ISSN 0240-8759

Vie et Milieu

Life and Environment

Vol. 44 nº 1 – Mars 1994

éiodique d'écologie - Publication trimestrielle

VIE ET MILIEU

Life and Environment

PÉRIODIQUE D'ÉCOLOGIE GÉNÉRALE
JOURNAL OF GENERAL ECOLOGY

LABORATOIRE ARAGO — UNIVERSITÉ P. et M. CURIE

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Publié avec le concours financier de l'Association Naturalia et Biologia
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ABONNEMENTS/SUBSCRIPTIONS 1994

	FRANCE	AUTRES PAYS
Un an (4 numéros) / *Annual subscription (4 issues)*...	660 F	870 F

Adresser le paiement à l'ordre de / *Address payment to the order of :*

Vie et Milieu, Laboratoire Arago, 66650 BANYULS-SUR-MER. FRANCE

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VIE ET MILIEU — Laboratoire Arago — F. 66650 BANYULS-SUR-MER

VIE MILIEU, 1994, 44 (1) : 1-9

VISUAL PREDATORS, ENVIRONMENTAL VARIABLES AND ZOOPLANKTON MORTALITY RISK

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ZOOPLANCTON
MORTALITÉ
LUMIÈRE
MODÈLE

RÉSUMÉ – Plusieurs aspects du risque de mortalité du zooplancton (taille, contraste propre, diminution de la lumière incidente et de la lumière diffuse, profondeur, intensité de la lumière ambiante, sélectivité, sasiété du prédateur) sont étudiés à partir d'un modèle de rencontre prédateur-proie dans lequel on suppose que le prédateur se nourrit à vue. Nous mettons en évidence que la pente du gradient vertical de risque décroit avec la taille du zooplancton et qu'il est 3 à 4 fois plus accusé pour les nauplii que pour les formes ayant la taille des Euphausiacés. A petite échelle une distribution verticale en taches se rencontre plutôt chez les petites formes. En raison de différences dans la détection, le risque de mortalité (et le taux de nutrition d'un prédateur non sélectif) dépend très nettement des différences de taille. Une strate turbide, comme par exemple une couche d'eau riche en phytoplancton, superposée à des eaux claires, peut offrir une zone de refuge pour le macroplancton et pour les Poissons de faible taille se nourrissant de plancton. De même, le risque de devenir une cible pour le microzooplancton diminue dans cette strate, mais persiste et s'accroit au-dessous de cette couche. En situation de faible contraste dans des eaux peu turbides, la réduction du contraste inhérent entraîne une meilleure protection.

ZOOPLANKTON
MORTALITY
LIGHT
MODEL

ABSTRACT – Several aspects of zooplankton mortality risk (body size, inherent contrast, beam and diffuse light attenuation, depth, ambient light level, selectivity, predator saturation) is studied from a predator-prey encounter model where the predator is assumed to feed by vision. It is shown that the steepness of the vertical gradient in risk decreases with zooplankton size, being 3-4 times steeper for nauplia than for krill-sized animals. Fine-scale vertical patchiness is thus more likely to be found for smaller forms. Due to differences in detectability, mortality risk (and feeding rate of an unselective predator) will be severely influenced by size differences. A turbid layer, such as a phytoplankton layer, overlying clear water may act as a refuge for macroplankton and small planktivorous fishes. Microzooplankton will also have gradually reduced objective risk in the layer, but even lower risk below the layer than inside it. Increased protection by reduced inherent contrast is only effective for very low contrasts and in water with low turbidity.

INTRODUCTION

Vertical distributions of pelagic animals must be understood in the context of maximizing life time reproductive output (McLaren 1963, Werner & Gilliam 1984, Clark & Levy 1988, Gabriel & Thomas 1988 a, b, Aksnes & Giske 1990). Giske *et al.* (1993) defined phenotypical fitness for an individual as the difference between its own rate of offspring production and the average rate of the population. A measure for these rates is the instantaneous rate of reproduction, r, which can be used both on the individual and the population levels. To describe the rate of individual (semelparous) offspring production over a life time, we may write

$$r = \ln (bS)/G \qquad (1)$$

where b is fecundity (offspring per mother) and S is probability of juvenile survival over generation time (G). The term bS thus represents the socalled net reproductive rate (R_0), which is the ratio of individuals separated by one generation. Survival probability (S) can be expressed as the product of mortality risk (Z) and generation time length,

$$S = e^{-GZ} \qquad (2)$$

Thus we may rewrite Eq.1 as (Giske *et al.* 1993)

$$r = \ln b / G - Z \qquad (3)$$

which is the individual approximation of the continuous population dynamics equation $r = b - d$. uEq . u3 states that a zooplankter will maximize its fitness by seeking a habitat which allows a high fecundity, a short generation time, and a low mortality risk, and the equation also expresses the relative importance of these three factors on lifetime fitness. For a zooplankter feeding on phytoplankton and preyed upon by visual predators, both feeding rate and mortality risk will generally decrease with increasing depth, so an attempt to increase b will generally also increase Z (and decrease G). While there has been a considerable effort in expressing the influence of environmental variables on fecundity and generation time of zooplankton (e.g. McLaren 1966, 1978, Bottrell *et al.* 1976, Vidal 1980 a, b, Huntley & Boyd 1984, Carlotti & Sciandra 1989, Carlotti & Nival 1992, Huntley & Lopez 1992), there have been considerably fewer attempts to describe local variations in zooplankton predation risk and mortality rate (Aksnes & Magnesen 1983, 1988, Aksnes & Giske 1990), although this is the potentially most important variable in Eq. 3.

The optimal trade-off between high fecundity or low mortality as expressed in Eq. 3 is based on the average over the whole life span of the individual. However, age, season and diel variability may impact the actual optimal trade-off between growth and fecundity versus survival : Gilliam (1982) and Werner & Gilliam (1984) showed that juvenile fish should choose the habitat that minimizes the ratio between their mortality risk and growth rate ("minimize μ/g", in their terminology). Aksnes & Giske (1990) and Giske and Aksnes (1992) showed that adult fish should emphasize survival even more, and minimize Z /ln (g) in their habitat choice. Such differences between juveniles and adults have also been indicated in experiments with gobies (Utne *et al.* 1993, Utne & Aksnes 1994). Aksnes & Giske (1990) also showed that if generation time is influenced by environmental temperature (Huntley & Lopez 1992), the major trade-off will be between mortality risk and temperature. Furthermore, Giske & Aksnes (1992) and Rosland & Giske (in pess) have shown that while risk-willingness of a juvenile mesopelagic fish in winter depends on the average life-history derived trade-off (Z/g) and stomach fullness, the adults seem to employ the strategy of maximizing probability of overwintering survival. Risk-willingness by animals facing the threat of starvation or exhaustion also exceed by far the average expectations from life history models (Stephens 1981, Metcalfe & Furness 1984). Thus the overall importance of avoiding mortality must be found from fitness assessments at the appropriate time scale, while the numerical value of the mortality risk should be assessed by mechanistical models of the predation process.

Two aspects of the environment distinguish the pelagic habitat from all others : 1) compared to air, the transparency of water is low. While visual range in air is mainly restricted by the horizon, an underwater image is attenuated at scales of millimeters to meters. 2) Also compared to littoral and benthic habitats, the pelagic does not contain obstacles allowing local shelter. Thus visual predation risk in the pelagic habitat may be approximated by underwater light and image transmission (Duntley 1962, Eggers 1977, Aksnes & Giske 1993). The scope of this paper is to analyse some environmental aspects of zooplankton mortality risk caused by visual predators, mainly based on the fish vision model of Aksnes & Giske (1993). Fish visual range depends on the visual ability of the fish, on the size and inherent contrast of its prey, but also on environmental variables as ambient light intensity, attenuation of light beams and attenuation of diffuse light. Fish vision is thus strongly depth dependent, and we will examine some objective aspect of mortality risk, irrespective of local distribution of predators and prey.

MODEL

We assume predators and prey to be randomly distributed on the local horizontal scale. The total number of encounters between predators and their prey over a time period T is then a function of local densities of predators (P) and zooplankton (N), their speed (V) and the ability of the predators to detect their prey (here interpreted as a prey detection area, A):

$$E = TNPAV \tag{4}$$

In the water column, the local rate of encounters (E/T) is strongly influenced by depth distribution of predators and prey. However, as both planktivores and plankton are mobile and can take any position in the vertical, the density-independent aspect of predator-prey contact rates is of fundamental importance, as it describes the objective (i.e. environmental) aspect of predation risk:

$$e = E \mathbin{/} (TNP) = AV \tag{5}$$

For a visual predator, the prey detection area A is determined by ambient light (depth), predator eye sensitivity, prey size and contrast, and the speed V is given by the predator and prey. Eq. 5 describes an objective function for food encounters for planktivores, where zooplankton mortality risk is not associated with the current vertical distribution of P. The physical variables underlying A will be crucial for the potential vertical variation in zooplankton predation risk.

Gerritsen & Strickler (1977) showed that the velocity component of contact rates can be described from swimming speeds of both predators and prey, and Rothschild & Osborn (1988) showed that turbulence may increase the contact rates considerably, especially for slow-moving predators. However, for the case of visual predators, predator swimming speed is generally an order of magnitude higher than turbulent velocity and zooplankton swimming speed, and we may write :

$$V \approx v \tag{6}$$

where v is planktivore swimming speed.

Aksnes & Giske (1993) have derived a simple model for how fish visual range R is influenced by the environment. The visual range depends on depth (z), light regime (air light intensity E_0, fraction of irradiance lost in the air-water interface ρ, diffuse attenuation coefficient K and beam attenuation coefficient c), the planktivore (sensitivity threshold for eye for detection of changes in irradiance $\Delta S_{e)}$ and the zooplankton (surface area a [$= \pi\ (L\ /2)^2$, L = body length] and contrast $|C_0|$:

$$R^2 e^{zK + cR} + \hat{c}R = \rho E_0 |C_0| \mathrm{a}\ \Delta\ S_e^{\ -1} \tag{7}$$

The prey detection area of a swimming visual predator is the cross-sectional area of the cylinder determined by its swimming path, its visual search range (R) and the search angle (θ).

$$A = \pi\ (R \sin\theta)^2 \tag{8}$$

(Luecke & O'Brien 1981, Dunbrack & Dill 1984, Aksnes & Giske 1993). There has been some attempts to measure θ (Hairston *et al*. 1982, Dunbrack & Dill 1984, O'Brien & Evans 1992), and although some of these results indicate that θ is not equal in all directions, we here assume a symmetrical forward oriented visual field. With this assumption, calculations of zooplankton mortality risk is straightforward, and mortality risk for a zooplankter from moving visual planktivores is proportional to the planktivore's prey detection surface, for which the visual range (given by Eq. 7) is the only environmental variable:

$$Z\ \alpha\ A\ \alpha\ R^2 \tag{9}$$

The proportionality factor is influenced by overall abundance of predators (P) and their swimming speed ($V = v$), on the (time or state-dependent) optimal trade-off between survival and other activities (c.f. Eq. 3), and possibly by availability of alternative prey items. Assessments of feeding of mesopelagic planktivores based on Eqs. 7-8 have been performed by Giske & Aksnes (1992) and Rosland & Giske (in press). We will here focus on risk assessment for the zooplankter after Eqs. 7-9.

ANALYSIS AND DISCUSSION

Body size and vertical gradients in mortality risk

For all sizes of plankton, visual based mortality risk will generally be reduced with depth according to a general decrease in ambient light. But the rate of reduction depends strongly on both prey size and actual depth. Generally, the easier a zooplankter is to see, the less change in detection range will be gained after a vertical relocation : the change of detection range of a predator when its prey moves one meter down is higher for smaller than for larger prey, and is also higher in deep water than in shallow water (Fig. 1 A). Consequently, the reduction in visibility with depth is much steeper for microplankton than for macroplankton (Fig. 1 B). Thus, one could predict

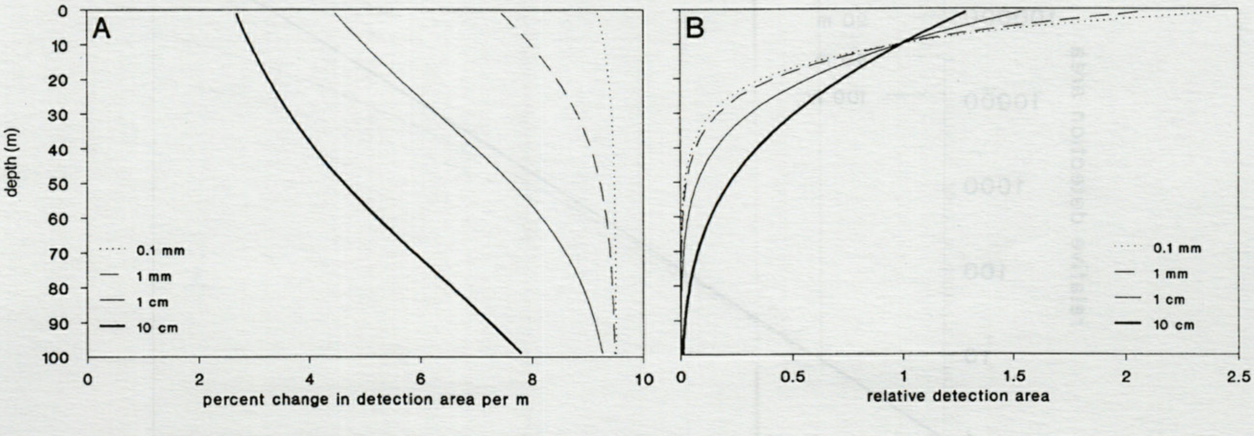

Fig. 1. – Effects of depth for detection risk of zooplankton. A, Relative vertical change in detection area. B, Detection area relative to area at 10 m depth. The parameter values in Eq.7 have the following standard values, if not varied in a simulation : E_0 : 1000 µmol m^{-2} s^{-1}, $\rho = 0.5$, $z = 1$ m, $K = 0.1$ m^{-1}, $c = 0.3$ m^{-1}, $C_0 = 0.5$, $\theta = 30^{\circ}$, $L = 0.1$ cm, $\Delta S_e = 2.5\ 10^{-5}$ µmol m^{-2} s^{-1}. Zooplankton is assumed sphaerical, so that its surface area $a = \pi\ (0.5L)^2$, where L is body length. Zooplankton wet weight is $W = 4/3\ \pi\ (0.5\ L)^3$, where L is length in cm (thus assuming a spheric zooplankter ; 1 g wet weight = 1 cm^3).

a more pronounced fine-scale vertical distribution of microzooplankton than of macrozooplankton. The benefit in terms of increased survival by adopting a narrow vertical range must eventually be balanced by costs of maintaining this vertical position, as small-sized individuals have higher swimming costs (Vlymen 1970).

Prey selectivity and size: relative visibility and body size

There has been a debate on whether planktivorous fish select their prey items on basis of energetic content (according to the optimal foraging theory) or visibility (Werner & Hall 1974, Confer & Blades 1975, Eggers 1982, Li *et al.* 1985, Wetterer & Bishop 1985, O'Brien & Evans 1992). Frequently, the term "selectivity" is used when the size – (or species-) composition of zooplankton in fish stomachs differs from zooplankton samples, irrespective of whether the difference is caused by detection limitations, zooplankton behaviour or the planktivore's food choice.

The range R at which an individual can be detected by a visual planktivore increases with zooplankton size and decreases with depth. At large depth, the detection range of the planktivore is proportional to L^2, since (when R is small and cR ! zK so that $cR + Kz \approx Kz$) $R^2 \propto a \propto L\,2$ (Eq. 7, Fig. 1). However, this proportionality does not hold for the largest plankton (i.e. when cR is of same magnitude as Kz), and the deviation from $R^2 \propto L^2$ appears first in shallow water (Fig. 2). This is because when R is large, $R^2 \propto L^2\, e^{-cR-zK}$ (Eq. 7). Thus, while a high representation of larger individuals in fish stomachs from shallow water may be explained by active prey selection, the same pattern in stomach composition at larger depth (or more generally at low irradiance levels) would be expected for encounter-based feeding. However, we should here remind that our prey is assumed passive and stationary, and quite different results could be obtained if prey swimming speed is of importance (e.g. Jakobsen & Johnsen 1988).

Inherent contrast and ambient light level

Transparent forms of zooplankton occur both in marine and limnetic habitats. Generally, the forms with higher inherent contrast experience higher mortality risk from visual predators (Nilsson 1960, Merret & Roe 1974, Mellors 1975) or are confined to habitats void of such predators (Fox 1948, Hobeak & Wolf 1991). The fitness cost associated with high fecundity and growth (many eggs or full gut) or extended habitat utilization (e.g. by UV protective pigments or red haemoglobin) depends on the water quality of the habitat and the size and position of the zooplankter. The benefit of reduced contrast is strongly dependent on the overall visibility of the animal. In decreasing order of importance, the dependency of contrast for mortality risk is influenced by overall

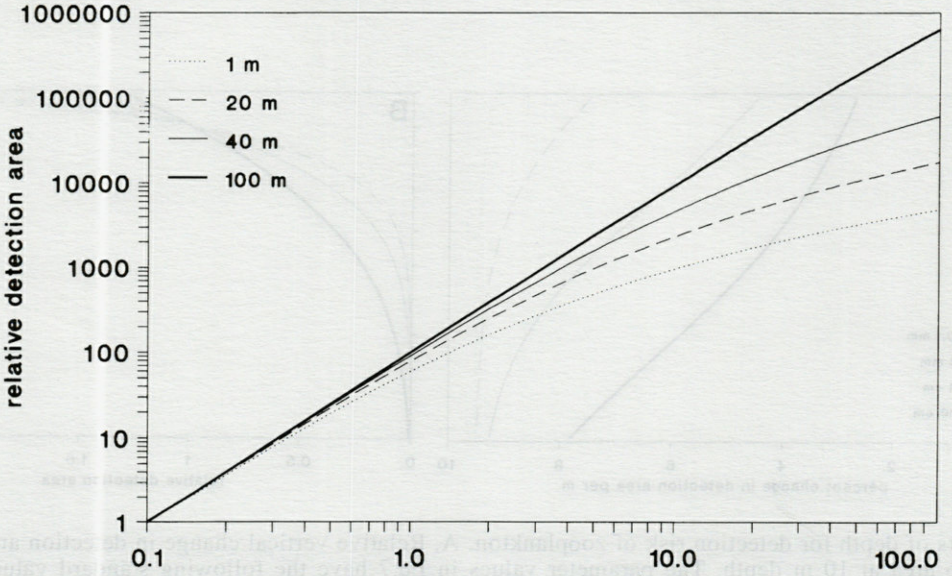

Fig. 2. – Effects of size for detection risk of zooplankton. Detection areas relative to 0.1 mm animal. Constant parameter values in Eq. 7 as in Fig. 1.

ambient light intensity, zooplankton size and water clarity. At low light intensities, change in mortality risk is proportional to change in contrast, while changes in contrast does not affect mortality risk so much in brightly illuminated water (Fig. 3 A). While minute zooplankters will gain a pronounced reduced predation risk by reduced inherent contrast, this will not influence risk of large-bodied individuals (Fig. 3 B). Changes in turbidity operate the same way a light intensity; contrast is of minor importance in highly turbid water, but will gradually increase in importance as water clarity increases (Fig. 3 C). An isoline for depths and inherent contrasts giving equal visibility and predation risk is shown in Fig. 4. This curve is independent of prey size and shows the potential increase in surface habitat exploitation for truly hyaline animals. The shape of the curve is also independent of absolute level of contrast, so that starting with less hyaline animals close to the surface will only shift the whole line to the right.

For the smaller size classes, reducing contrast is beneficial (Fig. 3 c), while migration may be relatively more costly (Vlymen 1970, Morris *et al.* 1985) due to drag coefficient and Reynolds number. An alternative strategy to diel vertical migration may then be diel variation in contrast, due to a diel pattern in feeding (Frost 1988, Haney 1988). There are several reports in the literature

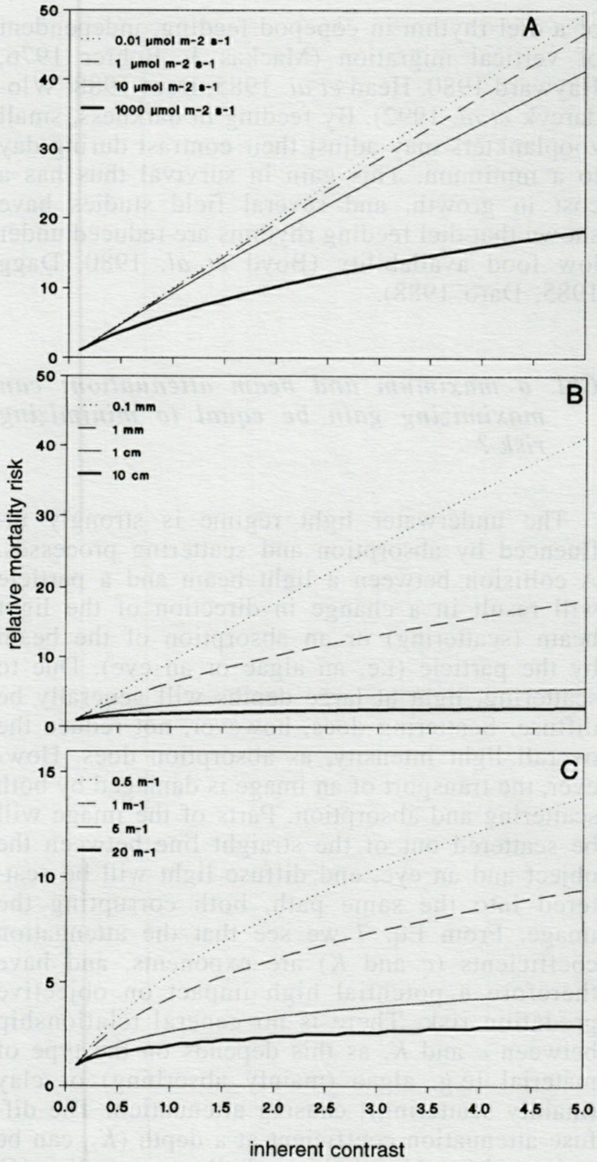

Fig. 3. – Effects of inherent contrast for detection risk of zooplankton. A, Relative detection areas under different light intensities. B, Relative detection areas under different body sizes. C, Relative detection areas under different beam attenuation coefficients. Constant parameter values for Eq. 7 as in Fig. 1.

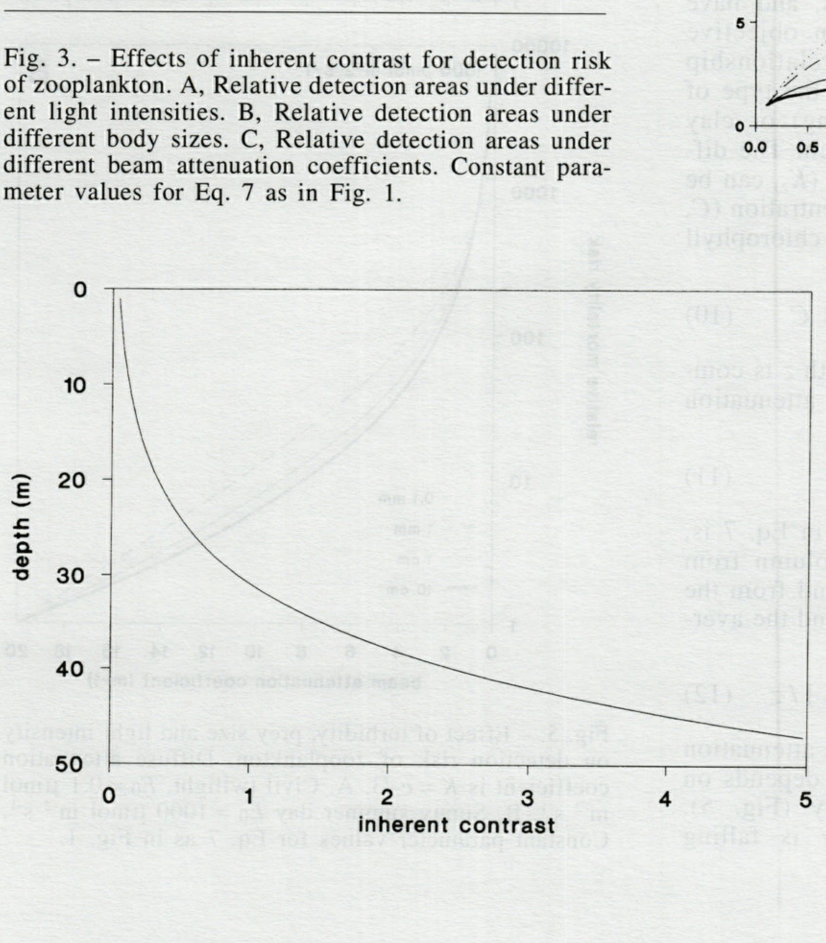

Fig. 4. – Isoline for equal visibility under varying inherent contrasts and depths. Constant parameter values in Eq. 7 as in Fig. 1.

of a diel rhythm in copepod feeding, independent of vertical migration (Mackas & Bohrer 1976, Hayward 1980, Head *et al.* 1985, Daro 1988, Wlodarcyk *et al.* 1992). By feeding in darkness, small zooplankters may adjust their contrast during day to a minimum. This gain in survival thus has a cost in growth, and several field studies have shown that diel feeding rhythms are reduced under low food availability (Boyd *et al.* 1980, Dagg 1985, Daro 1988).

Chl. a maximum and beam attenuation: can maximizing gain be equal to minimizing risk ?

The underwater light regime is strongly influenced by absorption and scattering processes. A collision between a light beam and a particle will result in a change in direction of the light beam (scattering) or an absorption of the beam by the particle (i.e. an algae or an eye). Due to scattering, light at large depths will generally be diffuse. Scattering does, however, not reduce the overall light intensity, as absorption does. However, the transport of an image is damaged by both scattering and absorption. Parts of the image will be scattered out of the straight line between the object and an eye, and diffuse light will be scattered into the same path, both corrupting the image. From Eq. 7 we see that the attenuation coefficients (c and K) are exponents, and have therefore a potential high impact on objective predation risk. There is no general relationship between c and K, as this depends on the type of material [e.g. algae (mainly absorbing) or clay (mainly scattering)] causing attenuation. The diffuse attenuation coefficient at a depth (K_z) can be estimated from local chlorophyll concentration (C, mg m^{-3}) and extinction caused by non-chlorophyll particles (k_0, m^{-1}) :

$$K_z = k_0 + 0.054\ C^{2/3} + 0.0088\ C \qquad (10)$$

(Riley 1956). Beam attenuation at depth z is commonly 2-4 times the local diffuse attenuation (Kirk 1980), and we assume here

$$c_z = 3\ K_z \qquad (11)$$

The diffuse attenuation coefficient in Eq. 7 is, however, the average of the water column from the surface to depth z, and is thus found from the local attenuation coefficient at depth and the average of the column above:

$$K = K_{0-z} = [\ (z-1)\ K_{0-(z-1)} + K_z\ ]\ /\ z \qquad (12)$$

The overall importance of the beam attenuation coefficient in surface water ($z = 1$ m) depends on prey size and overall light intensity (Fig. 5). While mortality risk of small prey is falling rapidly with increased attenuation in the whole range 0.2 – 20 m^{-1}, large prey will gain much more by an increase in c from 0.2 to 2 m^{-1} than from 2 to 20 m^{-1}. The overall light intensity is also of importance : the lines for the large 1 and 10 cm prey at 0.1 µmol m^{-2} s^{-1} (civil twilight, Fig. 5 A) are identical to the lines for the small 0.1 and 1 mm prey at 1000 µmol m^{-2} s^{-1} (sunny summer day, Fig. 5 B), respectively.

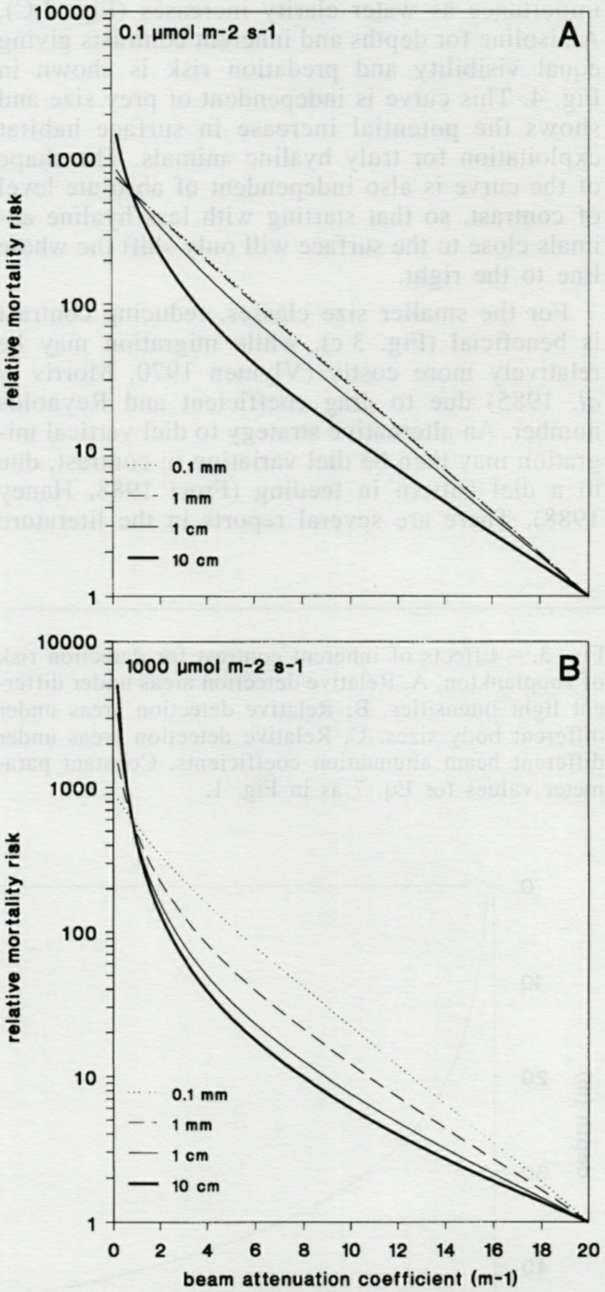

Fig. 5. – Effect of turbidity, prey size and light intensity on detection risk of zooplankton. Diffuse attenuation coefficient is $K = c\ /3$. A, Civil twilight, $E_0 = 0.1$ µmol m^{-2} s^{-1}. B, Sunny summer day $E_0 = 1000$ µmol m^{-2} s^{-1}. Constant parameter values for Eq. 7 as in Fig. 1.

Mortality risk at a depth depends on ambient light ($E_z = E_0\rho e^{-K_z}$) and the local attenuation coefficients (K_z and c_z). As shown in Fig. 1 A, the decrease in mortality risk does with increasing depth is low for large prey in shallow water, while they are quite sensitive to changes in the beam attenuation coefficient in water of low or moderate turbidity (Fig. 5). Thus a situation may arise where mortality risk increases downwards. This may happen if attenuation in a distinct vertical layer is high (e.g. a layer of brackish water or a sharp chlorophyll peak). Such a situation is sketched in Fig. 6 A. Due to a subsurface chlorophyll maximum, beam attenuation c_z is high at 1 - 5 m and low at surface and below 5 m and average diffuse attenuation coefficient increases through the turbid layer. The objective effect of this layer of high turbidity on the vertical predation risk profile is highly size-dependent, reflecting the different size-dependent impact of K and c (Fig. 6 B). For minute zooplankters, a layer of high turbidity acts to reduce overall light intensity below, and mortality risk below this layer is much less than above. For macrozooplankton, the layer works as thick fog where they can hide. In the graphical example, mortality risk is 10-30 times higher below the layer than inside it, while risk is not much less below than above the layer. Thus macrozooplankton benefit from the high cz in the layer, while microzooplankton gain from the increase in $K_{0\text{-}z}$ through the layer.

The turbid layer may be a very beneficial habitat for macroplankton, especially if they feed on the abundant turbidity-generating particles (such as phytoplankton). If macroplankton and small pelagic fishes feed on microplankton, the turbid layer may act as a high risk area for microplankton, as their predators may gain protection by staying there without reduction in their prey encounter rates. This was observed by Miner & Stein (1993), who found predation intensity of larval bluegill sunfish on crustacean zooplankton to increase in situations with high turbidity and high light intensity.

ACKNOWLEDGEMENTS – JG received financial support by a Norwegian Fisheries Research Council grant to Hein Rune Skjoldal. We thank Rune Rosland for valuable discussions.

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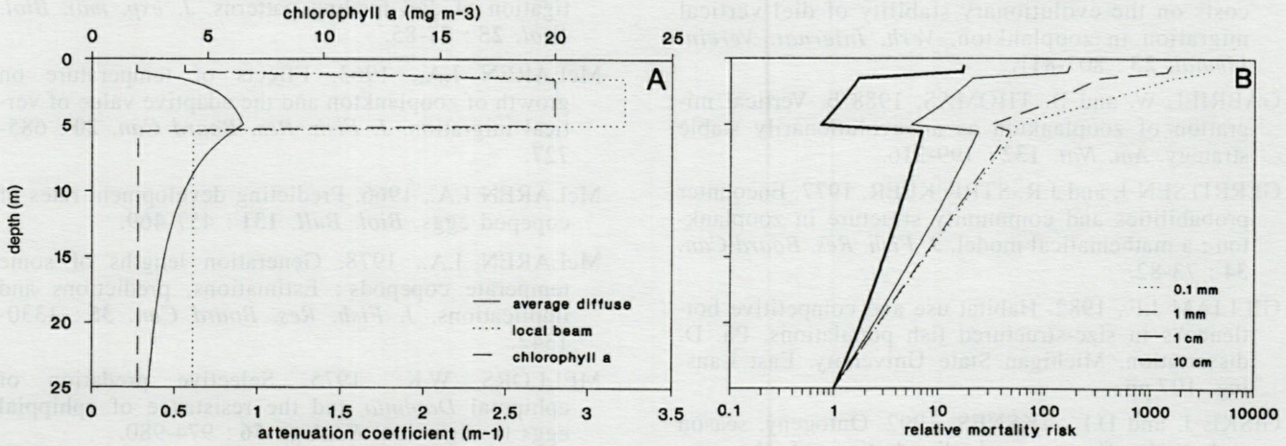

Fig. 6. – Effect of turbidity on vertical distribution of mortality risk. A, Vertical profile of attenuation coefficients. The local beam attenuation coefficient c_z and the average diffuse attenuation coefficient $K_{0\text{-}z}$ are calculated from chlorophyll concentration and non-chlorophyll extinction after Eqs. 10-12. Non-chlorophyll extinction k_0 is sat at 0.5 m^{-1} in the turbid layer and 0.1 m^{-1} above and below. B, Size-dependent relative detection risk for zooplankton. Constant parameter values for Eq. 7 as in Fig. 1.

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Reçu le 14 mai 1993 ; received, May 14, 1993
Accepté le 30 juillet 1993 ; accepted, July 30, 1993

VIE MILIEU, 1994, 44 (1) : 11-20

REVIEW AND COMPARISON OF GOAL FUNCTIONS IN SYSTEM ECOLOGY

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ÉCOLOGIE DE SYSTÈME
FONCTIONS CIBLES
ASCENDANCE
EXERGIE
ÉNERGIE
CHANGEMENTS STRUCTURAUX
EFFET INDIRECT

RÉSUMÉ – Cinq fonctions cibles différentes sont analysées et comparées par trois modèles différents de lacs suivant 15 versions différentes. Les fonctions cibles sont : exergie, exergie structurale, émergie, ascendance et rapport entre effets indirects et directs. Les définitions de ces concepts sont exposées. Toutes les fonctions cibles examinées sont fortement corrélées, mais l'émergie montre des coefficients de corrélation plus faibles vis à vis de l'ascendance et des effets indirects/directs que les autres couples de fonctions. La corrélation entre l'ascendance et l'exergie est la plus élevée, ce qui est en accord avec les résultats précédents. La corrélation entre l'exergie structurale et le rapport effets indirects/directs est également forte avec un coefficient d'une valeur égale à 0,99. Ces corrélations confortent l'idée d'intégrer les théories à propos des écosystèmes à un pattern, ainsi que l'a proposé Jorgensen (1992).

SYSTEM ECOLOGY
GOAL FUNCTIONS ASCENDENCY
EXERGY
ENERGY
STRUCTURAL CHANGES
INDIRECT EFFECT

ABSTRACT – Five different so-called goal functions are reviewed and compared by three different lake models in totally 15 different versions. The goal functions are : exergy, structural exergy, emergy, ascendency and the ratio indirect to direct effects. The definitions of these concepts are given in the paper. It was found that all the investigated goal functions are highly correlated, although emergy shows smaller correlation coefficients with ascendency and indirect /direct effects than other pairs of goal functions. Particularly the correlation between ascendency and exergy is very strong, which is consistent with previous results. The correlation between structural exergy and the ratio indirect to direct effects is also high with a correlation coefficient of 0.99. These correlations support the idea to integrate existing ecosystem theories to a pattern, as suggested by Jorgensen (1992).

INTRODUCTION

Goal functions are understood as functions, that can describe the direction of the ecosystem development. This must not be interpreted as ecosystems have predetermined goals, but rather that the selforganization ability of ecosystems makes it possible to meet perturbations by directive reactions.

Jorgensen (1992) gives an overview of several goal functions, proposed during the last 1-2 decades by several systems ecologists. It has furthermore been proposed (Jorgensen, 1992), that the different goals functions at least to a certain extent are just different view points of the same matter. It is not surprising, that the very complex ecosystems need several different view points to be described properly, when a relatively simple physical phenomena as light needs two descriptions : waves and particles.

This paper attempts to review and compare several different goal functions for totally 15 different editions of three lake models with different complexity. The following goal functions have been included : emergy, exergy, structural exergy, ascendency, both the total ascendency and the contributions from the through-flow (T), the ratio indirect to direct effect and buffer capacities. A few examinations of the correlation between two-three of the above mentioned goal functions have been carried out previously. These examinations will be summarized and compare with the results of this investigation.

DEFINITIONS AND REVIEW OF GOAL FUNCTIONS

The two goal functions emergy and exergy are based upon thermodynamics. Biomass or the free energy of combustion would only correspond to the energy of the ecosystem as "fuel", while emergy and exergy include an energy quality factor. Emergy considers how much solar radiation it costs to build a considered organisms (biomass) (see Odum, 1983). Figure 1 illustrates the concept of emergy. The biomass or rather the free energy of the biomass is multiplied with a factor, found from the amount of solar energy it costs to construct one unit of energy in the considered organism. Figure 1 gives only a simplified example. Much more elaborate examples can be found in Odum (1983). Patten (1992) shows how the cycling of energy in the ecological network can be used for calculation of the emergy. The factors used in the calculations shown below of emergy or emergy 1 are based upon Brown and Clanahan (1992), but also the factors derived from considerations as those shown in Fig. 1 have been used to calculate a different emergy, named emergy, 2, i.e., phytoplankton was given the quality factor 10, zooplankton 100 and fish 1000.

Exergy considers besides the free energy of the biomass as fuel the information embodied in the biomass structure. Figure 2 illustrates the idea behind this concept. The more information (knowledge) you put into the system, the more exergy will you obtain. A cathedral requires much more free energy included in the form of information, than to build a house of the same bricks. A house again has more exergy than just a cube of bricks a.s.o. The thermodynamic definition of exergy is the free energy that the considered system has relatively to its environment. The free energy hidden in the cathedral may be regained by a clever plan of converting the potential energy of all the bricks into work (free energy).

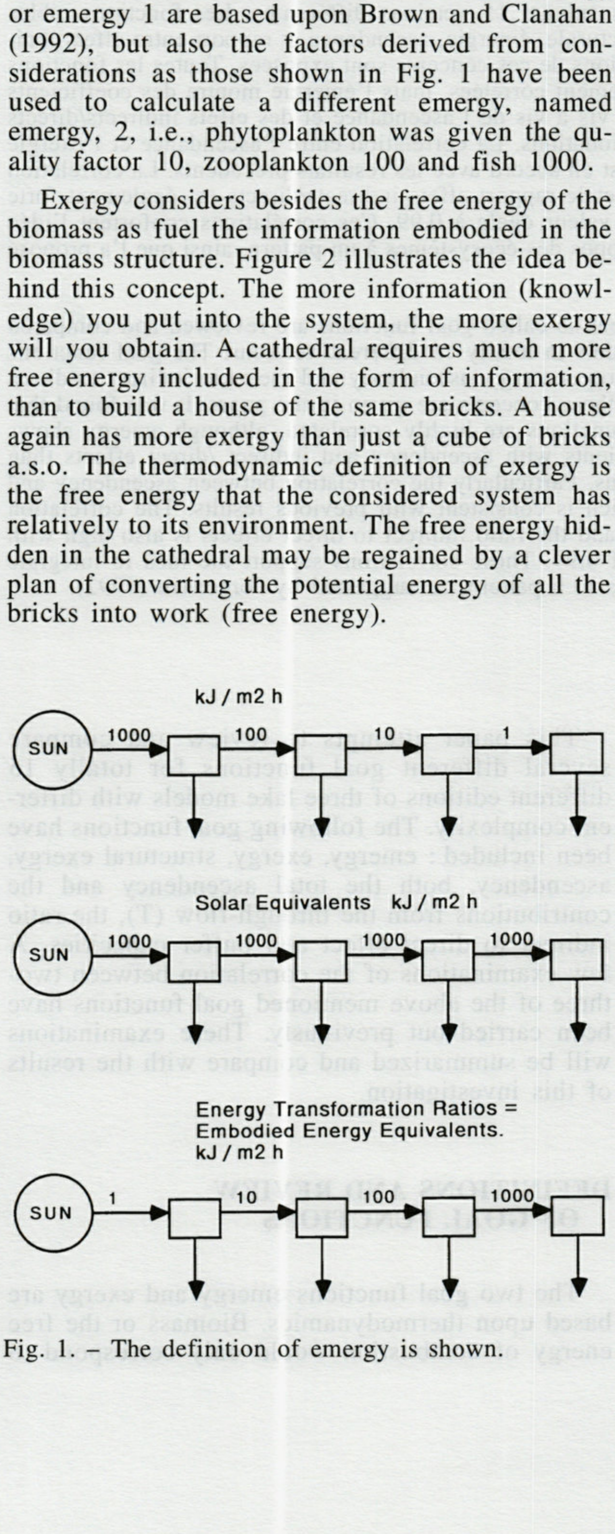

Fig.1. – The definition of emergy is shown.

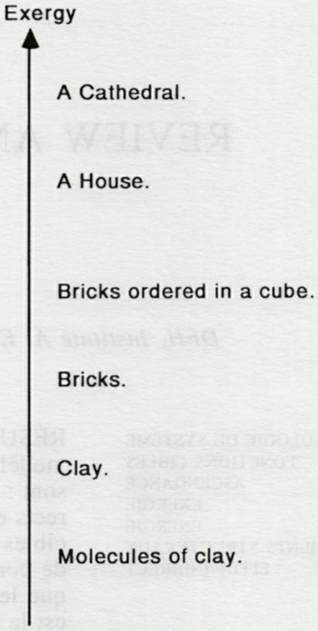

Fig. 2. – Exergy increases with increasing level of organization.

