. Recall that four samplings were made by tidal period; so, we see

Table 7.5

Indexes of diversity and fluctuations (bit)

Sampling number	H	D_1	D_2	$D_0 \times 2$	$D_0^* \times 2$	$S^2\sigma^2 \times 1.443$
1	1.81	1.59	1.75	0.218	0.231	1.018
2	1.04	0.18	0.97	0.508	0.455	2.972
3	1.59	1.27	1.59	0.120	0.087	1.457
4	1.88	1.66	1.78	0.322	0.357	0.923
5	2.18	2.11	1.96	0.554	0.663	0.296
6	0.66	- 0.67	0.53	1.016	0.889	4.147
7	1.50	1.44	1.35	0.172	0.319	1.227
8	1.77	1.58	1.71	0.182	0.210	1.025
9	1.34	0.84	1.28	0.312	0.305	2.060
10	0.67	- 0.70	0.53	1.026	0.910	4.195
11	1.23	0.53	1.19	0.446	0.370	2.481
12	1.81	1.78	1.41	0.686	1.026	0.756
13	2.11	2.01	2.00	0.272	0.349	0.432
14	1.69	1.50	1.63	0.444	0.377	1.140
15	1.27	0.61	1.17	0.956	0.799	2.377
16	1.72	1.62	1.34	0.800	1.078	0.968
17	1.76	1.60	1.55	0.758	0.820	1.000
18	1.13	0.40	1.09	0.446	0.370	2.670
19	1.36	0.87	1.33	0.184	0.157	2.010
20	1.88	1.68	1.29	1.084	1.559	0.897
21	1.50	1.10	1.46	1.980	1.90	1.809
22	1.26	1.10	1.31	0.384	0.208	1.802
23	0.70	- 0.57	0.48	2.406	1.971	4.008
24	1.07	0.40	1.04	0.474	0.365	2.672

six minima and six maxima. The mean current direction is also given, in Figure 7.24, successively we get current directions NW , SW , SE and NE . At first sight, the minima of the diversity corresponds to NW current direction. As the station M06 where the hauls were made is close to the Westerschelde Estuary, the NW current brings water from the Estuary where the diversity of *Mysidacea* is smaller than in water coming from the sea. So the transport of *Mysidacea* with a weak diversity is well visualized by the minima of the index of diversity. For the first three tidal cycles, the correspondance between the minima and the NW current is perfect, in this case, the sea is calm, whereas for the last three

