

UCL No. 20000
6/11/78

ON UPWELLING, EUTROPHIC LAKES, THE PRIMITIVE BIOSPHERE, AND BIOLOGICAL MEMBRANES

Ramón Margalef

Department of Ecology, University of Barcelona, Gran Via 585, Barcelona (7), Spain

Marta Estrada

Instituto de Investigaciones Pesqueras, Paseo Nacional, Barcelona (3), Spain

Mapping the pelagic environment on an ecological space defined by the distribution of phytoplankton.

Organisms are excellent sensors of properties of the environment. We feel that the picture provided through the filters of sophisticated pieces of equipment should be complemented by some appreciation of the biota. As an example, interesting by itself, and convenient for further discussions, we introduce the result of a new analysis of a series of more than 600 phytoplankton samples collected during two cruises in NW Africa (Margalef, 1978a; tables). The original data were compressed in the following way: For each pair of neighboring stations, closeness in the taxonomic composition of phytoplankton was assessed using Spearman's rank correlation coefficient. Boundaries were drawn between the stations with more dissimilar plankton, dividing the area in a number of small regions (fig. 2). The corresponding depths of all stations inside each region were pooled, using arithmetic averages, into an average profile.

A principal component analysis has been performed on such set of data, based on the correlation matrix of the distributions (^{logarithm} transformed abundances) of 33 species or groups of species (names in figs. 1, 2) in the whole set of samples. In total, more than 300 species were identified, but only the species or groups of species present at least in 30 of the pooled samples have been retained for the analysis. One of us (Estrada, 1978) made a principal component analysis of another set of samples collected in one of the cruises (Atlor II, March 1973) and the results have encouraged us to work with a larger material. Although we are aware of the pitfalls and lack of subtlety of the method, we feel it works well describing on a large scale areas of great contrast, as upwelling and non upwelling regions are.

The three first components account for the 53% of the total variance. The first component is strongly related to total abundance. The distribution of species and groups of species on the plane defined by components 2 and 3 (fig. 1) shows a clustering apart of the taxonomic groups and inside them the assumedly common segregation between congeneric species. The most important result is that this distribution can be projected without much distortion on an ordination of phytoplankton species that has been advocated in other papers (Margalef, 1978b). In it, the different life-forms of phytoplankton are associated with concentration of nutrients and with the coefficient of vertical turbulent diffusion.

It seems that the components 2 and 3 are related to agents significant in the selection of the different life-forms, embodied by different genera and species. We stress the total independence of the paths that lead to congruent distributions, and we see here a reason for hope in further developments.

A second principal component analysis was done with the values of gradients, computed as $(\log N_{z_1} - \log N_{z_2}) / (z_2 - z_1)$, where N are densities (in cells per ml) and z the depths. The rationale behind was the possible effect of upwelling on the vertical distribution of species and their gradients. The three first components added to a 33.5% of the variance, and the result of the analysis do not provide particular insights. Some relation is found with the precedent analysis, probably because in more turbulent water, not only concentration of cells is higher, but also the stratification is more blurred. Species of Rhizosolenia appear closer together in this analysis, perhaps because all favour certain patterns of layering.

Using the scores of each one of the composite samples, defined by survey and region (key in fig. 2) and depth, computed on the basis of the representation of the 33 species or groups of species, the position of the different composite samples has been constructed in a multicomponent space. The

. The resulting distribution makes much sense. Unfortunately its complexity makes difficult a representation on paper. The two surveys appear neatly segregated, excepting only the upwelling spots, that partage always some common characters, marked by a high score on the first component in the surface layers. The regions N are rich in phytoplankton and are placed close to the core of upwelling. Warm areas and offshore waters can be associated with a lower density of phytoplankton and a higher proportion of dinoflagellates. In the region S (Southern) seasonal differences are maximum, as they were actually at sea. The areas with abundant cryptomonads are well segregated from the rest and show strong vertical gradients. It is general that differences between surveys and between regions decrease in depth (100 m). Stratification can be best visualized by plotting the scores for the different components against depth in the form used by Denman and Platt (1978). The differences between surveys consist of seasonal changes in the communities including a different participation of diverse water masses in upwelling (Margalef, 1975).

A repetition of the analysis using gradients, as mentioned before with reference to species, added nothing important. Upwelling regions stand out. Differences in the position of the layers of maximal densities in the different regions resulted in complicated patterns of interlocking loops. An ordination of the samples based not on the matrix of correlation between gradients of species, but on that of gradients of chemical variables, resulted in a pattern with features either trivial or that we were unable to interpret.