The difference between emergy and exergy is that while the prior considers how much solar energy it costs to construct the biomass at different trophic levels, the latter attempts to account for the actual free energy of the biomass including the free energy stored in the information. Different organisms can have different strategies to obtain a certain level of total free energy. For instance a plant growing in the shade will have larger leaves and/or higher chlorophyll concentration to be able to gain the same free energy as plants growing in full sunshine. The two types of plants will have the same exergy (approximately) but very different emergy. Exergy seems therefore theoretically more correct, but emergy on the other side is relatively easy to interpret, when the energy network is known. In addition, when emergy is calculated for entire ecosystems, the differences in "strategies" between organisms at the same trophic level will to a certain extent neutralize each other.

Shieh and Fen (1982) have suggested to estimate the exergy contents in structurally complicated material on basis of the elementary composition. This has, however, the disadvantage that a higher organism and a microorganism with the same elementary composition will get the same exergy. We want to account for the higher organization (level of information) of higher organisms in our exergy calculation, because the exergy used for construction can be regained by a proper use of this organization. It seems therefore more appropriate to use the following expression for calculation of the exergy in an ecosystem with through-flow (Mejer and Jørgensen, 1979) :

$$Ex = R*T*\sum (c_i*\ln (c_i/c_{i,eq}) + (c_i - c_{i,eq}), \quad (1)$$

where R is the gas constant, T is the absolute temperature, c_i is the concentration in the ecosystem of component i and $c_{i,eq}$ is the corresponding equilibrium concentration at thermodynamic equilibrium. The problem by this equation is related to the size of $c_{i,eq}$. If we use approximately the same value for $c_{i,eq}$ for all types of organisms, we get a close relationship between exergy and biomass, but if we can find values of $c_{i,eq}$, which can account for the higher organization in higher organisms, we will account for the higher exergy contribution of the higher organisms.

For detritus, which it given the index 1, it can be found from classical thermodynamics :

$$\mu_1 = \mu_1{}^{eq} + RT \ln c_1/c_1{}^{eq} \quad (2)$$

where μ indicates the chemical potential. The difference $\mu_1 - \mu_1{}^{eq}$ is known for organic matter, detritus, which is a mixture of carbohydrates, fats and proteins.

Generally, $c_i{}^{eq}$ can be calculated from the definition of the probability P_i to find component i at thermodynamic equilibrium :

$$P_i \equiv c_i{}^{eq}/\sum_{i=0}^{N} c_i{}^{eq} \quad (3)$$

If we can find the probability, P_i, to produce the considered component i at thermodynamic equilibrium, we have determined the ratio of $c_i{}^{eq}$ to the total concentration. As the inorganic component, c_0, is very dominant by thermodynamic equilibrium, equation (2) may be rewritten as :

$$P_i \approx c_i{}^{eq}/c_0{}^{eq} \quad (4)$$

By a combination of equations (2) and (4), we get :

$$P_1 = [c_1/c_0{}^{eq}] \exp [-(\mu_1 - \mu_1{}^{eq})/RT] \quad (5)$$

For the biological components, 2, 3, 4...N, the probability, P_i, consists of the probability for produce the organic matter (detritus), i.e., P_1, and the probability, P_a, to obtain the information embodied in the genes, which again determine the amino acid sequence. Living organisms use 20 different amino acids and each gene determines the sequence of averagely 700 amino acids. P_a, can be found from the number of permutations among which the characteristic amino acid sequence for the considered organism has been selected. It means that we have the following two equations available to calculate P_i :

$$P_i = P_1 \, P_{i,a} \quad (6)$$

and

$$P_{i,a} = 20^{-700g} \quad (7)$$

where g is the number of genes.

Equation (4) is reformulated to :

$$c_i{}^{eq} = P_i \, c_0{}^{eq} \quad (8)$$

Equations (8) and equation (1) are combined :

$$Ex \approx R*T*\sum_{i=1}^{N} [c_i * \ln (c^i/P_i \, c_0{}^{eq}) + (c_i - P_i \, c_0{}^{eq})], \quad (9)$$

This equation may be simplified by the use of the following good approximations (based upon $P_i << c_i$, $P_i << P_0$ and $1/P_i >> c_i$, $1/P_i >> c_0{}^{eq}/c_i$) : $c_i/c_0{}^{eq} \approx 1$, $c_i \approx 0$, $P_i c_0{}^{eq} \approx 0$ and the inorganic component can be omitted. We obtain :

$$Ex \approx -R*T*\sum_{i=1}^{N} [c_i * \ln (P_i) \quad (9)$$

By a combination of this equations with equations (5) and (6), we obtain the following expression for the calculation of exergy :

$$Ex/RT = (\mu_1 - \mu_1{}^{eq}) \sum_{i=1}^{N} c_i/RT - \sum_{i=2}^{N} c_i \ln P_{i,a} \quad (10)$$

This equation can now be applied to calculate exergy for important ecosystem components. If we consider only detritus, we know that the free energy released pr. g of organic matter is about 18.5 kJ/g. R is 8.4 J/mol. and the average molecular weight of detritus is presumed to be 100,000. We get the following contribution of exergy by detritus pr. liter of water, when we use the unit g/1 for the concentrations :

$$Ex_1 = 18.5 \, c_i \text{ kJ/1 or } Ex_1/RT = 7.34*10^5 \text{ ci g/l} \quad (11)$$

A typical algae has on average 850 genes. We use purposely the number of genes and not the amount of DNA pr. cell, which would include unstructured and nonsense DNA, which is different for different organisms. In addition, a clear correlation between the number of genes and the complexity has been shown (Li and Grauer, 1991). If it is presumed that an algae has 850 genes, the contribution of exergy pr. liter of water, using g/1 as concentration unit would be :

$$\begin{aligned} Ex_{algae}/RT &= 7.34*10^5 \; c_i -{}_{ci} \ln 20^{-595000} \\ &= 25.2*\, 10^5 \; c_i \text{ g/l} \end{aligned} \quad (12)$$

Organisms with more than one cell will have DNA in all cells determined by the first cell. The number of possible microstates becomes therefore just proportional to the number of cells. Zooplankton has 100,000 cells approximately and (see Table IA) 50 000 genes per cell. ln $P_{zoo,a}$ can therefore be found as :

$$- \ln P_{zoo,a} = - \ln \left(20^{-50\,000*700} * 10^{-5}\right) \approx 1\,049 * 10^{5} \tag{14}$$

As seen the contribution from number of cells is insignificant. Similarly, it can be found that $P_{fish,a}$ is (use the figures in Table I) :

$$- \ln P_{fish,a} = - \ln \left(20^{-120\,000*700} * 10^{-5}\right) \approx 2517 * 10^{-5} \tag{15}$$

The application of these values for a model consisting of inorganic material, IM, phytoplankton, P, zooplankton, Z, fish, F, and detritus, D would yields :

$$\begin{aligned} Ex/RT = {} & P\,(1.79*10^{6}) + Z\,(104.9*10^{6}) + F\,(2.52*10^{8}) \\ & + (D+P+Z+F)*\,(7.34*10^{5}) \quad g/l \end{aligned} \tag{16}$$

The contributions from phytoplankton, zooplankton and fish to the exergy of the entire ecosystem are significant and far more than corresponding to the biomass. Notice that the unit of Ex/RT is g/l. Exergy can always be found in Joules pr. liter, provided that the right units for R and T are used. Equation (16) can be rewritten by converting g/1 til g detritus/ 1 by dividing by $(7.34*10^{5})$:

$$Ex/RT = P\,(3.4) + Z\,(144) + F\,(344) + (D) \quad \text{g detritus/l} \tag{17}$$

Exergy just as emergy will increase with increasing concentrations of nutrients. If we, however, want to get a measure of the ability to use the *available resources*, we can apply structural exergy, which is exergy divided by $\Sigma\, c_i$, i.e., the exergy relative to the biomass or nutrient level. It is an intensive attribute opposite exergy, which is an extensive variable. It accounts for the free energy of the structure, including the contribution from the information, but it is independent of the nutrient level, i.e., the available resources.

Organisms	**10^{-12}g DNA / cell**	**Number of genes**	**Number of cell type**
Bacteria	0.005	600	1-2
Algae	0.009	850	6-8
Yeast	0.02	2000	5-7
Fungus	0.03	3000	6-7
Sponges	0.1	9000	12-15
Jellyfish /zooplankton	0.9	50,000	23
Annelid worms	20	100,000	60
Fish	20	120,000	70
Field mouse	50	140,000	100
Human	90	250,000	254

A

B

Model	Number of st.var.	Variable param	Parameter value	Input conc. of nutrients	ß-Ex	ß-phyt
1	3	μ-max	0.2	12	0.86	0.83
2	3	μ-max	0.25	12	0.90	0.90
3	3	μ-max	0.15	12	0.80	0.80
4	3	μ-max	0.4	12	0.93	0.93
5	3	μ-max	0.6	12	0.95	0.96
6	3	μ-max	1.0	12	0.96	0.97
7	3	μ-max	1.0	10	0.95	0.97
8	4	μZ-max	0.35	12	0.59	1.18
9	4	μZ-max	0.42	12	0.59	0.23
10	4	μZ-max	0.42	10	1.22	-0.86
11	5	PRED	0.14	12	0.78	-3,80
12	5	PRED	0.20	12	0.64	-0.96
13	5	PRED	0.115	12	0.77	-16.6
14	5	PRED	0.14	10	0.70	-3,22
15	5	PRED	0.14	15	0.88	-4.60
16	4	μZ-max	0.56	12	violent oscillations	

Table I. – A, The evolution of g DNA/cell, number of genes and cell types. Approximate figures are given. B, Parameters and buffer capacities of the 15 examined models.

Ulanowicz (1986) has introduced the concept of ascendency, A, to account for the throug-flow of energy in an ecosystem, T, and the network. The definition is given in Fig. 3. Ascendency accounts for the size of the network, T, and I for the information stored in the network. A is an extensive variable. The size term, T, is most dominant in most calculations. (A-T)/T = I – 1 is an intensive attribute and accounts to a certain extent only for the structure or information embodied in the network, i.e., the complexity of the network, independent of the energy through-flow. It might therefore be expected that the structural exergy is well correlated to A-T, while the exergy would be better correlated to the size term, T, although probably also well to A, as the size term is most dominant.

Patten (1991) has shown that the indirect effects, I, dominate the direct ones, D. The details of the calculations of the direct and the indirect effects are given in Patten (1991) and Jorgensen (1992). The direct effect on the influence of nutrient on the growth of phytoplankton is the growth rate of phytoplankton, regulated by the nutrient concentrations. The indirect effect is the role of the cycling of nutrients through the food chain and mineralization an infinite number of times. The indirect effect is a result of the entire network and originates from all other links than the direct ones. The ratio indirect to direct effect will give a measure of the network complexity. The more pathways the network has, the bigger role will the indirect effect plays, compared with the direct one. The ratio I/D is therefore expected due to its dependence on the structure (the network) to be well correlated to structural exergy.

$$\textbf{Ascendency} = T * I$$

$$T = \sum_{j=0}^{n} \sum_{i=1}^{n+2} T_{ji}$$

$$I = \sum_{j=0}^{n} \sum_{i=1}^{n+2} (T_{ji} / T) * \log((T_{ji} * T) / (T_j * T)$$

Fig. 3. – Definition of ascendency.

COMPARISON OF GOAL FUNCTIONS

The three different eutrophication models used for the examination are shown in Figs. 4-6. As seen they differ by the number of state variables. Model number one has only three state variables, namely phytoplankton, detritus and nutrients, while model number two has added zooplankton and model number three contains zooplankton and fish in addition to the state variables in model number one. Figure 7 shows the equations used for model number three.

Different editions of the three models were developed by changing one of the key parameter and by changing the input of nutrient. Totally 16 cases have been examined. They are shown in Table IB. The key parameter for model 1 was considered the maximum growth rate of algae. The key parameter for model number two is considered to be the maximum growth rate of zooplankton. For the last model was used the growth rate of fish has as the key parameter. The last case study in Table IB, case study 16, has not

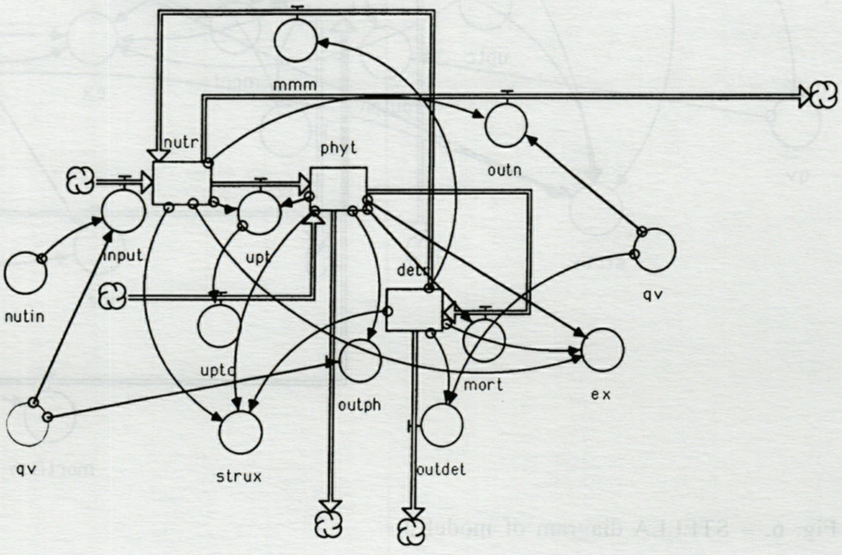

Fig. 4. – STELLA diagram of model 1.

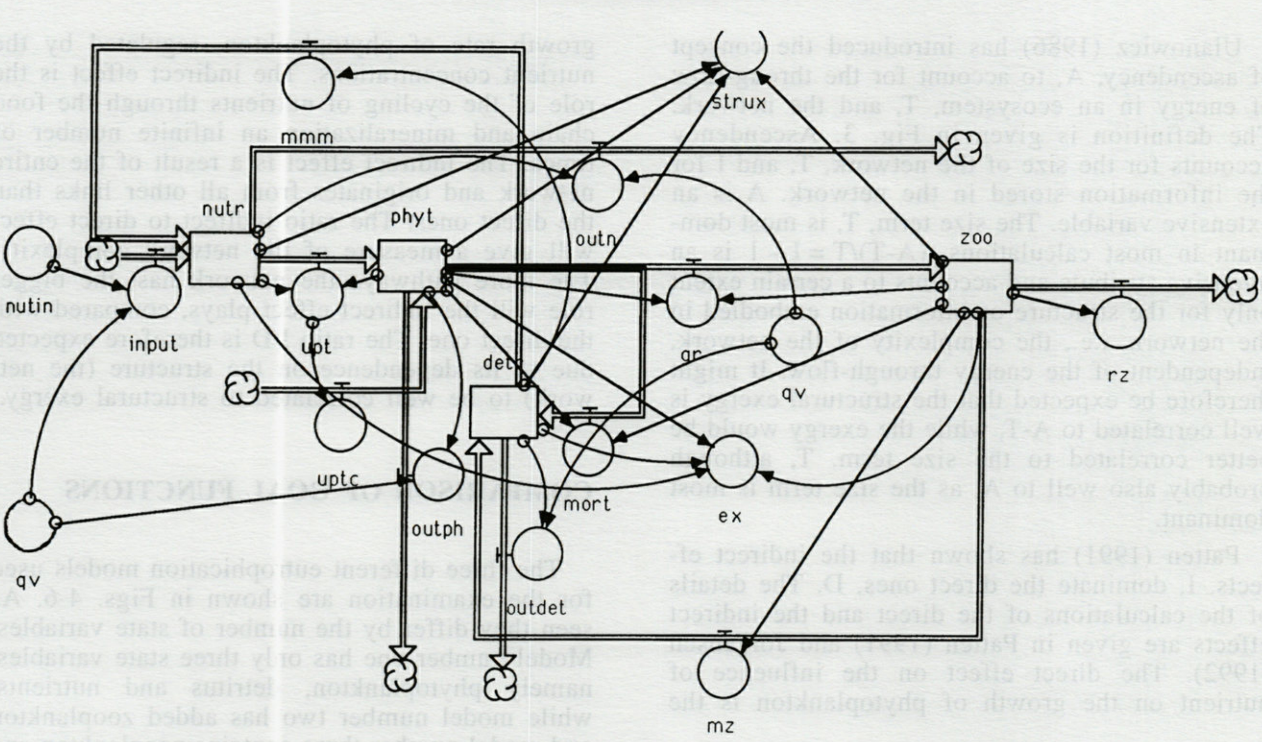

Fig. 5. – STELLA diagram of model 2.

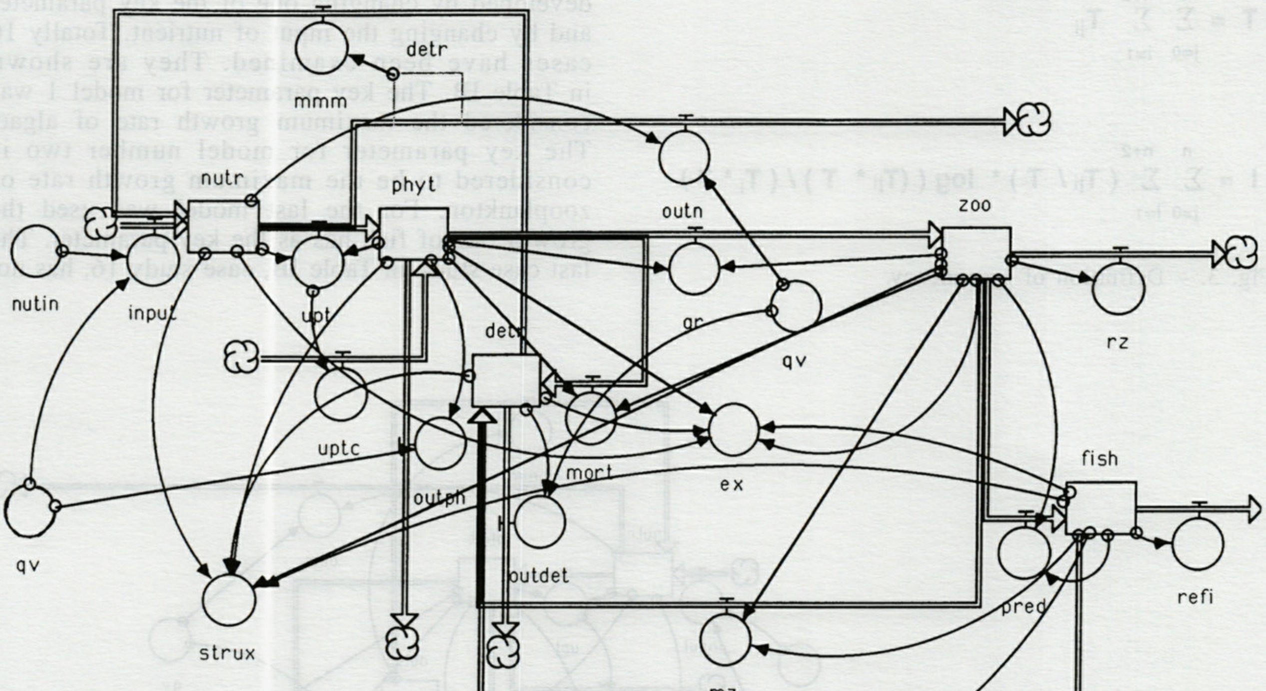

Fig. 6. – STELLA diagram of model 3.

```
☐ detr(t) = detr(t - dt) + (mort + mz + mortfish - mmm - outdet) * dt
  INIT detr = 16
  INFLOWS:
     ⇸ mort  =  0.25*phyt+0.17*(phyt-0.1)*zoo/(phyt+2)
     ⇸ mz  =  0.2*zoo+0.04*fish*(zoo-0.1)/(1+zoo)
     ⇸ mortfish  =  0.02*fish
  OUTFLOWS:
     ⇸ mmm = 0.1*detr
     ⇸ outdet = detr*(qv+0.9)
☐ fish(t)  =  fish(t - dt)  +  (pred - mortfish - refi) * dt
  INIT fish = 1
  INFLOWS:
     ⇸ pred  =  0.1*fish*(zoo-0.1)/(1+zoo)
  OUTFLOWS:
     ⇸ mortfish  =  0.02*fish
     ⇸ refi  =  0.06*fish
☐ nutr(t)  =  nutr(t - dt)  +  (input + mmm - upt - outn) * dt
  INIT nutr = 1.6
  INFLOWS:
     ⇸ input  =  nutin*qv
     ⇸ mmm  =  0.1*detr
  OUTFLOWS:
     ⇸ upt  =  IF nutr > 0.2 THEN 1.0*phyt*(nutr-0.1)/(5+nutr) ELSE 0
     ⇸ outn = nutr*qv
☐ phyt(t)  =  phyt(t - dt)  +  (upt + uptc - mort - outph - gr) * dt
  INIT phyt = 35
  INFLOWS:
     ⇸ upt  =  IF nutr > 0.2 THEN 1.0*phyt*(nutr-0.1)/(5+nutr) ELSE 0
     ⇸ uptc = 9*upt
  OUTFLOWS:
     ⇸ mort  =  0.25*phyt+0.17*(phyt-0.1)*zoo/(phyt+2)
     ⇸ outph = phyt*qv +0.1*phyt
     ⇸ gr  =  0.4*(phyt-0.1)*zoo/(phyt+2)
☐ zoo(t) = zoo(t - dt) + (gr - rz - mz - pred) * dt
  INIT zoo = 10
  INFLOWS:
     ⇸ gr  =  0.4*(phyt-0.1)*zoo/(phyt+2)
  OUTFLOWS:
     ⇸ rz = 0.125*zoo
     ⇸ mz  =  0.2*zoo+0.04*fish*(zoo-0.1)/(1+zoo)
     ⇸ pred  =  0.1*fish*(zoo-0.1)/(1+zoo)
○ ex =
  0.001*(phyt*(1100000+LOGN(phyt))+detr*(48+LOGN(detr))+zoo*(65000000+LOGN(zoo))+nutr*(LO
  GN(nutr)-LOGN(phyt+nutr+fish+zoo+detr))+fish*(130000000+LOGN(fish)))
○ nutin = 15
○ qv = 0.05
○ strux =
  0.001*(phyt*(1100000+LOGN(phyt))/(nutr+phyt+detr+zoo+fish)+detr*(48+LOGN(detr))/(nutr+phyt
  +detr+zoo+fish)+zoo*(65000000+LOGN(zoo))/(nutr+phyt+detr+zoo+fish)+nutr*(LOGN(nutr)-LOGN(ph
  yt+nutr+fish+zoo+detr))/(nutr+phyt+detr+zoo+fish)+fish*(130000000+LOGN(fish))/(nutr+phyt+detr
  +zoo+fish))
```

Fig. 7. – Equations of model 3.

stat var.	exergy	struc.ex.	emergy1	T	A	I/D	A-T/T	emergy2
3	36095	859	41682	10.29	17.95	1.68	0.7444	41682
3	37126	866	42881	10.59	18.77	1.69	0.7724	42881
3	34123	845	39397	9.74	16.55	1.65	0.6992	39397
3	38500	875	44462	10.98	19.81	1.68	0.8042	44462
3	39180	880	45265	11.19	20.31	1.67	0.8150	45265
3	39700	882	45387	11.32	20.71	1.67	0.8295	45387
3	32910	881	38008	9.39	15.65	1.67	0.6666	38008
4	704655	14867	142000	16.1	29.5	2.92	0.8323	82123
4	1728500	34960	264000	24.48	53.32	7.7	1.1781	84120
4	1470000	36000	229000	19.88	39.61	7.7	0.9925	69970
5	1995530	38989	602007	22.7	47.07	7.5	1.0736	93527
5	159669	3463	137870	11.44	21.2	1.8	0.8531	55130
5	1857800	37460	373544	23.2	48.8	8.1	1.1034	88594
5	1507661	35618	502379	17.56	32.4	7.5	0.8451	78542
5	2676843	41694	730720	30.0	64.6	7.5	1.1533	124090

Table II. – The goal functions calculated for the 15 cases.

A

Data File: goal functions

ex	1,000	0,978	0,933	0,982	0,971	0,952	0,896	0,954
struc. ex	0,978	1,000	0,888	0,941	0,924	0,990	0,866	0,901
emergy	0,933	0,888	1,000	0,880	0,862	0,841	0,757	0,917
T	0,982	0,941	0,880	1,000	0,998	0,912	0,944	0,960
A	0,971	0,924	0,862	0,998	1,000	0,899	0,959	0,946
I/D	0,952	0,990	0,841	0,912	0,899	1,000	0,859	0,841
A-T/T	0,896	0,866	0,757	0,944	0,959	0,859	1,000	0,860
Emergy 2	0,954	0,901	0,917	0,960	0,946	0,841	0,860	1,000

Data File: spec goal functions

exergy	1,000	0,456	0,999	1,000	1,000	0,361	0,999
strux	0,456	1,000	0,447	0,456	0,461	0,351	0,436
emergy	0,999	0,447	1,000	0,999	0,998	0,378	0,998
T	1,000	0,456	0,999	1,000	1,000	0,356	0,999
A	1,000	0,461	0,998	1,000	1,000	0,355	0,999
I/D	0,361	0,351	0,378	0,356	0,355	1,000	0,372
A-T/T	0,999	0,436	0,998	0,999	0,999	0,372	1,000

B

Table III. – A, Correlation coefficients of the 15 different case studies, representing 3 different models. B, Correlation coefficient for the seven case studies of model 1.

been included in the final analysis of correlations, as this edition of model two showed a chaotic behavior with many, violent and irregular fluctuations. Case studies 9 and 12 also showed fluctuations, although without chaotic behavior, as the fluctuations were repeated regularly.

All 16 models cases except model case 16, were run until steady state or until the fluctuations were repeated several times (for case study 9 and 12). Exergy, structural exergy, emergy 1, T, ascendency, A, the ratio indirect to direct effects, A-T/T and emergy 2 were calculated. The results are shown in Table II.

The results of a correlation analysis of the goal functions are shown in Table IIIA. Notice, that the correlation between structural exergy and I/D is 0.99. The relation between the two concepts is shown in Fig. 8A. The correlation between exergy and ascendency is 0.971 and the corresponding relation is shown Fig. 8 B.

A correlation analysis of the first 7 cases of model number one also was carried out. The results are summarized in Table IIIB. Particularly the correlations between any pair of exergy, ascendency, T, emergy and A-T/T are here very strong as indicated in Table V. The relation between exergy and ascendency is shown in Fig. 8 C.

DISCUSSION OF THE RESULTS AND REFERENCE TO PREVIOUS INVESTIGATIONS OF RELATIONS BETWEEN GOAL FUNCTIONS

The results show that for all 15 cases there are good correlations between exergy, structural exergy, T, ascendency and I/D. Exergy also is well correlated with both emergies, although slightly better with emergy 2 than with emergy. Emergy is less correlated to the other concepts – lowest to I/D and A-T/T.

The results are consistent with Salomonsen (1992), who found that the ratios of ascendency and exergy between an eutrophic lake and an oligotrophic lake were both approximately 10. Christensen, (1992) also has shown a relatively good correlation between ascendency and exergy for 42 different steady state models for a number of different types of ecosystems. Jorgensen (1993) showed that the correlation was even improved (a correlation coefficient of 0.97 was obtained), when only models of the same type of ecosystem (it was 15 different lakes) were considered. When we consider the same model but different cases, the correlations became even stronger. Exergy is

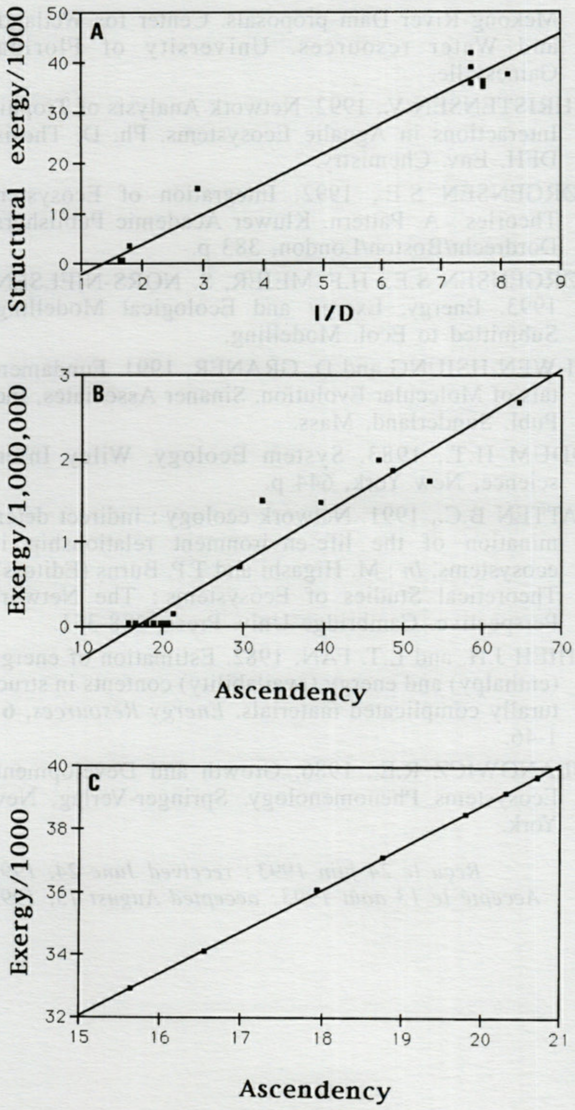

Fig. 8. – A, Correlation between structural exergy and I/D for all 15 cases. B, Correlation between structural exergy and A for all 15 cases. C, Correlation between exergy and ascendency for the seven cases of model 1.

calculated on basis of the biomass and information stored in the biomass, while ascendency is calculated from the through-flow and the flows in the network. More biomass (and information) generates more flows and the more biomass a system must maintain, the more through-flow is needed for maintenance. The found correlations between exergy and ascendency is therefore explainable.

The correlation of emergy to the other concepts became more acceptable, when different cases of the same model were examined. This is not surprising because the differences between the goal functions of the three models are wider than the differences between the goal functions of the same model, but with different parameters and/or inputs. It is, however, noticeable, that the correlation between I/D on the one side and exergy, structural exergy, T and ascendency on the other side is much weaker for the cases of the same model (Table IIIB) than when all the results are considered : compare Table IIIA,B. This is according to the results found by Jørgensen (1992) : the same network gives independent of the input and to a certain extent of the parameters the same ratio I/D, while the exergy and to a less extent also the structural exergy will reflect the differences in inputs. The ratio I/D is dependent on the number of linkages in the network, but is very little influenced by any changes within the framework of the same network.

The weaker correlation between emergy and the other goal functions for the 15 examined cases can be explained by the use of the quality factors from Brown and Clanahan (1992). If the quality factors are derived from the network, see the correlation coefficient for emergy 2 and exergy in Table IIIA, the correlation is improved between the two concepts.

The general results seem to support the idea presented in the introduction, that the different goal functions express different view points of the same matter, namely the self organization ability of the ecosystem.

It was found that the goal functions were all relatively small for the case number 16, see Table IB. This is the case, where the system behaves chaotic, i.e., with violent and irregular fluctuations. Regular fluctuations opposite steady state situations seem to coincide with relatively low buffer capacities ; see Table IB. It may be anticipated, that series of different buffer capacities should be included, if a correlation to the goal functions should be found. The present results do not give any clear picture of such relationships.

CONCLUSIONS

Different goal functions have been proposed, but as the all aim toward an expression for the information embodied in the ecological network, it is not surprising that they are strongly correlated. Exergy measures the information of the system, based upon the genes of the organisms, that are forming the ecological network. Structural exergy is exergy relatively to the total biomass, and should therefore be related to the information in the network, independent of the size of the network = biomass represented by the network. Emergy accounts for the information of the network, measured by the amount of solar energy, that it has costed to construct the network. Ascendency looks into the complexity of the networks itself, included the amount of mass or energy, that is flowing through the network. The ratio of indirect to direct effect measures the importance of cycling relatively to the direct cause and this ratio is therefore also a measure of the information of the network. The different concepts give slightly different information and are deducted from different viewpoints, but they all contribute to a pattern of ecosystem theory, as also proposed in Jørgensen (1992).

Particularly, the structural exergy and the indirect effect/direct effect ratio for all cases and exergy and ascendency, T and (A-T)/T for different cases of the same model, are well correlated. Structural exergy and I/D for different models are based upon the structure of the network independent of the size. This strong correlation is therefore not surprising. Exergy and ascendency measure both the complexity and the size and the level of information of the system, although the latter is based upon the flows and the former on the storage. The strong correlation between the two concepts is therefore explainable.

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Reçu le 24 juin 1993 ; received June 24, 1993
Accepté le 13 août 1993 ; accepted August 13, 1993

VIE MILIEU, 1994, 44 (1) : 21-27

THE IMPACT OF DISTURBANCE ON MEASUREMENTS OF VARIABILITY IN MARINE NEMATODE POPULATIONS

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ANALYSE DE LA VARIANCE
DISTRIBUTION SPATIALE
POLLUTION
PERTURBATIONS
DE L'ENVIRONNEMENT
NÉMATODES MARINS

RESUME – Le rôle de la répartition en agrégats dans la régulation de la biodiversité est l'un des thèmes majeurs de l'écologie ; des théories récentes, telle celle de la mosaïque spatio-temporelle, ont souligné l'importance des perturbations dans la création d'agrégats en tant que processus de structuration des communautés benthiques marines. De récents articles ont suggéré que l'utilisation de mesures paramétriques de la variabilité pouvait rendre compte de l'impact de perturbations naturelles ou anthropiques dans toute étude de la répartition en agrégats. Nous avons voulu contrôler ces assertions à partir de cinq séries de données concernant des Nématodes marins de milieux abyssaux et littoraux soumis à des perturbations quantifiées. Il apparaît que la variabilité entre échantillons, mesurée par le rapport variance sur moyenne des abondances spécifiques, est liée à la perturbation du milieu. Néanmoins, des données complémentaires sur les processus intervenant sur la distribution agrégative à petite échelle sont nécessaires pour utiliser cette approche en test de pollution.

VARIANCE TESTING
SPATIAL DISTRIBUTION
POLLUTION
DISTURBANCE
MARINE NEMATODES

ABSTRACT – The role of patchiness in the maintenance of biodiversity is a major theme in ecology and modern theories such as the spatial-temporal mosaic theory have stressed the importance of disturbance in the creation of patchiness as a process structuring marine benthic communities (Grassle and Morse-Porteous, 1987 ; Grassle, 1989). Some recent papers (Lambshead and Gooday, 1990 ; Rice and Lambshead, in press ; Warwick and Clarke, in press) have suggested that investigation of patchiness by parametric measures of variability can be used to assess the impact of natural and anthropogenic disturbance. We test these assertions on five marine nematode data sets from deep-sea and shallow-water environments subjects to known levels of disturbance. We conclude that variability between samples as measured by the variance/mean ratios of the abundance of the individual species in communities is linked to environmental disturbance. However, more information on the processes influencing small-scale patchiness under different disturbance regimes is required before this could be recommended as a reliable pollution test.

INTRODUCTION

The spatial and temporal variability in biological populations is a central area of interest in ecology (Andrewartha and Birch, 1954 ; 1984 ; Begon *et al.*, 1986). However, the way variability is measured can considerably influence ecological interpretations (Taylor, 1961) such that there is as much interest in the measurement of variability as in the type and amount of spatial variability generated by various ecological processes (*e.g.* Hanski, 1990 ; Taylor, 1984 ; Taylor and Woiwod, 1982).

Patchiness is the most common manifestation of spatial variability and disturbance is now considered to be one of the primary processes influencing patchiness, and hence diversity and community structure. If disturbance is the main cause of patchiness, this offers the prospect of using spatial variability to assess natural and anthropogenic disturbance (Lambshead and Gooday, 1990). In this paper, we test the use of some measures of patchiness based on the parametric variance which have been suggested for the detection of disturbance (Rice and Lambshead, in press ; Warwick and Clarke, in press). We compare five nematode data sets with different, known levels of disturbance to see whether these measures of variance are good assessors of disturbance.

TESTED HYPOTHESES

Using the five data sets it is possible to test three hypotheses :

1) That more species in a deep-sea community are significantly aggegated in a more disturbed system than a less disturbed system (Lambshead and Gooday, 1990 ; Rice and Lambshead, in press).

2) That fewer species would tend to be aggregated in a shallow-water community than a deep-sea community due to the high levels of disturbance experienced in coastal seas.

3) That the rate of aggregation with abundance for marine communities increases with higher levels of disturbance (Warwick and Clarke, in press).

CHOICE OF DATA SETS

A potential source of error that cannot be avoided is the interaction between sampler-size and organism patch-size. The measured variance not only measures the degree of aggregation in a patch but also the size of the patch relative to the sampler : a sampler hugely larger that the patches will tend to sample many patches together, reducing measured variability, and a sampler considerably smaller than the patches risks replicates being taken from within a single patch, also reducing measured variability. Employing a fixed core size for all habitats is not a viable strategy partly because of sediment characteristics, partly because abundances change markedly from place to place, and partly because we have no evidence that nematode patches are the same size in all environmental conditions. How much of a problem sample-size/patch-size interactions are in practice is unclear.

Choice of data sets is critical for comparisons of variance because estimates of variance are directly influenced by sampling strategy. Taylor (1961, 1984) introduced the power law $S^2 = aM^b$ for the variance (S^2) and mean (M) of population samples where "a" and "b" are constants. It was originally considered that, although "a" was sample-protocol dependent, "b" described the aggregation of the organisms and was thus independent of sample protocols. However, Sawyer (1989) demonstrated that "b" was also influenced by sample protocols so all variance analysis results reflect sampling strategy as well as underlying organism distributions. It is, therefore, necessary to standardise sampling protocols before any meaningful comparisons can be made between different populations. Accordingly, we investigate a single taxon, marine free-living nematodes, which have all been collected by similar specialist meiofauna corers, either hand held for the shallow-water samples (Platt and Warwick, 1988), or remote for the *Alvin* (Thistle and Eckman, 1990) and multiple corer deep-sea samples (Barnett *et al.*, 1984), which should function with similar efficiency. Six, independently sampled, replicates were taken for each site.

Five sets of data met the criteria for this analysis, including two matched pairs of disturbed/control stations. The criteria are : (i) same organisms, (ii) similarly efficient samplers, (iii) similarly efficient extraction technique, (iv) standardized taxonomy, particularly of unknown species, and (v) known disturbance regime of the site sampled. The first matched pair is the DEEPSEAS stations in the north-east Atlantic (Rice and Lambshead, in press). The 4,856 m deep northern Porcupine Abyssal Plain site (PAP) at 48°50'N : 16°30'W is subject to a major seasonal input of phytodetrital material. The 4,850 m southern Madeiran Abyssal Plain site (MAP) at 31°N : 21°W has an organic supply which is both lower and less periodic. These stations were selected to test for the effect of different food regimes on abyssal fauna. The multiple core sampler employed had an internal diameter of 5.7 cm.

The third deep-sea data set comes from the San Diego Trough (SDT) from a 1,050 m station at 32°52'N : 117°45.5'W which is described in Thistle (1978). SDT is a physically undisturbed site with high productivity by deep-sea standards but the meiofauna are subject to biogenic disturbance from the abundant macrofauna (Thistle and Eckman, 1988 ; 1990 ; Eckman and Thistle, 1991 ; Thistle *et al.*, 1993 ; Lambshead *et al.*, submitted). It is difficult to scale the disturbance at SDT against PAP, biogenic disturbance against a seasonal input of food. However, we are on firmer ground in concluding that SDT experienced higher levels of disturbance than MAP, which could be used as a control in a paired comparison. The *Alvin* corer had a 6.6 cm internal diameter.

Finally, the second matched pair were shallow-water stations from the Clyde inland sea area. These stations are described in Lambshead (1986). Briefly, the samples were taken from two geographically close areas, Ettrick Bay (EB) and Ayr Bay (AB), which were similar in the major ecological parameters (salinity and grain size) except that Ayr bay suffered from sub-catastrophic contamination from industrial and sewage effluent. The hand-corer employed had a 2.2 cm inner diameter.

The two matched data sets employed here (MAPvPAP and EBvAB) were collected during projects specifically designed to test disturbed sites against reference sites so the reference sites are as valid controls as may be practically achieved. Even so, they suffer from the usual pseudoreplication problems associated with field ecology in a marine environment (Green, 1979 ; Hurlbert, 1984). Briefly, it is extremely difficult to set up randomised plots with differing treatments in the marine environment because the water medium tends to disperse the treatment.

In addition to the two matched sets, MAP can be used as a reference station for all four data sets on two grounds. First, it is a low organic supply, unperiodic, physically undisturbed station and it can confidently be concluded that it experiences lower levels of disturbance than any of the other stations. Second, it represents the most common nematode habitat, given that a significant portion of the globe is covered by this type of environment.

STATISTICAL ANALYSIS OF VARIANCE

The most direct way to assess variability is to quantify it with a robust and mathematically tractable measure and explicitly test the significance of comparisons. The measure of variability used most is the variance of some measure of abundance in samples, or associated statistics such as standard deviation. There are several methods for explicitly testing variance, many of which have been reviewed by Van Valen (1978) and Zar (1984). However, most require specific types of data which limits how they can be used. Hence, in this paper we consider only those which are least affected by sample protocol and have been suggested for assessing the impact of disturbance on populations of marine organisms.

Lambshead and Gooday (1990) used the simple F-test, the most standard method, to show that deep-sea Foraminifera samples from the Porcupine seabight are more variable after a phytodetritus drop. The problem with the F-test is that it is extremely sensitive to deviations from normality (Box, 1953 ; Pearson and Please, 1975) and distributions of organisms can deviate considerably from normality (Taylor, 1961 ; Van Valen, 1978). For this reason this method is not recommended and is not employed here.

The first approach we used was variance to mean ratios (Hessler and Jumars, 1974 ; Jumars, 1975, 1976 ; Gage, 1977 ; Thistle, 1978). The variance to mean ratios multiplied by the degrees of freedom (number of samples-1) gives a good estimate of the Chi Squared statistic. Aggregated or regular distributions can then tested for using the Chi Squared distribution, with 5 degrees of freedom (n-1). A probability of < 2.5 % indicates significant aggregation, > 97.5 % indicates a regular distribution, and any other result indicates a distribution that cannot be distinguished from random.

The results from the previous analyses listed mostly indicated randomly distributed organisms but Jumars and Eckman (1983), in their seminal paper, note that the low abundances in the deep-sea communities analysed by these authors make a Type II error likely, i.e. the resolving power of the test becomes so low that non-random distributions cannot be distinguished from random. This is a strong argument for turning to a taxon with abundant species, such as marine nematodes. Rice and Lambshead (in press) followed Jumars and Eckman (1983) in plotting variance to mean ratios against mean for the nematode assemblages at MAP and PAP. Even using such an abundant taxon many rare species have to be eliminated from the analysis as they drop below the resolving power of the test. Rice and Lambshead adopted a sum of ten animals in the six cores as the lower limit for testing. They reported that only 5 species (28 % of the total species tested) were significantly aggregated at the undisturbed site (MAP) while at disturbed PAP, 28 species (72 %) were significantly aggregated (Chi Squared test, using 2.5 % significance levels). Rice and Lambshead tentatively concluded that analysis of the patch dynamics of nematode populations might be developed as "a general monitoring method for [disturbance assessment in] the deep sea".