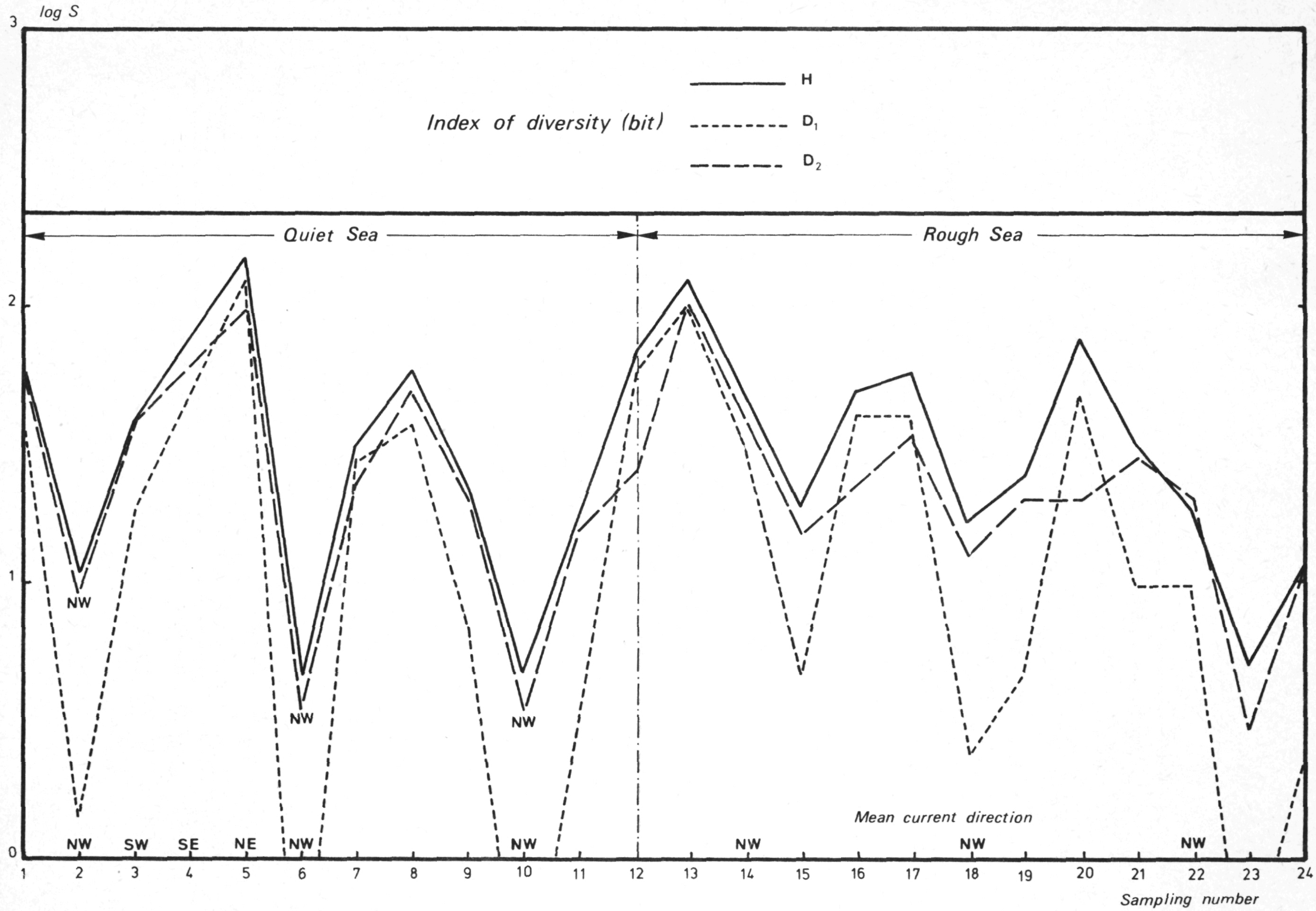

fig. 7.24.- H is the Shannon-Weaver index of diversity, D_1 is the development of H around the mean up to the second order and D_2 is the development of H around the reference state up to the second order.