The species and the samples have been positioned in a common frame using the

analysis of correspondence or reciprocal averaging (fig. 2). We see the results as less satisfying than the precedent ordination, although the pattern and general relations are substantially the same. The first axis is always much related to the abundance or density of populations. The analysis of correspondence using log-transformed data emphasized the distinction of particular regions in relation with local dominance of particular species (Thalassiosira parthenea, Oscillatoria thiebautii).

We feel worthwhile to examine the possibility of developing a project along these lines, but including more taxonomic groups (species or groups of species), perhaps 80 to 100, and extended over the principal upwelling areas in the world ocean. Since we have more interest now in ecology than in evolution and biogeography, taxonomic units are more important as "ecological species" typifying life-forms. The high proportion of cosmopolitan species is an advantage, although it is in part apparent and covers much local genetic and physiological differentiation. The study of the correlations in distribution between a number of core taxonomic units could provide the basis for the ordination of a large number of samples collected in routine work.

Variables different from the density of populations are, of course, not excluded, and we believe that variables that can be monitored in an automatic way, like fluorescence or particle counts, could be specially valuable in surveys for practical purposes.

Upwelling areas as systems under stress and their comparison with other ecosystems.

The precedent section provides a good introduction to the subject, insofar that it shows how, between different spots in the sea, an ecological distance can be computed that is not proportional to the metric distance between the same points, or even to some distance computed on the distribution of hydrographic properties. We are led to a vision of different fields, each one to be described with reference to others, and suspect that upwelling systems would emerge as strongly deformed fields, in relation with any chosen frame of reference.

Upwelling areas and eutrophic lakes are the most productive planktonic ecosystems. Both are force-fed, with nutrients provided, respectively, from deep layers or from neighboring terrestrial ecosystems. Reactions that depend on concentrations are accelerated, with resulting significant shifts in ratios like phytoplankton/nutrients, zooplankton/phytoplankton. The ratios that are usually labeled as "efficiencies", generally drop, and food-chains may be shortened. The set of interactions, and the amount of the components, appear more or less displaced from what is considered normal and steady state in otherwise comparable ecosystems. The forced system works as if opposing to the extra input of nutrients, not only by an acceleration of the functions, but also circulating one fraction of the elements through loops external to the ecosystem of reference: oxygen and nitrogen through the atmosphere, organic carbon and phosphate through the sediment (Margalef, 1975).

This behavior can be shown more didactically through physical models (hydraulic, electrical) than through the usual mathematical models, probably because we need come closer to the field where ecology meets thermodynamics. All force-fed ecosystems, including marshes and cropland, behave the same way. Fertilization of agricultural ecosystems accelerates turnover, intensifies denitrification and part of the phosphorus present is removed from circulation in the form of highly insoluble phosphates (Eidt, 1977). The activity of the biosphere in the past has resulted in the formation of an atmosphere rich in nitrogen and in oxygen, and in vast deposits of reduced carbon.

The fundamentals of plankton ecology are simple. Any atom has a higher probability of travelling down when it forms part of a particule than when it is in solution. Phytoplankton cells sink; on the average, zooplankton feeds at a layer that is closer to the surface than the level at which excrete, and the compacted fecal pellets of copepods, often the dominant plankters, sink at relatively high speed. Reducing power acquired in the photic zone is transferred down mechanically, under the action of gravity. Thus, the whole thickness of the ecosystem, viz. of the biosphere, consists of an electron transport system. The spectrum of the intensity of this transport, measured over different spaces, or over different ways of integrating organismic components, might be useful as a criterium of organization and to assess how far an ecosystem is forced or stressed from outside. The vertical gradients in pE (Eh) and in pH are very valuable ecological indicators. Accumulation of organic matter in the sediment is related not only to the productivity of the supplying system, but to its degree of stratification as well, a conclusion important in paleoecology (Degens and Stoffers, 1976).

Electromagnetic radiation and gravity combine in the functional organization of the marine biosphere. The biosphere can be compared to a biological membrane, where different forces are at work in a physical matrix that is more rigid, what explains the different scales involved. The comparison may be perhaps attractive for the molecular ecologist. It may suggest that, in both entities, local perturbations associated with rapid exchanges of energy (upwelling, the winter chimneys in the Mediterranean) can propagate in the form of waves on a plane perpendicular to the main (vertical) gradient.