A further informative manipulation of the Chi Squared analysis can be performed (Jumars, 1975 ; Thistle 1978 ; Jumars and Eckman, 1983 ; Rice and Lambshead, in press). Briefly, all the species can be treated as replicates and their Chi-Squares added together to obtain a "total Chi-Squared". The total Chi-Squared indicates whether species on the average depart from Poisson distributions in per-core abundances. The Chi-Squared for the nematode species pooled together into "nematodes per core" can be calculated. The "pooled Chi-Squared" indicates whether the per-core abundances of the individual species summed by core produce a Poisson distribution. They will do this if each individual species' abundances are independent and individually Poisson distributed. The pooled Chi-Squared is subtracted from the total Chi-Squared to give the Heterogeneity Chi-Squared. This tests whether the total number of individuals per sample is essentially constant indicating whether the individual species tend to aggregate in the replicates at random, or in concordance (i.e. tendency to agree where to aggregate) or in discordance (i.e. tendency to disagree where to aggregate).

The second method tested here was devised by Warwick and Clarke (in press) who investigated the variability of several shallow water sites with respect to contamination : meiobenthos in organically enriched mesocosms ; macrobenthos around oilfields in the North sea ; reef corals following the 1982-3 El Nino ; and fish on coral reefs in the Maldive islands subjected to mining. Warwick and Clarke use a variant of Taylor's power law where log (1 + variance) is plotted against log (1 + mean) for each species in a community and a regression line is fitted through these points. Warwick and Clarke concluded that the slope of the regression line for a community was greater when it was subject to disturbance, i.e. the degree of aggregation against abundance increases from reference to disturbed sites.

There are two potential problems with this method, one theoretical and the other methodological. The theoretical problem is that it is not clear whether single species data conforms to a straight line. There are other possibilities such as quadratic functions, augmented Poisson or negative binomials (Gaston, pers. com.) so it is equally unclear whether multi-species data should theoretically conform to a straight line either. A problem could arise if the variance-mean relationship was non-linear and data sets which were considerably different in abundances were compared. This is discussed by McArdle *et al.* (1990), who demonstrate the problems in making between-species comparisons. The same arguments may apply to between-communities comparisons. But Warwick and Clarke show on empirical grounds that the fit to their data is good. So over the range of values likely to be used in practice the theoretical problem of non-linearity is probably unimportant.

The methodological problem is that Warwick and Clarke included low-abundance species in the data sets analysed, as well as species completely absent from at least one site. Where the number of species in one set of samples is much less than another and the samples are more heavily dominated by a few species (as often happens in contamination situations), the multiple points with zero-mean and zero-variance for absent species and the species with low abundance can have a hugely disproportionate influence on the regression line, anchoring it to the origin and turning the method into a test for relative species richness.

In this paper we repeat Rice and Lambshead's (in press) analysis. The abundance below which species are excluded in this paper is a slightly less conservative "cut-level", than that used previously. Species with mean abundance of 0.50 or less per core are rejected as this is at the lower limit where deviations from randomness can be detected. Warwick and Clarke's method is also repeated using the same cut level to avoid artefacts associated with low abundances.

RESULTS

Plots of variance against mean are shown for the five data sets in Fig. 1. This data confirms Warwick and Clarke's (in press) view that the data is reasonably linear so fitting regression lines are sensible. Table I shows the results of the Chi Squared analysis showing whether nematodes had aggregated, random or regular distributions. Many species were present in too low an abundance to be tested. All species tested were either aggregated or randomly distributed except a single species at SDT that was regularly distributed. This solitary result is probably a statistical artefact (with multiple testing some results will be significant by chance). Table I also shows the percentage of species that fit into the aggregated and random groups. SDT and PAP showed more species aggregating than the undisturbed MAP. The unpolluted shallow station, EB, also showed many species aggregating but the polluted station, AB, showed fewer species that were significantly aggregated. The data sets were tested for aggregation versus random distributions using the reference site, MAP. A two sample Chi-Squared test was employed using Yates" correction for one degree of freedom. PAP was significantly different from MAP ($p <$ %) but SDT was not ($p > 10$ %). MAP was also significantly different from the unpolluted EB ($p < 0.1$ %) but not the polluted AB ($P>10$ %). If the results for the two shallow sites are compared using the same method then they are also significantly different ($p < 1$ %).

Table II shows the analysis of the heterogeneity Chi-Squared test. Apart from the most undisturbed station (MAP), nematode species tend to the significantly discordant (i.e. species significantly tend to avoid aggregating in the same places). Table III shows the slopes and intercepts of the regression lines for graphs (Fig. 1) of the log (variance) plotted against the log (mean). The regression lines for SDT, PAP, EB and AB were tested against the line for MAP for statistical differences

Table I. – Numbers of species significantly aggregated, significantly regular and neither of the above (random), in five benthic nematode communities, with the percentage of the species tested which were aggregated. Abbreviations of site names : MAP - Madeira Abyssal Plain (undisturbed deep sea) ; SDT - San Diego Trough (biogenic disturbance in deep sea) ; PAP - Porcupine Abyssal Plain (highly seasonal detritus input in deep sea) ; EB - Ettrick Bay (unpolluted shallow water) ; AB - Ayr Bay (polluted shallow water).

site	signif. aggregated	neither	signif. regular	insufficient data	percentage aggregated
MAP	8	30	0	34	21
SDT	21	40	1	54	34
PAP	31	27	0	67	53
EB	41	25	0	27	62
AB	12	26	0	19	32

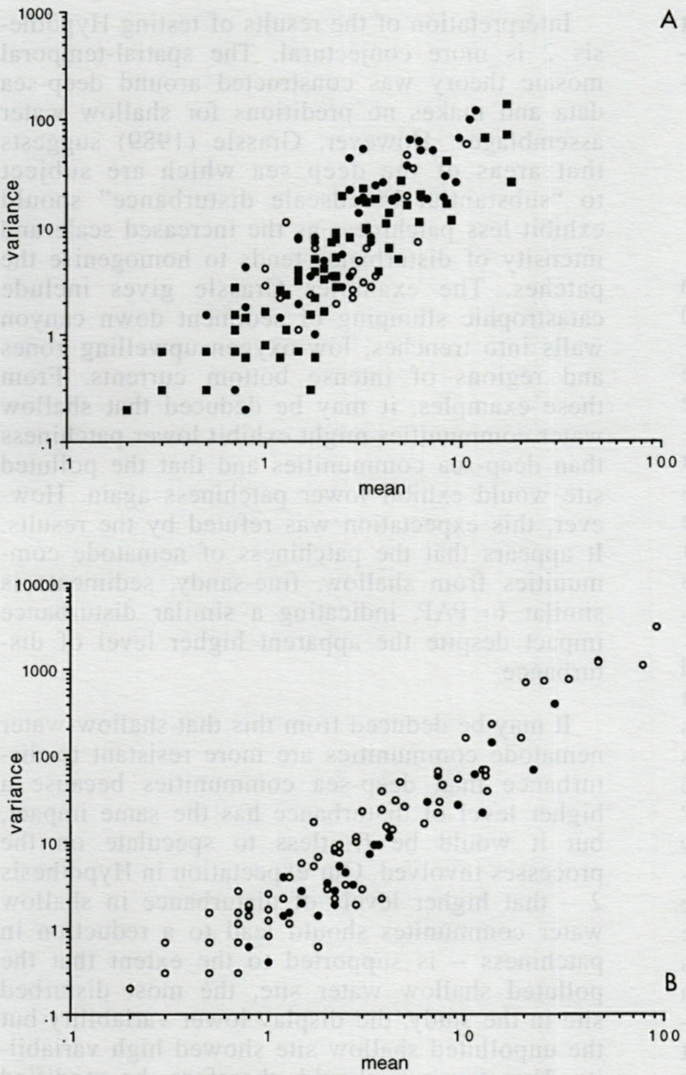

Fig. 1. – Logarithmic plot of variance versus mean abundances of marine nematode species from matched samples. A, Deep sea samples : empty circles - Madeira Abyssal Plain (undisturbed) ; filled circles - Porcupine Abyssal Plain (highly seasonal detritus input) ; filled squares - San Diego Trough (biogenic disturbance). B, Shallow water samples : empty circles - Ettrick Bay (unpolluted) ; filled circles - Ayr Bay (polluted). Parameters of regression lines for this data and their statistical significance are presented in Table III.

Table II. – Comparison of patchiness in total nematode population, individual species independently and individual species as a community, as measured by the "Total Chi Squared", "Pooled Chi Squared" and "Heterogeneity Chi Squared" respectively (Jumars and Eckman 1983). Abbreviations of site names : MAP - Madeira Abyssal Plain (undisturbed deep sea) ; SDT - San Diego Trough (biogenic disturbance in deep sea) ; PAP - Porcupine Abyssal Plain (highly seasonal detritus input in deep sea) ; EB - Ettrick Bay (unpolluted shallow water) ; AB - Ayr Bay (polluted shallow water). Abbreviations of distribution statistics : A - aggregated ; R - randomly aggregated ; D - discordantly aggregated ; * - $P < 0.05$; ** - $P < 0.01$; *** - $P < 0.001$.

site	total Chi Squared	pooled Chi Squared	heterogeneity Chi Squared
MAP	A***	A***	R
SDT	A***	A***	D***
PAP	A***	A***	D***
EB	A***	A***	D***
AB	A***	A***	D***

Table III. – Comparison of slopes and intercepts of regression lines for logarithmic plots of mean versus variance for five benthic nematode communities. Values with the same letter as superscript are not significantly different at $P < 0.05$. Abbreviations of site names : MAP - Madeira Abyssal Plain (undisturbed deep sea) ; SDT - San Diego Trough (biogenic disturbance in deep sea) ; PAP - Porcupine Abyssal Plain (highly seasonal detritus input in deep sea) ; EB - Ettrick Bay (unpolluted shallow water) ; AB - Ayr Bay (polluted shallow water). Abbreviations of distribution statistics : A - aggregated ; R - randomly distributed ; * - $P < 0.05$; ** - $P < 0.01$; *** - $P < 0.001$.

site	intercept	slope
MAP	0.11^{A}	1.45^{a}
SDT	0.23^{A}	1.41^{a}
PAP	0.56^{B}	1.63^{a}
EB	0.49^{B}	1.63^{a}
AB	0.25^{A}	1.49^{a}

in slope and intercept. There were no significant differences for slope for any of the lines. However, PAP and EB showed significantly higher intercepts, as might be expected from Table I.

DISCUSSION

The lack of any significant differences between the slopes of the regression lines of log (variance) plotted against log (mean) lead us to reject Hypothesis 3. There is no evidence that disturbance changes the rate of aggregation with abundance for marine nematode communities and so this approach should be regarded with caution as a test for pollution induced disturbance. This result was unexpected because the disturbances tested here were resource linked. SDT and PAP have higher organic enrichment than MAP. Both shallow sites are more enriched than the deep-sea sites and AB, in particular, is subject to sewage pollution. Resource-linked disturbances might be expected to increase the rate of aggregation plotted against abundance provided that it is the resource that is driving the aggregation. "The more resources there are, the higher the abundance and the more clumped the animals around the patchy resources" Lambshead and Rice (in press). It is not clear why this postulated change in the tendency to aggregate could not be detected but it may be because of the discordancy shown by all the nematode communities affected by disturbance. If species tend to avoid aggregating in the same patches then the species are responding differently to environmental stimuli. So a disturbance event might cause different species to respond in different ways, some species aggregating more and some aggregating less, leaving the community unaltered as a whole. Hence, a regression line will be unaltered.

The analyses seem to support Hypothesis 1. Both methods of analysis show significantly more species aggregated at PAP than MAP. This hypothesis is drawn from Grassle and Morse-Porteous (1987), who suggested that high species richness in the deep-sea benthos (and possibly tropical rainforests) was the result of small scale disturbance acting against a low productivity background over large areas. They suggested that this would produce a mosaic pattern of patchy disequilibria. Grassle (1989) suggested that a disturbance event of increased patchy resources, such as the phytodetritus drop at PAP, might act as a source of patchiness. This process was detected by both the methods of variance analysis tested here. However, the fact that SDT could not be distinguished from MAP suggests that the higher biological activity at SDT did not have the same disturbance impact on the nematode species as the episodic food availability at PAP.

Interpretation of the results of testing Hypothesis 2 is more conjectural. The spatial-temporal mosaic theory was constructed around deep-sea data and makes no preditions for shallow water assemblages. However, Grassle (1989) suggests that areas of the deep sea which are subject to "substantial broadscale disturbance" should exhibit less patchiness as the increased scale and intensity of disturbance tends to homogenise the patches. The examples Grassle gives include catastrophic slumping of sediment down canyon walls into trenches, low-oxygen upwelling zones and regions of intense bottom currents. From these examples, it may be deduced that shallow water communities might exhibit lower patchiness than deep-sea communities and that the polluted site would exhibit lower patchiness again. However, this expectation was refuted by the results. It appears that the patchiness of nematode communities from shallow, fine-sandy, sediments is similar to PAP, indicating a similar disturbance impact despite the apparent higher level of disturbance.

It may be deduced from this that shallow-water nematode communities are more resistant to disturbance than deep-sea communities because a higher level of disturbance has the same impact, but it would be fruitless to speculate on the processes involved. Our expectation in Hypothesis 2 – that higher levels of disturbance in shallow water communites should lead to a reduction in patchiness – is supported to the extent that the polluted shallow water site, the most disturbed site in the study, did display lower variability but the unpolluted shallow site showed high variability. Hypothesis 2 should, therefore, be modified in the light of these results.

Finally, it should be noted that these conclusions rest on only five data sets. The hypotheses need to be tested with more data before methods could be recommended as a reliable way of assessing disturbance. Also, there is a limit to the information that can be gleaned from the examination of replicates of single-sized cores that only examine patchiness at one scale. Multiple-sized corers are required to investigate the processes influencing small-scale patchiness under different disturbance regimes and this is easier in mesocosm experiments than in the field.

ACKNOWLEDGEMENTS – The authors would like to thank Tim Ferrero, Kevin Gaston, Nicole Gourbault and Gordon Paterson for helpful advice. The DEEPSEAS data were collected in a grant supported by the CEC MAST I Contract -0037-C. The San Diego Trough data were collected with the aid of NATO Grant CRG 900050. The paper was improved considerably by penetrating reviews from two referees. DEEPSEAS Contribution N° 7.

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Reçu le 28 septembre 1993 ; received September 28, 1993
Accepté le 29 octobre 1993 ; accepted October, 1993

VIE MILIEU, 1994, 44 (1) : 29-37

MESOCOSMS AND ECOSYSTEM MODELLING

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MODÉLISATION
DYNAMIQUE DE L'OXYGÈNE
ANALYSE DE SYSTÈME
MÉSOCOSMES
PRODUCTION PRIMAIRE
CONSOMMATION D'OXYGÈNE
ENSOLEILLEMENT

RESUME – Une modélisation dynamique utilisant différents niveaux d'agrégation est appliquée au résultat d'une expérience en mésocosme reproduisant les effets de l'enrichissement en nutrients sur les variables caractéristiques du système (composition et biomasse algale, zooplancton et zoobenthos). Un modèle de la dynamique de l'oxygène correspondant à un haut niveau d'agrégation a été employé pour analyser une série temporelle de mesures d'oxygène. Ensuite, un modèle de production primaire (niveau moyen d'agrégation) a été appliqué à ces données d'oxygène augmentées de données biologiques. Les modèles à forte agrégation aussi bien que les modèles d'écosystèmes sont utiles pour étudier le comportement de mésocosmes. Le choix du modèle et du niveau d'agrégation dépendent de la question spécifique posée. Les modèles à forte agrégation donnent une estimation des paramètres les plus fiables, tandis qu'une agrégation faible permet une meilleure analyse des processus de l'écosystème.

MODELLING
OXYGEN DYNAMICS
SYSTEM ANALYSIS
MESOCOSMS
PRIMARY PRODUCTION
OXYGEN CONSUMPTION
REAERATION
INSOLATION

ABSTRACT – Dynamic model analysis at two different levels of aggregation was applied to the results of a mesocosm experiment on the effects of nutrient loading on coastal benthic ecosystems. An oxygen dynamics model with a high level of aggregation was first used to analyze oxygen time series. The productivity estimates of the first model were then linked with additional biotic and abiotic data to estimate the separate contributions of three groups of primary producers to the total production. Highly aggregated models as well as more detailed models proved to be useful to study ecosystem behaviour in mesocosms. The choice of the model depends on the specific question addressed. Models with high aggregation levels supply more reliable parameter estimates, while low aggregation models lead to better insight in ecosystem processes.

INTRODUCTION

Many tools and methods are available to study ecosystems and ecosystem processes. They vary from large scale ecosystem studies in the field to studies on single species in the laboratory. Mesocosms are considered to be the link between these two extremes. Medium scaled experimental enclosures integrate many processes, but are possible to control, at least to a certain extent. Generally, mesocosms are not suited to study processes at a species level, although species can be monitored accurately. The results resemble reality more than laboratory experiments do, due to the more natural behaviour of organisms (Brock *et al.*, 1993). However, system behaviour cannot be predicted absolutely, because certain field conditions may be suppressed in mesocosms, e.g. the effects of wind.

The system behaviour in mesocosms is generally studied by monitoring chemical and biological state variables in the system, such as phosphorus concentration, algal cell counts, zooplankton densities and benthic filter feeder biomass or numbers (Bratbak *et al.*, 1993 ; Carlsson & Granéli, 1993 ; Doering *et al.*, 1989 ; Hansen & Blackburn, 1991 ; Hinga, 1992 ; Vanni & Findlay, 1990 ; Widbom & Elmgren, 1988). These results may be analyzed using (multiple) regression analysis techniques and non-deterministic models such as time-related polynomes (Roberts, 1992). However, these methods generally fail to describe the dynamic interrelations that are active in the system. In addition to the state variables, one has to pay attention to the underlying processes such as primary production rates, sediment/water fluxes of inorganic compounds and zooplankton community filtering rates (Niederlehner & Cairns, 1990 ;

Keller *et al.*, 1990 ; Kelly *et al.*, 1985 ; Nilsson *et al.*, 1991 ; Oviatt, 1986 ; Sampou & Oviatt, 1991 ; Sullivan *et al.*, 1991).

The system behaviour in the mesocosm can be subsequently described by using models which include both data on state variables and on processes. The models applied may differ in the degree of aggregation and the degree of integration. A model with a high level of integration incorporates all processes which are thought to be important, and thus describes the entire ecosystem. Models with a low level of integration are restricted to sub-processes such as air/water exchange, sediment oxygen demand and benthic primary production. Models with a high aggregation level lump many processes, whereas models with low levels of aggregation describe processes in more detail. Consequently, an ecosystem model which covers the entire ecosystem and describes processes in detail is considered to be a model with a high level of integration and a low level of aggregation.

Outdoor marine mesocosm facilities were constructed on the island of Texel to study shallow estuarine ecosystems, such as the Wadden Sea. These experimental ecosystems are used to examine the responses of such ecosystems to changes in environmental conditions. In 1990, the project BEST (Benthic Eutrophication STudies) was set up to study the response of coastal benthic systems to eutrophication, with special emphasis on the hypertrophic situation in the Venice Lagoon in Italy. Fieldwork in the Venice Lagoon itself was supported by experimental work in mesocosms at Texel. The mesocosms were installed to closely resemble a relatively unpolluted situation in the Venice Lagoon. During this experiment, several state variables and processes were regularly measured in all mesocosms, at least once every 5 weeks. In addition, oxygen concentrations were measured at a very high frequency, viz. every 30 seconds. The oxygen time series may be analyzed by using models that describe the relevant processes of changes in oxygen concentration and their effects at the different levels of aggregation (Van Straten, 1986 ; Van Straten & Kouwenhoven, 1991 ; Keesman, 1989).

This paper describes the results of the analysis of the oxygen concentration time series, using two models with a similar high level of integration but with a different level of aggregation. Finally, the application of these models for mesocosm studies are discussed in relation to their predictive power.

MATERIAL AND METHODS

Mesocosms

Eight 21 m^2 basins, 0.5 m water depth, and 0.5 m sediment, were set up identically, the only difference being the additional nitrogen and phosphorus input of each system (Fig. 1). The basins were flushed continuously with Wadden Sea water, the residence time of the water was one week. The response of the mesocosm ecosystems to the different nutrient additions was monitored from March to September 1992. Oxygen, insolation and water temperature were measured every 30 seconds, and 15 minutes averages of these samples were recorded (Fig. 2). The main biological and chemical variables of the ecosystem and the additional supply water were monitored at regular intervals ranging from 1 to 5 weeks, viz. nutrient concentrations in the water and sediment, light attenuation coefficients, biomass and species composition of the phytoplankton, microphytobenthos, macroalgae, zooplankton and zoobenthos, and the production, respiration and nutrient fluxes.

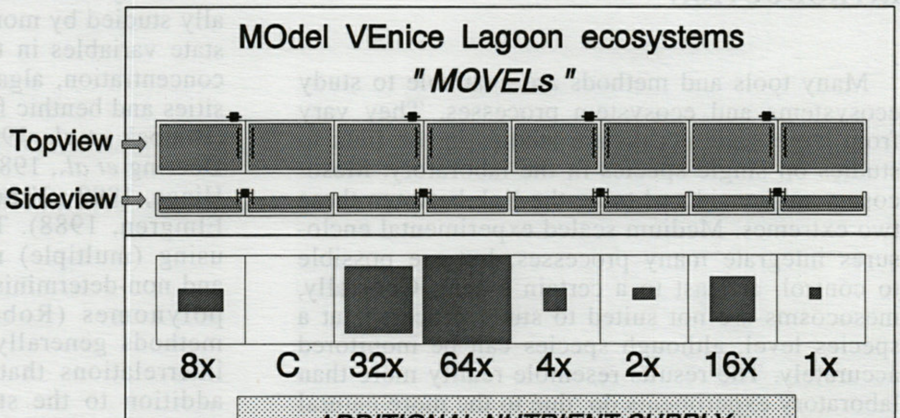

Fig. 1. – Design of the mesocosm experiment with eight different levels of nutrient loading.

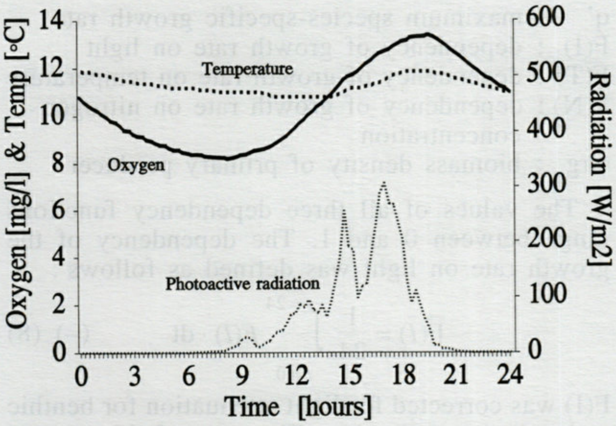

Fig. 2. Dissolved oxygen concentration (mgO$_2$ · l^{-1}), global radiation (W · m^{-2}) and water temperature (°C) in MOVEL00 at daynumber 122 in 1992.

Model analysis

Model 1 : Analysis of oxygen dynamics

The first model which was used to analyze the oxygen time series (Fig. 3), was characterized by a high level of aggregation. The single aim of this analysis was to estimate general system characteristics, viz. total oxygen production and total consumption rates. The basic processes which were included in this oxygen dynamics model are primary production, oxygen consumption and reaeration, i.e. oxygen exchange between atmosphere and water (Fig. 3). Since all processes are lumped into these three groups, the model results give virtually no information on the underlying processes. Such a model is therefore only valid if the underlying processes or variables do not significantly change during the experimental period.

Primary production is a species-dependent function of several environmental conditions such as light, temperature and nutrient concentrations. It was assumed that light is the only control variable that changes during a period of 24 hours. Therefore the primary production reads :

$$\mathit{Production} = q \cdot I_0 \qquad (\mathrm{mg}(\mathrm{O}_2) \cdot \mathrm{l}^{-1} \cdot \mathrm{d}^{-1}) \qquad (1)$$

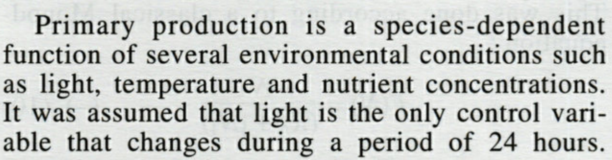

Fig. 3. – Scheme of model I.

where I_0 is the global radiation, expressed as W · m^{-2}. The photosynthetic parameter q (mg(O$_2$) · l^{-1} · day^{-1} · (W · m^{-2})$^{-1}$) consequently lumps all the remaining relationships, e.g. temperature, nutrient concentrations and light attenuation in the water column.

Consumption includes the degradation of organic matter (detritus) by pelagic and benthic bacteria, and the respiration by primary producers and pelagic and benthic fauna. The consumption rate R reads :

$$\mathit{Consumption} = R \qquad (\mathrm{mg}(\mathrm{O}_2) \cdot \mathrm{l}^{-1} \cdot \mathrm{d}^{-1}) \qquad (2)$$

Reaeration depends, amongst other factors, on temperature, salinity and oxygen saturation concentration in the water :

$$\mathit{Reaeration} = k_r \cdot [C_\infty\ (T,\ Sal) - C_t] \qquad (\mathrm{mg}(\mathrm{O}_2) \cdot \mathrm{l}^{-1} \cdot \mathrm{d}^{-1}) \qquad (3)$$

where k_r is the reaeration coefficient (day^{-1}), and C∞ is the oxygen saturation concentration in the water. The temperature (T) and salinity (Sal) dependency of C_∞ was taken into account. The coefficient k_r itself is also temperature dependent, but the variation with temperature is much smaller than that of C_∞.

Combining the three basic groups of processes, the oxygen dynamics model reads :

$$\frac{dC}{dt} = q \cdot I_0 - R + k_r \cdot [C_\infty\ (T,\ Sal) - C] \qquad (\mathrm{mg}(\mathrm{O}_2) \cdot \mathrm{l}^{-1} \cdot \mathrm{d}^{-1}) \qquad (4)$$

The input and output of matter was not included in this analysis, since the residence time of the water exceeded the period of each analysis.

The values of the parameters q, R and k_r could subsequently be estimated from the oxygen time series. The differential equation (4) was solved by means of two methods : (1) by simulating C(t) and (2) from data-point (t) to data-point (t + 1).

When simulating C(t), only the starting value C(0) was thought to be known, or may be estimated. After the simulation, the set of measured values of the oxygen concentration C(t) was compared with the set of estimated values C_i (t).

By the second method, the differential equation (4) was solved from data-point (t) to data-point (t + 1) :

$$C_{t+1} = (1 - \Delta t \cdot k_r) \cdot C_t + \Delta t \cdot q \cdot I_{0,t} + + \Delta t \cdot k_r \cdot C_{\infty,t} - \Delta t \cdot R \qquad (5)$$

where C(t) is the measurement at time t. Thus, each measurement C(t) was a new starting point for the computation of C_i(t + 1). It was assumed that T, Sal and I were continuous and could be differentiated at [t, t + Δt].

Parameters values for both methods were obtained by minimizing the sum of squares S of residues R_i :

$$S = \sum_{i=1}^{m} R_i^2 = \sum_{i=1}^{m} (\hat{C}_i - C_i)^2 \qquad (6)$$

for all m observations, where $\hat{C}_i$ was the computed oxygen concentration and C_i the measurement. The simulation and subsequent parameter estimation according to the first method was performed by means of the STEM software package (ReMeDy, 1991). This program uses a Nelder-Mead (Simplex) minimization procedure which is robust, but not very fast. Application of the second solving method, which was done using the Matlab scientific software tools (MATLAB, 1991), usually results in smaller residues than when solving the equation according to the first method, because estimations are started with the measured situation at t = t for each separate time interval [t, t + Δt].

When applying a model, errors principally occur in the data, in the model, and in the parameters. The errors in the data appeared to be of minor importance (Zuur, 1993). The errors in the model may be found by examining the structure of R_i of equation (6). In general, a regular (non-white noise) structure of the residues R_i implies that at least one important factor was not, or not correctly, described by the model. Errors in parameters may be due to interchangeability : parameters are highly interchangeable when the same quality of the simulation results is found when using different combinations of parameter values. In such cases, the data are insufficient to discriminate between the several processes that are incorporated in the model. Uncertainty analysis was applied in order to examine errors in parameters (Draper & Smith, 1981).

Model II : analysis with incorporation of biotic data

The second model used to analyze mesocosm data was characterized by a lower level of aggregation than the first model. Here the productivity estimates were linked with additional data in order to estimate the contributions of the primary producers in the mesocosms to the total production. The primary producers were divided into three groups, viz. benthic microalgae (benthic diatoms), pelagic microalgae (diatoms and flagellates) and pelagic macrocalgae (Enteromorpha and Ulva). The oxygen production of each group of primary producers reads :

$$Production = q' \cdot \overline{F}(\overline{I}) \cdot F(T) \cdot F(N) \cdot Org \qquad (mg(O_2) \cdot l^{-1} \cdot d^{-1}) \quad (7)$$

q' : maximum species-specific growth rate
F(I) : dependency of growth rate on light
F(T) : dependency of growth rate on temperature
F(N) : dependency of growth rate on nitrogen concentration
Org : biomass density of primary producer

The values of all three dependency functions range between 0 and 1. The dependency of the growth rate on light was defined as follows :

$$\overline{F}(\overline{I}) = \frac{1}{24} \int_{t=0}^{t=24} F(I) \cdot dt \qquad (-) \quad (8)$$

F(I) was corrected for light attenuation for benthic and pelagic production. The sum of the oxygen production of the three groups of primary producers should be equal to q · F(I_0) as was defined in equation (1).

Additionally, a nitrogen budget was included into the computations :

$$\frac{dN}{dt} = -\gamma_N \cdot [Production - Respiration] + Flux + Inp - Outp + Addit \qquad (mg(N) \cdot l^{-1} \cdot d^{-1}) \quad (9)$$

Inp, Outp : natural inflow and outflow of nitrogen (mg · l^{-1} · d^{-1}).
Addit : amount of nitrogen added to the basin (mg (N) · l^{-1} · d^{-1}).
Flux : contribution due to sediment/water exchange (mg (N) · l^{-1} · d^{-1}).
γ_N : N/O ratio in all algae (g(N)/g(O_2).

The amount of nitrogen added to the basins and the natural inflow of nitrogen was measured, and the outflow of nitrogen was calculated from the actual nitrogen concentration in each basin and the water outflow. The remaining relationship to be described was the dependency on N-availability. This was done according to a classical Monod-equation :

$$F(N) = \frac{N}{(K_N + [N])} \qquad (-) \quad (10)$$

where K_N is the Monod-parameter.

The reaeration coefficient (eq. 3) was reduced in proportion to the coverage of the water surface by macroalgae. Macroalgae produce and use oxygen, some of which may be exchanged with the atmosphere instead of the water column. Nitrogen supply and release, however, is always coupled to the water. A correction factor was used to take the partial oxygen loss into account.

Six parameters are of interest in our approach, viz. the K_N parameters and the maximum growth parameters q' of respectively phytoplankton, microphytobenthos and macroalgae. It was impossible to estimate all six parameters because the K_N values and the production rate parameters appeared to be highly interchangeable. This was mainly due to the limited number of biomass measurements. We assumed therefore that K_N equalled 14 µg · l^{-1} for all three primary producers (De Vries *et al.*, 1988).

The primary production was coupled to the actual N-concentration through the above-mentioned Monod-function. However, N-data were too variable, which corrupted the estimation of q'-values. In order to improve the estimation, N-concentrations were estimated by setting dN/dt = 0 in eq. (9), and computing the necessary [N]. Subsequently, the difference between measured and computed [N]-values were minimized according to eq. (6). Thus, not only the q values from section I, but also the measured [N]-values were used in the minimization computation. The minimization target F reads.

$$F = \Sigma\,(q - q'F(T) \cdot F(N) \cdot Org)^2 + \\ + \beta_N \cdot \Sigma\,([N]_{meas} - [N]_{comp})^2 \qquad (11)$$

with β_N as a weighting factor.

RESULTS

Model I

Comparison of the measured and calculated oxygen concentrations reveals that the calculated oxygen concentrations were lower than the measured concentrations in the morning hours, and higher than the measured concentration in the afternoon hours (Fig. 4). This difference may be due to an underestimation of production and/or an overestimation of consumption during the morning, or vice versa.

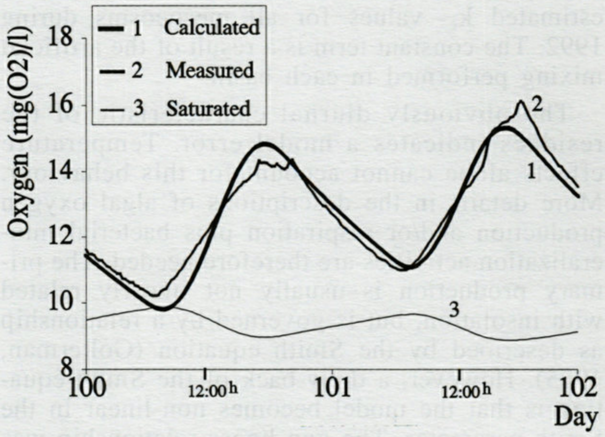

Fig. 4. – Measured, calculated and saturated dissolved oxygen concentration (mgO_2 · l^{-1}) in MOVEL00 at from daynumber 100 to 102 in 1992, as estimated by the original model I by simulating C(t).

Although the individual confidence intervals of the parameter estimates q, R and k_r are rather small, the combined 90 % confidence countours of parameter estimates allow a much larger deviation from the best estimates (Fig. 5).

Especially the reaeration coefficient k_r and the consumption rate R show a strong interchangeability. Since the k_r – parameter is mainly dependent on the wind velocity, the parameter exchangeability between k_r and R was eliminated by computing instead of estimating k_r. All daily reaeration coefficients were assumed to be related to wind velocity according to

$$k_r = \frac{1}{depth} \cdot \{0.517 + 0.129 \cdot Uwi\} \qquad (d^{-1}) \quad (12)$$

where Uwi was the wind speed (m · s^{-1}) at 10 m (KNMI, 1992). Equation (12) was based on all

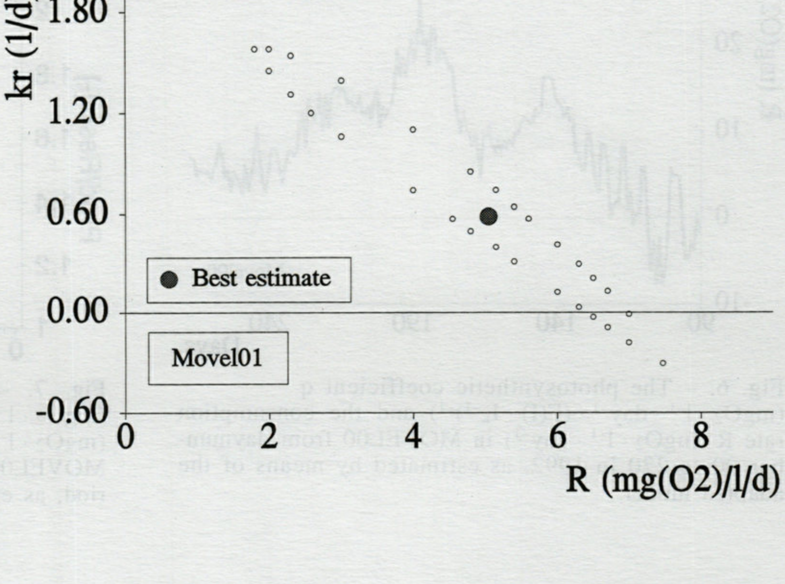

Fig. 5. – Confidence intervals (90 %) and best estimates of parameter combination of the consumption rate R (mgO_2 · l^{-1} · day^{-1}) and the reaeration coefficient K_r (mgO_2 · l^{-1} · day^{-1}) as estimated by means of the original model I. Day 122, Movel 01.

estimated k_r – values for all mesocosms during 1992. The constant term is a result of the artificial mixing performed in each basin.

The obviously diurnal characteristic of the residues indicates a model error. Temperature effects alone cannot account for this behaviour. More details in the descriptions of algal oxygen production and/or respiration plus bacterial mineralization activities are therefore needed. The primary production is usually not linearly related with insolation, but is governed by a relationship as described by the Smith equation (Golterman, 1975). However, a draw-back of the Smith-equation is that the model becomes non-linear in the Smith-parameter. The non-linear relationship was therefore approximated by means of the linear relation:

$$F(I_z) = \begin{pmatrix} \frac{I}{I_k} : I < I_k \\ 1.0 : I > I_k \end{pmatrix} \qquad (-) \quad (13)$$

where I_k ($W \cdot m^{-2}$) was the photosynthetic parameter.

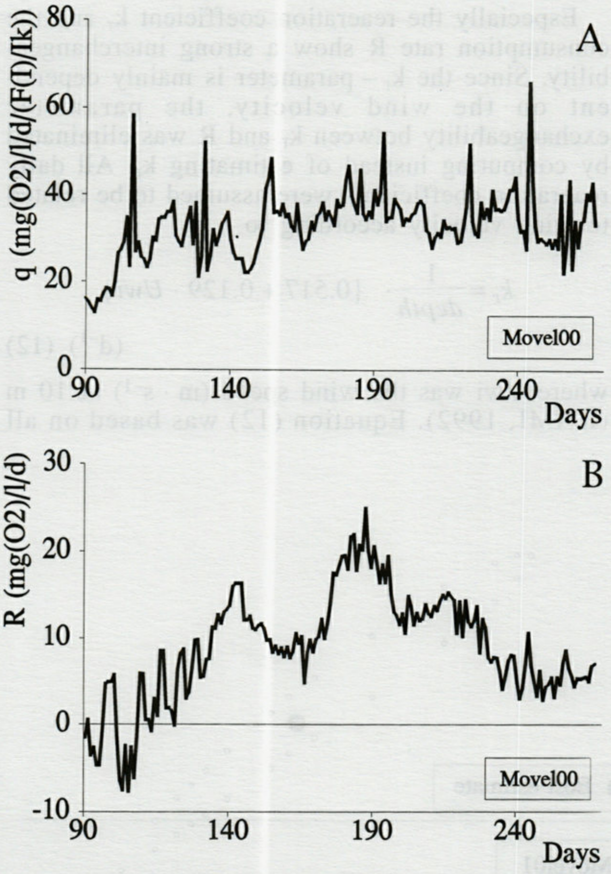

Fig. 6. – The photosynthetic coefficient q ($mgO_2 \cdot l^{-1} \cdot day^{-1} \cdot (F(I) \cdot I_k^{-1})^{-1}$) and the consumption rate R ($mgO_2 \cdot l^{-1} \cdot day^{-1}$) in MOVEL00 from daynumber 90 to 270 in 1992, as estimated by means of the adapted model.

These two adaptions to the original model resulted in better parameter estimates. When the residues of the original and adapted model were compared, both after eq. (5), the adaption not only led to smaller residues, but also to a more white characteristic of this noise.

As an example, the values of the photosynthetic coefficient q and the consumption rate R for MOVEL00 (reference basin) during the entire research period in 1992 are shown in Fig. 6.

The average production rate as well as the average respiration rate seem to increase with increasing nutrient loading (Fig. 7). The ratio

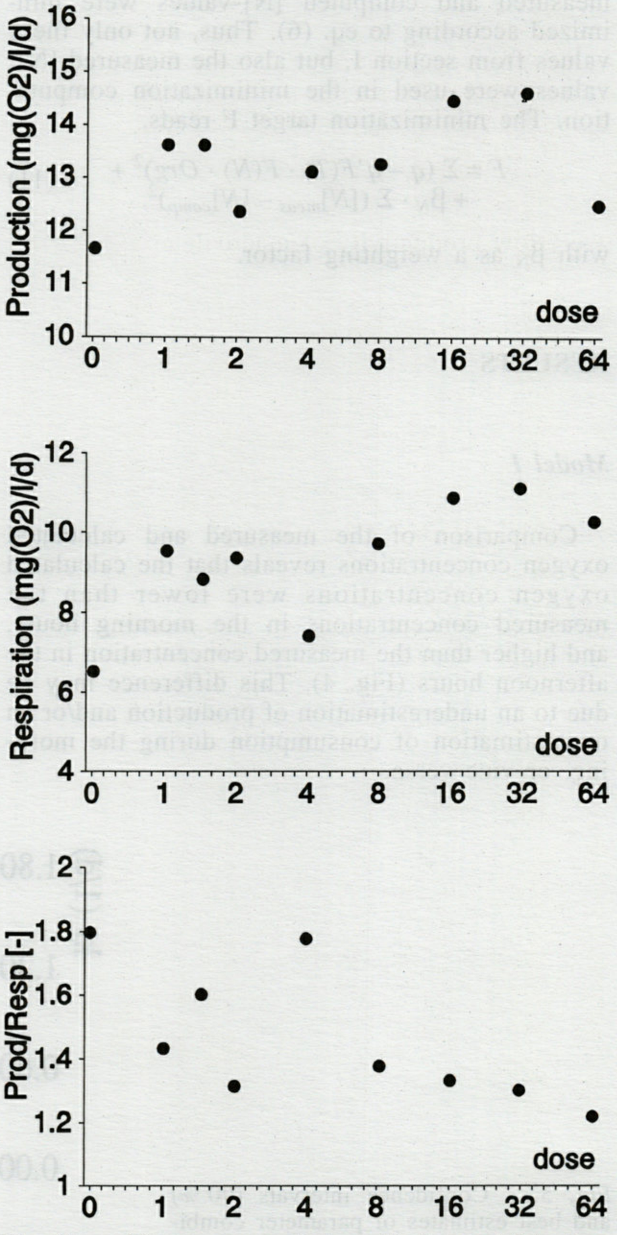

Fig. 7. – The average photosynthetic coefficient q ($mgO_2 \cdot l^{-1} \cdot day^{-1}$), the average consumption rate R ($mgO_2 \cdot l^{-1} \cdot day^{-1}$) and the ratio between q and R in MOVEL00 to MOVEL64 for the entire experimental period, as estimated by means of the adapted model I.

(production/respiration) decreased with increasing loading.

Model II

Assuming that the Monod constants K_N equalled 14 µg · l^{-1} for all three groups of primary producers, the photosynthetic coefficient q (q' · F(T) · F(N) · F(shade) · [Org]) as estimated by means of model II seems to be reasonably related to the photosynthetic coefficient q (oxygen model), as estimated by means of the adapted model I (Fig. 8).

The estimates for the maximum growth parameters of phytoplankton, microphytobenthos and macroalgae respectively, were 17.72, 9.66 and 0.29 d^{-1}. The subsequent calculation of the average primary production of each group of algae during the experimental period showed that microphytobenthos was the main producer of oxygen in most mesocosm ecosystems (Fig. 9). The relatively low productivity of macroalgae of 0.29 d^{-1} was compensated by their large biomass. This, in contrary to phytoplankton, which combined high productivity with low biomass. The average production of phytoplankton, microphytobenthos and macroalgae was not clearly related to the nutrient loading.