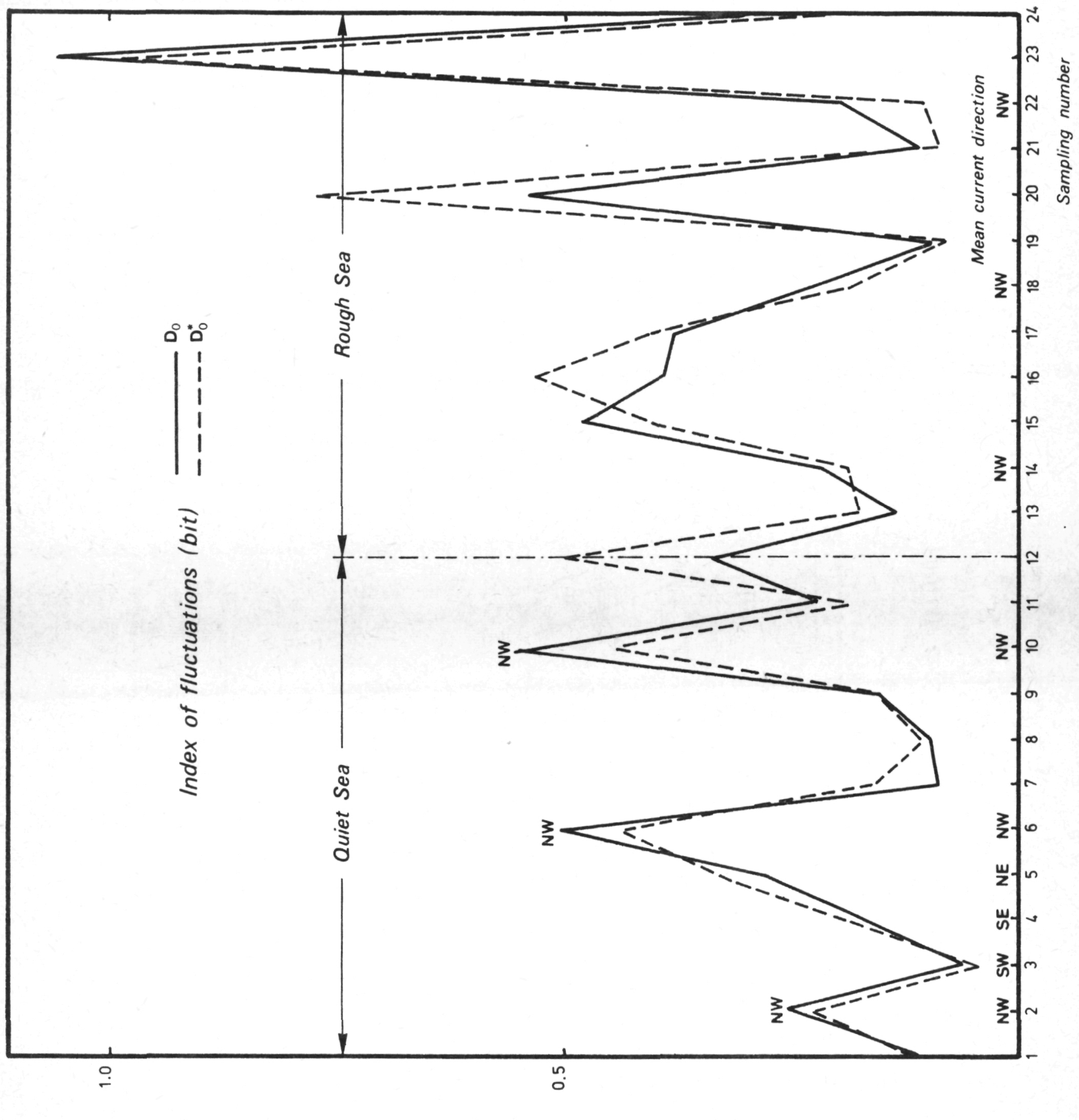

fig. 7.25.- D_o is the index of fluctuations and D_o^* represents the second order term of D_2 .

tidal cycles the effect of the turbulence of the sea is seen by a shifting of these minima. Moreover, the intensity of the oscillations of the diversity is relatively constant with time.

In Figure 7.25, the indexes of fluctuations D_0 and D_0^* are plotted in function of the time as in Figure 7.24. But, contrary to Figure 7.24, we observe oscillations of the index with the tidal cycles, only under calm conditions and the maxima of fluctuations occur when the NW current brings *Mysidacea* from the Estuary. So, maxima of the index of fluctuations corresponds to minima of the index of diversity, and so, the index of fluctuations gives a very attractive measure of perturbations of an ecological system around its reference state. On the other hand, for the turbulent sea region, the maxima of the index of fluctuations corresponds no more to NW current direction. Moreover, the maxima of the variation of the index becomes very large; at sampling number 23, the index is 1.203 whereas the other maxima are around 0.5 .

Now let us compare the behaviour of the index of diversity with the index of fluctuations. In the calm sea region the two indices follow the tidal cycle and the minima of the diversity correspond to the maxima of the index of fluctuations which occur with the NW current direction transferring *Mysidacea* of weak diversity from the Estuary.

On the other hand, in the turbulent sea region, no such correspondance exists between the two indexes, the index of diversity keeps the same behaviour as in the calm sea region whereas the index of fluctuation increases strongly with turbulence. Moreover, in sampling numbers 6 and 23, the indexes of diversity are the same 0.66 and 0.70 respectively and the indexes of fluctuations are 0.508 and 1.203 respectively. So, two identical values of the index of diversity can correspond to two strongly different values of the index of fluctuations. The second index gives more information about the deviation of an ecosystem from its reference state.