The vertical functional structure of a pelagic ecosystem is basically defined by the distribution of primary production and total respiration. The non-overlap of both distributions reflects mainly the vertical transport (sinking of particulate material) and also some horizontal transport. If the overall distributions are more or less preserved, the excess of particulated organic matter travelling down has to equal the supply of nutrients to the top. Considerable interest exists in making estimates of the flow of particulated material (Bishop *et al.*, 1977; Eppley and Peterson, 1979), and of the fraction of the

total production that is recycled in deep water or, respectively, in layers close to the surface, although it is more useful to think in terms of a vertical continuum than in discrete compartments. In more productive, more stressed ecosystems, in coastal waters, closed basins, upwelling areas and eutrophic lakes, a larger fraction of the material is recycled down. In other words: organic matter sinking from the upper layers penetrates to a greater depth just in the areas of more intensive ascent of deep water (Sapotschnikov, 1975). It would appear easy to compute an index to express the intensified exchange by countercurrent, based on actual gradients of light, nutrients and plankton. A very rough index was devised and applied to the area of our study in NW Africa (Margalef, 1975b), and we have so far failed in our attempt to find a more elegant index that could be computed on information available generally. The flow of elements (N, O, C, P) to the external loops, is proportional to the steepness of the vertical gradient of redox potential. Upwelling areas drive out more effectively than unstressed marine systems a fraction of its components in the boundaries. The evidence is found in the composition of the sediments beneath upwelling areas. Direct estimates of the flow of N and O to the atmosphere seem to be absent.

Although what has been said is not new, it bears repetition with the purpose of pulling together different streaks of reasoning, leading to complementary ways of comparing upwelling and non-upwelling areas. Comparison should extend to the whole water column. The relationship between organization and function of the ecosystem and the input of external energy should be emphasized. The role of external, exosomatic or non-photosynthetic energy in ecology is suggested by the correlation between the yield of crops and the subsidy that farming receives. Forced systems

use much energy in environmental transport, mostly horizontal in eutrophic lakes and in marshland, vertical in upwelling areas, and mixed in the intertidal ecosystems rich in macrophytes. Production drops when forcing stops.

The work done in an upwelling area could be quantified combining different approaches: 1) Work done against gravity by the displaced water, 2) Changes in the kinetic energy of boundary currents in relation with an upwelling event, 3) Exchange of heat through the surface of the sea. The last possibility seems particularly promising. Mapping the distribution of the different components of the total exchange of heat around a machine, the parts where work is done, for instance, the pistons, stand out. The maps published by Hastenrath and Lamb (1978), as well as some former maps in Budyko (1974), show fairly good spatial correlations with the distribution of marine productivity and the position of the main upwelling areas. Perhaps monitoring of ocean production from space may be more effective if based indirectly on heat exchange than in direct estimates of the chlorophyll content, besides a straightforward reliance on biological indicators, counting number of fishing boats per square mile.

Fertilization of water can be associated with external work in the ranges of

1 to 100 W m^{-2} . A log/log relation between external available energy and primary production can be suggested, but the relation is not monotonous, since an excess energy in mixing leads to the well known effect of Gran and Braarud. The contribution of the different depths to the mass of upwelled water, the organization of eddies required to accommodate the transformation of vertical flow into diverging more superficial movements, the relatively small amount of water introduced in the productive layers, are subjects of lively recent research. All this provides the physical frame for the organization of the ecosystem. There is a contribution of the photosynthetic energy to the recycling, through the animals, but the effect of animals (net vertical transport downwards versus recycling) is difficult to assess at this stage. Even if the net inflow of nutrients is relatively small, there is enough energy available for mixing and recycling several times before the added materials sink or disperse over neighboring areas. The spatial organization of recycling results in lenses of oxygen depleted water and much local heterogeneity.

The double role of external energy: driving in nutrients and stirring and recycling the materials is more distinct in eutrophic lakes: The input of materials, including transportation plus production in some far away place, is always present, but the productive lake may be more or less stratified. If stratification is strong more materials are lost to the atmosphere and to the sediment. If more energy is available for mixing, production is kept at a higher level and the cycle losses less materials. Any definition of what is advection and what is turbulence in the spectrum of movement is closely related with the organization of the ecosystem.

The energy involved in upwelling is not only a part of the local income of electromagnetic radiation, but results from focussing of a part of energy received over much larger areas, in the same way as energy used by downtown Los Angeles is supplied from other parts of the country. An upwelling area is dependent on an area extending over thousands of km, as well as on a mechanism of transfer. Simple computation leads to this result and we have wondered often if local winds can drive upwelling or if rather upwelling drives coastal winds.

If the precedent assumptions are correct, definite relations are to be expected between the energy locally available to do work, primary production, turnover, differential acceleration of turnovers at different trophic levels, organization of significant vertical gradients, and separation of biogenetic elements at the boundaries of the system of reference. All these expectations are realized in qualitative terms, but the usefulness of a theory demands a capacity for closer description and prediction. Our conviction is that description should be kept simple. One can think of the propagation of light through an anisotropic medium: a guiding principle states that the actual path is the one that takes less time. Besides the intricacies at a small scale, marine ecosystems may appear some day as simple as that, in relation with oceanic fields and with available energy. But reliable prediction may be

limited to situations characterized by a steadily decay of turbulence, that from the practical point of view may be devoid of interest. On the contrary, inputs of energy, as in upwelling, lead to essentially unpredictable situations.