CONCLUSIONS

This paper shows that it is possible to derive information on ecosystem behaviour from oxygen time series by means of a dynamic oxygen model with a high level of aggregation. The results of model I analysis showed that the values of the photosynthetic coefficient q and the consumption rate R varied during the experimental period and that they were related to the additional nutrient supply. The model with a medium aggregation level, model II, revealed additional information on the contribution of the primary producers to the values of the photosynthetic coefficient q.

Finally, ecosystem models with a low aggregation level may be used to estimate parameters of more detailed processes in the mesocosm ecosystems, e.g. flows of matter, fluxes and process rates. These parameter estimates may be subsequently tested for the effects of the treatment and results may be used to estimate mass budgets for the mesocosm ecosystem.

However, several drawbacks appear when lowering the level of aggregation. Even in mesocosms, not all state variables and processes which are necessary for parameter estimation can be measured, or can be measured frequently enough. Part of his problem may be solved by using data from literature, or employing "best guesses". In addition, individual parameter uncertainties generally increase with a decrease in aggregation level. Therefore, ecosystem models with low levels of aggregation may be used to estimate ecosystem parameters, but one should be very careful in assigning strict values to the results and always be aware of parameter uncertainties.

Highly aggregated models, as well as ecosystem models, are useful to study the behaviour of mesocosm ecosystems, extending the knowledge of the system and allowing the interpolation and a better interpretation of the biotic and abiotic data. The predictive power of models with a high

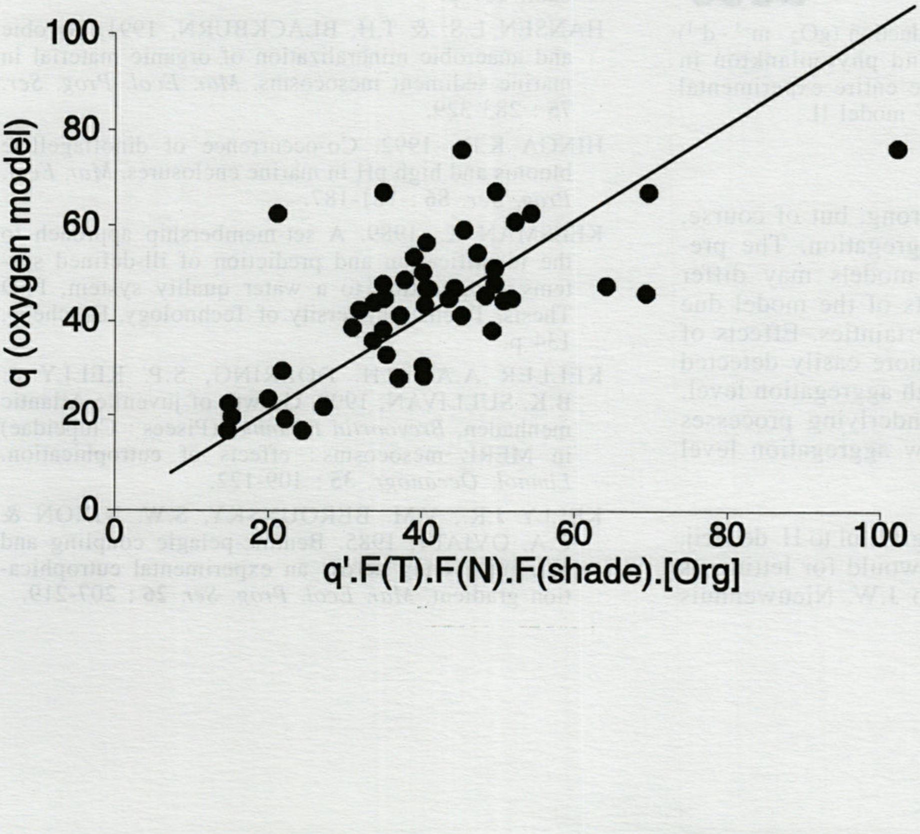

Fig. 8. – The relationship between the photosynthetic coefficient q (q' · F(T) · F(N) · F(shade) · [Org]) as estimated by means of model II and the photosynthetic coefficient q (oxygen model) as estimated by means of the adapted model I.

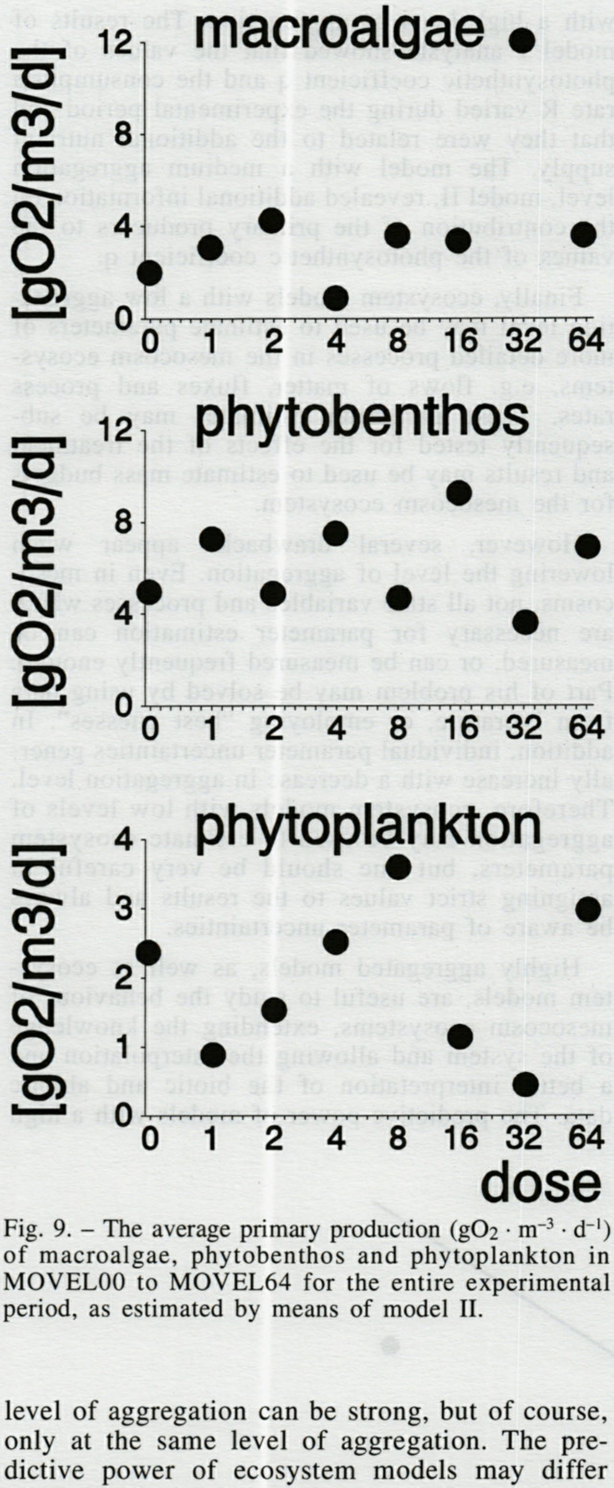

Fig. 9. – The average primary production ($gO_2 \cdot m^{-3} \cdot d^{-1}$) of macroalgae, phytobenthos and phytoplankton in MOVEL00 to MOVEL64 for the entire experimental period, as estimated by means of model II.

level of aggregation can be strong, but of course, only at the same level of aggregation. The predictive power of ecosystem models may differ substantially for different parts of the model due to differences in relative uncertainties. Effects of treatments will therefore be more easily detected by means of models with a high aggregation level. If more detailed insight in underlying processes is required, application of low aggregation level models should be favoured.

ACKNOWLEDGEMENTS – We are grateful to H. de Heij, R. Jak and H. van het Groenewould for letting us use their unpublished data, to J.W. Nieuwenhuis for this contribution to the data analysis, to J. Schoonheden for his assistance in the acquisition of the oxygen time series, to two anonymous referees for their critical comments on the manuscript, to A. van Leeuwen for linguistic corrections and to S.M.J.M. Brasseur for the French translation of the abstract. The BEST project (STEP CT-91-0120) project was granted by the EC.

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Reçu le 26 juillet 1993 ; received July 26, 1993
Accepté le 30 novembre 1993 ; accepted November 30, 1993

VIE MILIEU, 1994, 44 (1) : 39-58

DESIGNING A SIMPLE MICROBIOLOGICAL-PHYSICAL MODEL FOR A COASTAL EMBAYMENT

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MODÈLE
MICROBIOLOGIE
PHYTOPLANCTON
REMINÉRALISATION
GOLFE DE FOS
ÉCOSYSTÈME CÔTIER
MÉDITERRANÉEN

RÉSUMÉ – Dans l'optique d'une meilleure compréhension du devenir de la matière organique lors de son transit en zone côtière, une nouvelle approche de type numérique a été tentée dans une baie du sud de la France, le Golfe de Fos, largement ouvert sur la Méditerranée et par lequel transite une partie des eaux rhodaniennes. Le modèle décrit les principaux processus physiques de circulation estuarienne, de stratification thermohaline et de remise en suspension, l'ensemble étant couplé à des processus biologiques de croissance des microalgues, Bactéries et Protozoaires sous le contrôle des sels nutritifs et de la lumière disponible, ainsi que des processus de reminéralisation dans la colonne d'eau et le sédiment. Des simulations ont permis de mettre en évidence : 1) le rôle important que joue le golfe de Fos dans le recyclage des nutrients en provenance du continent, avant leur exportation en direction du large ; 2) l'intervention des processus de remise en suspension, d'une part, dans la limitation de la lumière disponible pour la photosynthèse et, d'autre part, dans l'exportation de matière organique contenue dans les sédiments locaux ; et 3) la variabilité haute fréquence qui caractérise ces sytèmes peu profonds et largement forcés par le vent.

MODEL
MICROBIOLOGY
PHYTOPLANKTON
REMINERALISATION
GULF OF FOS
MEDITERRANEAN COASTAL
ECOSYSTEM

ABSTRACT – Numerical modelling provides a means of studying the processes that cycle nutrients and organic material as they pass through the coastal zone on their way from the land to the sea. The Gulf of Fos is an embayment on the Mediterranean coast of France, receiving part of the discharge of the Rhône river. We discuss the design of a simple numerical model for the Gulf. The model couples the physical processes of estuarine circulation, density stratification, and particulate resuspension, with the microbiological processes of light – and nutrient – controlled growth of pelagic micro-algae, bacteria and protozoans, and the detrital remineralisation of nutrients in water-column and sediment. Simple numerical experiments are used to show (1) the rôle of the Gulf in cycling land-derived nutrients before they reach the open sea ; (2) the importance of particulate resuspension in controlling light availability for photosynthesis and the export of organic material ; and (3) the high frequency of variability in this shallow, wind-forced system.

INTRODUCTION

The coastal zone moderates the interaction between land and ocean (Holligan 1990). The inner coastal zone is most subject to terrestrial influence and to extreme marine effects such as stirring by waves, and plays an important role in ameliorating the consequences of anthropogenic discharge. It is thus important to understand the main processes that control the functioning of shallow-water marine ecosystems. It is also important to understand the links amongst these processes, which include water transport, sediment dynamics, and the biological cycling of material. Numerical models provide tools for studying such links, and data to parameterise and test these models can more easily be acquired in shallow waters than in the deep ocean. In this paper we describe a Mediterranean coastal embayment, the Gulf of Fos, near Marseille, and discuss the factors that led us to choose a particular representation of the physical and microbiological processes controlling the cycling of carbon and nitrogen in this bay. Our case for focusing on the early steps in the development and testing of a coupled model is that these steps are part of the scientific process of forming and testing hypotheses, and are thus useful in developing ideas about ecosystem function, even if the model does not, at this stage, make accurate predictions.

THE GULF OF FOS

The Gulf of Fos is situated on the Mediterranean coast of France at 43.25°N, 4.56°E. It is a semi-enclosed shallow area, influenced by freshwater from the Rhône river and occasionally from the Etang de Berre (Fig. 1). Mean depth is 8 m and the approximate area is 45×10^6 m^2. A navigation channel divides this area into two parts : the western Carteau Cove, dominated, since 1983, by shellfish farming ; and the north-eastern part, bordered by an important industrial chemical complex.

The discharge of freshwater into the Gulf by the Rhône Canal was estimated by Arfi (1989) as being 1 % of the total Rhône flow. This flow is, however, highly variable with time. During 1986, the mean flow in the Rhône at Beaucaire, near Arles, was 1700 m^3 s^{-1} with spring peaks of up to 6300 m^3 s^{-1} (Fig. 2 A).

The mean tidal range in this region is less than 0.3 m, so tidal forcing is weak, with typical velocities of order 10^{-2} m s^{-1}. Instead, winds provide the main input of kinetic energy. The mean wind speed in 1986 was about 5 m s^{-1}, mainly from the NW and SE (Fig. 2 B), and only 4 % of days were without wind. Physical modelling and current meter studies (Grenz, 1989) show the importance of wind-driven circulation within the Gulf. Salinity profiles sometimes show strong salinity layering (Fig. 3). Salinometers moored in Carteau Cove from 18-29 October and 3-17 December 1993, and recording at 15 minute intervals, showed surface-bottom salinity differences exceeding 4 psu during 30 % of the time.

The sediments are muddy sands (25 % particles less then 63 µm) and sandy muds (50 to 90 % < 63 µm) depending on location and depth (Grenz in Massé, 1993). Water content varies between 35 and 60 % of total wet weight. Organic content in the upper sediment varied over space and time between 2 % and 15 % of ash-free dry weight, with molar C : N ranging from 15 : 1 to 25 : 1 (Plante-Cuny *et al.*, in press).

When winds are strong, stirring suspends inorganic and organic particles (Grenz, 1989). This suspended particulate material (SPM) could be trapped within the Gulf by the local circulation, or exported to the open sea. Conversely, during calm periods, the Gulf could act as a trap for sedimenting material. It seems likely that the alternation of resuspension and deposition is important in controlling production and consumption in the Gulf. Firstly, resuspension could enhances the microbial decomposition of organic detritus. Secondly, although no precise optical data are available, light availability for primary producers must be substantially reduced during periods of high SPM load.

The shallow, organic-rich, sediments of the Gulf sustain a high oxygen demand and nutrient release rate. Measurements during 1987 and 1988, by means of *in situ* benthic chambers, showed typical fluxes of – 2 to – 12 mmol O_2 m^{-2} d^{-1} and + 1.5 mmol nitrate + nitrite + ammonium (dissolved inorganic nitrogen, DIN) m^{-2} d^{-1}. The oxygen fluxes represent sediment demand ; they are however less than total respiration because of daytime gross photosynthesis of + 11 to + 26 mmol O_2 m^{-2} d^{-1}. The DIN flux, from the sediment to the water, could contribute up to 15 % of the

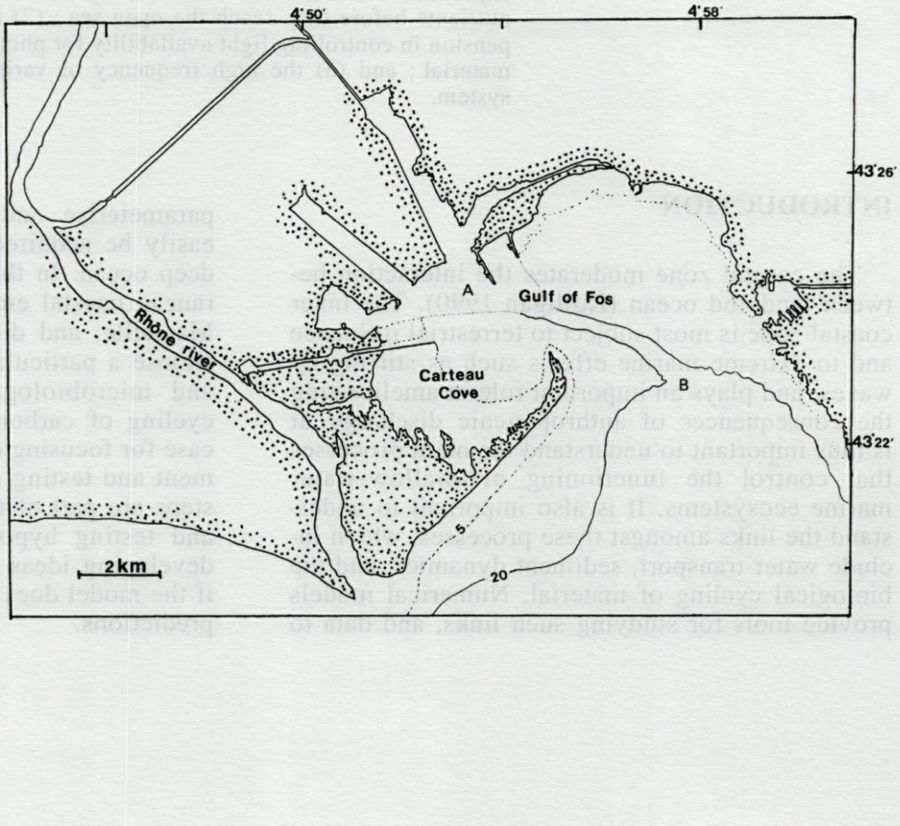

Fig. 1. – Map of the Gulf of Fos and position of sampling stations A and B used in April 1991 for data in Figure 4.

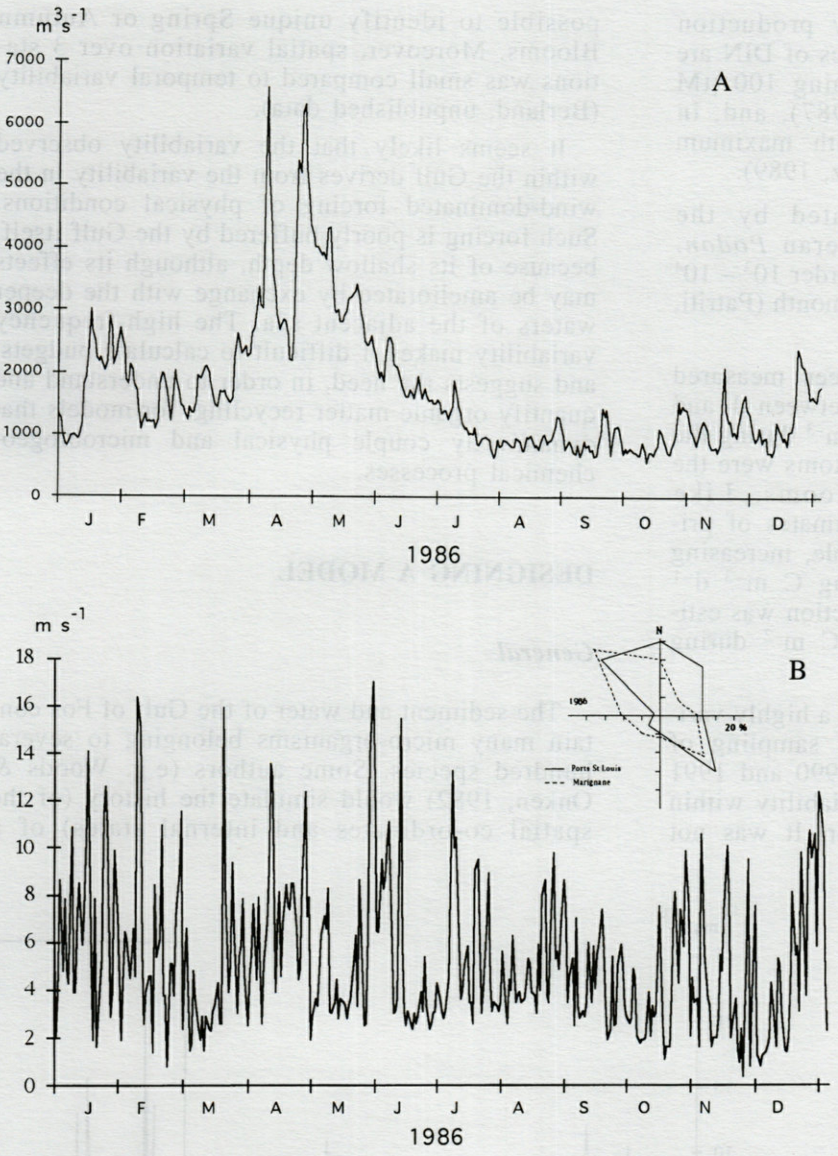

Fig. 2. – A, Flow in the Rhône recorded at Beaucaire during 1986 (data from Compagnie Nationale du Rhône-Lyon). B, Wind speed (and directional rose) at Marignane during 1986 (data from Météo France).

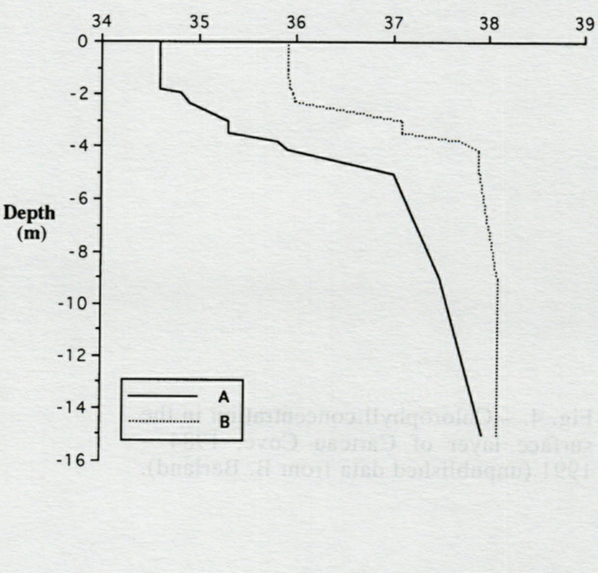

Fig. 3. – Profiles of salinity on 5 April 1991 ; for station positions see Fig. 1.

nitrogen requirement for primary production (Baudinet *et al.*, 1989). Other sources of DIN are the Rhône water, typically containing 100 µM nitrate (El Habr & Golterman, 1987), and, in winter, the Mediterranean sea, with maximum 5 µM nitrate (Cruzado & Velanquez, 1989).

Mesozooplankton are dominated by the copepod *Acartia* and the cladoceran *Podon*. Biomasses during 1980-81 were of order 10^3 – 10^4 animals m^{-3}, depending on site and month (Patriti, 1984).

Water-column chlorophyll has been measured since 1984. Typical values were between 1 and 5 mg chl a m^{-3}, with up to 22 mg m^{-3} during the Spring Bloom of 1990 (Fig. 4). Diatoms were the main type of algae during blooms. Like chlorophyll concentrations, ^{14}C estimates of primary production were highly variable, increasing during Spring Blooms to 400 mg C m^{-3} d^{-1} (Folack *et al.*, 1989). Annual production was estimated as between 71 and 140 g C m^{-2} during 1984 (Folack, 1986).

As such data indicate, the Gulf is a highly variable environment. High frequency sampling of water column chlorophyll during 1990 and 1991 showed that there was as much variability within a month as during the entire year. It was not possible to identify unique Spring or Autumn Blooms. Moreover, spatial variation over 3 stations was small compared to temporal variability (Berland, unpublished data).

It seems likely that the variability observed within the Gulf derives from the variability in the wind-dominated forcing of physical conditions. Such forcing is poorly buffered by the Gulf itself, because of its shallow depth, although its effects may be ameliorated by exchange with the deeper waters of the adjacent sea. The high-frequency variability makes it difficult to calculate budgets, and suggests the need, in order to understand and quantify organic matter recycling, for models that dynamically couple physical and microbiogeochemical processes.

DESIGNING A MODEL

General

The sediment and water of the Gulf of Fos contain many micro-organisms belonging to several hundred species. Some authors (e.g. Woods & Onken, 1982) would simulate the history (of the spatial co-ordinates and internal states) of a

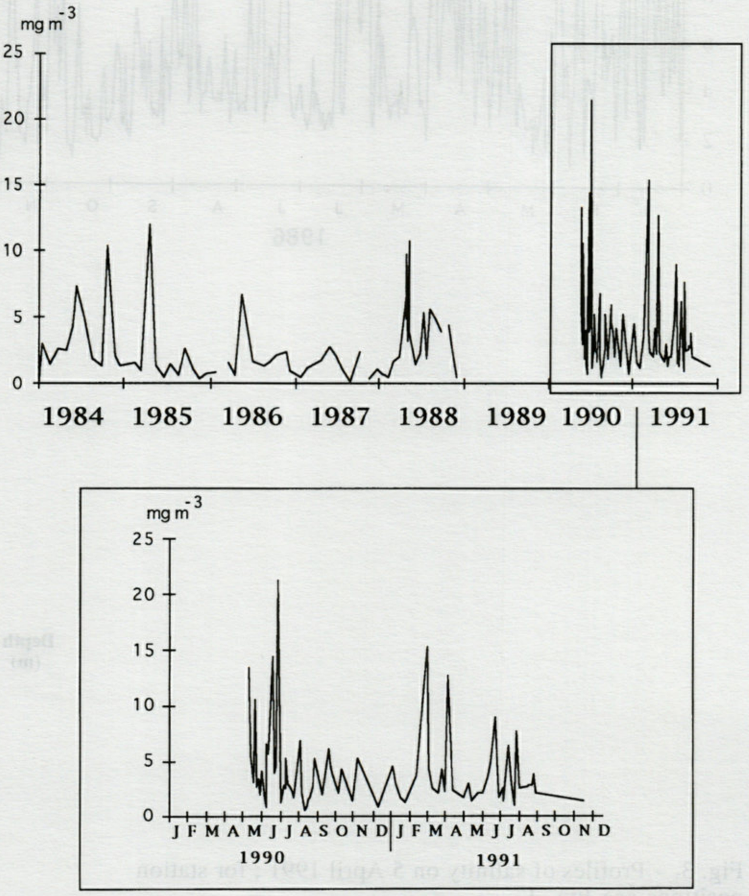

Fig. 4. – Chlorophyll concentration in the surface layer of Carteau Cove, 1984 – 1991 (unpublished data from B. Berland).

sample of typical individuals. Nevertheless, there is, as yet, no evidence that the extra computing costs of such an exercise are justified by substantially better predictions. The conventional approach, which we adopt here, is to group organisms. Each group is described by a time-varying mean state. Rates of formation, transformation and removal are specified by continuous functions of the mean state, and movements are forced by average water motions.

The fundamental problem in designing a biological model is thus to decide how to group the organisms. If the bulking is taxonomic, should it take place at the level of species, classes, phyla or kingdoms ? How many state variables should be used to describe each bulked entity ? Should values of these state variables be calculated at the nodes of a two – or three – dimensional mesh, or averaged over large parts of the Gulf ? Are the mean physical transports best described by applying equations for advection and turbulent diffusion at each node, or by computing exchanges across compartment boundaries ? Should the compartment boundaries be fixed or dynamic ?

Such questions are not easily answered. Nevertheless, a general guide is given by Occam's razor and Popper's epistemology of science (Popper, 1972) : add complexity only when forced by circumstances, but strive to discover such circumstances. For example, our initial physical model did not include exchange between the Gulf and the Mediterranean. Compared with observations, the model predicted water temperatures that were too high in summer, and too low in winter. Adding marine exchange resulted in better agreement (Fig. 5).

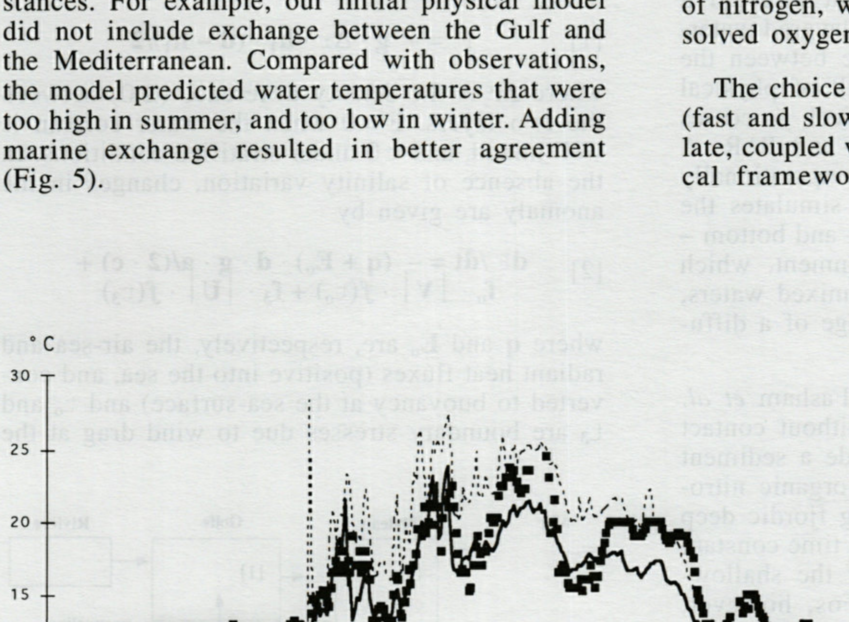

Fig. 5. – Surface temperatures in the Gulf of Fos during 1986. Dots correspond to values observed in Carteau Cove, the dashed line to model-prediction without circulation, and the solid line model-prediction with circulation.

This emphasis on avoiding unnecessary complexity led to a model in which :

- variables were averaged horizontally over the Gulf, and vertically over one or two water-column layers of variable thickness, and one sediment layer of constant thickness ;
- physical transports were represented by exchanges between the layers, and between them and the sea, the vertical exchanges including upwelling, entrainment and particulate sinking in the case of the water column, and deposition/resuspension of particulates, and diffusional exchange of solubles, in the case of the sediment-water interface ;
- particulate material was divided into three types : inorganic particulates not subject to biological gains or losses but influencing photosynthesis through effects on water turbidity ; organic detrital material subject to slow mineralisation by associated heterotrophic micro-organisms ; and 'microplankton' including fast-recycling micro-heterotrophs as well as phytoplankton ;
- organic particulates were quantified in terms of carbon and nitrogen, and, in the case of the microplankton, as chlorophyll ; combined nitrogen, was conserved by cycling through ammonium and nitrate ; and the production or consumption of organic carbon, and the oxidation or reduction of nitrogen, were associated with changes in dissolved oxygen.

The choice of 3 elements (C,N and O) and two (fast and slow cycling) types of organic particulate, coupled with a simple, boundary-layer physical framework, may be contrasted with the plankton models of Anderson & Nival (1989), Fasham *et al.* (1990), and Ross *et al.* (1993). Anderson & Nival and Fasham *et al.* represent only one element (nitrogen) ; Ross *et al.* also include carbon. All three models explicitly include zooplankton amongst their 4 (Ross *et al.*, Fasham *et al.*) or 8 (Anderson & Nival) types of organic particulate.

Both Fasham *et al.* and Ross *et al.* used a simple physical framework. In the case of Fasham *et al.* this was an oceanic mixed layer with depth variation (and consequent entrainment) supplied as a forcing function. Ross *et al.* described fjordic hydrography by a three-layer structure with fixed compartment volumes and interface depths. Entrainment and diffusional exchanges were supplied as forcing functions. Anderson & Nival's model of a Mediterranean coastal pelagic ecosystem was driven by vertical turbulent diffusion, with time-constant but depth-varying eddy diffusivities. Biological concentrations were predicted at a series of grid points representing a vertical profile, rather than averaged over 1 or 2 boundary layers as in our case.

In none of these models was the biology dynamically coupled to the physics. Observations had shown highly variable density stratification in the Gulf of Fos, which is shallow compared with the systems described by the other models. We thus needed a physical model that allowed a switch from a vertically mixed to a layered water-column, and in which the interface between the layers was free to move as a result of physical forcing that also drove the biological processes through effects on nutrient supply and PAR. A boundary-layer physical model is computationally simpler than a diffusion model. It simulates the transport of water between surface – and bottom – mixed layers by anisotropic entrainment, which may be more realistic, in strongly mixed waters, than the vertically isotropic exchange of a diffusion model.

Finally, Anderson & Nival and Fasham *et al.* modelled deep-water ecosystems without contact with the benthos. Ross *et al.* include a sediment layer which mineralised deposited organic nitrogen and returned it to the overlying fjordic deep water by a first order process with a time constant of about 3 months. In the case of the shallow-water ecosystem of the Gulf of Fos, however, resuspended organic material may make an important contribution to remineralisation. In order to investigate this, we allowed processes suspending inorganic particulates also to act on sediment-layer detritus.

Table I lists the symbols used for the state variables, and Table II gives the main equations, of the model for the Gulf of Fos. Parameters are defined in Table III.

The physical model

The physical compartmentalisation is illustrated in Fig. 6. The first version of the model simulated only the column labelled "Golfe", omitting lateral exchanges. In this case the physics was that of the model L3VMP, as described by Tett (1990a), and was driven by two main processes : surface heating or cooling as a result of solar irradiance and air-sea heat exchange ; and the injection of turbulent kinetic energy (t.k.e.) into surface and bottom layers as a result of boundary stresses. Resulting changes in water-column potential energy and heat content brought about changes in layer temperature and thickness. An increase in, for example, the thickness of the surface layer due to greater wind stirring, resulted in the entrainment into the surface layer of water from the bottom layer. Bottom stress caused particulate resuspension when the stress exceeded a critical value, otherwise particulates were allowed to deposit. Solutes exchanged between pore water and water-column by a diffusional process scaled by an arbitrary parameter representing bioturbation.

The stratification model derives from the mixed-layer model of Kraus & Turner (1967), as modified to include tidal stirring by Simpson & Bowers (1984). Clarke (1986) provided the two-layer algorithms. The potential energy anomaly of a two layer system is defined by :

$$[1] \qquad \mathrm{F} = -\, \mathbf{g} \cdot \Delta \mathrm{r} \cdot \mathbf{h_1} \cdot (\mathbf{d} - \mathbf{h_1})/2$$

where $\mathbf{\Delta r}$ is the density difference (≤ 0) between the two layers. $\mathbf{F} = 0$ when the water column is well mixed, and < 0 under stratified conditions. In the absence of salinity variation, changes in the anomaly are given by

$$[2] \qquad \mathbf{d}\mathrm{F}\,/\mathbf{dt} = -\,(\mathbf{q} + \mathbf{E_o}) \cdot \mathbf{d} \cdot \mathbf{g} \cdot \mathbf{a}/(2 \cdot \mathbf{c}) + \mathbf{f_o} \cdot \left|\mathbf{V}\right| \cdot f(\mathrm{t_o}) + \mathbf{f_3} \cdot \left|\mathbf{U}\right| \cdot f(\mathrm{t_3})$$

where **q** and $\mathbf{E_o}$ are, respectively, the air-sea and radiant heat fluxes (positive into the sea, and converted to buoyancy at the sea-surface) and $\mathrm{t_o}$ and $\mathrm{t_3}$ are boundary stresses due to wind drag at the

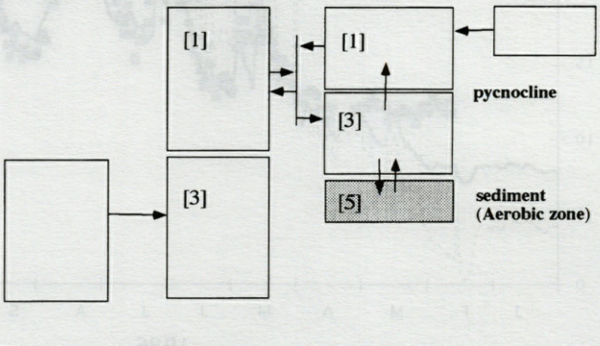

Fig. 6. – Physical compartmentalisation in the model.

Table I. – State, forcing and main intermediate variables.

Symbol	Description	Units
State variables		
A	Concentration of inorganic particles	mg m^{-3}
B	Concentration of microplankton carbon	mmol C m^{-3}
C	Concentration of detrital carbon	mmol C m^{-3}
h	Layer thickness	m
I	PAR irradiance	$\mu E\ m^{-2}\ s^{-1}$
M	Concentration of detrital nitrogen	mmol N m^{-3}
N	Concentration of microplankton nitrogen	mmol N m^{-3}
O	Concentration of dissolved oxygen	mmol N m^{-3}
NH_S	Concentration of dissolved ammonium	mmol N m^{-3}
NO_S	Concentration of dissolved nitrate	mmol N m^{-3}
t	Time	d
X	Chlorophyll concentration*	mg m^{-3}
Φ	Potential energy anomaly†	J m^{-2}
θ	Temperature	°C
σ	Salinity	psu
* not independent - function of B and N in layer		
† not independent - function of θ, σ and h over water-column layers		
Forcing variables		
D	Elevation rate due to freshwater discharge	m d^{-1}
E_0	Sea-surface solar irradiance (all wavelengths)	W m^{-2}
G	Mesozooplankton grazing pressure	0.2 d^{-1}
q	Air-sea heat flux	W m^{-2}
${}^{tide}U$	Maximum tidal current speed	0.01 m s^{-1}
V	Wind speed	m s^{-1}
Intermediate variables		
E	Entrainment velocities between layers	m d^{-1}
Q	Nutrient quota, N/B	mmol N (mmol C)$^{-1}$
u	Microplankton nutrient uptake rate	mmol N (mmol C)$^{-1}$ d^{-1}
W	Pycnocline elevation rate due to circulation	m d^{-1}
w	Particle sinking speed	m d^{-1}
λ	PAR attenuation coefficient	m^{-1}
μ	Microplankton growth rate	d^{-1}
τ	Boundary stresses	kg m^{-3} s^{-4}

sea surface and tidal and other movements at the sea-bed. $|\mathbf{V}|$ gives the absolute wind speed ; because $t_o = {}^{air}\mathbf{p} \cdot \mathbf{k_0} \cdot \mathbf{V}^2$, the intensity of wind stirring is proportional to $\mathbf{V}^3$. Likewise, the intensity of bottom stirring is proportional to $\mathbf{U}^3$, where, in the original version for North-West European shelf seas, **U** was the maximum tidal velocity.

Tides are weak in Fos, but wind effects can easily reach the sea-bed in these shallow waters. Thus, we used algorithms from CERC (1974, in Railland, 1991) to compute the additional bottom stress (and consequent t.k.e. injection and particulate resuspension) due to the orbital motion of wind-waves. The joint velocity became :

$$\mathbf{U} = \sqrt{({}^{tide}\mathbf{U}^2 + {}^{orb}\mathbf{U}^2)}$$

where ${}^{orb}\mathbf{U}$ is the horizontal component of the orbital velocity at the sea-bed.

In our initial 1-site model, simultaneous solution of equations [1] and [2], starting from known initial conditions, predicted $\Delta\mathbf{h_1}/\Delta\mathbf{t}$ and thus the vertical entrainment velocities **E** defined in Table II. As already mentioned, the 1-site model failed to predict water temperatures accurately, so we added the circulation shown in Fig. 6, which includes an additional water column ("Plateau") in the Gulf of Lions, and allowed for the effects of freshwater on potential energy in equations [1] and [2] (see Table II). The landwards boundary conditions included a varying discharge of freshwater, which was assumed to be immediately mixed throughout layer [1] of the "Golfe" water-column. Sea-water was introduced as a bottom wedge ; the resulting upwards displacement of the pycnocline was opposed by turbulence in the surface layer, which entrained salt into the surface layer. An entrainment multiplier, computed from

Table II. – Main equations of the model.

The equations are given in two versions. The generalized version is for a mixed water-column and without lateral exchanges; subscripts are mostly omitted. In the detailed equations for stratified conditions, purely numeric subscripts refer to the "Golfe" water column. Layers in adjacent water-columns have complete subscripts. Fig. 7 shows column names and layer numbers. See Tett (1990a) for details of sediment processes, boundary exchanges, and functions not given in full.

Physical model

Structure and transports

h_1, h_3 : thicknesses (m) of layers above and below pycnocline;
d : total depth of watercolumn : $d = h_1 + h_3$
$E_{1,3}, E_{3,1}$: 'entrainment velocities' (m d^{-1}), into layer [1] from [3], or *vice versa* :

$$E_{1,3} = \Delta h_1/\Delta t : \Delta h_1 \geq 0 \text{ and } h_1 \leq d; = 0 : \Delta h_1 < 0 \text{ or } h_1 = d;$$
$$E_{3,1} = \Delta h_3/\Delta t : \Delta h_3 \geq 0 \text{ and } h_3 \leq d; = 0 : \Delta h_3 < 0 \text{ or } h_3 = d;$$

$\Delta h/\Delta t$ evaluated by simultaneous solution of equations for potential energy, salinity and temperature.
$E_{3,5}$: sediment erosion velocity (m d^{-1}), the rate at which the water column entrains sediment: a function of tidal and wind-wave stirring at the sea-bed; see also text.
f^d : fraction of sinking material that is deposited, a function of tidal and wind-wave stirring.
W : rate of uplift (m d^{-1}) of pycnocline due to salt wedge intrusion into "Golfe" column:

$$W = m_E.(\sigma_{plateau[1]} - \sigma_1).D$$

Suspended (fine inorganic) sediment : A mg m^{-3}

$$dA/dt = (E_{3,5}.A_5 - f^d.{}^A w.A)/d$$
$$dA_1/dt = (E_{1,3}.(A_3 - A_1) - {}^A w.A)/h_1$$
$$dA_3/dt = (E_{3,5}.A_5 + E_{3,1}.(A_1 - A_3) + {}^A w.(A_1 - f^d.A_3))/h_3$$

No lateral exchange of this sediment.

PAR, Photosynthetically Effective IrRadiance : I μE m^{-2} s^{-1} (mean over layer and 24 hr)

$$I = I_0.(1 - e^{-\lambda.h})/(\lambda.h)$$

I_0 : (photosynthetically active) irradiance at top of layer, 24 hr mean. For sea surface layer,

$$I_{0[1]} = m_0.m_1.m_2.E_0$$

For layer [3], $I_{0[3]} = I_{0[1]}.e^{-\lambda 1.h1}$

λ: diffuse attenuation coefficient (m^{-1}):

$$\lambda = {}^{SW}\lambda + {}^{A}\varepsilon.A + {}^{X}\varepsilon.X + {}^{C}\varepsilon.C$$

Potential energy anomaly : Φ J m^{-2}

$\Phi = 0$ (mixed)
$\Phi = -g.\Delta\rho.h_1.(d - h_1)/2$ (stratified)

$$\Delta\rho = \rho.(a.(\theta_1 - \theta_3) - b.(\sigma_1 - \sigma_3))$$
$$d\Phi/dt = -q.d.g.a/(2.c) - g.\Delta\rho.W.d/2 + \{stirring\};$$
$$\{stirring\} = 0 \qquad : \Phi = 0;$$
$$\{stirring\} = V^3.{}^{air}\rho.f_0.k_0 + f(U).\rho.f_3.k_3.4/(3.\pi) \qquad : \Phi < 0.$$

where:
$f(U) = {}^{tide}U^3$ ("Plateau"), $= |U|.({}^{tide}U^2 + {}^{orb}U^2)$ ("Golfe", with wind-wave stirring).
${}^{orb}U$: maximum wind-wave orbital velocity at sea-bed, from wind speed **V** and fetch and water column depth, using algorithms in Raillard (1991);

$$|U| = \sqrt{({}^{tide}U^2 + {}^{orb}U^2)}.$$

Salinity : σ psu

$d\sigma/dt = 0$ (mixed, no circulation)
$d\sigma_1/dt = (-D.\sigma_1 + E_{1,3}.(\sigma_3 - \sigma_1))/h_1$ (stratified, circulation)

$d\sigma_3/dt = (E_{3,1}.(\sigma_1 - \sigma_3) - W.(\sigma_3 - \sigma_{plateau[1]}))/h_3$: $h_3 > 0$;
$\sigma_3 = \sigma_{plateau[1]}$: $h_3 = 0$.