Finally, in Figure 7.26 we have plotted H_0 and H_1 which are defined as

$$(61) \qquad H_0 = - \sum_{i=1}^{S} \overline{p_i} \ln \overline{p_i}$$

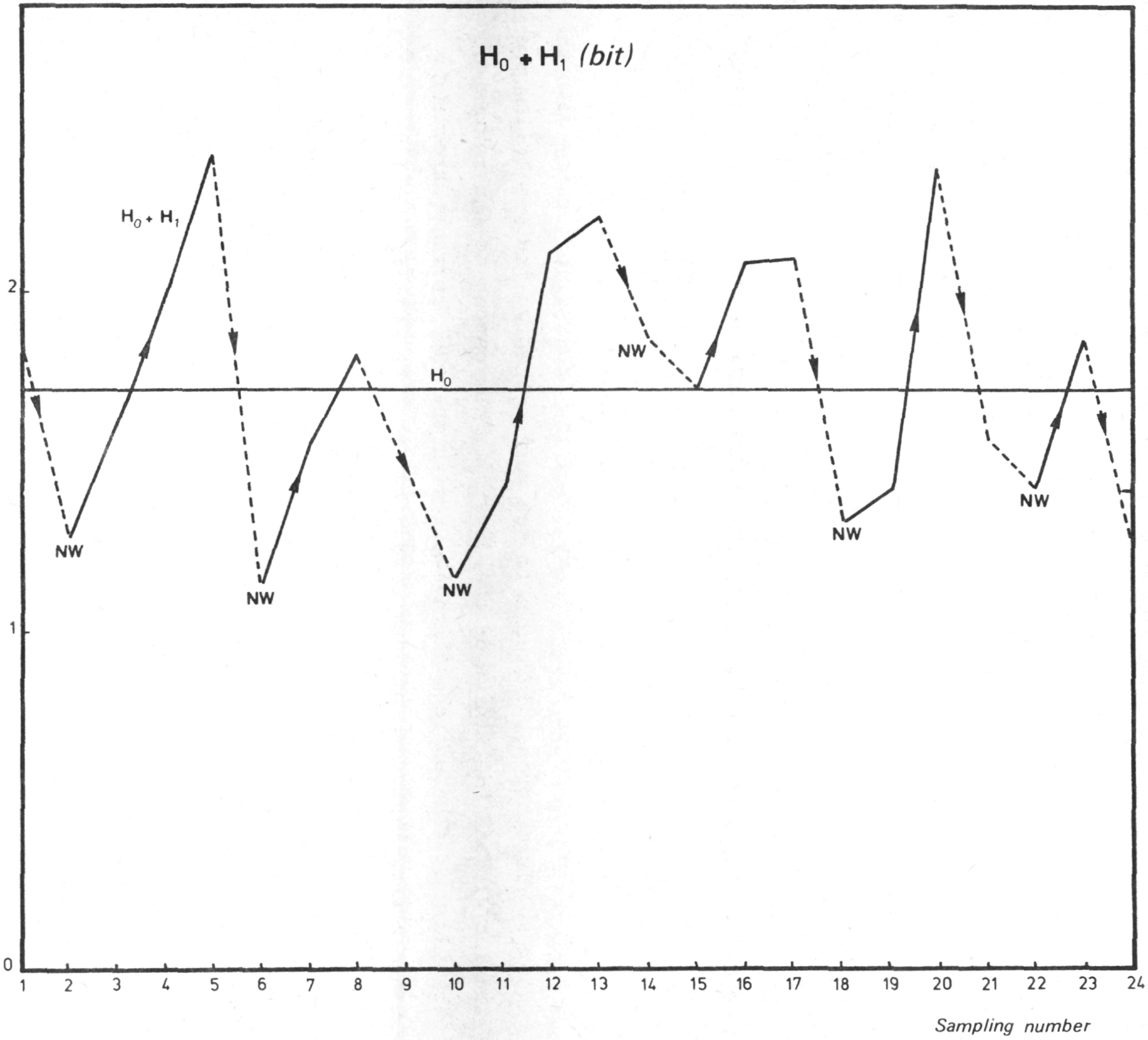

fig. 7.26.- H_0 and H_1 represent the first two terms of D_2 .

and

$$(62) \qquad H_1 = - \sum_{i=1}^{S} (\ln \bar{p}_i)(p_i - \bar{p}_i)$$

which are the first two terms of the series development of H around the reference state [equation (22)]. H_0 is the diversity of the reference state and is a constant with time whereas H_1 is a function of time.

In conclusion, two opposite phenomena influence the value of the diversity; first we observe a decrease of the diversity with time which corresponds to a flow of diversity from the Estuary (the diversity of the *Mysidacea* in the Estuary is smaller than in the sea). Second, the diversity increases because of diffusion phenomena. Thus the flow of diversity is, on the average, sufficient to maintain the ecosystem at its reference state and compensate the diffusion processes.

9.- Conclusion

Defining a "reference state" for a distribution of species as the ensemble of space-time average proportions of species $\bar{p}_i$, an index of diversity is derived from the Shannon-Weaver formula, which reduces to a simple relation depending on the total number of species S and the variance of distribution σ^2 around the mean.

For the study of fluctuations around the reference state, we introduce an index of fluctuations D_0 which is a positive definite function in the sense of Lyapunov, and zero at the reference state.

Considering the well-known model of Volterra-Lotka to describe a "predator-prey" population, the index of fluctuations D_0 is applied explicitely. Moreover, another function $D_0^{(2)}$, symmetrical to D_0 , is presented.

The discussion of the time derivative of the index of fluctuations D_0 leads to the non-asymptotic stability of the Volterra-Lotka model in the case of small perturbations of the stationary state : D_0 is a constant of motion. Moreover, the function $D_0^{(2)}$ is surprisingly a constant of motion of the Volterra-Lotka model for any arbitrary perturbation received from the environment.

Thus, the index of fluctuations D_0 can be used as a practical criterion of stability of an ecosystem. Moreover, an average of the index of diversity of an ecosystem $\overline{H}$ can be written as :

$$\overline{H} = H_0 - \overline{D_0}$$

where H_0 is the diversity of the reference state and $\overline{D_0}$ the average of the index of fluctuations D_0

$$\overline{D_0} = \frac{1}{T} \int_0^T dt \sum_{i=1}^{S} p_i \ln \frac{p_i}{\overline{p_i}} \quad .$$

Finally, all these indexes are compared on an experimental example : the variation of the distribution of *Mysidacea* at a point of the North Sea. The index of fluctuations appears to be a very attractive measure of the effects on the ecosystem of external perturbations.

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