Temperature : θ °C

$$d\theta/dt = q/(\rho.c.d)$$

$$d\theta_1/dt = (q/(\rho.c) + E_{1,3}.(\theta_3-\theta_1))/h_1$$

(assumes that $\theta_{\text{rivière}} = \theta_1$)

$$d\theta_3/dt = (E_{3,1}.(\theta_1-\theta_3) - W.(\theta_3-\theta_{plateau[1]}))/h_3 \qquad : h_3>0$$

$$\theta_3 = \theta_{plateau[1]} \qquad : h_3=0$$

Biological model

Microplankton carbon biomass : **B** mmol C m^{-3}

$$dB/dt = (\mu - G - ({}^{B}w/d)).B \qquad \text{(mixed)}$$

$$dB_1/dt = (\mu_1 - G - (({}^{B}w_1+D)/h_1)).B_1 + (E_{1,3}.(B_3-B_1))/h_1 \qquad \text{(stratified, circulation)}$$

$$dB_3/dt = (\mu_3 - G - ({}^{B}w_3/h_3)).B_3 + ({}^{B}w_1.B_1 + E_{3,1}.(B_1-B_3) - W.(B_3-B_{plateau[1]}))/h_3 \qquad : h_3>0;$$

$$B_3 = B_{plateau[1]} \qquad : h_3=0.$$

${}^{B}w$:(nutrient-dependent) sinking rate of microplankton: between 0 and 5 m d^{-1};
G : zooplankton grazing pressure (d^{-1}) on microplankton - supplied from observations;
μ : microplankton specific growth rate (d^{-1}):

$$\mu = f(Q) \qquad : f(Q) < f(I);$$
$$= f(I) \qquad : f(Q) \geq f(I).$$

where

$$f(Q) = \mu'_{max}.f(\theta).(1-(Q_{min}/Q))$$
$$f(I) = \alpha.I.{}^{X}Q^{B}-r^{B}$$

$Q = N/B.$
${}^{X}Q^{B}$: microplankton chlorophyll:carbon ratio (mg chl (mmol C)$^{-1}$);
r^{B} : microplankton biomass-related respiration (d^{-1}):

$$r^{B} = r^{B}_0 + r.\mu \qquad : \mu \geq 0;$$
$$= r^{B}_0 \qquad : \mu < 0;$$

$f(\theta)$: Arrhenius-type function of temperature.

Chlorophyll concentration **: X** mg chl m^{-3}

$$X = {}^{X}Q^{B}.B$$

where

$${}^{X}Q^{B} = Q.({}^{X}Q^{N}_{max}.Q^* + {}^{X}Q^{N}_{min}.(1-Q^*)$$

and $$Q^* = (Q-Q_{min})/(Q_{max}-Q_{min})$$

Detrital carbon concentration : **C** mmol C m^{-3}

$$dC/dt = ((1-\gamma).G + ({}^{B}w/d)).B - ({}^{C}r - (f^{d}.{}^{C}w/d)).C + (E_{3,5}.C_5/d)$$

$$dC_1/dt = (1-\gamma).G.B_1 - ({}^{C}r_1 + (({}^{C}w_1+D)/h_1)).C_1 + E_{1,3}.(C_3-C_1)/h_1$$

$$dC_3/dt = ((1-\gamma).G + ({}^{B}w_3/h_3)).B_3 - {}^{C}r_3.C_3 + ({}^{C}w_1.C_1 + E_{3,5}.C_5 - f^{d}.{}^{C}w_3.C_3)/h_3 + (E_{3,1}.(C_1-C_3) - W.(C_3-C_{plateau[1]}))/h_3 \qquad : h_3>0;$$

$$C_3 = C_{plateau[1]} \qquad : h_3=0.$$

${}^{C}r$: detrital C respiration rate (d^{-1}), function of temperature, oxygen, and detrital N:C ratio:

$${}^{C}r = f(\theta).({}^{C}r_{max}.O/(O_{1/2,max}+O).f(M/C) + {}^{C}r_{min}.O/(O_{1/2,min}+O))$$

where

$$f(M/C) = (1-({}^{M}Q^{C}_{min}.C/M))^2$$

Detrital nitrogen concentration: **M** mmol N m^{-3}

$$dM/dt = ((1-\gamma).G + ({}^{B}w/d)).N - ({}^{M}r - (f^{d}.{}^{C}w/d)).M + (E_{3,5}.M_5/d)$$

$$dM_1/dt = (1-\gamma).G.N_1 - ({}^{M}r_1 + (({}^{C}w_1+D)/h_1)).M_1 + E_{1,3}.(M_3-M_1)/h_1$$

$$dM_3/dt = ((1-\gamma).G + ({}^{B}w_3/h_3)).N_3 - {}^{M}r_3.M_3 + ({}^{C}w_1.M_1 + E_{3,5}.M_5 - f^{d}.{}^{C}w_3.M_3)/h_3 + (E_{3,1}.(M_1-M_3) - W.(M_3-M_{plateau[1]}))/h_3 \qquad : h_3>0;$$

$$M_3 = M_{plateau[1]} \qquad : h_3=0.$$

${}^{M}r$: detrital N respiration rate (d^{-1}), function of temperature and detrital N:C ratio:

$${}^{M}r = f(\theta).{}^{M}r_{max}.f(M/C)$$

Microplankton nitrogen biomass: **N** mmol N m^{-3}

$$dN/dt = u.B - (G + {}^{B}w/d).N$$
$$dN_1/dt = u_1.B_1 - (G + (({}^{B}w_1+D)/h_1)).N_1 + (E_{1,3}.(N_3-N_1)\ )/h_1$$
$$dN_3/dt = u_3.B_3 - (G + ({}^{B}w_3/h_3)).N_3$$
$$+ ({}^{B}w_1.N_1 + E_{3,1}.(N_1-N_3) - W.(N_3-N_{plateau[1]}))/h_3 \quad : h_3>0;$$
$$N_3 = N_{plateau[1]} \quad : h_3=0.$$

u : microplankton nitrogen uptake rate (mmol N (mmmol C)$^{-1}$ d^{-1}), given by

$$u = {}^{NH}u + {}^{NO}u$$

where superscripts **NH** and **NO** refer to ammonium or nitrate; the generalized uptake equation is:

$$u = u_{max}.(1-(Q/Q_{max})).(S/(S_{1/2}+S))$$

Dissolved oxygen concentration: **O** mmol O m^{-3}

$$dO/dt = ({}^{O}q^{B}.\mu + {}^{O}q^{NO}.{}^{NO}u).B - {}^{O}q^{NH}.{}^{NH}r.{}^{NH}S - {}^{O}q^{C}.{}^{C}r.C$$
$$+ (\{air\text{-}sea\ flux\} - \{sediment\ flux\})/d$$
$$dO_1/dt = ({}^{O}q^{B}.\mu_1 + {}^{O}q^{NO}.{}^{NO}u_1).B_1 - {}^{O}q^{NH}.{}^{NH}r_1.{}^{NH}S_1$$
$$- {}^{O}q^{C}.{}^{C}r_1.C_1 + (E_{1,3}.(O_3-O_1) + \{air\text{-}sea\ flux\})/h_1$$
$$dO_3/dt = ({}^{O}q^{B}.\mu_3 + {}^{O}q^{NO}.{}^{NO}u_3).B_3 - {}^{O}q^{NH}.{}^{NH}r_3.{}^{NH}S_3 - {}^{O}q^{C}.{}^{C}r_3.C_3$$
$$+ (E_{3,1}.(O_1-O_3) - W.(O_3-O_{plateau[1]}) - \{sediment\ flux\})/h_3 \quad : h_3>0;$$
$$O_3 = O_{plateau[1]} \quad : h_3=0.$$

Ammonium concentration: ^{NH}S mmol N m^{-3}

$$d{}^{NH}S/dt = -{}^{NH}u.B - {}^{NH}r.{}^{NH}S + e.\gamma.G.N + {}^{M}r.C + (\{sediment\ flux\})/d$$
$$d{}^{NH}S_1/dt = -{}^{NH}u_1.B_1 - {}^{NH}r_1.{}^{NH}S_1 + e.\gamma.G.N_1 + {}^{M}r_1.C_1$$
$$+ (E_{1,3}.({}^{NH}S_3-{}^{NH}S_1)\ )/h_1$$
$$d{}^{NH}S_3/dt = -{}^{NH}u_3.B_3 - {}^{NH}r_3.{}^{NH}S_3 + e.\gamma.G.N_3 + {}^{M}r_3.C_3$$
$$+ (E_{3,1}.({}^{NH}S_1-{}^{NH}S_3) - W.({}^{NH}S_3-{}^{NH}S_{plateau[1]}) - \{sediment\ flux\})/h_3 : h_3>0;$$
$${}^{NH}S_3 = {}^{NH}S_{plateau[1]} \quad : h_3=0.$$

^{NH}r : ammonium nitrification rate (d^{-1}), function of temperature and oxygen concentration:

$${}^{NH}r = f(\theta).{}^{NH}r_{max}.O/(O_{1/2,nit}+O)$$

Nitrate concentration: ^{NO}S mmol N m^{-3}

$$d{}^{NO}S/dt = -{}^{NO}u.B + {}^{NH}r.{}^{NH}S - (\{sediment\ flux\})/d$$
$$d{}^{NO}S_1/dt = -{}^{NO}u_1.B_1 + {}^{NH}r_1.{}^{NH}S_1 + (E_{1,3}.({}^{NO}S_3-{}^{NO}S_1)\ )/h_1$$
$$d{}^{NO}S_3/dt = -{}^{NO}u_3.B_3 + {}^{NH}r_3.{}^{NH}S_3$$
$$+ (E_{3,1}.({}^{NO}S_1-{}^{NO}S_3) - W.({}^{NO}S_3-{}^{NO}S_{plateau[1]}) - \{sediment\ flux\})/h_3 : h_3>0;$$
$${}^{NO}S_3 = {}^{NO}S_{plateau[1]} \quad : h_3=0.$$

the difference (Δ**s**) between model-predicted salinities in the surface layers of the "Golfe" and "Plateau" columns, coupled the entrained flux of sea water (**W**) to the freshwater discharge (**D**) into the Gulf :

$$\mathbf{W} = \mathbf{m_E} \cdot \Delta s\,.\mathbf{D} \qquad [3]$$

Both the flux and the discharge are expressed per unit surface area of the Gulf, and are thus best understood as the rate of elevation of the pycnocline by the intruding salt wedge from the "Plateau" site (**W**) and the potential rate of elevation of the sea-surface in the Gulf due to the freshwater discharge (**D**). Since the simulated depth **d** of the "Golfe" water column remains constant, conservation of mass requires that the "Golfe" [1] layer exports water at **D + W** per unit area.

In the absence of data from the Gulf of Lions, the model was run to simulate seasonal cycles of water temperature and thermocline depth for the "Plateau" column, which was given a depth of 50 m. The seawards boundary condition was equivalent to a dilution of the deep water in the Gulf of Lions at about 2 % per day, by water of 10 °C and 38 psu in a Liguro-Provencal current (Massé, 1993) of constant properties.

Table III. – Parameter and initial values.

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physical structure

Surface area of Gulf of Fos and thus of "Golfe" column : 45 x 106 m^2.
d : mean depth of Gulf of Fos and thus of "Golfe" water-column : 8 m.
Depth of "Plateau" water-column: 50 m.
h_5 : thickness of benthic (oxic sediment) layer in Gulf : 0.05 m.

exact or approximate physical constants

a : coefficient of thermal expansion of seawater (at 15°C and 35 psu): 0.00021 °C^{-1};
b : coefficient of haline contraction of seawater (at 15°C and 35 psu): 0.00078 psu $^{-1}$;
c : specific heat of seawater : 3900 J kg^{-1} °C^{-1};
g : gravitational acceleration : 9.81 m s^{-2};
$^{air}\rho$, ρ : air and seawater densities : 1 and 1025 kg m^{-3};

other physical and optical parameters

A_5 : concentration of fine inorganic sediment in benthic layer : 200 kg m^{-3}; [1]
f_0, f_3 : efficiencies of surface, wind (0.0029 or 0.0020 [a]) and seabed, tidal (0.004) mixing; [2]
k_0, k_3 : surface, wind (0.0014 or 0.0007 [a]) and seabed, tidal (0.0025) drag coefficients; [2]
m_0 : 1.91 μE PAR per J total solar irradiance; [3]
m_1 : optical coefficient (0.95) allowing for surface reflection; [3]
m_2: factor (0.37) correcting for near-surface deviations from exponential decay of light; [3]
^{A}w : sinking rate of fine inorganic sediment : 1.5 m d^{-1}. [1]
$^{A}\varepsilon$: attenuation cross-section of suspended inorganic sediment: 0.1 m^2 g^{-1}; [4]
$^{C}\varepsilon$: attenuation cross-section of organic detritus: 0.001 m^2 (mmol C)$^{-1}$; [5]
$^{X}\varepsilon$: attenuattion cross-section of microplankton: 0.02 m^2 (mg chl)$^{-1}$; [5]
$^{SW}\lambda$: attenuation coefficient due to clear coastal seawater : 0.10 m^{-1}; [4]

[1] : estimated by least-squares fit of model predictions to observed inorganic SPM.
[2] : Clarke, 1986, or [a] reduced from Clarke values in case of shallow water of Gulf.
[3] : Tett (1990b)
[4] : estimated by fitting model to North Sea data - Tett & Walne, submitted.
[5] : Tett (1990a)

microbiological parameters

e : excreted fraction of grazed and assimilated microplankton nitrogen : 0.5;
$O_{1/2,max}$: half-saturation constant for nitrogen-dependent detrital carbon respiration : 10 mmol dissolved oxygen m^{-3};
$O_{1/2,min}$: half-saturation constant for minimum detrital carbon respiration : 1 mmol dissolved oxygen m^{-3};
$O_{1/2,nit}$: half-saturation constant for ammonium oxidation: 30 mmol dissolved oxygen m^{-3};
Q_{max} : maximum microplankton nitrogen to carbon: 0.20 mmol N (mmol C)$^{-1}$;
Q_{min} : minimum microplankton nitrogen to carbon : 0.05 mmol N (mmol C)$^{-1}$;
$O_q{}^B$: photosynthetic quotient for carbon assimilation : 1 mmol O (mmol C)$^{-1}$;
$O_q{}^C$: respiratory quotient for detrital carbon : 1 mmol O (mmol C)$^{-1}$;
$O_q{}^{NH}$: 'respiratory' quotient for nitrification : 2 mmol O (mmol N)$^{-1}$;
$O_q{}^{NO}$: photosynthetic quotient for nitrate assimilation : 2 mmol O (mmol N)$^{-1}$;
$^{M}Q^{C}{}_{min}$: minimum detrital nitrogen : 0.06 mmol N (mmol C)$^{-1}$;
$^{X}Q^{N}{}_{max}$: maximum microplankton chlorophyll to nitrogen: 2.0 mg chl (mmol N)$^{-1}$;
$^{X}Q^{N}{}_{min}$: minimum microplankton chlorophyll to nitrogen: 1.0 mg chl (mmol N)$^{-1}$;
r : factor relating microplankton respiration to growth rate: 0.6; [a]
$r^{B}{}_{0}$: microplankton biomass-related basal respiration : 0.04 d^{-1} ;
$^{C}r_{max}$: maximum (nitrogen-dependent) detrital carbon respiration at 20°C: 0.08 d^{-1}; [a]
$^{C}r_{min}$: minimum detrital carbon respiration at oxygen saturation & 20°C: 0.0005 d^{-1};
$^{M}r_{max}$: maximum relative rate of detrital nitrogen remineralization at 20°C: 0.06 d^{-1}; [a]
$^{NH}r_{max}$: maximum relative rate of ammonium oxidation at 20°C: 1.0 d^{-1};
$S_{1/2}$: half-saturation constant for nutrient uptake : 0.24 mmol ammonium m^{-3}, 0.32 mmol nitrate m^{-3};
u_{max} : maximum microplankton nutrient uptake rate : 1.0 mmol ammonium (mmmol C)$^{-1}$ d^{-1}, 0.4 mmol nitrate (mmmol C)$^{-1}$ d^{-1};
^{C}w : detrital sinking rate : 0.5 m d^{-1}; [b]
α : microplankton photosynthetic 'efficiency' : 0.07 mmol C (mg chl)$^{-1}$ d^{-1} (μE PAR m^{-2} s^{-1})$^{-1}$;
γ : fraction of grazed microplankton that is assimilated by zooplankton: 0.7; [a]
μ'_{max} : maximum microplankton relative growth rate at 20°C: 2.0 d^{-1};

Source : Tett (1990a) with [a] some modifications; detrital sinking rate [b] estimated for Gulf from least squares fit of model predicted to observed organic SPM.

Initial values of state variables for "Golfe"

$\mathbf{B_1 = B_3}$: 1.0 mmol (organic) C m^{-3};
$\mathbf{C_1 = C_3}$: 1.0 mmol (organic) C m^{-3};
$\mathbf{C_5}$: 1.5 kmol (organic) C m^{-3};
$\mathbf{M_1 = M_3}$: 0.1 mmol (organic) N m^{-3};
$\mathbf{M_5}$: 0.093 kmol (organic) N m^{-3};
$\mathbf{N_1 = N_3}$: 0.2 mmol (organic) N m^{-3};
$\mathbf{O_1 = O_3 = O_5}$: 300 mmol O_2 m^{-3};
$\mathbf{^{NH}S_1 = {}^{NH}S_3}$: 0.0 mmol (ammonium) N m^{-3};
$\mathbf{^{NH}S_5}$: 10.0 mmol (ammonium) N m^{-3};
$\mathbf{^{NO}S_1 = {}^{NO}S_3}$: 4.0 mmol (ammonium) N m^{-3};
$\mathbf{^{NO}S_5}$: 10.0 mmol (ammonium) N m^{-3};
Dissolved concentrations in layer [5] refer to pore water, which made up 80% of volume in the layer.

The value of the entrainment multiplier coefficient ($\mathbf{m_E}$) was estimated as 3 psu^{-1}, by least-squares fit of salinities predicted by the model to salinities (n = 10) observed in the Gulf during 1986. The mean dilution time-scale of 20 days for the surface layer calculated for the estuarine circulation in 1986 may be contrasted with the 1 day time-scale estimated (from currents predicted by the 2D, vertically-integrated, model of Millet (*in* Grenz, 1989)) for replacement of the entire contents of the Gulf by a Mistral wind of 15 m s^{-1}. These results imply that periods of slow estuarine circulation (which perhaps exists, in reality, only in the deeper parts of the Gulf) alternate with episodes of rapid, wind-driven flushing.

The microbiological model

The biological model (Fig. 7) is that of L3VMP (Tett, 1990a). It describes autotrophic and heterotrophic microbial processes producing and consuming organic carbon and chlorophyll, and

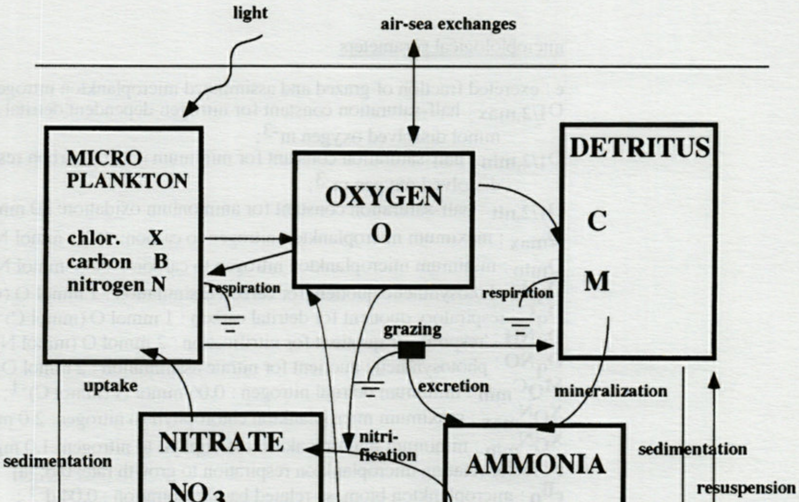

Fig. 7. – Biological and chemical compartmentalisation in the model.

cycling nitrogen through inorganic and organic forms. The fast-cycling compartment is called **microplankton** because it includes water-column micro-heterotrophs as well as micro-algae. The heterotrophs are bacteria and protozoa with growth that depends directly on algal production, and with a growth rate which is sufficiently tightly coupled to algal growth for the micro-heterotrophic metabolism to be treated simply as an extra source of respiration on a one-day timescale. Ammonium excreted by the protozoa is assumed to be immediately taken up by the algal component of the microplankton.

This combination of phytoplankton and fast-growing micro-heterotrophs avoids the need to model in detail the algal extra-cellular production, and the growth and consumption of bacteria and protozoa, required by an explicit description of the "microcycle" (Williams, 1981). As a result, the primary production predicted by L3VMP, from the product $\mu \cdot \mathbf{B}$ of microplankton relative growth rate and biomass, is "net microplankton community production", approximately what would be measured by the ^{14}C method with 24-hour incubations (Tett *et al.*, 1993).

The microplankton compartment is quantified by concentrations of organic carbon **B**, nitrogen **N** and chlorophyll **X**. Microplankton growth is predicted with a 'cell-quota, threshold-limitation' equation :

$$\mu = L\{\mu'_{\mathbf{max}} \cdot (\mathbf{1\text{-}k_Q/Q}), \\ (a \cdot \mathbf{I} - \mathbf{r^B{}_0}) \cdot x/(\mathbf{1 + b})\} \tag{4}$$

originally proposed for algae, and here modified from Tett & Droop (1988). In this equation, which assumes linear averaging of relevant processes over 24 hours, the "least-of" operator *L{...,...}* stipulates that the rate of growth is controlled by *either* a saturation function of the cellular ratio **Q** of nitrogen to carbon, *or* the net rate of photosynthesis, whichever is computed to be the least on a particular day. Net photosynthesis includes losses due to algal and microheterotroph respiration. These losses are assumed to be mainly proportional to growth rate while the 24-hr mean irradiance **I** experienced by the microplankton exceeds the compensation irradiance $\mathbf{I_c}$ at which $a \cdot \mathbf{I} = \mathbf{r^B{}_0}$.

Microplankton carbon thus increases as a result of growth, or decreases because of basal respiratory loss when $\mathbf{I' < I_c}$. Microplankton nitrogen increases as a result of nutrient uptake, which is a saturation function of sea-water concentrations of nitrate and ammonium, modified by the capacity of the microplankton for nitrogen storage. Ammonium uptake is given a lower half-saturation constant than nitrate uptake, but there is no competitive inhibition. Microplankton chlorophyll content **c** is made dependent on nitrogen content, with a higher yield of new chlorophyll from assimilated nitrogen when the simulated cells are nitrogen-replete, thus providing as simple mechanism for light and shade adaptation as a response to a changing balance between light and nutrient limitation of growth. Microplankton sinking rate is also made a function of increasing nitrogen content. Pending further investigation, model parameters for maximum cell nitrogen quota, maximum nitrogen uptake rate, and chlorophyll : nitrogen ratios, were made 80 % of values (Tett & Droop, 1988) appropriate for algae, in order to compensate for the inclusion of microheterotroph biomass in the microplankton.

Because the aim is to model microbial dynamics as simply as possible, L3VMP contains no explicit compartment for mesozooplankton. In-

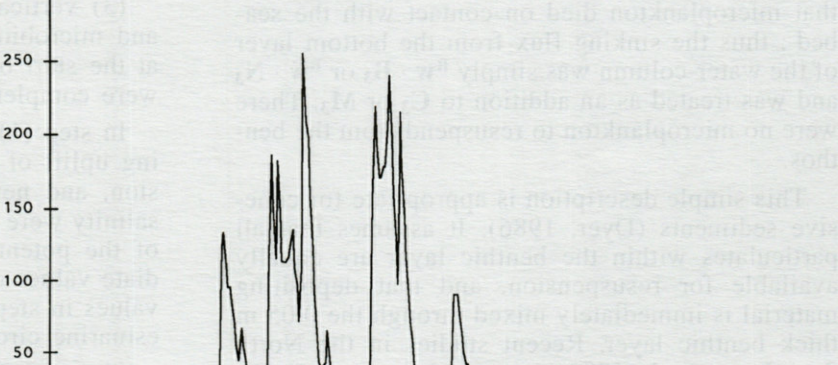

Fig. 8. – Predicted (solid line) suspended particulate matter (SPM) in 1986, compared with observations (squares) in Carteau Cove.

stead, the impact of these animals is parameterised by a grazing pressure **G**, which may either be calculated from observed abundances of mesozooplankton (Tett, 1990a ; Tett *et al.* 1993) or be used as a free variable in fitting the model to observations of chlorophyll concentration (Woods & Tett, submitted). Grazing converts some nitrogen instantly to ammonium, simulating mesozooplankton excretion ; another part of the microplankton particulate material is converted to detritus. All microplankton sinking from the bottom water-column layer are assumed to die, and thus to be converted instantly to detritus, on contact with the sea-bed.

As already mentioned, detritus may deposit into the sediment layer, or be resuspended, according to the bottom stress. Detrital mineralisation processes are assumed to be qualitatively similar in the water-column and in the benthos, but to take place more slowly in the latter because of the lower concentrations of oxygen in the sediment pore-water. Details are given by Tett (1990a). At this stage the model does not include anoxic processes such as denitrification, and hence the simulated sediment cannot act as a nitrate sink.

The resuspension model

We modelled the net sediment-water flux of a particulate as the difference between deposition and resuspension. Under stratification, the resuspension flux of inorganic sediment is $\boldsymbol{f}_{\mathbf{e}}(\mathtt{t}_3,\mathtt{t}_c) \cdot \mathbf{A}_5$, and the deposition flux is $\boldsymbol{f}_{\mathbf{d}}(\mathtt{t}_3,\mathtt{t}_c) \cdot {}^{A}\mathbf{w}.\mathbf{A}_3$, where $\mathbf{A}_5$ is the concentration in the benthic layer and $\mathbf{A}_3$ is the concentration in the overlying water layer. Erosion takes place when the actual bottom stress $\mathtt{t}_3$ exceeds a critical stress $\mathtt{t}_c$; otherwise there is deposition. The erosion function $\boldsymbol{f}_{\mathbf{e}}$ has the units of velocity, whereas the deposition function $\boldsymbol{f}_{\mathbf{d}}$ is a fraction (0-1) which reduces the free-water sinking rate. Similar descriptions were used for detrital carbon and nitrogen. It was assumed that microplankton died on contact with the sea-bed ; thus the sinking flux from the bottom layer of the water-column was simply ${}^{B}\mathbf{w} \cdot \mathbf{B}_3$ or ${}^{B}\mathbf{w} \cdot \mathbf{N}_3$ and was treated as an addition to $\mathbf{C}_3$ or $\mathbf{M}_3$. There were no microplankton to resuspend from the benthos.

This simple description is appropriate for cohesive sediments (Dyer, 1986). It assumes that all particulates within the benthic layer are equally available for resuspension, and that depositing material is immediately mixed through the 0.05 m thick benthic layer. Recent studies in the North Sea (Jago *et al.*, 1993) suggest that resuspension models should include a layer of recently settled "fluff" as a buffer between SPM in the water-column and the consolidated material in the benthic layer. Finally, L3VMP ignores the contribution that the micro-phytobenthos makes (Plante-Cuny & Bodoy,1987) to production in these shallow waters.

Optical model

In shallow, potentially turbid or potentially eutrophic waters such as the Gulf of Fos, it is important to take into account the contributions of phytoplankton and suspended particulates to light attenuation. Following Tett (1990b), mean photosynthetically available radiation (PAR) in the surface layer was calculated from

$$[5] \quad \mathbf{I}_1 = \mathbf{m}_0 \cdot \mathbf{m}_1 \cdot \mathbf{m}_2 \cdot \mathbf{E}_0 \cdot (\mathbf{1\text{-}e}^{-\mathtt{l}\mathbf{1} \cdot \mathbf{h1}})/(\mathtt{l}\mathbf{1} \cdot \mathbf{h}_1)$$

where $\mathbf{E}_0$ is the 24-hour mean of the total solar irradiance at the sea surface, and PAR diffuse attenuation is given by

$$[6] \quad \mathtt{l}_1 = {}^{sw}\mathtt{l} + {}^{X}\mathtt{e} \cdot \mathbf{X}_1 + {}^{A}\mathtt{e} \cdot \mathbf{A}_1 + {}^{C}\mathtt{e} \cdot \mathbf{C}_1.$$

which shows the contributions of particle-free seawater, chlorophyll, inorganic SPM, and organic detritus. The $\mathtt{e}$ terms are attenuation cross-sections, the amount of diffuse attenuation caused by unit concentration of each light absorber.

USING THE MODEL

Numerical methods

Solutions to the equations were found by numerical integration, forced by time-varying boundary conditions, and starting from the initial conditions given in Table III. The equations were separated into groups of terms, which were then solved sequentially for a time-step of 1 day. The order was :

(1) lateral inputs and estuarine circulation, using Euler forward-difference ;

(2) vertical mixing, using algorithms based on Clarke (1986) ;

(3) vertical (boundary fluxes, layer exchanges) and microbiological processes, preserving values at the start of the time-step until all calculations were completed.

In step (1), $\mathbf{h}_1$ was replaced by $\mathbf{h}_1$-$\mathbf{W}$, simulating uplift of the pycnocline by salt-wedge intrusion, and new values of layer temperatures and salinity were calculated, leading to a revised value of the potential energy anomaly. These intermediate values of $\mathbf{h}_1$ and $\mathbf{F}$ were then used as initial values in step (2). Step (1) was omitted when the estuarine circulation was "turned off".

Slow processes in group (3) were integrated by the Euler forward-difference method. Sediment-water exchanges of oxygen and DIN, which were very rapid in relation to the buffering capacity of the sediment pore-water, were integrated by the same method, but with reduced time-step to avoid instability. Equations for 'fast' microplankton processes such as growth, or nutrient uptake, were integrated analytically to allow calculation with a time-step of 1 day (corresponding to the process time-scale assumed by the cell-quota, threshold limitation, model) without numerical instabilities. For example, in the case of microplankton biomass, the change $\Delta\mathbf{B}$ was calculated from :

$$[7]\ (a)\quad \mathbf{B'} = \mathbf{B_t} \cdot (exp((\mu\text{-}G) \cdot \Delta t) - 1)/(\mu\text{-}G)$$

$$(b)\qquad \Delta\mathbf{B} = (\mu - G) \cdot \Delta t \cdot \mathbf{B'} - \phi/h$$

where **B'** is the mean biomass over the time-step Δt, at the beginning of which the biomass was $\mathbf{B_t}$. The sinking flux from unit surface area of, for example, layer [1] was computed from :

$$(c)\ \phi_1 = (1 - exp\,(-\,^{B}w_1 \cdot \Delta t/h_1)) \cdot B_1' \cdot h_1.$$

The scheme for separating the main terms of the equations implies that model predictions were not necessarily precise for any one time-step ; however, the property of conserving carbon and nitrogen ensured the accuracy of predictions on longer time-scales.

The solutions were written as a Pascal program to run on an Apple Macintosh computer using the 'Think Pascal' programming environment. Initial values and forcing meteorological and grazing data were read in from text files. Daily values of the state variables and derived fluxes were stored as text files, and subsequently further processed using Microsoft 'Excel'.

Parameter values and boundary conditions

As noted in Table III, most parameter values were taken from the literature. The boundary conditions were the concentrations in the "Rivière" and "Mer" boxes in Fig. 6, and the inputs from these to the "Golfe" [1] and "Plateau" [3] layers. As already mentioned, the freshwater discharge for the standard simulation was assumed to be 1 % of the Rhône flow, taking the latter from the 1986 data shown in Fig. 2 A. The nitrate concentration in this freshwater was taken as a constant 100 µM (El Habr & Golterman, 1987). Temperature, salinity and nitrate in the "Plateau" [3] layer were forced towards the constant 10 °C, 38 psu and 5 µM nitrate assumed for the "Mer" box by a simple relaxation condition, exemplified for temperature by

$$[8]\quad \mathbf{d\theta_{plateau[3]}/dt = -\ k \cdot (\theta_{plateau[3]} - \theta_{mer})}$$

where **k** was 0.02 d^{-1}. Meteorological data for 1986 (Fig. 2 B) were obtained from Météo France at Marignane, close to the Gulf of Fos. A test of the stratification and circulation models is shown in Fig. 5, which compares observed and predicted temperatures in the surface layer of the Gulf. Additionally, forcing the model with 1990 meteorological and river data predicted salinity stratification in the Gulf exceeding 4 psu on 20 % of days, and less than 1 psu on 34 % of days. The mean difference between layer [1] and [3] was 2.3 psu. This may be compared with the short-period observations in Carteau Cove during Autumn 1993, which showed the mean surface-bottom difference as 3.7 psu, with > 4 psu in 30 % of records and < 1 psu in 38 % of records.

Parameter values for detrital mineralisation and pore-water exchange were adjusted to give nutrient fluxes corresponding to those observed during the 1987 studies with benthic chambers (Baudinet *et al.* 1989 ; Barranguet & Aliot, ms). Resuspension parameters were estimated by least-squares fit of model predictions for inorganic and organic SPM to observations in 1986. As Fig. 9 shows, the observations were made during periods

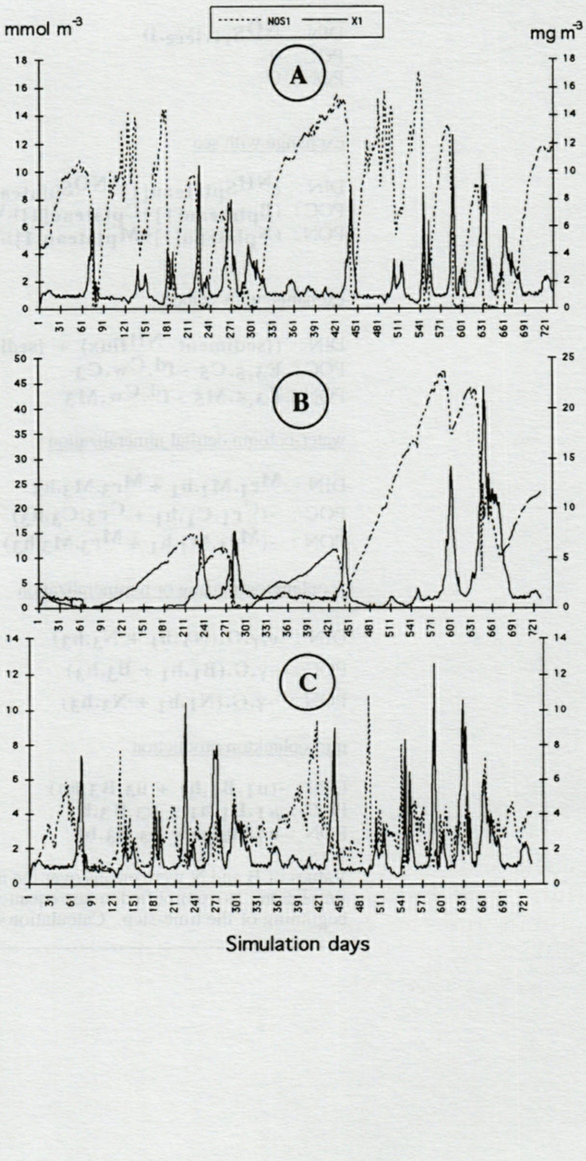

Fig. 9. – Chlorophyll and nitrate predicted over 2 years from 1986 meteorological and river flow data : A : standard run ; B : without circulation ; C : without resuspension of inorganic sediment.

of fair weather, and we have no way of checking the predictions for periods of high wind stirring.

It was decided not to impose a seasonal cycle of mesozooplankton grazing at this stage. Instead, the grazing pressure, **G**, was estimated as a constant 0.2 d^{1} on the basis of mean abundances in Patriti (1984).

The standard simulation

The "standard run" of the model (Fig. 9 A) included all the features already mentioned, including freshwater-driven circulation, and wind-wave-driven resuspension of particulates at the "Golfe" site. In order to initialise conditions at the "Plateau" site the model was run for this site alone for a preliminary two years. Table V gives the predicted organic carbon and nitrogen budgets for the "Golfe" site during the next two simulated years, starting from typical observed mid-Winter values of the state variables. Equations used for calculating fluxes are listed in Table IV. At 69 to 86 g C m^{-2} yr^{-1}, predicted microplankton production was at the lower end of the range of 71 to 140 g C m^{-2} yr^{-1} estimated using $_{14}C$ by Folack (1986).

All simulated years were forced by 1986 meteorological and river flow data in order to test the long-term stability of the model. Consequently, the decrease in total nitrogen at the

Table IV. – Flux equations.

POC : particulate organic carbon (in microplankton and detritus);
DIN : dissolved inorganic nitrogen - nitrate and ammonium;
PON : particulate organic nitrogen (in microplankton and detritus);

Terms are given for stratified conditions and predict fluxes in mmol m^{-2} d^{-1}. A positive value indicates a gain by the "Golfe" water-column.

input from river

DIN : ${}^{NO}S_{\text{rivière}}.D$
POC : 0
PON : 0

exchange with sea

DIN : $({}^{NH}S_{plateau[1]}+{}^{NO}S_{plateau[1]}).W - ({}^{NH}S_{1}+{}^{NO}S_{1}).(D+W)$
POC : $(B_{plateau[1]}+C_{plateau[1]}).W - (B_{1}+C_{1}).(D+W)$
PON : $(N_{plateau[1]}+M_{plateau[1]}).W - (N_{1}+M_{1}).(D+W)$

exchange with seabed

DIN : $(\{\text{sediment } {}^{NH}\text{flux}\} + \{\text{sediment } {}^{NO}\text{flux}\})$
POC : $E_{3,5}.C_{5} - f^{d}.{}^{C}w.C_{3}$
PON : $E_{3,5}.M_{5} - f^{d}.{}^{C}w.M_{3}$

water-column detrital mineralization

DIN : ${}^{M}r_{1}.M_{1}.h_{1} + {}^{M}r_{3}.M_{3}.h_{3}$
POC : $-({}^{C}r_{1}.C_{1}.h_{1} + {}^{C}r_{3}.C_{3}.h_{3})$
PON : $-({}^{M}r_{1}.M_{1}.h_{1} + {}^{M}r_{3}.M_{3}.h_{3})$

zooplankton grazing or remineralization

DIN : $e.\gamma.G.(N_{1}.h_{1} + N_{3}.h_{3})$
POC : $-\gamma.G.(B_{1}.h_{1} + B_{3}.h_{3})$
PON : $-\gamma.G.(N_{1}.h_{1} + N_{3}.h_{3})$

microplankton production

DIN : $-(u_{1}.B_{1}.h_{1} + u_{3}.B_{3}.h_{3})$
POC : $\mu_{1}.B_{1}.h_{1} + \mu_{3}.B_{3}.h_{3}$
PON : $u_{1}.B_{1}.h_{1} + u_{3}.B_{3}.h_{3}$

Values of **B** and **N** were means over the time-step (**Δt** = 1 day) used in the numerical simulations, as exemplified in text equation [6]. Other concentrations were those at the beginning of the time-step. Calculation of uptake rates obeyed: **u.B.Δt < S**.

"Golfe" site, from an initial value of 4.7 mol N m^{-2}, to 1.7 mol N m^{-2} after two years (Table V), shows that the model is not able, with current parameter values, to provide an explanation for the maintenance of nitrogen in the Gulf of Fos which can be deduced from observed long-term constancy in mean sediment and water-column organic content.

The explanation is that the model exports more nitrogen from the "Golfe" site than is imported in freshwater. This loss is most evident in particulate organic nitrogen. The error seems to lie mainly in the resuspension model, which injects large amounts of benthic detrital nitrogen into the water-column during periods of strong wind-stirring. Much of this suspended particulate nitrogen is exported by the simulated estuarine circulation. In reality, the benthos should, during a year, receive a net input of particulate organic nitrogen, as sedimenting detritus, sufficient to compensate for the export of mineralised DIN from the sediment into the water-column.

Some simple numerical experiments

Despite this fault, which itself gives some insight into the importance of organic deposition and resuspension in shallow-water coastal ecosystems, we can still use the model to carry out simple numerical experiments. Two obvious tests are to remove (1) the estuarine circulation, and (2) the resuspension of light-absorbing inorganic particulates.

The effect of turning off the estuarine circulation is to reduce primary production in the first simulated year (to 38 g C m^{-2} yr^{-1}). Production is however restored (to 75 g C m^{-2} yr^{-1}) during the second year. As Fig. 9 B shows, the explanation is that nutrient levels are decreased in year 1 by the lack of a contribution from the Rhône, but that more nutrients are available in year 2 as a result of sustained benthic remineralisation without export of water-column DIN or particulate nitrogen.

The effect of turning off the resuspension of inorganic particulates (Fig. 9 C) is that now only self-shading or nutrient depletion can limit microplankton growth. Predicted chlorophyll concentrations are generally higher, and annual production is more than doubled (130 - 190 g C m^{-2} yr^{-1}).

Short-term dynamics

The difficulties in creating a long-term balance in nitrogen do not prevent us employing the model to gain insights into the short-term dynamics of microplankton. Model results emphasise the high-frequency variability of the pelagic ecosystem in the Gulf of Fos. The pattern of change is very different from the seasonality expected at this latitude. In the case of the oceans, deep mixing in Winter prevents phytoplankton growth until the vernal onset of stratification allows the Spring Bloom. Nutrient depletion thereafter restricts microalgal biomass in the surface mixed layer until

Table V. – Results of the standard run.

A. Total nitrogen budget		at day	*0*	*365*	*730*	
	in water-column		34	130	128	mmol N m^{-2}
	in sediment layer		4651	2840	1526	
	total		4685	2970	1654	
	change over year			-1715	-1316	
	explained by fluxes			-1714	-1317	
	numerical error			-1	1	

B. Annual fluxes	Exchanges -------------------------				In water column -----------------------		
	from River	from Sea	from Benthos ------------- Suspension	Pore water	Detrital mineralization	Zooplankton grazing/remin.	Microplankton production
day 1-365							
Particulate organic C	0	-27989	26537	0	-1813	-2262	5739
Nitrate + ammonium	1198	-878	0	386	127	182	-951
Particulate organic N	0	-1852	1422	0	-127	-364	951
day 366-730							
Particulate organic C	0	-14906	12962	0	-2361	-2889	7142
Nitrate + ammonium	1198	-1149	0	719	200	234	-1199
Particulate organic N	0	-1132	598	0	-200	-468	1199

Notes

1. Fluxes are given in mmol m^{-2} yr^{-1}. Positive values are gains by "Gulfe" water-column.
2. Total nitrogen is sum of microplankton N, detrital N, nitrate, and ammonium.

thermocline ventilation encourages an Autumn Bloom. In the case of the Gulf of Fos, however, shallow waters potentially allow phytoplankton growth at any time of the year. Restrictions are imposed by turbidity and nutrient depletion.

A characteristic sequence of events is thus as follows. (1) High SPM levels following storms cause a decrease in submarine PAR, with the result that microplankton growth rates are less than losses due to grazing and export. Benthic and water-column remineralisation, and the Rhône inflow, bring about an increase in water-column DIN. (2) As particulate material is exported, or re-deposited to the sediment, the water clears, resulting in rapid growth of phytoplankton. (3) Chlorophyll concentrations increase until self-shading, or nutrient depletion, restricts further growth. Fig. 10 shows a predicted sequence of such events, each lasting 10 - 30 days and separated by 30 - 80 days. These time-scales must result from the interval between major storms and from the typical 20 days residence time of water in the Gulf. Of course, these predictions do not include the effects of wind-driven water exchange, but these latter are likely to intensify the episodic nature of change.

CONCLUSIONS

Although, as Fig. 10 demonstrates, detailed agreement between simulated and observed chlorophyll concentrations was poor, the Figure does suggest that the simulated timescale of chlorophyll variability is about right. Precise prediction was not the aim at this stage. Instead, the construction of a simple, holistic, model that coupled physical and microbiogeochemical processes has given us some important insights into ecosystem function in the Gulf of Fos and has provided guidance about sampling strategies. The insights concern (1) the rôle of the Gulf in cycling land-derived nutrients before they reach the open sea ; (2) the importance of particulate resuspension in controlling light availability for photosynthesis and the export of organic material ; and (3) the frequency of variability in a shallow, wind-forced system. The third insight has, in particular, shown the need to sample more frequently than the monthly intervals initially employed to study conditions in the Gulf. Our new knowledge of the importance of high-frequency variation also emphasises the requirement to take account of wind-driven lateral exchange. Finally, the difficulties in maintaining the long-term constancy of ecosystem nitrogen point to the need for a better resuspension model.

ACKNOWLEDGEMENTS – Work described here was partly supported by : the Groupement Scientifique : *Cycles biogéochimiques. Devenir de la matière organique en zone littorale* (G.S. – CNRS – SN Elf Aquitaine – Univ. Aix-Marseille II & III) ; and the Programme National d'Océanographie Côtière – Chantier Méditerranéen (PNOC-CNRS). We are grateful to D.Bowers (University of Wales, Bangor) for advice on the physical model.

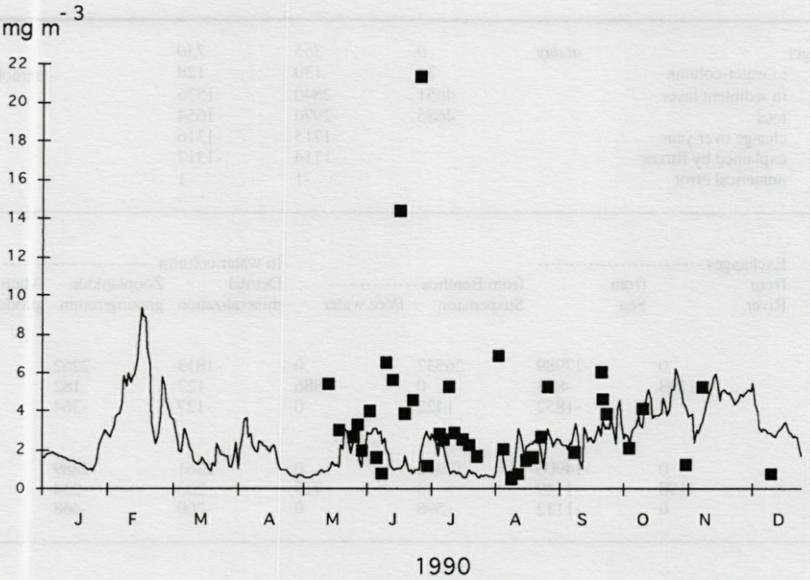

Fig. 10. – Chlorophyll concentrations during part of 1990. Predictions (solid line) forced by 1990 meteorology and river flows. Observations in Carteau Cove shown by squares.

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Reçu le 16 juillet 1993 ; received July 16, 1993
Accepté le 10 janvier 1994 ; accepted January 10, 1994

VIE MILIEU, 1994, 44 (1) : 59-68

ARE SIZE-SPECTRA OF MESOZOOPLANKTON A GOOD TAG FOR CHARACTERIZING PELAGIC ECOSYSTEMS ?

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STRUCTURE DE TAILLE
COPÉPODES
RÉPARTITION LATITUDINALE

RÉSUMÉ – La description des écosystèmes est passée progressivement d'une approche systématique à une représentation plus abstraite. La théorie structurale dimensionnelle de Sheldon permet de faire l'hypothèse d'une répartition prédictible des spectres de biomasses le long de gradients latitudinaux. La répartition des classes de taille des Copépodes a été faite à partir du matériel de quatre missions du N/O " Marion – Dufresne " dans l'Océan Indien et son secteur antarctique, recoupant cinq zones hydrologiques. Une analyse factorielle montre que chaque zone est caractérisée par un spectre de taille (classes de taille, nombres d'individus et biomasses). Le nombre des Copépodes montre une tendance décroissante des petites vers les grandes tailles pour chacune des zones – à l'exception des îles – sans toutefois atteindre le niveau d'égalité des biomasses dans la gamme du spectre entre petites et grandes formes (pente – 0,3 au lieu de la valeur théorique de – 1).

COPEPODA
SIZE STRUCTURE
LATITUDINAL DISTRIBUTION

ABSTRACT – The description of ecosystems, from a realistic picture of species has progressively changed to an abstract characterization. The structural theory leads to hypothesizing a predictable distribution of biomass-spectra along latitudinal gradients. Four cruises of the R/V "Marion-Dufresne" in the Indian Ocean provided the biological material to compare the latitudinal distribution of Copepoda size-classes.The large surveyed area overlaps five latitudinal hydrological zones. A factorial analysis shows that each of these zones is characterized by a size spectrum (distribution of size-classes, number of individuals and biomasses). In the considered area, the concentration of Copepoda over the whole size range shows a tendancy to decrease from the smallest size classes to the largest ones. But the level of equal biomass is not achieved (slope – 0.3 in state of the theoritical one – 1).

The description of ecosystems has progressively changed from a realistic picture of species to an abstract characterization. Specific individuals are replaced by more general features, as biomass, trophic categories, size classes or chemical composition, which agree with a simplification of ecosystem and describe "an ecology without species" (Steele & Frost, 1977).

In an attempt to analyse ecosystems and identify the pathways of energy and material flow, the natural environment initially was reduced to trophic levels (Lindeman, 1942). Next, the size-efficiency hypothesis (Brooks & Dodson, 1965) stated that the structure of ecosystems is built according to trophodynamic interactions grounded on hierarchic order of size, i.e the size of each step is smaller than the following one, and on inter- or intraspecific competition (Kerr, 1974 ; theory reviewed by Hall *et al.*, 1976). These ideas have been stretched to a large extent, due to the growing interest in food webs and productivity of seas, from the first symposium on Marine Food Chains (Steele, 1970) to the late theoretical developments of Pimm *et al.* (1991). Thus in ecosystems, the biological and metabolical parts of the size-spectra have to be taken into account in the flow-matter or biomass energy flow from smaller to larger scales (Kerr, 1974 ; Platt & Denman, 1978).

The structural theory based on the size classes in ecosystems was first stated by Elton (1927) as "pyramid of numbers". It was later emphasized by Sheldon *et al.* (1972) that "as an ecosystem approaches a steady state, the biomass / size-classes ratio approximates to a constant". It then follows that the number of particles will be decreasing with increasing sizes "from bacteria to whales". Since then, the analysis of size-spectra in scaling pelagic ecosystems has been used also : 1) for biochemical purposes : as an attempt to approximate weight of zooplanktonic standing stock (Pearre, 1980) and vertical transport of organic matter that is also size-dependant (Rudyakov & Tseytlin, 1980), or to simulate models of

C and N fluxes (Moloney & Field, 1991) ; 2) for prediction of fish productivity from direct observations (Borgman, 1982), as an indicator of the prey-predator size preferences by larval fishes (Nishiyama & Hirano, 1983) ; 3) for estimating production, or losses, of main groups of oceanic organisms (Kamenir & Khaylov, 1987). If at first, most of the size-frequencies diagrams were devoted to the restricted range of phytoplankton and microzooplankton, easily displayed by automatic particles counters (Sheldon & Parsons, 1967), further pelagic size spectra have been extended to the range of mesozooplankton and macrozooplankton. Sheldon *et al.* (1972) and Witek & Krajewska-Soltys (1989) have emphazised that the distribution of biomass-spectra is predictable along latitudinal North - South gradients in the oceans. Changes in size-spectra may thus become a tag to display disturbances in steady the states of ecosystems : examples are given for feed-back interactions between particles (Silvert & Platt, 1980), prey availability in pelagic food web (Hargrave *et al.*, 1985), eutrophy versus oligotrophy (Sprules & Munawar, 1986), variability due to vertical and seasonal changes (Rodriguez & Mullin, 1986) or a spring bloom (Rodriguez *et al.*, 1987).

According to the basic size – spectrum model, the plankton categories (phyto- to macro-plankton) display a "more or less flat" pattern. The copepods community makes up the bulk of the mesozooplankton, so it may be expected to follow the overall pattern of zooplankton.

Several cruises of the french R/V "Marion-Dufresne" in wide areas of the Southern Ocean provided us with the biological material to compare the latitudinal distribution of mesozooplankton size-classes and to cope with the questions : 1) Are the size frequency diagrams of copepods, in association with their biomasses and densities, representative of latitudinal differences between oceanic areas ? 2) How does the Sheldon relation apply to the mesozooplankton category considered as the single group of copepods ?

MATERIAL AND METHODS

Field sampling

Zooplankton samples were provided by four oceanographical cruises of the R/V "Marion-Dufresne" from low (about 10°N) to high latitudes (66°S) in the Indian Ocean (Fig. 1, Table I).

Copepods were sampled using a non-closing WP2 - net (200 µm mesh sized gauze), between respectively 100 m, 200 m and 500 m and the

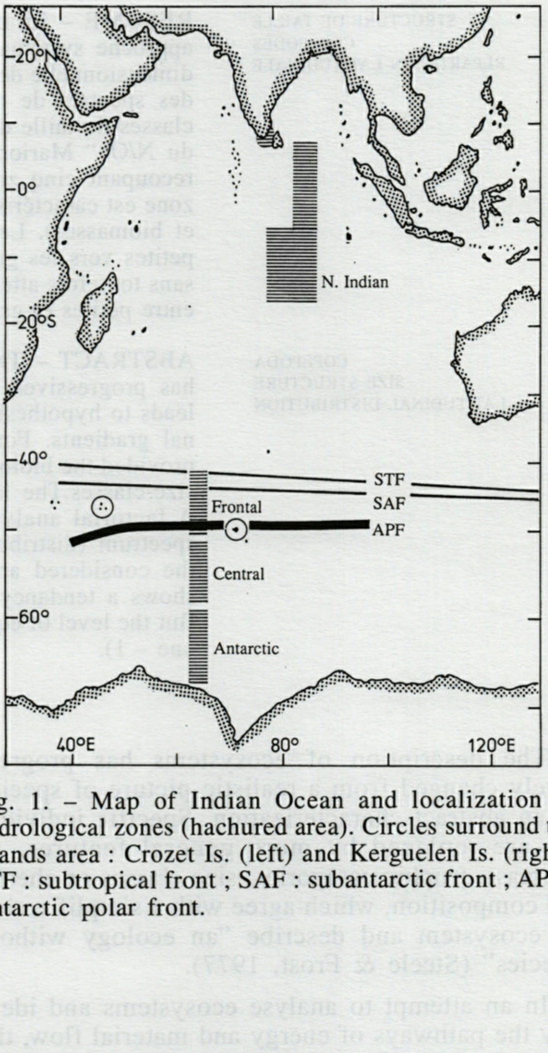

Fig. 1. – Map of Indian Ocean and localization of hydrological zones (hachured area). Circles surround the Islands area : Crozet Is. (left) and Kerguelen Is. (right). STF : subtropical front ; SAF : subantarctic front ; APF : Antarctic polar front.

Table I. – Location of mesozooplankton sampling areas (N = number stations).

Cruises	Localization	Dates
ANTIPROD I (N = 25)	42° 52 S-66°25 E to 62° 14 S-66°33 E	1 - 28 III 1977
ANTIPROD II (N = 10)	40° 57 S - 66°32 E to 63° 44 S - 66° 29E	24 II / 20 III 1980
SAFARI (N = 41)	7° 05 N - 78° 58" E to 14° 56S - 83°38 E	27 VII / 24 VIII 1981
BIOMASS (N = 23)	46° 40 S - 51° 48 to 45° 44 - 49° 37 E	29 I / 13 III 1982

surface at each station ; each vertical haul was duplicated in order to provide two samples, one for measuring dry biomass and the other to be preserved in formalin 5 % for further enumeration and dimensional measurements. Densities of copepods (dry biomasses, enumeration) were expressed per square meters. In this paper, biomasses and numbers are accounted only for the water layer from where the measured animals originated.

Laboratory methods

Biomasses expressed in mg dry weight (D.W.) were obtained after filtration of whole fresh samples and desiccation at 60 °C, while the numerations were done on an aliquot part of the preserved ones.

One hundred copepods of the 100 m - surface hauls were systematically picked at random and measured individually with a digitizer interfaced with a microcomputer. Measurements were also conducted on copepods from 200 m - and 500 m - surface hauls sampled in the Islands and north Indian Ocean zones.

A Student's test "t" has shown that the size frequency distributions of the 100 - 200 - and 500 m depth hauls in these sectors are not significatively different. Despite one exception – for the Islands sector, where the distribution of the smallest size classe (S1/2) appears statistically different between 100 m - and 200 m - surface layers- the sampling depth has not been considered in scaling and analyses of the size classes of Copepoda.

Assuming that vertical hauls are integrating the whole water mass, the diel vertical migration of copepods have not been considered.

With the use of automatic counters (Sheldon & Parsons, 1967) or successive size fractionation through decreasing mesh-size screen (Witek & Krajewska – Soltys, 1989 ; Rodriguez & Mullin, 1986), the biovolume of planktonic organisms is usally expressed as the equivalent spherical volume or as its equivalent spherical diameter (ESD). So, to standardize our measurements, a specific program has been written that gives individual biovolumes (calculated according to the Shmeleva's (1965) formula), individual equivalent spherical diameter and frequency distribution of these parameters.

Considering all the cruises, in order to avoid classes with no individual or even only a very few of them, the number of classes (with ESD intervals of 100 µm) was reduced to seven, named S1/2, S3....S9/10 (Table II).

Table II. – Size classes of Copepods, as equivalent spherical diameters (ESD in µm) and biovolumes.

Size - classes	ESD (μm)		Biovolumes
	Ranges	Mean Ø	($\mu m^3 . 10^6$)
S1/ 2	200 - 300	250	8, 2
S03	301 - 400	350	22
S04	401 - 500	450	48
S05	501 - 600	550	87
S06	601 - 700	650	144
S7/ 8	701 - 900	800	268
S9/10	901 - 1300	1100	697

Factorial Correspondence Analysis

Factorial Correspondence Analysis (FCA) (Hill, 1974 ; Lebart *et al.*, 1984) can be viewed as finding the best simultaneous representation of data sets that comprise the rows and columns of a data matrix. FCA is applied to contingency tables and provides an accurate analysis of the matrix with binary coding. In this study FCA was used to describe and evaluate associations of length and quantitative structures and geographical areas. The rule of homogeneity of variables and units was obtained by coding the variables into classes. The easiest way to standardize a set of heterogeneous data (measurements, numbers, weights) is to use a generalized logical description (Jambu & Lebeaux, 1983). The measurement of each variable was replaced by a partition divided into classes (a, b, c, d). As the histograms of the variables did not show any clear separation, then division into classes of equal numbers was carried out in order to have marginal distribution of nearly equal classes. FCA has been performed on the 99 stations sampled during the four considered cruises. This method and the interpretation of its results are clearly related to overaging method as described by Hill (1973).

Biovolumes spectra in sampling area

An estimate of the total biovolume of each size class is calculated according to the expression : (Copepoda / m^2 × percent of individuals / class) × nominal biovolume (μm^3). The nominal (individual) biovolume calculated with mean ESD roughly doubles from one size-class to the next one, yielding unequal class widths. The biovolumes are standardized (linearized) using a logarithmic scale transformation, that gives a mean class width of 0.3 (interval between $\log_{10}$ biovolume classes). The relation in log-log coordinates, between total biovolume of each class normalized by the nominal biovolume, i.e the equivalent of the numerical density of individuals in the class, and the mean nominal biovolume of individuals has been computed as : log (normalized biovolume or copepod number / m^2) = a + b log (nominal biovolume in μm^3). This correspondence is valid only for an arrangement of weight (or biovolume) classes where each class is double of the previous one (Platt & Denman, 1978). The values of the slope for the "denormalized" curve will differ from b by + 1.

RESULTS AND DISCUSSION

Size classes latitudinal distribution

Mikhaylovsky (1989) in the southern Pacific Ocean and Valdès *et al.* (1990) on the north – western Spanish coast have shown that geographical zones may be characterized by their size frequencies distributions.

In the Indian Ocean, the five determined latitudinal zones are in good agreement with five hydrologically defined latitudinal zones (Table III and Fig. 2). In the text, the different areas will be written in italics.

The tropical zone of Indian Ocean (*North Indian*) is the farthest northern zone studied in this survey. A succession of convergences and divergences are induced locally by a complex system of currents, seasonally changing monsoon gyre or westward drift of the South Equatorial Current (Wyrtki, 1973), which, in turn, might change the mesoscale biological activity (Piontkovskii *et al.*, 1985).

The Frontal Zone (*Frontal*) in the Kerguelen Is. vicinity is determined by a large scale, very complex hydrological situation due to the joining of the subtropical Convergence, the transition frontal zone confined between 44°40 S and 46°40 S and

Table III. – Overlay of the sampling area in sectors identified according to the latitude and hydrological characteristics.

Sectors	Location
North Indian (MD 27)	7° 05 N to 14° 56 S
Frontal Zone (pro parte MD 12+ MD 21)	42° 09 to 46°47 S
Islands Zone (MD 30 + some stations MD 21)	45° 44 to 48° 33 S
Central Zone (pro parte MD 12 + MD 21)	47° 32 to 57° 34 S
Antarctic Zone (pro parte MD 12 + MD 21)	58° 24 to 63° 44 S

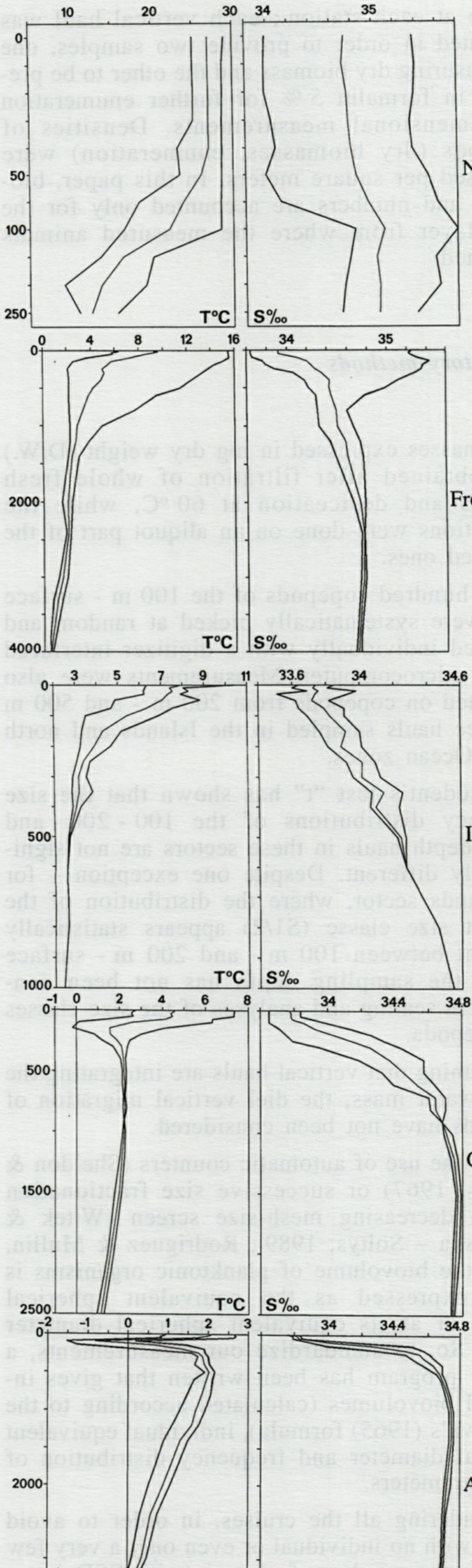

Fig. 2. – Hydrological profiles of temperature (°C) and salinities (S ‰) with depth (m) on the vertical axis.

the Polar front (Park *et al.*, 1991). The lay-out of the water masses surrounding the Crozet Archipelago and the north of the Kerguelen Islands is modified by numerous islets and the complex submarine topography (Plancke, 1974 ; Deacon, 1983). This peculiar situation justifies the identification of the concerned sectors as the Islands area (*Islands*). On the contrary, the Central zone (*Central*), belonging to the open ocean, is characterized by a regular thermal gradient from the Front to about 60° S where begins the Antarctic zone (*Antarctic*), the so-called "krill area".

Histograms of ESD frequencies for the different above mentioned sectors are summarized in Fig. 3. 77 % of copepods from the *North Indian* sector are partitioned between classes S1/2 and S03-S04 classes (250 - 450 µm) with the dominant mode, (32 %) in S03 (350 µm). In the *Frontal* zone a bimodal situation is observed with a first peak (31 % of copepods) in S03 and a second smaller one (16 %) in the very large size S9/10 category (≥ 1,100 µm). The frequency distribution in the *Central* area looks like that in *Frontal*. It is also bimodal but with a light shift of the mode (36 %) toward S04 (450 µm). This may confirm the biological transition character of the fronts. The *Islands* zone appears as the most harmonious : 26 % of animals in the modal class S06 (650 µm), 19 % in S05, 17 % in S04, and 21 % in the largest ones, S7/8 and S9/10. *Calanus simillimus* and *Drepanopus pectinatus* populations at any development stages constitute the bulk of the Copepoda (pers. obs.), probably due to the islands effect (Wolanski & Hamner, 1988). Despite what one could expect, the histograms in the *Antarctic* zone are very similar to those of the *North Indian* : 37 % in S03 and 30 % in S04.

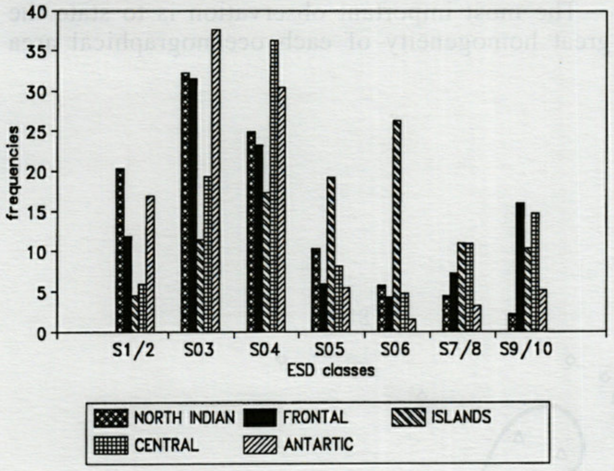

Fig. 3. – Histogram of the size classes frequencies of Copepods in the five identified zones of the Indian Ocean. S1/2....S9/10 : size classes.ESD : equivalent spherical diameter.

Biomasses (mg Dry Weight) and concentrations associated with the size spectra describe some biological characteristics of the areas (Fig. 4).

If the mean concentrations (2 g and about 0.5 10^5 individuals m^{-2}) in the central oceanic sector are considered as representative of the open ocean, the abundance of mesozooplankton is decreasing (1 g and from < 0.5 10^5 individuals m^{-2}) symmetrically northwards – to Fronts and N. Indian – and southwards – to the very antarctic part of the Indian Ocean (Razouls & Razouls, 1982 ; Razouls, 1984). On the contrary, the highest mean values (about 7 g and 2 10^5 individual m^{-2}) occur around the Crozet Is. and the North of the Kerguelen Is., associated with the

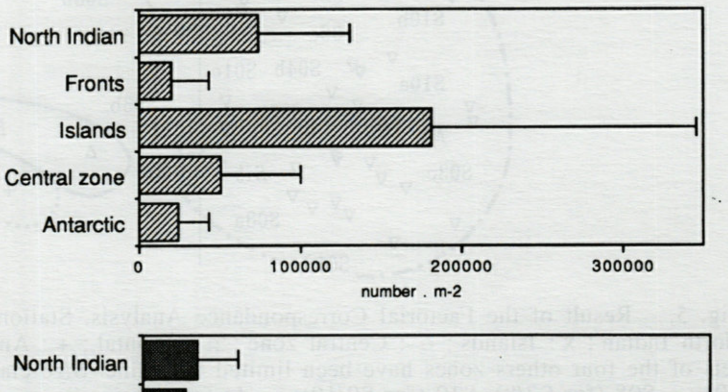

Fig. 4. – Biological features in the different hydrological zones, for the 100 m depth water masses. Copepods number and biomasses (expressed as dry weight D.W.), standardized by square meter (vertical bars : Sd).

maximum observed values of 16 g and 5 10^5 individuals m^2. These results match well with those found by Grindley & Lane (1979) around Marion Is. or by Boden & Parker (1986) near Prince Edward Is.

FCA applied to the whole data set (size classes, biomasses, concentrations and stations) summarizes and clarifies the distribution of the biological parameters versus latitude (Fig. 5), station location being not used as a characterization. This figure is the diagrammatic illustration of the contingency table after binary coding of the importance (concentrations and biomass) and the distribution of size classes of Copepoda with sampling stations. It shows the principal relationships among the profiles on the basis of the two first axes. The plane F1/F2 explains 22 % of the total variance, with the percentages affected to the axes : F1 = 13.8 % ; F2 = 9.3 %.

According to the number of stations and variables, and also to the binary coding, this value gives a good measure of the information. Despite this small percentage, the corresponding axes restore the bulk of the information contained in the data set. The other axes explain respectively 7.4 % (F3) and 6.8 % (F4) of the variance.

The proximity between two "variables" points indicates that these variables shows a similar profile of distribution for all the stations ; the proximity between two "station" points indicates a similar profile of distribution for all the variables. It is possible to interpret the relative position of one point in a certain set with respect to all the other points in the other set ; in any case it may be dangerous to compare without any precautions the proximity of two points in the same set.

The most important observation is to state the great homogeneity of each oceanographical area

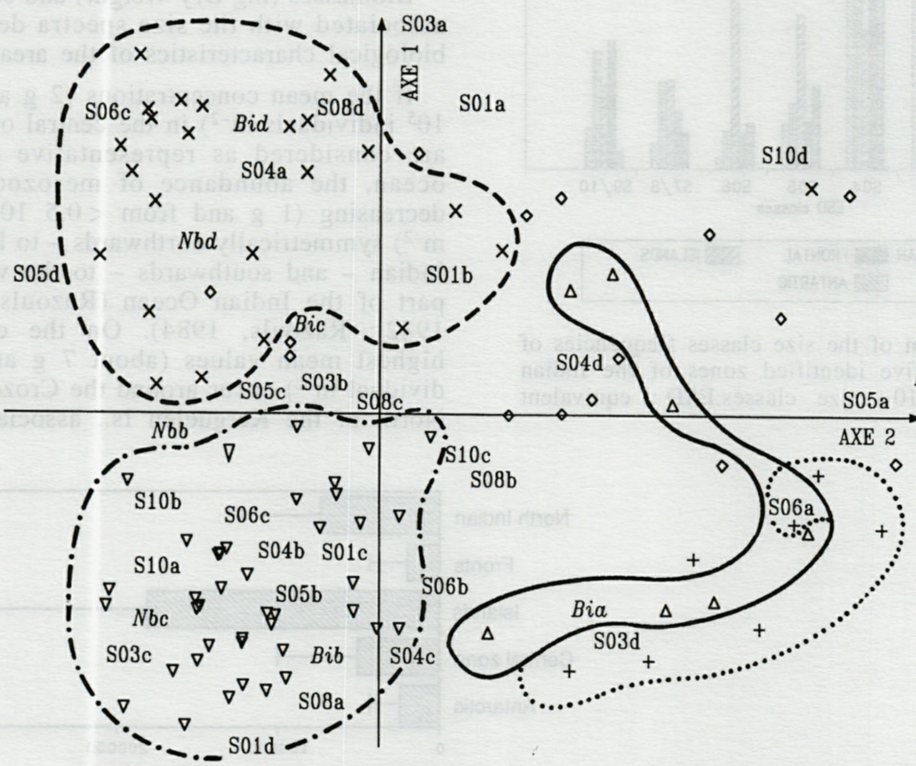

Fig. 5. – Result of the Factorial Correspondance Analysis. Stations from the different zones are designed as : , : North Indian ; **x** : Islands ; e : Central zone ; n : Frontal ; + : Antarctic. Except for the Central zone stations, the sets of the four others zones have been limited by a line. Size classes in ESD (μm) are plotted as S01 (for S1/2), S03,....,S08 (for S7/8), S10 (for S9/10). a - d : frequencies (in per cent) of presence of the size class. *Nb* : Copepods numbers. m^{-2} ; *Bi* : Biomasses (dry weight · $m^{-2)}$ · *a, b, c, d* : indices of abundance in an increasing order.

with S01 a : ≤ 4 % ; b : 5-12 % ; c : 13-20 % ; d : 21-40 %. S03 a : ≤ 15 % ; b : 16-27 % ; c : 28-35 % ; d : 36-54 %. S04 a : ≤ 17 % ; b : 18-25 % ; c : 26-34 % ; d : 35-62 %. S05 a : ≤ 6 % ; b : 7-11 % ; c : 12-14 % ; d : 15-37 %. S06 a : ≤ 3 % ; b : 4-6 % ; c : 7-13 % ; d : 14-65 %. S08 a : ≤ 4 % ; b : 5-7 % ; c : 8-11 % ; d : 12-35 %. S10 a : ≤ 2 % ; b : 3-4 % ; c : 5-10 % ; d : 11-79 %. *a : Nb* : 0-30,000 individuals ; Bi ≤ 813 mg.m^{-2}. *b : Nb* : 31-52 × 10^3 individuals ; Bi : 814-1600 mg.m^{-2}. *c : Nb* : 53-100 × 10^3 individuals ; Bi : 1601-2600 mg.m^{-2}. *d : Nb* : 101-800 × 10^3 individuals ; Bi : 2601-19,000 mg.m^{-2}.

in terms of biometrical data. On the plane defined by the F1/F2 axes, stations are partitioned into 4 quadrants corresponding to geographical or latitudinal affinity : *North Indian, Islands, Central* and *Antarctic* zones are very well identified and are very little overlapping. The *Frontal* area stations are positioned as the classical horseshoe picture mainly characteristic of an area with heavy gradient.

The population of the *North Indian* sector shows a mean level of biomass (Bib = 800 - 1,600 mg), with relatively numerous copepods (Nbc = 52,000 to 100,000 individuals/m^2) in all classes, while 35 - 40 % of individuals lie in classes S01 to S03, 4 % in S08 and 2 % in S10 respectively. On the opposite, the *Islands* sector is dominated by heavy biomasses (Bid ≥ 2,600 mg) and populations with middle to large sizes : 35 % in S05, 65 % in S06 and 35 % in S08.

The *Central* area shows a higher dispersion ; centered around a dominant S04 class (to 62 % of individuals), it includes also an important proportion of higher class (to 79 % in S10), the biomasses (Bic) standing around 2,100 mg. One station of the *Islands* area, located very far from the shore, shows also an unusual proportion of the highest class S10, and then could be considered as belonging to both sets of samples.

The *Antarctic* sector is discriminated by weak biomass and abundance of animals (Bia < 800 mg and Nba < 30,000), associated with small sizes (to 54 % in S03 and 3 % in S06) ; this could be explained in the most southern stations (beyond 60° S) by either competition for food or a spatial exclusion between Euphausia and Copepoda.

The *Frontal* zone presents biomasses ranging from Bia < 800 mg to Bic 2,600 mg ; the size structure changes also from less than 10 % in S01 (a,.b classes) to more than 62 % of combined S03 and S04). This area thus appears as a transition between the *Central* and the *Antarctic* zone.

So, the size distribution of Copepoda appears to be a possible tool in identifying pelagic ecosystem. A confirmation is shown in the size distribution of Copepods in the two overlapping cruises "Antiprod" I and II (Table I). Their size-class distribution remains distributed in the same pattern within a three years interval (Table IV), even if absolute abundance parameters differ.

Table IV. – Size classes distribution in cruises Antiprod I (1977) and II (1980).

	S1/ 2	S03	S04	S05	S06	S7/8	S9/10
ANT.I	6.3	20	36.8	14.8	6.0	7.2	8.9
ANT. II	11.0	27.2	30.4	5.48	3.24	8.8	13.9

Relationships between body size distribution and biomass

The distribution of copepods numbers into the biovolume classes, arranged in log.- log. scale, is established for the five already defined zones (Fig. 6).

Apart from the *Islands* area, the four others sectors display similar profiles and a Kendall test of concordance shows that the distributions of animals in biovolume classes are not independant from each other, and that are not due to chance.

The size of the S1/2 class, appears everywhere as lower than those of the next classes. This paradox could be explained by an underestimation of the sampling power of the net in the mean range 250 µm ESD. If the set of data from the *Islands* stations is discarded, the number of copepods presents a slight but continuous decrease in the classes between S03 and S06, while the individual biovolumes increase ; this tendancy is reversed in the classes above S06.

The regression between the nominal biovolume classes and the animals' abundances is expressed by the equation : log number / m^2 = log a – b. log Biovolume. The correlation is significant if the values from *Islands* sector are excluded (Eq. 1) : $r = -0.44$ ($N = 28$), but it becomes better when the first class (S1/2) is not considered (Eq. 2) : $r = -0.60$ ($N = 24$). In spite of two exceptions – the lowest size class and the *Islands* sector – our results indicate a significant tendancy of Copepoda concentration to decrease inversely with size, as was expected.

The slope b of theses log.- log. curves are less negative than the theorical value, (– 1) which characterizes a steady state. The computed values are respectively : $b = -.31$ for Eq. 1, and $b = -.55$ for Eq. 2. A "t" test shows that these values are significantly ($P < 0.05$) different from the theoretical one. Accordingly, the slopes (b + 1)

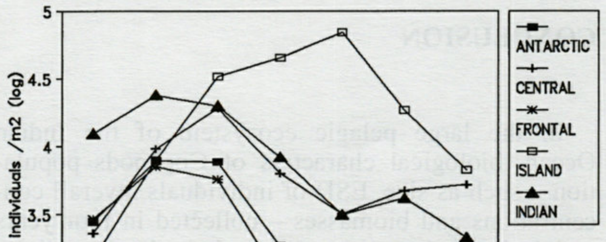

Fig. 6. – Distribution of the Copepods numbers in the seven size classes, expressed in log. of the biovolumes (µm^3).

describing the changes in biomass related to biovolume classes become positive (.69 and .45) : these coefficients are the far from the value "0", indicative of a theoretically constant biomass.

The departure of our data from the stability of biomass – if we accept the Sheldon's hypothesis – may be explained by some bias : in the limit of catch for smallest or largest sized copepods, in the integration of heterogeneous distributions – if any – in vertical hauls, in the coarse bodily pattern used for copepod calibration (Schmeleva, 1965) or the restricted size range from 10^7 to 10^9 µm^3 in biovolumes (or 200 to 1,300 µm ESD) of copepods. The heterogeneity of the water masses is also to be considered as a disturbing factor as it is shown for different zones from Greenland to Antarctic peninsula by Witek *et al.* (1989). They find "generally equal biomasses level" for individual body volumes of plankton ranging over eleven orders of magnitude – from 4 µm^3 to 5 10^{11} µm^3 (or 1 µm to 10^6 µm ESD) with some irregularities in specific geographical zone.

The Sheldon's conceptual model was first elaborated using nanno – and phytoplankton before being extended to micro – and mesozooplankton, up to 4,000 µm ESD (Sheldon *et al*, 1972). But Platt & Denman (1978) hypothesized also that the biomass distribution was not flat but decreased with a factor $(b + 1) = - 0.22$. Rodriguez & Mullin (1986) computed a value of – 0.16 to express the slight divergence from the flatness for the relation between biomass and body weight in terms of Carbon, in plankton populations over a range of eight orders of magnitude. The criterion of slope 0 or near 0 consitutes a reference for characterizing the stability of a zone : Canadian lakes (Sprules & Munawar, 1986), North Pacific gyre (Rodriguez & Mullin, *op. cit.*). The departure of 0 could indicate on the contrary a variability due to the season (Rodriguez *et al.* 1987) or related to the depth and diel variation.

CONCLUSION

In the large pelagic ecosystem of the Indian Ocean, biological characters of Copepods population – such as size, ESD of individuals, overall concentrations and biomasses – collected in four years and during four surveys along a latitudinal gradient, have been taken in account. For the whole copepods communities the latitudinal hydrological zones are characterized by these biological features. At least for the period of the collected data. But the "model" given for any area as a structural representation should be improved on the basis of seasonal variations for integrating the changes due to dynamics of populations Frost (1980).

From a more general point of view it is obvious that the concept of energy flow through a hierarchical trophic order – the largest feed on the youngest or smallest ones – is not valid for the isolated taxon of Copepods. It is rather expected that Copepods are related by competition, which can affect the size composition (Kerr, 1974), or by coexistence in narrow ecological niches (Steele & Frost, 1977). Likewise, Platt (1985) claims for autotrophs that "the concept of trophic level assumption appears to be an unjustified simplification"

Even if size scale of the numerous taxon of Copepods yields a partial description of any pelagic local ecosystem, other allometric rules – growth rates, development stages, generation time – are to be considered for a better understanding of the specific copepods spectra, though the weak relationship observed between size spectra and abundance, seems to characterize pools of invertebrates populations (Blackburn *et al.,* 1993).

ACKNOWLEDGEMENTS – We thank the TAAF (now the IFRTP) for facilities to participate to oceanographical cruises on the R/V "Marion Dufresne". Our thanks too to M.J Nattéro, N. Batailler for their technical help and to Ph. Lemerle for computaring program.

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Reçu le 2 mars 1994 ; received March 2, 1994
Accepté le 23 mars 1994 ; accepted March 23, 1994

VIE MILIEU, 1994, 44 (1) : 69-91

ANALYSES MULTIVARIEES DES RELATIONS ESPECES-MILIEU : STRUCTURE ET INTERPRETATION ECOLOGIQUE

Multivariate analyses of species-environment relationships : structure and ecological interpretation

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ÉCOLOGIE
COMMUNAUTÉ
RELATIONS ESPÈCES-MILIEU
ORDINATION
GRADIENT
ANALYSES MULTIVARIÉES
AMPLITUDE D'HABITAT
DIVERSITÉ

RÉSUMÉ – L'étude des relations entre les communautés animales ou végétales et leur environnement implique souvent un ensemble d'échantillons associant un certain nombre d'espèces et un certain nombre de variables de milieu. Le présent article passe en revue une large part des méthodes multivariées, basées sur le modèle linéaire, qui permettent l'analyse des tableaux relevés × espèces, en offrant différentes possibilités de couplage avec les tableaux relevés × variables de milieu correspondants. L'accent est mis sur la structure des modèles statistiques, sur la robustesse et la flexibilité des méthodes, sur leur choix, sur leur adéquation aux problématiques biologiques, et sur l'interprétation des résultats en relation avec les concepts écologiques.

ECOLOGY
COMMUNITY
SPECIES-ENVIRONMENT
RELATIONSHIPS
ORDINATION
GRADIENT
MULTIVARIATE ANALYSIES
HABITAT BREADTH
DIVERSITY

ABSTRACT – The study of the relationships between animal or plant communities and their environment often supposes a set of samples that associate several species and several environmental variables. This paper reviews the main multivariate methods, based on the linear model, allowing the analysis of samples × species matrices, and offering different possibilities of coupling these matrices with the corresponding sample × environmental variables matrices. The emphasis is placed on the structure of the statistical models, on the robustness and flexibility of the methods, on the choice among them, on their relevance to biological problems, and on the interpretation of the results in relation with ecological concepts.

1. INTRODUCTION

L'écologie des communautés a longtemps entretenu l'espoir que des modèles type analyse des systèmes, en éliminant les aspects descriptifs liés à la prise en compte des multiples cas d'espèces, pourraient faire de l'écologie une science « dure » (McIntosh, 1987). Mais la prise de conscience de la diversité des mécanismes impliqués et de l'importance des facteurs historiques ou aléatoires, notamment des perturbations (Connell 1978, Denslow 1985, Pickett et White 1985), ont engendré une période de doute et d'introspection bien résumée par McIntosh (*ibid.*). De fait, le corpus théorique en écologie des communautés est en plein renouvellement. Malgré l'intérêt de concepts comme ceux d'espèces « clés » *(key-stone species)* (Paine 1966), de groupes fonctionnels ou de guildes (Simberloff et Dayan 1991), l'indispensable analyse de la dynamique des communautés ne saurait se réduire à une juxtaposition ou une amplification d'approches « fonctionnelles » de type dynamique des populations. Les approches empiriques gardent toute leur importance, et l'échantillonnage des communautés doit reprendre son rôle central, qui est de fournir les informations de base sur leur variabilité spatio-temporelle.

Dans ce contexte, l'objectif de cet article est de fournir au lecteur écologiste non statisticien une approche pédagogique, mais néanmoins critique, d'une large part des méthodes actuelles d'analyse statistique en écologie des communautés. Un premier problème pratique est de mettre en évidence, résumer et quantifier la diversité et la variabilité floro/faunistique contenue dans un ensemble de relevés. Un deuxième problème est de mettre cette variabilité et cette diversité en relation avec des variables de milieu. Pour cela, l'utilisation des méthodes statistiques multivariées est naturelle et souvent préférable à celle des méthodes de classification, ne serait-ce que parce que les variations des facteurs environnementaux sont le plus souvent graduelles dans l'espace ou le temps.

Si les analyses factorielles, particulièrement l'Analyse des Correspondances, sont largement utilisées en écologie, c'est trop souvent sans prise de conscience de leurs propriétés en tant que modèles écologiques. Les exposés pédagogiques usuels reposent sur des notions abstraites de calcul matriciel ou de géométrie dans l'espace sans connotation écologique directe. Nous soulignerons plutôt les liens étroits avec des concepts de base de l'écologie des communautés, et par conséquent l'adéquation entre méthode statistique et modèle écologique, montrant par exemple que l'Analyse des Correspondances est à l'intersection des notions d'*optimum écologique* et d'*espèce indicatrice*. Nous envisagerons ensuite l'intervention dans l'analyse des variables mesurées dans le milieu : c'est le domaine des analyses à plusieurs tableaux, où sont analysées les relations entre *vie* et *milieu*, c'est-à-dire entre tableaux floro/faunistiques et tableaux des variables externes. Nous évoquerons enfin divers développements méthodologiques récents, en proposant quelques éléments de réflexion sur le choix des méthodes, sur leur interprétation en termes écologiques, et sur les possibilités de passer de la simple description exploratoire à la modélisation de phénomènes définis et aux tests d'hypothèses.

2. CORRESPONDANCE ENTRE ESPÈCES ET RELEVÉS

Comment mettre en évidence l'information contenue, sous forme de variabilité floro/faunistique, dans un tableau espèces × relevés, autrement dit comment faire apparaître la structure d'un tableau souvent volumineux et illisible ? Certaines espèces sont-elles liées à certains groupes de relevés ? Existe-t-il donc un classement des espèces tel qu'on puisse lui faire correspondre un classement des milieux ? Bref, peut-on mettre en *correspondance* les espèces et les relevés ?

2.1. Optimum écologique et ordination des espèces

Considérons la répartition d'une espèce dans divers relevés différant entre eux par une variable écologique quelconque. Sur l'axe représentant cette variable, chaque relevé est à la valeur x_i prise par la variable en question (éventuellement en classes). Il y a donc ordination *a priori* des relevés. La distribution des relevés contenant une espèce donnée sur cet axe figure ce qu'on peut appeler le « profil écologique » (Gounot 1969) de l'espèce (*cf.* Romane 1972, Daget et Godron 1982). L'optimum de l'espèce sera logiquement estimé par un paramètre de position de la distribution, le plus souvent la *moyenne* par souci de simplicité. On pourrait aussi utiliser le mode de l'approximation gaussienne du profil de l'espèce (Gauch *et al.* 1974, Ter Braak et Looman 1986), mais cette méthode est difficilement utilisable si l'on dispose de plus de deux ordinations concurrentes des relevés. Remarquons que la moyenne ne constitue un « résumé » satisfaisant de la position de l'espèce sur le gradient que si la distribution de cette dernière est unimodale.

Dès qu'on envisage plusieurs espèces se pose le problème de leur classement. Il est logique de les ordonner d'après les moyennes de leurs distributions, c'est-à-dire les moyennes des x_i des relevés où on les trouve. On obtient ainsi, à partir de l'ordination *a priori* des relevés, une ordination *a posteriori* y_j des espèces sur un axe-espèces correspondant (Fig. 1a). Sur cet axe, des espèces dont les optimums écologiques sont proches auront des y_j proches. Cette méthode de classement des espèces sur un gradient par leurs positions moyennes (moyennes pondérées, ou moyennes simples si les relevés sont en présence-absence), ou « *averaging* » simple (*weighted averages*), est classique (Whittaker 1948, *in* Whittaker 1960 ; « méthode des barycentres », Daget 1977). D'une façon générale, l'étude de la distribution des espèces sur un gradient écologique défini *a priori* est appelée « analyse de gradient directe ». Cette définition *a priori* s'effectue en général à partir d'une variable du milieu dont l'importance est reconnue (humidité, altitude, stade d'une succession écologique, etc). On a également imaginé utiliser une combinaison *a priori* de variables à l'aide d'indices synthétiques comme dans la méthode des « scalars » (cf. Togerson 1958, McIntosh 1967, Austin *et al.* 1984).

D'un point de vue statistique, le classement obtenu par les moyennes *maximise la corrélation* entre les indices x_i des classes et les indices y_j des espèces. Mais la méthode ne fournit aucune information sur les ressemblances et différences floro/faunistiques entre relevés (c'est-à-dire entre les x_i puisque ceux-ci sont définis *a priori*). De plus, chaque espèce est considérée indépendamment des autres.

2.2. Espèces indicatrices et ordination des relevés

Selon un raisonnement symétrique du précédent, on peut désirer ordonner un ensemble de relevés d'après les espèces qu'ils contiennent, si les préférences de ces espèces concernant une variable écologique donnée sont connues (notion d'espèce « caractéristique »). La présence d'une espèce est alors considérée comme *indicatrice* d'une certaine valeur probable de la variable. Dans ce cas, ce sont les y_j (optimums des espèces sur ce facteur, autrement dit leur « valeurs indicatrices ») qui sont fixés *a priori*. On en déduit l'ordination *a posteriori* des relevés, la coordonnée x_i d'un relevé étant égale à la moyenne des y_j des espèces qu'il contient.

Ainsi Ellenberg (1948), désirant prédire l'acidité d'un sol d'après la présence de certaines plantes, classe d'abord ces espèces de 1 (très acidophiles) à 9 (très alcalophiles) ; la moyenne des indices des espèces d'un échantillon lui donne une estimation semi-quantitative de l'acidité du sol (voir aussi Ter Braak et Gremmen 1987). Whittaker (1960), ou Whittaker et Niering (1965), étudiant un gradient d'aridité, attribuent aux espèces les indices $y_j = 1$ (« mésiques ») à 4 (« xériques »), puis ordonnent les stations d'après la moyenne de ces indices. De même, Demarq et Mourer-Chauviré (1976), cherchant à reconstituer les variations paléoclimatiques d'après des faunes d'oiseaux fossiles, indexent les espèces de $y_j = 1$ (« arctiques ») à 4 (« méditerranéennes ») ; ils utilisent la moyenne des indices des espèces comme « indice thermique » de l'échantillon (voir d'autres exemples de « *habitat adaptation numbers* » ou « *species position indices* » *in* McIntosh 1967 et Goff et Cottam 1967).

Mais pour une matrice relevés x espèces donnée, la corrélation globale entre les indices x_i des relevés et y_j des espèces ne peut être optimale dès lors que l'on fixe *a priori* soit les uns, soit les autres. La qualité des ordinations obtenues par le calcul des moyennes dépend en effet de la qualité de l'ordination *a priori*. Elle dépend donc étroitement de l'expertise de l'écologiste et de la connaissance qu'il possède, ou croit posséder, soit des espèces, soit des relevés.

2.3. De l'ordination réciproque des espèces et des relevés à l'Analyse des Correspondances

On peut donc n'accorder qu'une confiance relative à l'ordination *a priori* des relevés (ou des espèces), et préférer s'en remettre à une méthode objective pour obtenir la meilleure ordination réciproque des espèces et des relevés possible. Ainsi, Dix et Smeins (1967), étudiant l'influence du drainage sur la végétation, commencent par ranger « à l'estime » leurs relevés dans les 6 classes d'une échelle approximative d'humidité. Ils choisissent alors 48 espèces indicatrices, c'est-à-dire ayant un mode bien marqué sur cette échelle provisoire, et les ordonnent de 1 (celles dont le mode est dans des stations très sèches) à 6 (très humides). Ils en déduisent une nouvelle ordination des relevés, placés à la moyenne des indices de leurs espèces, « *more accurate than that based on the original visual assessment of topography and drainage* » (Gauch 1982). Il s'agit-là d'un raisonnement qui conduit, par itérations, à l'*averaging* réciproque, autrement dit à l'AFC.

Une des techniques de l'AFC (Hill 1973a) consiste en effet, à partir d'une ordination *a priori* des espèces, à ordonner les relevés d'après la moyenne des espèces qu'ils contiennent. Cette nouvelle ordination des relevés est utilisée pour réordonner les espèces par la même technique, qui conduit à une nouvelle ordination des relevés. On réitère ces deux étapes jusqu'à ce que les deux ordinations se stabilisent (Fig. 1b). La solution, unique, ne dépend plus des ordinations initiales. Digby et Kempton (1987 p. 72), sur un exemple, visualisent la convergence vers une ordination unique, après une dizaine d'itérations, en partant de deux ordinations initiales distinctes.

Ici, l'écologiste renonce donc à intervenir *a priori* dans l'ordination. Il en résulte trois propriétés importantes :

a) La solution dépend exclusivement de la structure interne du jeu de données. Elle est donc objective. Elle est aussi optimale. En effet, à chaque itération, la corrélation entre les indices x_i des relevés et y_j des espèces augmente, jusqu'à stabilisation où cette corrélation r est maximale. On obtient alors une ordination réciproque des espèces et des relevés, qui correspond au *premier couple de facteurs de l'AFC*. Cette ordination réciproque peut être visualisée par le graphe de corrélation canonique relevés x espèces (Fig. 2a). L'ordination est optimale : tout déplacement d'une ligne ou d'une colonne aurait pour effet de faire baisser la corrélation globale relevés x espèces (qui n'est autre que la racine de la valeur propre du facteur considéré de l'analyse). Le maximum de points (de « présences ») est situé vers la diagonale. Les lignes (ou colonnes) sont d'autant plus proches que leurs moyennes sur le gradient sont plus proches : la proximité sur l'axe est donc une mesure de ressemblance à la fois pour les espèces et pour les relevés.

b) Au coefficient *1/r* près, chaque espèce a une abscisse y_j égale à la moyenne des abscisses x_i des relevés où on la trouve. Réciproquement, chaque relevé a une abscisse x_i égale à la moyenne des y_j des espèces qu'il contient (Tabl. I). Si r est suffisamment élevé, on peut représenter espèces et relevés sur le même axe : les espèces sont alors au milieu de leurs relevés, et réciproquement. Mais on peut aussi choisir l'axe-espèces de variance unité et l'axe-relevés de variance égale à la valeur propre, auquel cas les points-relevés sont au barycentre des espèces qu'ils contiennent (mais non l'inverse). Si l'axe-relevés est de variance unité, et l'axe-espèces de variance égale à la valeur propre, ce sont les espèces qui sont au barycentre des relevés où elles sont présentes.

c) Le « facteur » ainsi mis en évidence par l'analyse est un facteur purement abstrait qui ne traduit que la structure principale du jeu de données. Les coordonnées représentent de nouvelles variables synthétiques floro/faunistiques, de variance maximale. Le problème consistera à mettre en évidence *a posteriori* d'éventuelles corrélations de ce facteur abstrait (qu'on appelle quelquefois « variable latente ») avec les variations de variables externes mesurées sur le terrain (voir plus loin paragraphe 4).

La littérature offre des exemples de tentatives *ad hoc* visant le même but que l'AFC. Ainsi Glowacinski (1975), après avoir fixé *a priori* l'ordre des colonnes (= stades d'une succession écologique) de son tableau, permute les lignes-espèces « *with the principle of splitting up the columns of each succeeding community to the smallest pos-*

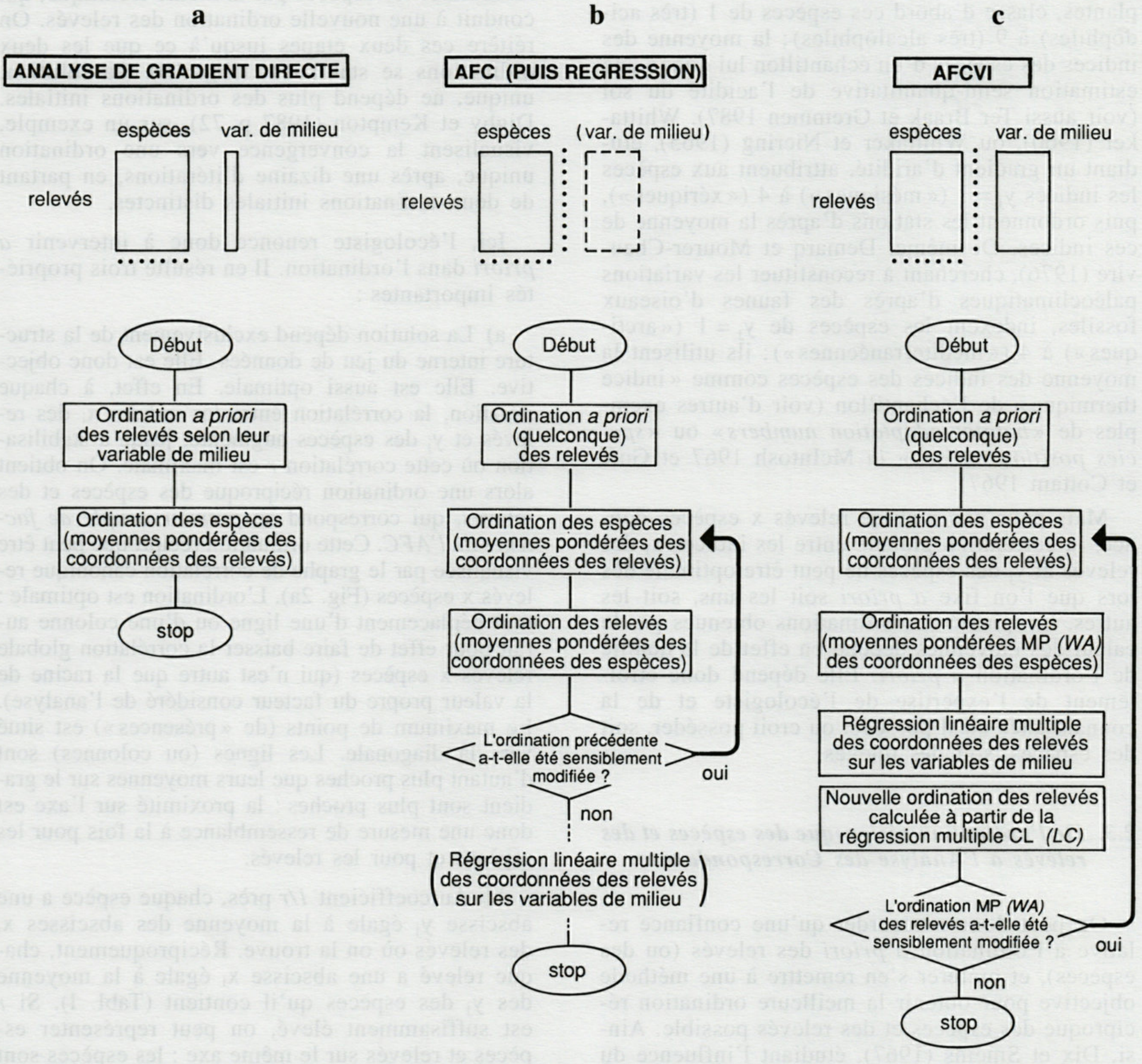
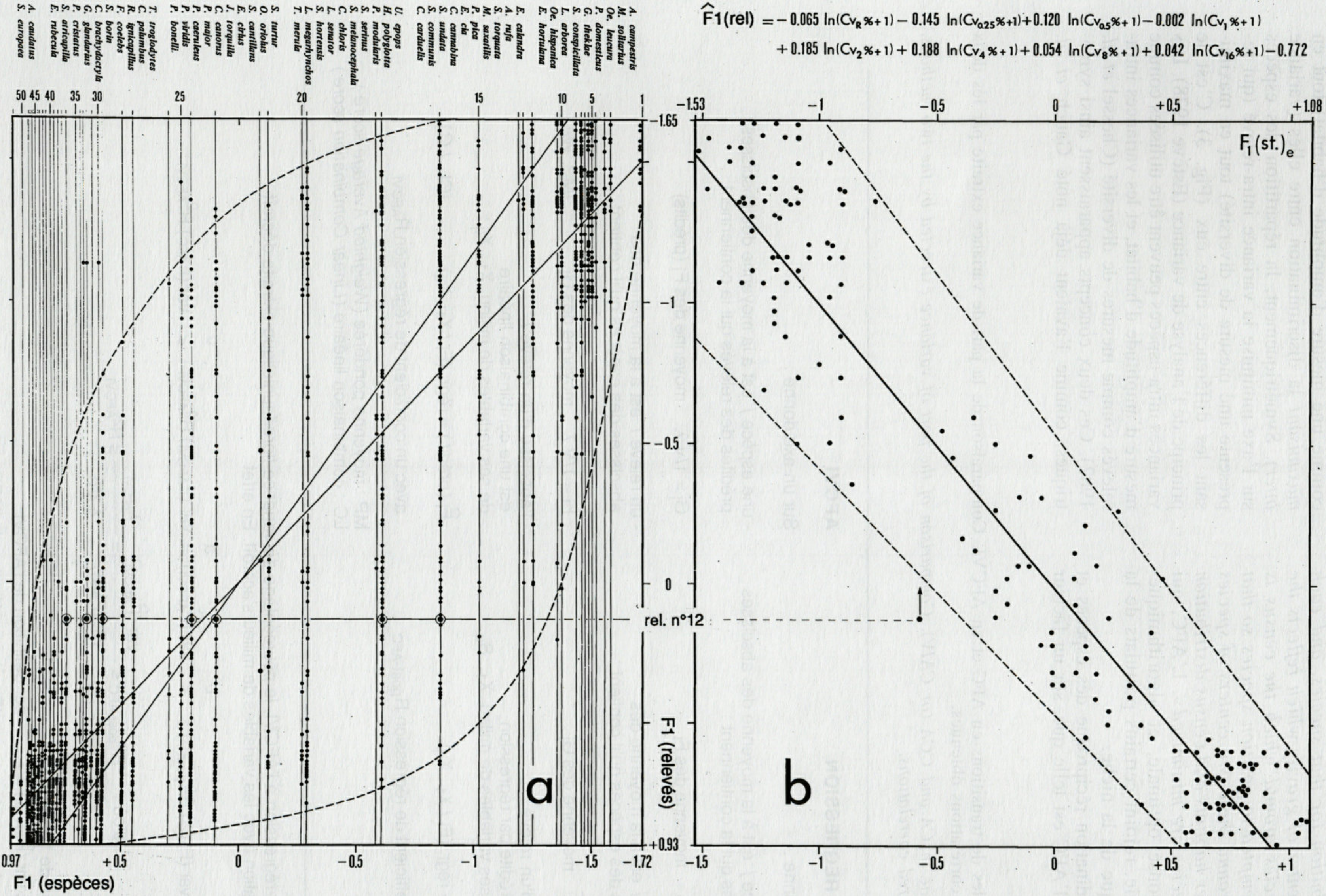


Fig. 1. – Algorithmes correspondant à l'analyse de gradient directe avec *averaging* simple (a), à l'Analyse Factorielle des Correspondances (AFC) éventuellement suivie d'une régression (b), et à Analyse Factorielle des Correspondances sur Variables Instrumentales (AFCVI) ou Analyse Canonique des Correspondances (ACC) (c) (modifié et complété d'après Palmer, 1993).

Algorithms for direct gradient analysis by Weighted Averaging (WA) (a), for Correspondence Analysis (CA) eventually followed by a regression (b), and for Correspondence Analysis with respect to Instrumental Variables (CAIV), or Canonical Correspondence Analysis (CCA) (c).



$$\widehat{F1}(\mathrm{rel}) = -0.065\ \ln(Cv_R\% + 1) - 0.145\ \ln(Cv_{0.25}\% + 1) + 0.120\ \ln(Cv_{0.5}\% + 1) - 0.002\ \ln(Cv_1\% + 1) + 0.185\ \ln(Cv_2\% + 1) + 0.188\ \ln(Cv_4\% + 1) + 0.054\ \ln(Cv_8\% + 1) + 0.042\ \ln(Cv_{16}\% + 1) - 0.772$$

Fig. 2. – a, Exemple de graphe canonique montrant la corrélation entre l'ordination des espèces (axe-espèces horizontal) et l'ordination des relevés (axe-relevés vertical) selon le premier facteur de l'Analyse Factorielle des Correspondances d'un gradient avifaunistique pelouses-forêts. Une seule des lignes correspondant aux 182 relevés (celle du relevé n° 12) a été tracée. b, Graphe de régression multiple de l'ordination des relevés selon le premier facteur de l'AFC sur 8 variables de milieu (recouvrements de 8 strates végétales dans cet exemple) (d'après Prodon et Lebreton 1981).

a. Example of canonical graph showing the correlation between the species ordination (species-axis horizontal) and the sample ordination (sample-axis vertical) corresponding to the first factor of Correspondence Analysis of an avifauna gradient. Being too numerous, the lines corresponding to the 182 samples are omitted. b. Multiple regression graph of the relevé ordering, according the first axis of CA, on 8 environmental variables (vegetation cover values in this example).

sible (vertical) extent» ; et Cody (1975) : «*each row... has a center of gravity which reflects the center of distribution for that species, and each column has a center of gravity which reflects the rank of the species around which the census is centered... I attempted to position species so that the variances around these two centers of species distributions over habitats and census distribution over ranked species are minimized*». L'AFC, qui fournit une réponse optimale, et algorithmiquement bien définie, rejoint certains postulats de la théorie écologique de la niche.

En effet, l'ordination réciproque des espèces et des relevés par l'AFC est telle que, sur un facteur donné, la répartition des relevés *minimise* les variances intra-espèces (qui peuvent alors être utilisées comme une mesure d'amplitude d'habitat) tout en *maximisant* la discrimination entre elles (variance *inter*). Symétriquement, la répartition des espèces sur l'axe minimise la variance intra-relevé (qui représente une mesure de diversité) tout en maximisant les différences entre eux (Fig. 3). C'est le principe de l'analyse de variance (Estève 1978). Les variances intra-espèces peuvent être utilisées comme mesure d'amplitude d'habitat, et les variances intra-relevés comme mesures de diversité (Chessel *et al.* 1982). Ces deux concepts apparaissent ainsi symétriques, comme l'avaient déjà noté Gauch *et al.*

Tabl. I. – Formules de transitions en AFC et en AFCVI. Comparaison de la part de variance extraite par les deux méthodes, et des corrélations obtenues.

Transition formulae in CA and CCA (or CAIV). Comparison of the part of variance extracted by the two methods, and of the measured correlations.

AFC, PUIS REGRESSION	**AFCVI**
Sur un axe donné :	Sur un axe donné :
1) - une espèce *j* est à la moyenne des abscisses des relevés qui la contiennent :	- une espèce *j* est à la moyenne des abscisses prédites des relevés qui la contiennent:
$G_j = 1/\sqrt{\lambda}$ moyenne des F_i	$G_j = 1/\sqrt{\lambda}$ moyenne des $\widehat{F}_i$ (prédits)
- un relevé *i* est à la moyenne des abscisses des espèces qu'il contient :	- un relevé *i* est à la moyenne des abscisses des espèces qu'il contient :
$F_i = 1/\sqrt{\lambda}$ moyenne des G_j	$F_i = 1/\sqrt{\lambda}$ moyenne des G_j [MP, *WA*]
2) l'abscisse d'un relevé *i* peut être prédite par régression à partir de ses variables de milieu $X_1...S_q$:	- l'abscisse d'un relevé *i* est une combinaison linéaire de ses variables de milieu $X_1...X_q$:
$\widehat{F}_i$ (*prédit*) = régr. (F_i / $X_1...X_q$)	$\widehat{F}_i$ (*prédit*) = régr. (F_i / $X_1...X_q$) [CL, *LC*]
avec un coefficient de régression $R_{post\text{-}AFC}$	avec un coefficient de régression R_{AFCVI}
	MP : moyenne pondérée (*Weighted Average score*) LC : combinaison linéaire (*Linear Combination score*)

De l'AFC-puis-régression à l'AFCVI, le pourcentage de variance floro/faunistique extraite décroît, mais la corrélation avec les variables de milieu s'accroît. En effet :

$$\mathrm{var}\,(\widehat{F}_{AFC}) \overset{a}{=} \mathrm{var}\,(F_{AFC})\,R^2{}_{post\text{-}AFC} \overset{b}{\leq} \mathrm{var}\,(\widehat{F}_{AFCVI}) \overset{a}{=} \mathrm{var}\,(F_{AFCVI})\,R^2{}_{AFCVI} \overset{c}{\leq} \mathrm{var}\,(F_{AFC})\,R^2{}_{AFCVI}$$

$$\text{d'où : } R^2{}_{post\text{-}AFC} \leq \frac{\mathrm{var}\,(\widehat{F}_{AFCVI})}{\mathrm{var}\,(F_{AFC})} = \frac{\lambda_{AFCVI}}{\lambda_{AFC}} \leq R^2{}_{AFCVI}$$

a) par définition de la régression

b) $\mathrm{var}\,(\widehat{F}_{AFC}) \leq \mathrm{var}\,(\widehat{F}_{AFCVI}) = \lambda_i$ par définition de l'AFCVI

c) $\mathrm{var}\,(F_{AFCVI}) = \lambda_{AFCVI} < \lambda_{AFC} = \mathrm{var}\,(F_{AFC})$ par définition de l'AFC

(1977). Il est possible d'en donner une représentation graphique simultanée dans un plan factoriel sous forme d'ellipses de dispersion (Thioulouse et Chessel 1992).

2.4. L'aspect multidimensionnel de l'Analyse des Correspondances

S'il existe bien une et une seule meilleure ordination réciproque des espèces et des relevés, il en existe aussi d'autres possibles, non corrélées à la première, et de coefficients de corrélation moins élevés. L'AFC fournit ces ordinations sous forme de couples de facteurs successifs.

Certains de ces facteurs peuvent être artefactuels. Ainsi, lorsque la première ordination extrait presque toute la variabilité de la matrice, c'est-à-dire lorsque la structure du tableau est essentiellement unidimensionnelle. Le second axe, contraint par le calcul d'être non corrélé au premier, en est alors une fonction quadratique : les points espèces et relevés

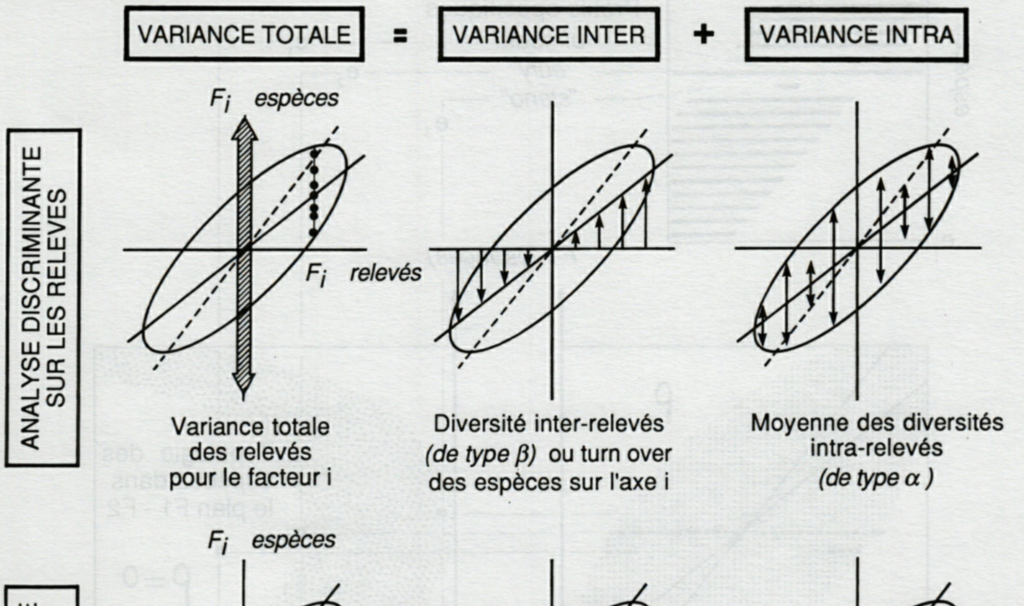


Fig. 3. – L'Analyse Factorielle des Correspondances comme double analyse discriminante (sur les espèces et sur les relevés).

Correspondence Analysis as a double discriminant analysis (on the species and on the samples).

sont disposés en parabole dans le plan des 2 premiers facteurs. C'est l'« effet Guttman » ou « *arch effect* ». Cet effet peut s'observer même lorsqu'il existe bien un deuxième gradient écologique ; il suffit pour cela que la séparation des espèces soit meilleure sur le premier gradient « replié » sous forme quadratique que sur ce deuxième gradient, lequel se voit alors relégué à un rang ultérieur. La figure 4 illustre les différents modes de représentation selon les premier et deuxième axes-espèces et axes-relevés dans le cas d'un gradient simple avec effet Guttman. Dans ce cas, le second

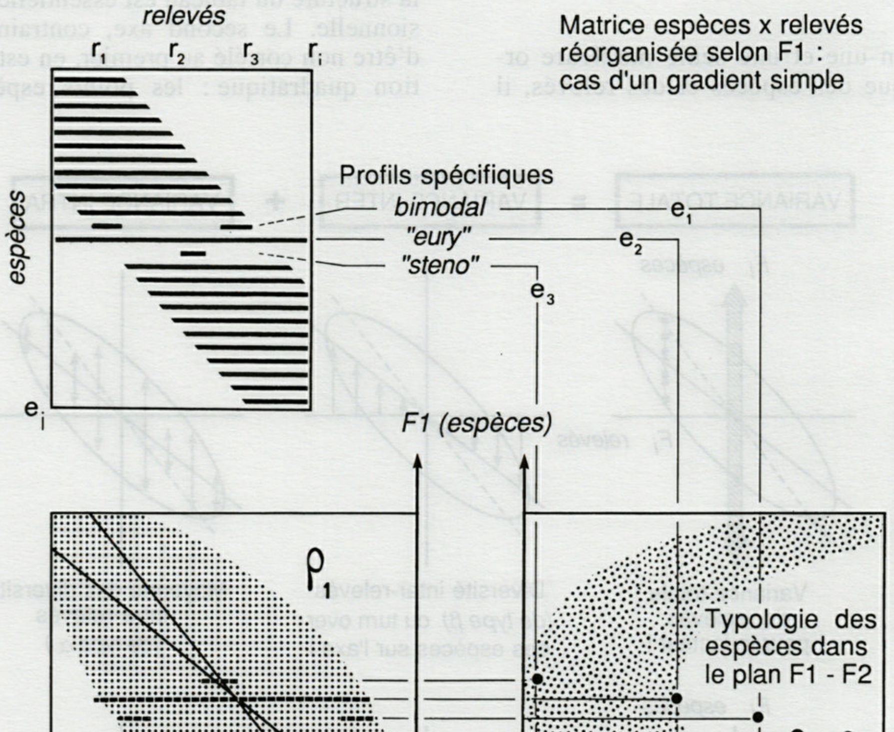


Fig. 4. – Graphes de corrélations canoniques et plans factoriels correspondant aux deux premiers facteurs d'une Analyse Factorielle des Correspondances dans le cas d'un gradient unidimensionnel avec « effet Guttmann » (ρ = corrélation correspondant à un graphe donné).

Canonical correlation graphs and factorial planes corresponding to the two first factors of Correspondence Analysis in the case of an unidimensional gradient with an « arch effect » (ρ = correlation corresponding to a given plot).

axe sépare néanmoins au centre deux groupes d'espèces/de relevés situés au milieu du premier axe :

— les points correspondants aux espèces ou aux relevés à faibles variances conditionnelles (respectivement à faibles amplitudes d'habitat et faibles diversités) caractéristiques du milieu du gradient, et de lui seul, sont à l'extérieur de la parabole,

— les espèces/les relevés à forte variance conditionnelle (forte amplitude d'habitat/forte diversité) sont à l'intérieur de la parabole.

Le classement similaire de ces deux groupes écologiquement différents au milieu du premier axe est une conséquence logique de l'ordination d'après la moyenne des profils.

Mais la relation parabolique entre les deux premiers axes n'est pas toujours un artefact de calcul ; elle peut simplement résulter de relations non linéaires entre variables du milieu (*cf.* par exemple Prodon et Lebreton 1981, Balent 1986, Lebreton *et al.* 1988a). C'est pourquoi on ne saurait conseiller l'utilisation de l'AFC « détendancée » *(Detrended Correspondence Analysis)* de Hill et Gauch (1980). Dans cette modification *ad hoc* de l'AFC, une étape supplémentaire est introduite dans le calcul itératif pour supprimer toute relation parabolique entre les deux premiers axes. Lebreton et Yoccoz (1987), Wartenberg *et al.* (1987) et Palmer (1993) dénoncent l'arbitraire d'une telle manipulation, d'ailleurs rendue inutile par l'avénement des analyses factorielles sous contrainte linéaire (*cf.* paragraphe 4.2.1.).

3. GRADIENTS D'ABONDANCE : L'ANALYSE EN COMPOSANTES PRINCIPALES

Au lieu que les distributions des espèces soient unimodales, leurs optimums se succédant le long du gradient, les variations d'abondance de ces espèces peuvent être continues le long du gradient (c'est-à-dire monotones croissantes ou décroissantes, voire même linéaires après transformation éventuelle). Ce sera le cas si l'on étudie un tronçon de gradient suffisamment court pour que les optimums de la plupart des espèces soient en dehors des bornes de l'échantillonnage. Dans ce cas, on peut raisonner directement en termes de *corrélation* entre les abondances des espèces et le facteur responsable du gradient. Si le facteur écologique responsable est bien identifié, sa corrélation directe avec une variable-espèce donnée est aisée à calculer. S'il ne l'est pas, on recherchera une « variable latente » (autrement dit un « gradient sous-jacent ») qui soit en meilleure corrélation linéaire possible avec l'ensemble des variables-espèces. La méthode naturelle pour cette analyse indirecte de gradient est l'Analyse en Composantes Principales (ACP).

Ter Braak (1987b, 1988) montre que la recherche de ce facteur latent peut s'effectuer, comme dans l'AFC, par une suite d'itérations. Soit y_{ij} l'abondance d'une espèce j dans un relevé i :

— on commence par une indexation x_i arbitraire, *a priori* et de variance unité, des relevés,

— on calcule, par *régression* linéaire classique, la pente b_j exprimant les variations des abondances des espèces. Les x_i étant centrés, cette équation s'écrit $y_{ij} = b_j.x_i$,

— on calcule les nouveaux indices x_i des relevés par régression inverse de x en y (c'est-à-dire par *calibration*),

— et ainsi de suite jusqu'à stabilisation de b_j et des x_i, qui alors ne dépendent plus des valeurs initiales arbitraires.

Comme dans l'AFC, l'ACP met en évidence des facteurs successifs non corrélés, facteurs qui résument la réponse commune de l'ensemble des espèces à des facteurs communs.

Dans les cas, fréquents en écologie, où se succèdent sur un gradient des espèces à distribution essentiellement unimodales (c'est-à-dire où le tableau des espèces est susceptible d'être réorganisé de façon à ce que les présences soient plus ou moins concentrées sur la diagonale, et les absences dans deux angles) l'utilisation de l'ACP devient inappropriée et l'AFC s'impose. En effet, la distance euclidienne sous-jacente à l'ACP rend cette analyse très sensible aux forts effectifs et aux doubles zéros ; il apparait de fausses similarités entre échantillons par absences d'espèces. L'utilisation de cette distance pour mesurer les similarités entre espèces ou entre relevés d'un gradient induit des distortions curvilinéaires maintes fois dénoncées, en particulier une involution des extrémités d'un gradient simple sur le plan des deux premiers facteurs (effet « fer à cheval ») (Beals 1973, Whittaker et Gauch 1973, Gauch *et al.* 1977, Wartenberg *et al.* 1987) (voir aussi Fig. 5). La distance du khi-2, sous-jacente à l'AFC, est moins sensible à ce problème ; son comportement l'apparente d'ailleurs plutôt à une distance simple déduite du coefficient de Jaccard (1901), de la forme 1 – w/u (où w est le nombre d'espèces présentes dans les deux relevés comparés, u le nombre d'espèces présentes dans l'un ou l'autre). Cette distance, qui exclut les doubles absences, ou celle assez proche dérivée de l'indice de Sörensen (Bray et Curtis 1957, Beals 1973), a démontré depuis longtemps son efficacité en tant que mesure de similarité dans des tableaux de comptage (Shi 1993). En pratique, on réservera donc l'ACP (en général normée) à l'analyse des tableaux de variables de milieu, dont les variations sont souvent monotones.

4. MISE EN RELATION DES VARIATIONS FLORO/FAUNISTIQUES AVEC LES VARIATIONS DES VARIABLES DE MILIEU

L'échelle des axes factoriels issus de l'analyse factorielle d'un tableau espèces x relevés est une «échelle d'intervalle» où unité et position de l'origine sont arbitraires. Certains auteurs, à la suite de Hill (1973), graduent par commodité leurs axes de 0 (choisi à un extrême de l'axe) à 100 (à l'autre extrême). C'est une graduation abstraite, et il n'y a pas de raison de supposer *«that (the habitat) characteristics change twice as much from 0 et 2 as they do from 0 to 1»* (Routledge 1984). L'ambiguité est augmentée par l'usage du mot facteur, qui dans l'analyse ne se réfère pas à un «facteur du milieu» (c'est-à-dire une variable externe) explicite. Quelle est donc la signification écologique d'un axe factoriel? Plus précisément, est-il possible de mettre en correspondance l'ordination floro/faunistique avec des variables de milieu, en ne se contentant pas, comme trop souvent, d'interpréter qualitativement les axes grâce aux connaissances acquises par ailleurs sur l'écologie des espèces?

Une solution *ad hoc* efficace consiste, sur le plan factoriel issu de l'AFC du tableau floro/faunistique, à associer chaque point-relevé à la valeur (ou la modalité) prise par la variable étudiée, ou à calculer la moyenne des coordonnées des relevés porteurs de la même modalité (Ayyad et Dix 1964). Selon cette représentation, on représentera les variables de milieu (codées en classes) de la même façon que les espèces participant à l'analyse, mais sans influer sur celle-ci. Les proximités des espèces et des relevés avec les points représentatifs des classes de variables peuvent alors donner d'utiles indications.

Mais, pour rester dans la logique du modèle linéaire, il est préférable de chercher à relier par régression les ordinations du tableau des espèces aux variables contenues dans le tableau des variables de milieu. Ce problème d'étalonnage des axes de l'analyse floro/faunistiques (AFC ou autre) par rapport à une ou plusieurs variables quantitatives décrivant le gradient (altitude dans le cas d'un gradient en montagne, durée d'émersion moyenne dans une étude de la zone intertidale, volume de la végétation pour un gradient successionnel, etc.) se pose dans les mêmes termes lorsque les variables sont qualitatives. Dans ce cadre simple de régression d'axes factoriels par rapport à des descripteurs de milieu, plusieurs approches sont possibles; elles correspondent à une imbrication plus ou moins poussée de l'étape analyse factorielle et de l'étape régression.

4.1. Analyse factorielle, puis régression

Dans cette approche, la régression *suit* l'analyse factorielle du tableau relevés x espèces, qui peut être une Analyse des Correspondances (Fig. 1b) ou toute autre analyse factorielle. On peut ainsi faire la régression d'un axe de l'AFC floro/faunistique sur un facteur du milieu (régression simple après une ordination *ad hoc* : Ayyad et Dix 1964, ou après ACP : Ibanez 1968), ou sur plusieurs variables (régression multiple), ou chercher une combinaison linéaire de plusieurs axes avec plusieurs variables (corrélation canonique). Ainsi Prodon et Lebreton (1981) relient-ils des variations de composition de l'avifaune (AFC) avec des variations de densités de plusieurs strates de végétation. De même Chang et Gauch (1986), après une AFC «détendancée», relient les axes de variations floristiques à des facteurs thermiques, hydriques et édaphiques. Lorsque certains facteurs ont des variations non linéaires, il en résulte une certaine perte d'information, que l'on cherchera à limiter par des transformations appropriées.

Cette approche se résume en trois formules : les deux formules de transition de l'AFC reliant coordonnées des espèces et des relevés (Tabl. I), et la formule de régression simple ou multiple (voir l'exemple de la Fig. 2b). Lorsque le coefficient de corrélation multiple, noté $R_{\text{post-AFC}}$, est élevé (ce qui sera souvent le cas dans une étude de gradient si les variables ont été bien choisies), les coordonnées des relevés obtenus par l'AFC (F_i observés, c'est-à-dire les moyennes pondérées des scores des espèces) et celles prédites par régression (F_i prédits) seront proches. Les axes factoriels pourront alors être considérés comme des variables de milieu synthétiques.

Cette approche est efficace lorsque l'adéquation entre le, ou les, premier(s) axe(s) de l'analyse et le gradient étudié est bonne, ce que seule une planification appropriée des observations est à même de garantir. Sinon, il est possible que des variations imprévues de composition taxonomique viennent dans l'analyse masquer le phénomène d'intérêt principal : des présences d'espèces rares peuvent fragmenter en blocs relevés x espèces un gradient *a priori* régulier; des variations de paysage peuvent venir perturber l'effet d'un gradient d'altitude, etc. L'éventuelle incapacité à expliquer le premier (ou un des premiers) facteur(s) de l'analyse par les variables de milieu mesurées n'implique donc pas forcément l'absence d'effet floro/faunistique de ces variables.

Il en est un peu de même pour une autre approche consistant à réaliser indépendamment une analyse factorielle pour chacun des deux tableaux (par exemple une AFC pour le tableau floro/faunistique, et une ACP pour celui des variables de milieu), puis à calculer la régression de la première ordination sur la deuxième. Cette méthode, souvent efficace, assure une bonne relation entre les deux tableaux puisque la réduction extrait de chacun d'eux les sources non aléatoires de variation. Elle assure une bonne robustesse puisque les processus d'optimisation inhérents aux deux méthodes n'interviennent pas dans la liaison entre les deux tableaux. Mais il n'y a toutefois pas de raisons qu'une combinaison linéaire des variables du deuxième tableau soit précisément celle qui explique au mieux les variations du tableau floro/faunistique (Lebreton *et al.* 1991).

4.2. Régression au sein d'une analyse factorielle : les analyses sous contrainte linéaire

4.2.1. Principe général

Pour être plus sûr de bien détecter l'action des variables de milieu, une imbrication plus poussée de l'analyse factorielle et de la régression est possible. Ainsi, dans le cas de l'AFC, on peut contraindre les coordonnées factorielles des relevés à être une combinaison linéaire de ces variables : c'est «l'Analyse Canonique des Correspondances» (Ter Braak 1986, 1987), ou «Analyse Factorielle des Correspondances par rapport à des Variables Instrumentales» (AFCVI ; Lebreton *et al.*, 1988a), ou encore «AFC sous Contrainte Linéaire» (Sabatier 1987). Dans cette analyse, les formules de transition incorporent désormais une régression (Tabl. I). Ces trois formules se prêtent à un calcul itératif, qui donne le premier couple de facteur de l'AFCVI (Fig. 1c), tout comme le double *averaging* conduisait au facteur de l'AFC (cf. ci-dessus 2.3.). La même imbrication des deux étapes, ordination et régression, peut d'ailleurs être réalisée à partir de toute ACP du tableau relevés x espèces, dans ce qu'on appelle du nom générique d'ACPVI (Sabatier 87, Sabatier *et al.*, 1989 ; Lebreton *et al.*, 1991).

Dans l'AFCVI, à la différence de l'AFC, on obtient explicitement *deux* coordonnées pour chaque relevé : celle obtenue par moyenne pondérée à partir des coordonnées de ses espèces, comme dans l'AFC ordinaire (F_i observé, c'est-à-dire le *Weighted Average score (WA)* de Palmer 1993), et celle prédite à partir de la combinaison linéaire de ses variables de milieu (F_i prédit, le *Linear Combination score (LC)* de Palmer). Ces deux ordinations sont reliées par un coefficient de corrélation multiple noté R_{AFCVI}. Le gain correspondant à l'imbrication de la régression dans l'analyse elle-même est que R_{AFCVI} est toujours supérieur ou égal à $R_{post\text{-}AFC}$ (Tabl. I).

En pratique, les coordonnées prédite par la régression multiple *(«LC-scores»)* exprimeront bien l'influence des variables de milieu mesurées sur la composition taxonomique. L'AFCVI sera capable d'«ignorer» les autres sources de variation éventuelles, connues ou non, de cette composition taxonomique. Le gain sera peut-être limité dans le cas de gradient simple ; il pourra être important en cas de données complexes ou fortement bruitées (Palmer 1993). Insistons aussi sur trois autres avantages très importants de l'AFCVI par rapport à l'AFC simple :

a) une moindre sensibilité à l'«effet Guttman», avec la possibilité de séparer les cas artéfactuels des liaisons réellement curvilinéaires,

b) une moindre sensibilité aux espèces rares,

c) une moindre sensibilité à la troncature des gradients qui entraine un relatif tassement des espèces et des relevés aux extrémités des axes dans l'AFC simple.

Tous ces avantages rendent sans objet le recours aux analyses «détendancées» *(detrended analyses)*. Enfin, l'AFCVI facilite l'interprétation des résultats en permettant la représentation dans le même plan, et éventuellement sur la même figure, des points-espèces (typologie des espèces) et des points-relevés (typologie des relevés), comme dans une AFC, et des vecteurs-variables, dont les angles et les longueurs s'interprètent comme en ACP (représentation «*triplot*»).

4.2.2. Nombre, nature, et pertinence des variables

Lebreton *et al.* (1991) rappellent que le rapport des variances I(AFCVI)/I(AFC), ou des inerties, ou encore des traces (= somme des valeurs propres de tous les axes de l'analyse), est comme dans toute ACPVI un rapport de corrélation multivarié ; c'est une moyenne pondérée des carrés des coefficients de corrélation entre les profils de chaque espèce et les variables de milieu. Ce rapport peut être interprété comme le carré d'un coefficient de corrélation. Il constitue donc une mesure *globale* (c'est-à-dire qui tient compte de tous les axes) de l'influence de l'ensemble des variables de milieu sur le peuplement, et donc de la pertinence de leur choix.

En tant que moyenne, ce rapport des variances est relativement insensible au nombre de termes utilisés, c'est-à-dire au nombre d'espèces. Cette robustesse pour un nombre d'espèces élevé est une des propriétés essentielles des ACPVI pour l'analyse des relations espèces-milieu. Les analyses sous contraintes perdent cependant de leur robustesse lorsque le nombre de variables approche le nombre de relevés ; les coefficients des variables dans les régressions multiples inhérentes à la méthode deviennent alors instables, et les rôles respectifs des variables ne peuvent être déterminés (Ter Braak 1986, 1987, Mercier *et al.* 1992). Autrement dit, l'intensité de la contrainte linéaire varie avec le nombre de variables de milieu. Si leur nombre dépasse celui des espèces, il n'y a plus de contrainte du tout, et l'AFCVI reproduit les résultats de l'AFC. S'il n'y a qu'une seule variable, l'AFCVI reproduit le résultat d'un simple *averaging* direct, et les espèces sont alors à la moyenne de leur variable de milieu.

Lorsque les relevés sont groupés en *n* classes (par exemple selon 4 types de sol), on a alors une variable qualitative à *n* classes ou modalités (soit 4 variables en 0/1 dans notre exemple). Une telle variable qualitative, qui constitue un «facteur» au sens de l'Analyse de Variance (on parlera souvent de «covariables»), pourra être utilisée par elle-même dans l'analyse, ou en conjonction avec d'autres variables qualitatives ou quantitatives.

4.2.3. Analyses «partielles»

Supposons que l'on souhaite étudier l'effet d'un groupe de variables B (par exemple les différentes modalités de la variable qualitative exposition), sachant qu'un autre groupe de variables A (par exemple l'altitude et le type de végétation) influence déjà le tableau relevés x espèces dans une étude d'avifaune en montagne. Il s'agit donc de déterminer la part de variation dans le tableau relevés x espèces expliquée par B, une fois l'influence de A prise en compte. Inversement, B peut être un ensemble de covariables dont on souhaite éliminer l'effet, et A le tableau des variables quantitatives d'intérêt principal. Comme avec les techniques classiques de régression partielle, on peut réaliser des analyses canoniques partielles, ou des ACPVI Partielles (Ter Braak, 1988 ; voir également Yoccoz et Chessel 1988), c'est-à-dire conditionnellement à une variable multivariée donnée. On parlera par exemple de l'ACPVI du tableau X par rapport à B/A («B sachant A»), c'est-à-dire par rapport à B une fois tenu compte de l'influence de A, ou l'inverse. La décomposition en effets successifs lorsqu'on a affaire à des facteurs multiples est développée par Sabatier *et al.* (1989). C'est une des voies les plus prometteuses des ACPVI.

4.2.4. AFCVI et Analyse discriminante

Parmi les Analyses par rapport à des variables instrumentales, l'AFCVI a un statut très particulier pour l'écologiste du fait de ses relations étroites avec certaines analyses discriminantes classiquement utilisée en écologie des communautés. L'usage de l'analyse discriminante est licite pour comparer les habitats de diverses espèces dès lors que chaque relevé concerne un seul individu d'une espèce donnée, accompagné de ses variables de milieu (voir par ex. Nudds 1982). Chaque relevé constitue donc un «individu statistique» dans la classe espèce considérée. L'analyse discriminante entre les classes ainsi constituées fournit des axes discriminants qui sont des variables de milieu synthétiques, c'est-à-dire des combinaisons linéaires des variables de milieu. Chaque espèce est placée à la moyenne des relevés où elle est présente, et le chevauchement entre les distributions des différentes espèces est minimisé.

Ce sont ces propriétés que l'AFCVI généralise au cas de relevés comportant plusieurs espèces. L'AFCVI fournit la combinaison linéaire de variables du milieu qui maximise la dispersion des espèces, c'est-à-dire la discrimination entre elles, puis la suivante non corrélée à la première, etc. (Ter Braak 1987a,b). Dans l'analyse, chaque présence d'une espèce donnée constitue un individu statistique qui se voit attribuer les variables de milieu du relevé concerné (voir Tabl. I *in* Lebreton *et al.*, 1988a). A noter, *contra* Nudds (1982), que les tests associés à l'analyse discriminante ne sont plus valides du fait de l'interdépendance induite par la duplication des variables de milieu inhérente à cette analyse.

4.3. Autres méthodes pour relier deux tableaux : les analyses symétriques

En insérant la régression au sein même de l'analyse factorielle, l'approche précédente relie directement le tableau relevés × espèces et le tableau relevés × milieu par une analyse factorielle d'un type particulier. A ce titre elle ne constitue qu'une des analyses qui permettent de relier deux tableaux de données portant sur les mêmes unités statistiques, c'est-à-dire les mêmes relevés. Parmi ces analyses, dont on pourra trouver une revue synthétique dans Mercier (1991), certaines font jouer un rôle symétrique aux deux tableaux.

4.3.1. Analyse des corrélations canoniques

Une première méthode consiste à chercher les couples de facteurs (il y en a autant que de relevés), de corrélation maximale, formés d'une combinaison linéaire des variables du premier tableau, et d'une combinaison linéaire des variables du second tableau : c'est l'Analyse des Corrélations Canoniques. Cette méthode représente de façon théoriquement optimale les dépendances entre les deux tableaux. Mais, en pratique, ceci n'est vrai que quand le nombre de relevés est très élevé par rapport au nombre de taxons et au nombre de variables de milieu (Hitier 1993). Sinon, apparait un problème de robustesse qui se traduit par une nette tendance à l'instabilité des résultats (par exemple Gauch et Wentworth 1976, Gittins 1985) ; on pourra toujours s'en convaincre en comparant les résultats obtenus par les analyses séparées des deux moitiés d'un même jeu de données. De plus, les relations entre les abondances des espèces et les variables de milieu sont en général non linéaires, rendant la recherche directe de corrélations problématique (Austin 1968).

4.3.2. Analyses de Costructure (ou de Co-inertie)

Les Analyses de Costructures, introduites dans un cas simple par Tucker (1958), ont récemment été systématisées et généralisées par Chessel et Mercier (1993) dans le contexte de l'analyse de données écologiques. On peut en comprendre le principe en simplifiant à l'extrême l'approche par corrélation. Réduisons tout d'abord le tableau relevés x taxons Y et, indépendamment, le tableau relevés x variables de milieu X chacun à leur plus important axe de variation; celui-ci sera le premier axe factoriel d'une analyse appropriée, souvent une AFC pour Y, et une ACP normée pour X. Soient y et x ces deux axes; ils sont bien représentatifs de la variabilité de chaque tableau car, parmi les combinaisons linéaires possibles des variables des tableaux respectifs Y et X, ce sont par définition celles de variance maximale. On peut alors étudier la liaison entre y et x sur un simple graphique et, si elle est raisonnablement linéaire, la quantifier par un coefficient de corrélation r_{xy}. Mais on peut chercher, dans un second temps, à modifier les coefficients des combinaisons linéaires de x et y de façon à augmenter r_{xy}. Ici, x et y étant chacun de variance maximum (σ_x^2 et σ_y^2), toute modification de l'un ou de l'autre diminuera sa variance. En améliorant la liaison entre x et y, on amoindrit donc dans une certaine mesure leur représentativité en tant que résumés respectifs de X et Y. Un compromis consiste alors à maximiser le produit $\sigma_x\sigma_y r_{xy}$. C'est l'objet de l'Analyse de Costructure, qui cherche à rapprocher les F1 des deux ACP sans détruire trop leur représentativité en tant que résumés linéaires de X et Y. Le même raisonnement se poursuit pour les axes factoriels successifs. Les facteurs obtenus, tout comme ceux des ACP originelles, sont par construction bien corrélés avec les variables de Y et X respectivement. Pour cette raison, les analyses de costructure sont relativement insensibles au nombre de taxons et de variables de milieu. En comparaison, les ACPVI sont peu robustes pour un nombre élevé de variables dans X (le tableau relevé x variables de milieu dans notre cas). Elles supporteront par contre éventuellement plus de taxons que de relevés dans Y (voir un exemple dans Lebreton *et al.*, 1991).

Les deux approches symétriques ci-dessus peuvent être critiquées précisément pour leur symétrie. Un des avantages des ACPVI par rapport à elles est en effet de prendre en compte explicitement l'influence supposée des variables de milieu sur la composition spécifique, et non l'inverse. Le tableau floro/faunistique constitue la structure à expliquer, l'autre tableau contient les variables explicatives. Il est vrai que dans certains cas, on peut être aussi intéressé par les possibilités de prédiction des variables de milieu à partir du peuplement que l'inverse. De plus, si les méthodes symétriques s'adressent théoriquement à des tableaux X et Y obtenus par échantillonnage entièrement aléatoire des relevés, la recherche d'une liaison milieu – espèce conditionnellement aux variables de milieu (par exemple lorsque les relevés sont organisés selon un plan d'expérience) reste acceptable par les méthodes symétriques, avec l'avantage d'une robustesse très appréciable en cas de nombres de variables de milieu ou de taxons élevés (Tabl. II) (Chessel et Mercier 1993, p. 34).

Tabl. II. – Avantages et inconvénients des trois catégories d'analyses multivariées couplant deux tableaux (Y : tableau des espèces, X : tableau des variables de milieu), en particulier en matière de robustesse.

Advantages and drawbacks of the three categories of multivariate analyses coupling two matrices (Y : species matrix, X : environmental variable matrix), in particular with respect to robustness.

Méthodes de couplage de Y et X	ANALYSE CANONIQUE	ACPVI (s.l.) de Y/X	ANALYSES DE COSTRUCTURE
Robustesse pour un nombre d'espèces élevées	NON (1,2)	OUI (1, 2)	OUI (1)
Robustesse pour un nombre de variables de milieu élevé (a)	NON	NON	OUI (1)
Flexibilité concernant la nature des mesures dans Y et X	potentiellement OUI	OUI (3)	potentiellement OUI
Possibilités d'analyses conditionnelles (ou "partielles")	OUI	OUI (3, 4)	potentiellement OUI
Possibilités d'inférences	OUI (5)	OUI (2)	OUI (2)

Note :
(a) une variable de milieu qualitative à m modalités compte pour m-1 variables

Références : 1- Chessel et Mercier (1993); 2 - Hitier (1993); 3 - Sabatier *et al.* (1989); 4 - Ter Braak (1988); 5 - Seber (1984)

En terme de flexibilité (possibilité d'adaptation à différents types de données), les trois approches sont équivalentes. Il est ainsi parfaitement possible de réaliser une analyse canonique entre un tableau relevés x espèces en présences-absences, justifiable par exemple d'une AFC, et des variables de milieu qualitatives, et ceci en jouant sur les transformations préalables et les pondérations (*cf.* 5.2.). En ce qui concerne les possibilité de tests, l'analyse canonique l'emporte, au prix d'hypothèses restrictives sur la nature des distributions sous-jacentes (normalité, linéarité...). Pour les autres analyses, des tests de permutation approchés sont possibles, soit par tirages au hasard (Ter Brak 1988), soit en utilisant une approximation de la distribution de permutation (Hitier 1993). Pour l'instant, les meilleures possibilités sont celles du logiciel CANOCO (Ter Braak 1987c) dans le cadre de l'AFCVI.

Les avantages en matière de robustesse et pertinence des trois approches analyse canonique, ACPVI, analyses de costructure sont résumées dans le Tableau II.

5. CHOIX D'UNE STRATÉGIE POUR UNE ÉTUDE ESPÈCES X MILIEU

5.1. Planification, choix des variables

Les trois principales décisions à prendre lors de la mise en place d'une étude de relations taxons – milieu sont les suivantes (d'après Lebreton et Yoccoz, 1987 complété; voir aussi Wiens 1989) :

1) Quel ensemble de taxons échantillonner, et avec quelle méthode de mesure d'abondance ou de simple présence?

2) Quelles variables de milieu mesurer?

3) Selon quelle planification des relevés?

Les réponses à ces questions dépendent en partie des objectifs et des questions biologiques, et en partie de considérations statistiques dont Frontier (1983) offre une bonne vue d'ensemble. L'ensemble de taxons échantillonné est généralement un groupe systématique bien défini, ou un ensemble d'espèces sensibles aux mêmes variations de milieu, susceptibles d'interactions, et échantillonnables par une même méthode (Coléoptères capturés par des pots de Barber, passereaux forestiers chanteurs, poissons pêchés au chalut, etc). Dans des études de groupes taxonomiques homogènes en relation avec la théorie de la niche, un plan d'échantillonnage selon un ou plusieurs gradients sera souvent retenu, alors qu'en biologie de la conservation, un plan d'échantillonnage systématique sera souvent approprié pour couvrir la région d'étude d'une façon homogène.

Choix des variables de milieu et planification des relevés sont d'ailleurs intimement liés. En effet par variables de milieu, il faut entendre toute variable caractérisant les relevés, y compris des variables qualitatives qui sont en fait des facteurs au sens analyse de variance du terme. Ainsi par exemple on pourra choisir 30 relevés dans un type de forêt, et 30 autres relevés dans un autre type, ou bien associer une variable qualitative (le versant) à une variable quantitative (l'altitude). Pour éliminer l'effet d'une variable, il est bien sûr toujours possible de limiter en conséquence l'échantillonnage, mais il sera souvent intéressant de pouvoir «éliminer» ces effets *a posteriori* (*cf.* par ex. Yoccoz et Chessel 1988, Dolédec et Chessel 1989). Ainsi, dans la planification d'une typologie de stations forestières, pour étudier l'effet du type de sol sur la composition floristique, on pourra :

— soit minimiser l'action du facteur altitude en répartissant strictement tous les relevés à l'intérieur d'un même étage altitudinal,

— soit procéder à une analyse, par exemple sur des variables instrumentales définissant les types de sol, conditionellement à l'altitude (§ 4.2.3.).

C'est ainsi que dans une étude d'invertébrés fluviaux, Richardot-Coulet *et al.* (1986; voir également Lebreton *et al.*, 1988b) caractérisent des relevés par une série de facteurs qualitatifs croisés, ce qui permet par exemple de tester l'effet de différentes méthodes d'échantillonnage compte-tenu d'autres sources de variation de composition spécifique comme la saison, le courant ou la station (Sabatier *et al.* 1989).

On veillera aussi à limiter au maximum, par une planification soignée, les confusions de facteurs. Par exemple des comparaisons d'avifaunes entre régions par des méthodes de points d'écoute ne pourront faire l'économie, si les différences à mettre en évidence sont subtiles, d'un contrôle de l'effet observateur : croiser observateur et régions, chaque observateur effectuant une part des relevés de chaque région est idéal. Un seul observateur partout semblerait encore préférable, mais le risque est alors d'introduire une confusion région-saison en étalant les relevés dans le temps!

Il est bien sûr recommandé de réduire le nombre de variables de milieu, à la fois pour les raisons de robustesse déjà discutées, mais aussi pour ménager les possibilités de mise en évidence d'effets car au delà de 4 variables des interactions complexes empêchent souvent la construction d'un modèle raisonnable.

D'après Chessel (1992), études théoriques et analyses concrètes permettent d'énoncer d'autres principes importants à prendre en considération dans la construction des plans d'échantillonnage : miniaturisation du sondage élémentaire (pour tenir compte de l'hétérogénéité du milieu et pouvoir augmenter le nombre des échantillons), emboîtement des mesures (plans de type hiérarchique), «abandon impératif de l'échantillonnage au hasard (constat d'ignorance et entretien de celle-ci)», contrôle des structures à plusieurs échelles... Les problèmes d'échelle sont au cœur de l'étude des relations espèces-milieu, depuis la définition des questions posées jusqu'à l'interprétation des résultats. En dépendent en effet tous les patrons de variabilité mesurés (Wiens 1989).

5.2. Choix des transformations, des métriques, et de la méthode de couplage

Une fois les tableaux de données obtenus, trois questions concernant l'analyse statistique doivent être examinées :

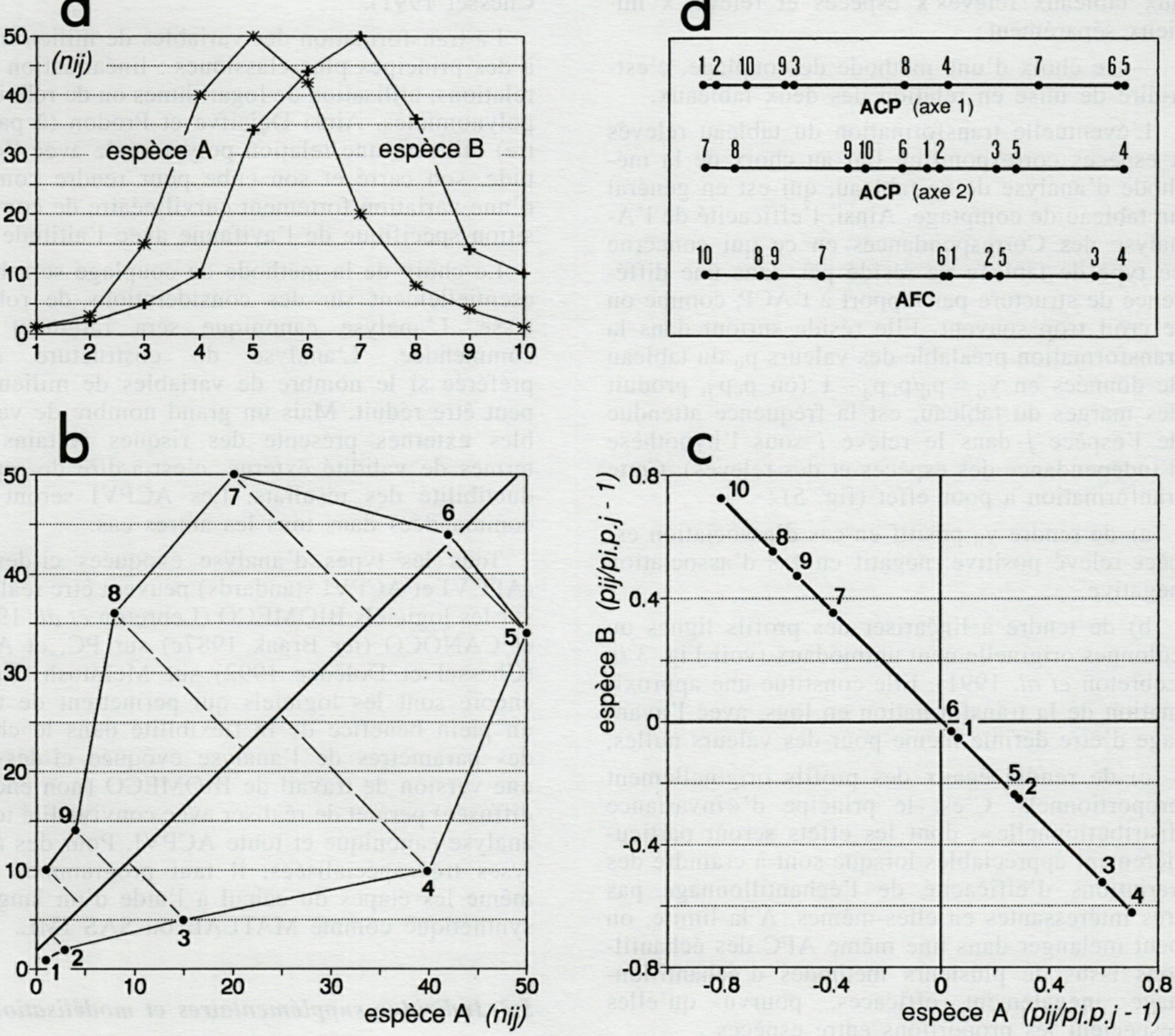


Fig. 5. – a, Exemple théorique d'un transect de 10 relevés (i = 1 à 10) contenant 2 espèces j_1 (« espèce A ») et j_2 (« espèce B ») en proportion variable (abondances de A : 1 ; 3 ; 15 ; 40 ; 50 ; 42 ; 20 ; 8 ; 4 ; 1, soit $n_{.1} = 184$, abondances de B : 1 ; 2 ; 5 ; 10 ; 34 ; 44 ; 50 ; 36 ; 14 ; 10, soit $n_{.2} = 206$).

b, Les 10 points-relevés dans l'espace défini par les deux axes-espèces, sans transformation des abondances brutes n_{ij}. L'ordination selon l'axe principal d'allongement du nuage est une approximation du premier facteur de l'ACP ; dans cet exemple, c'est un axe d'abondance trivial. L'ordination selon l'axe perpendiculaire au précédent est une approximation du deuxième facteur de l'ACP.

c, Les 10 points-relevés dans l'espace défini par les deux axes-espèces, après transformation des abondances en $y_{ij} = p_{ij}/p_{i.}p_{.j} - 1$ (avec $p_{ij} = n_{ij}/n_{..}$) : même sans les pondérations par les $p_{i.}$ et les $p_{.j}$ propres à l'AFC, l'ordination obtenue est une bonne approximation de l'AFC.

d, ordination des 10 points-relevés après ACP et après AFC. On remarque une certaine analogie entre l'ordination obtenue par AFC et celle obtenue sur le deuxième axe de l'ACP (inspiré et modifié de Wartenberg *et al.* 1987).

a, Theoretical example of 10 samples (i = 1 à 10) containing 2 species j_1 (species A) and j_2 (species B) in different proportions.

b, The 10 relevés in the space defined by the 2 species-axes, with the raw species abondance values. The ordering on the principal axis of the scatter of points is an approximation of the first axis of PCA. The ordering on the second principal axis is an approximation of the second axis of PCA.

c, The 10 relevés in the space defined by the 2 species-axes, after transformation of the abondances in $y_{ij} = p_{ij}/p_{i.}p_{.j} - 1$ (with $p_{ij} = n_{ij}/n_{..}$). Even without the weighting by $p_{i.}$ and $p_{.j}$, the resulting ordering is a good approximation of the CA ordering.

d, One-dimensional ordering of the relevés after PCA (first and second axes) and after CA.

— le choix d'une transformation des données, et le choix des pondérations. Ces deux choix sont inhérents aux analyses multivariées applicables aux tableaux relevés x espèces et relevés x milieux séparément ;

— le choix d'une méthode de couplage, c'est-à-dire de mise en relation des deux tableaux.

L'éventuelle transformation du tableau relevés x espèces correspond en fait au choix de la méthode d'analyse de ce tableau, qui est en général un tableau de comptage. Ainsi, l'efficacité de l'Analyse des Correspondances en ce qui concerne ce type de tableau ne réside pas dans une différence de structure par rapport à l'ACP, comme on le croit trop souvent. Elle réside surtout dans la transformation préalable des valeurs p_{ij} du tableau de données en $y_{ij} = p_{ij}/p_{i.}p_{.j} - 1$ (où $p_{i.}p_{.j}$, produit des marges du tableau, est la fréquence attendue de l'espèce *j* dans le relevé *i* sous l'hypothèse d'indépendance des espèces et des relevés). Cette tranformation a pour effet (fig. 5) :

a) de rendre y_{ij} positif en cas d'association espèce-relevé positive, négatif en cas d'association négative,

b) de tendre à linéariser des profils lignes ou colonnes originellement unimodaux (voir Fig. 3 *in* Lebreton *et al.* 1991). Elle constitue une approximation de la transformation en logs, avec l'avantage d'être définie même pour des valeurs nulles,

c) de rendre égaux des profils originellement proportionnels. C'est le principe d'« invariance distributionnelle », dont les effets seront particulièrement appréciables lorsque sont à craindre des variations d'efficacité de l'échantillonnage pas très intéressantes en elles-mêmes. A la limite, on peut mélanger dans une même AFC des échantillons issus de plusieurs méthodes d'échantillonnage inégalement efficaces, pourvu qu'elles respectent les proportions entre espèces.

En revanche, cette transformation peut être inopportune lorsque les variations d'abondance absolue présentent un intérêt en elles-mêmes, ou lorsque l'accent doit être mis sur les espèces les plus abondantes. Diverses autres variantes sont possibles pour des tableaux de comptage. Elles peuvent être vues comme des solutions intermédiaires entre ACP et AFC : par exemple les transformations $y_{ij} = p_{ij} - p_{i.} - p_{.j} + 1$ (ACP bicentrée), ou $y_{ij} = p_{ij}/p_{.j} - p_{i.}$ (Analyse non symétrique des Correspondances). L'exploration des performances pratiques de ces variantes est en cours.

Le choix d'une transformation préalable du tableau de comptage est donc essentiel. Celui des pondérations est moins critique (Blanc *et al.* 1976) et résultera souvent du choix de la méthode sélectionnée pour la transformation qu'elle implique. Ainsi, dans le cas de l'AFC, une pondération uniforme des relevés pourra être souhaitable pour donner un sens à des tests de permutations. Quoi qu'il en soit, les étapes qui suivent transformations et pondérations peuvent être décrites en tant qu'ACP généralisée (*cf.* Fig. 3 *in* Dolédec et Chessel 1991).

La transformation des variables de milieu obéit à des principes plus classiques : linéarisation des relations, utilisation de logarithmes ou de relations polynomiales. Ainsi Dejaifve et Prodon (à paraître) utilisent une relation polynomiale avec l'altitude, son carré et son cube pour rendre compte d'une variation fortement curvilinéaire de composition spécifique de l'avifaune avec l'altitude.

Le choix de la méthode de couplage sera basé esentiellement sur des considérations de robustesse. L'analyse canonique sera rarement recommendée. L'analyse de costructure sera préférée si le nombre de variables de milieu ne peut être réduit. Mais un grand nombre de variables externes présente des risques certains en termes de validité externe, c'est-à-dire de reproductibilité des résultats. Les ACPVI seront recommandées dans tous les autres cas.

Tous les types d'analyse évoquées ci-dessus (AFCVI et ACPVI standards) peuvent être réalisés sur les logiciels BIOMECO (Lebreton *et al.* 1990) et CANOCO (ter Braak 1987c) sur PC, et ADE (Chessel et Dolédec 1992) sur McIntosh. Rares encore sont les logiciels qui permettent de tirer un plein bénéfice de la flexibilité dans le choix des paramètres de l'analyse évoquée ci-dessus ; une version de travail de BIOMECO (non encore diffusée) permet de réaliser avec convivialité toute analyse canonique et toute ACPVI. Pour des analyses très spécialisées, il faut programmer soi-même les étapes du calcul à l'aide d'un langage synthétique comme MATLAB ou SAS IML.

5.3 Individus supplémentaires et modélisation

En analyse multivariée, où le modèle linéaire est partout sous-jacent, on oublie trop que le principal intérêt d'une équation de régression $y = a + bx$ est de pouvoir prédire y lorsque seul x est connu. L'analyse des relations espèces – milieux ne fait pas exception. Ainsi peut-on considérer la représentation obtenue dans une AFC suivie d'une régression, ou dans une AFCVI, comme un modèle des relations espèces milieu. La composition taxonomique permet de prédire les coordonnées de relevés suplémentaires par simple *averaging* des coordonnées des espèces. La mesure des variables de milieu permet une autre prédiction des coordonnées de ces mêmes relevés, qui peut être en forte liaison linéaire avec la première (cf. par exemple Prodon et Lebreton 1981). Comme toujours, ce sont les cas où le modèle est pris en défaut qui sont les plus instructifs. Ainsi, après perturbations, peut-on observer des distortions entre la composition faunistique et les variables de milieu (dans cet exemple la couverture végétale). Cette distortion est due ici à des effets de rémanence des avifaunes forestières après incendie (Prodon et Lebreton 1983).

La même approche pourrait être utilisée pour effectuer une validation croisée, c'est-à-dire pour obtenir, sur un lot de relevés consitutant une réplication du lot de départ, une estimation de la corrélation entre l'ordination floro/faunistique et les variables de milieu indépendante, et donc de validité externe maximale. C'est une manière de rétablir la robustesse des ACPVI en cas de doute dû à un grand nombre de variables de milieu.

6. DISCUSSION

« Par le choix d'une méthode, par la direction donnée à l'interprétation, l'analyse des données est modélisatrice »

Estève 1978

Parmi les méthodes d'ordination utilisées en écologie, on distingue classiquement deux catégories :

– les analyses directes (par ex. Whittaker 1967) ou « *environmental ordinations* » (Austin 1968) relient la distribution des espèces à des variables externes mesurables et d'importance reconnue. C'est l'« *extrinsic analysis* » de William et Lance (1968), ou « *ecological analysis* » (Whittaker et Gauch 1978). C'est le domaine des profils écologiques, de l'*averaging* simple ou de la régression logistique, de la régression simple ou multiple sur variables de milieu, espèce par espèce. Une telle approche peut être pertinente à condition que ces variables de milieu rendent bien compte de la variabilité floro/faunistique observée (Mercier *et al.* 1992). Mais l'analyse ignore les éventuelles covariations entre espèces, c'est-à-dire l'aspect intégré du peuplement.

— les analyses indirectes sont basées, comme dans la phytosociologie classique, sur une analyse du seul tableau relevés x espèces (« *intrinsic analysis* » de William et Lance 1968, « *taxonometric analysis* » de Whittaker et Gauch 1978 ou encore « *continuum analysis* » de McIntosh 1958). Pour cela, l'AFC et ses variantes éventuelles sont un des outils les mieux adaptés. L'influence éventuelle de variables de milieu, par exemple sous forme de gradients écologiques, peut alors être inférée *a posteriori.*

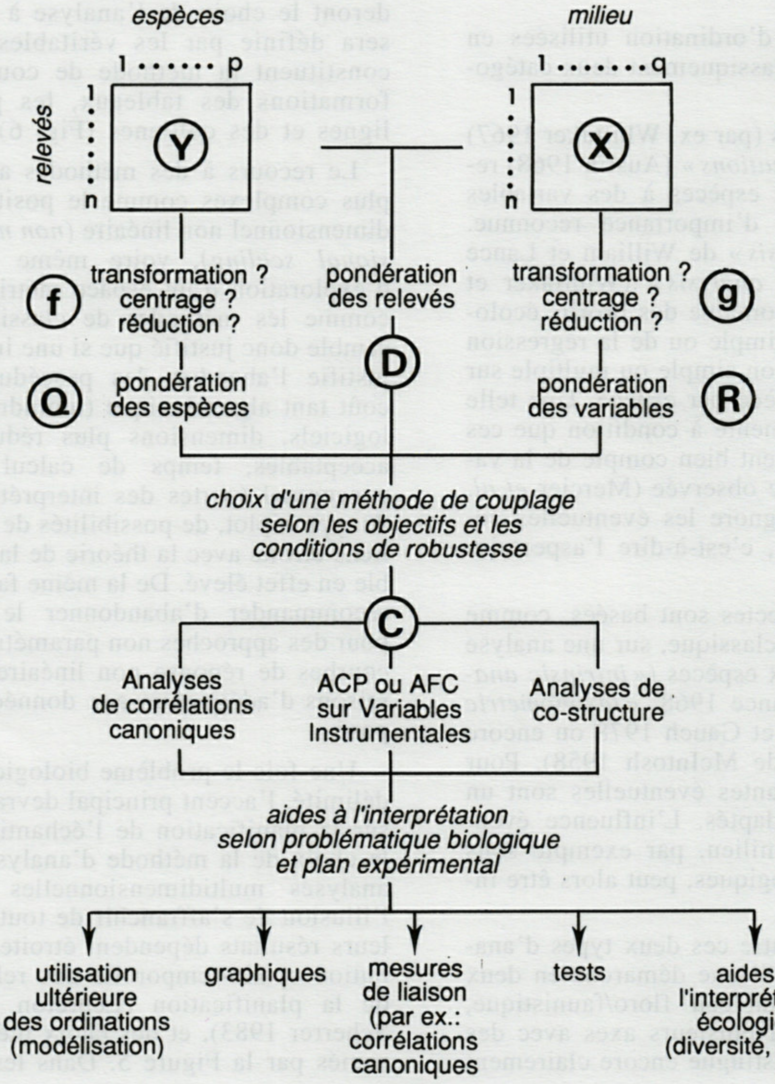
Mais la distinction entre ces deux types d'analyse tend à s'estomper. Si une démarche en deux temps (ordination du tableau floro/faunistique, puis corrélation d'un ou plusieurs axes avec des descripteurs externes) distingue encore clairement analyse interne et externe, les analyses sous contraintes comme l'AFCVI (pourtant qualifiées de directes par Ter Braak 1986), et plus encore les analyses symétriques, mêlent les deux approches. Elles rapportent en effet les principaux axes de la variabilité floro/faunistique à la variabilité du milieu, tout en fournissant des mesures de l'intensité de la relation entre les deux. Ainsi les multiples possibilités de couplage des deux tableaux réconcilient-elles méthodes d'ordinations directes et indirectes.

Comme le pressentaient Blanc *et al.* (1976) la flexibilité des analyses multivariées linéaires est loin d'avoir été épuisée. Permettant de se libérer des limites de telle ou telle méthode rigide, cette flexibilité rend possible en effet une meilleure mise en adéquation entre problématique et données d'une part, et analyse statistique d'autre part. Ce sont la nature des données (par exemple espèces notées en présence-absence), les considérations de robustesse (par exemple un nombre élevé de taxons), et surtout les questions biologiques (par exemple étude de l'effet de perturbations sur un gradient de milieux) qui guideront le choix de l'analyse à réaliser. Celle-ci sera définie par les véritables paramètres que constituent la méthode de couplage, les transformations des tableaux, les pondérations des lignes et des colonnes (Fig. 6).

Le recours à des méthodes algorithmiquement plus complexes comme le positionnement multidimensionnel non linéaire *(non metric multidimensional scaling)*, voire même à des méthodes d'exploration d'un espace métrique non linéaires comme les méthodes de classification, ne nous semble donc justifié que si une inadéquation claire justifie l'abandon des procédures linéaires. Le coût tant algorithmique (moindre disponibilité en logiciels, dimensions plus réduite des tableaux acceptables, temps de calcul important) que conceptuel (pertes des interprétations graphiques de type biplot, de possibilités de modélisation, des liens étroits avec la théorie de la niche) nous semble en effet élevé. De la même façon, on ne saurait recommander d'abandonner le modèle linéaire pour des approches non paramétriques ou pour des courbes de réponse non linéaires sans de solides raisons d'adéquation aux données et au problème posé.

Une fois le problème biologique à étudier bien délimité, l'accent principal devra porter davantage sur la planification de l'échantillonnage, que sur le choix de la méthode d'analyse elle-même. Les analyses multidimensionnelles peuvent donner l'illusion de s'affranchir de tout *a priori*. En fait, leurs résultats dépendent étroitement de la distribution spatio-temporelle des relevés, c'est-à-dire de la planification (Lebreton et Yoccoz 1987, Scherrer 1983), et des choix méthodologiques résumés par la Figure 5. Dans les analyses à deux tableaux, le choix des variables externes explicatives est, nous l'avons vu, particulièrement délicat. Or ces variables sont en nombre infini. Pour leur choix, il sera indispensable de faire appel aux connaissances *a priori* de l'écologiste et à son intuition. Il est aussi recommendé de se soucier de l'interprétation des résultats dès la planification : «*I suspect that a lot of unintelligible linear combinations have been lost somewhere between analysis and publication*» (Johnsson 1981). Il est donc clair que toutes les connaissances *a priori*, même intuitives, des espèces, de la région d'étude, ou de la littérature, doivent être mobilisées dans la phase de planification. Elles jouent un rôle essentiel et décisif que l'objectivité des calculs ultérieurs ne saurait masquer. On ne peut donc suivre Benzecri (1986) lorsqu'il affirme que «l'analyse statistique affranchit des idées *a priori*» en permettant de traiter le complexe «sans y projeter de structures *a priori*».

L'accent mis sur la planification résulte d'une évolution de l'outil statistique : on peut dire qu'avec le développement des méthodes de couplage entre tableaux, les méthodes d'ordination pour l'analyse des relations espèces milieux ont rejoint la statistique classique. En effet, utilisées au départ comme méthodes exploratoires pour révéler des gradients ou des groupements dans des ensembles de données complexes, les analyses factorielles tendent désormais à être utilisées en écologie pour tester des hypothèses sur les relations entre faune/flore et environnement, par exemple dans la modélisation de gradients définis *a priori* comme objets d'étude (Prodon et Lebreton 1981, Balent 1986a et b, Dakki 1986, Mercier 1988, etc). Le rapide développement de procédures inférentielles ne fera qu'accentuer cette tendance. Parmi les directions les plus prometteuses, l'utilisation dans des situations de type expérimental est à peine amorcée. Lavorel *et al.* (1991)



et Lavorel et Lebreton (1992) testent ainsi des hypothèses sur les mécanismes de succession végétale entre des relevés traités et des témoins. Les « variables de milieu » sont alors des variables qualifiant les relevés, c'est-à-dire des facteurs au sens exact de l'analyse de variance. Les mêmes auteurs associent également des facteurs hiérarchiques à différentes échelles spatiales et délimitent ainsi les échelles de plus forte variation de composition spécifique. A une échelle appropriée, est ensuite étudié l'effet de « variables de milieu » biotique, en l'occurrence le contenu de la banque de graines, sur la composition de la végétation épigée, pour tester des hypothèses concernant la niche de régénération.

Beaucoup de critiques sur l'utilisation de l'analyse multivariée dans l'étude des communautés résultent de l'abus qui en a été fait dans des situations uniquement descriptives. On rejoint ici les raisons de la crise de la phytosociologie classique. D'autres se rapportent aux difficultés inférentielles, c'est-à-dire à la difficulté de cerner la validité des résultats. La flexibilité se développant actuellement vaut-elle la peine de l'effort de compréhension que cela suppose de la part de l'écologiste ? La réponse peut être non en termes de compréhension des patrons principaux de variation, ou d'obtention de graphiques démonstratifs. L'échantillonnage dans l'étude des communautés est souvent si contrasté que les faits majeurs peuvent être appréhendés par bien des techniques statistiques différentes. Mais, même si l'évolution encore en cours des méthodes que nous avons passées en revue, et les difficultés qui en résultent pour l'écologiste, sont encore un frein, la réponse est certainement oui dans trois directions qui ne peuvent laisser indifférent :

— la possibilité d'un contrôle de la robustesse, c'est-à-dire de la validité externe des résultats, notamment lorsque les effets étudiés sont subtils,

— les liens étroits avec les concepts écologiques, par exemple avec les différents aspects de

Fig. 6. – Etapes de la réalisation et choix des options dans une analyse de relations espèces-milieu, basée sur un tableau relevés x espèces (Y) associé à un tableau relevés x variables (X).
Une telle analyse peut se résumer par la formule
C((f(Y), Q, D), (g(X), R, D))
dont les huit paramètres sont :
C méthode de couplage (canonique, variables instrumentales, co-inertie, régression après ACP de Y,...) (voir revue in Mercier 1991, Chessel et Mercier 1993)
f transformation (y compris centrage et réduction éventuels) du tableau relevés x espèces (par exemple $(p_{ij}/p_{i.}p_{.j} - 1)$ dans le cas de l'AFC)
Y tableau relevés x espèces
Q pondération (ou « métrique ») des espèces (inutilisée en analyse canonique) (par exemple $(p_{i.})$ en AFC)
D pondération (ou « métrique ») des relevés (c'est-à-dire des lignes de Y et de X)
g transformation des variables de milieu (y compris centrage et réduction éventuels) (par exemple en Logs)
X tableau relevés x variables de milieu
R pondération (« métrique ») des variables de milieu (inutilisée en analyse canonique et sur variables instrumentales) (par exemple Identité, c'est-à-dire poids uniformes, pour l'ACP).
Ainsi, par exemple :
ACPVI ($(p_{ij}/p_{i.}p_{.j} - 1)$, $(p_{.j})$, $(p_{i.})$), (X, Identité, $(p_{i.})$) est l'Analyse Canonique des Correspondances (ACC ; ter Braak 1986, 1987) ou Analyse Factorielle des Correspondances sur Variables Instrumentales (AFCVI ; Lebreton et *al.* 1988 a et b).

Steps and methodological options in the realization of a species-environment analysis, from a relevés × species matrix (Y) associated with a relevés × environmental variables (X). This analysis can be summarized by the formula
C((f(Y), Q, D), (g(X), R, D))
the eight parameters of which are :
C the method of coupling (canonical, instrumental variables, coinertia, regression after PCA of Y...) (see review in Mercier 1991, Chessel et Mercier 1993)
f transformation (including possible centering and reduction) of the sample-species matrix (e.g. $(p_{ij}/p_{i.}p_{.j} - 1)$ *for Correspondence Analysis)*
Y sample × species matrix
Q weighting of the species (unused in canonical analysis) (e.g. $(p_{i.})$ *for CA)*
D weighting of the samples (i.e. lines of Y and X matrices)
g transformation of environmental variables (including possible centering and reducing)
X sample × environmental variables matrix
R weighting of the environmental variables (unused in canonical analysis and instrumental variable analysis) (e.g. identity, i.e. uniform weighting, in PCA)
As an example :
CAIV ($(p_{ij}/p_{i.}p_{.j} - 1)$, $(p_{.j})$, $(p_{i.})$), *(X, Identity,* $(p_{i.})$*) is the Canonical Correspondence Analysis (CCA ; ter Braak 1986, 1987) or Correspondence Analysis with respect to Instrumental Variables (CAIV ; Lebreton* et al. *1988 a et b).*

la théorie de la niche et de la diversité, liens sur lesquels nous nous proposons de revenir,

— les possibilités d'utilisation comme modèle (étude des perturbations, des échelles spatiales et temporelles...).

On ne peut donc qu'encourager les écologistes à faire preuve d'imagination et à concevoir des plans d'observation ou d'expérience astucieux ciblés sur des problèmes précis.

REMERCIEMENTS – Nous remercions MM. J. Lepart, P. Chardy et S. Hitier pour les utiles remarques dont ils ont bien voulu nous faire part dans des délais très courts.

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Reçu le 16 mai 1994 ; received May 16, 1994
Accepté le 14 juin 1994 ; accepted June 14, 1994

Directeur gérant de la publication : A. Guille

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Printed in France *Dépôt légal : 3^e^ trimestre 1992* *Commission paritaire n^o^ 22217*

Imprimerie Louis-Jean, 05002 GAP cedex — Dépôt légal 589 — Juillet 1994

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VIE ET MILIEU, 1994, 44 (1)

Life and Environment

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