The necessity of an actual analysis at a small scale.

When we speak of ecosystems and imply some coordinated behavior of their diverse components, agents ~~more~~ mysterious than the restrictions imposed by physical laws are ^{not} accepted. Structure is generated at the smallest level, but properties as turbulence, heat exchange and temperature, control the preservation of structure and drive the appearance of the whole ecosystem along directions that often can be described in simple terms. For instance, if the supply of external energy is small, the system falls into a state of great local diversification and changes really important are unlikely. Only the ecosystems in which the internal transport (= communication) uses much energy and covers large spaces, behave in a way that looks like what we expect from a true "organization". The importance of organisms in controlling the ecosystem usually is inversely related to the importance of external energy. Pelagic ecosystems have the advantage that they can be studied as processes, with the hope that they are amenable to an abridged description that would be out of place for ecosystems with an historic accumulation of rigid and perdurable elements of structure, as forests are. We accept that mechanical energy is perhaps the most important driving force and that it is reflected in the resulting patterns (Margalef, 1967, 1978).

The study of distributions at a small scale is necessary in order to take profit from the experimental work on physiology of plankton, and combine its results with the interpretation of marine distributions. When we say, with reference to upwelling, that mechanical energy, decaying in the movement of water, forces the ecosystem and drives it out of equilibrium, some operational approach is necessary, in which the words force and equilibrium find a scientific meaning. The recent literature on theoretical ecology contains scores of papers on niches, niche overlap, segregation, and the like. Ecologists are really concerned about the isolating role of space, at all the scales. But the interest has to be extended to the consideration of the physical environment. The plankton works around a mechanism of segregation, transferring nutrients from illuminated zones to dark spaces, slowing down turnover in the process. Segregation of potential reactants (light, nutrient, cells) or, else, their forced superposition, control pelagic life. Development of the model of Riley, Stommel and Bumpus (1949) lead to expressions with a term $(A/\rho) \left(\sum_{i=1}^n (d^2 N_i / dx^2) \right)$, where A is turbulent diffusion and the N_i 's stand for the different reactants (nutrients, phytoplankton, zooplankton); its dimensions are power per unit surface (Margalef, 1978). This term may define the enhancement of production due to mixing, with destruction of small structure. The contents of the second brackets can be substituted by a measure of the covariance of the distributions of the different potential reactants. The whole expression,

of course, depends on the volume, that is, has a spectral quality, and appropriate understanding requires to push the analysis down to the smallest scale. Further, a knowledge of the statistical properties of the distributions at a small scale is necessary to set in proper perspective the results of the comparison of samples obtained in quite distant oceanographic stations.

The small scale analysis of the pelagic ecosystem is usually based on the study of transects. Eventual hypothesis about the distributions over three, or four dimensions, have to be tested against the results of the analysis of transects. It is usual to submit the sequence of values along a transect to a suitable analysis that expresses them as sums of periodic functions. Perhaps other possibilities should be explored (Margalef, 1978 b). Alternative expressions could provide a link with approaches followed in other areas of ecology. For instance, we can take the weighted average of the rates of change, and study how it changes along time: To escape problems of dimensionality, we scale $n_i = N_i / \sum N_i$, where n_i are the relative concentrations or densities, of species or of other components.

The expression $\frac{d}{dt} \sum (n_i \frac{dn_i}{dt})$ is a measure of stability, it approaches zero in systems that are considered stable. All depends on the definition of stability, but this criterium, introduced by Volterra in ecology, has gained some acceptance under the name of expressions of Liapunov. It has wider applications.

The rate of change can refer to space (gradients) and a distinction should be made between the vertical (z) and horizontal (x, y) coordinates. In analogy with the anterior formula a family of expressions can be constructed, combining partial derivatives in relation to t, z, x . The expressions combining time and space ($t, z; z, t; t, x; x, t$) would tend to zero if the plankton could be considered as an ergodic system. The expressions describing spatial structure, for instance $\frac{\partial}{\partial z} \sum (n_i \frac{\partial n_i}{\partial z}) = \sum (\frac{\partial n_i}{\partial z})^2 + \sum (n_i \frac{\partial^2 n_i}{\partial z^2})$

may have a particular interest for the analysis of profiles and because of the combination of second derivatives that appear in the second term, which are a measure of the conformity or lack of conformity in the distribution of potential reactants, under the opposite effects of mixing and of segregation of residuals.

The important mechanisms operate at a very small scale, but organization of systems of transport and the spectrum of turbulence make the passage from such elemental and potential mechanisms to the realities of plankton distribution.

REFERENCES

- Bishop, J. K. B., J. M. Edmond, D. R. Ketten, M. P. Bacon and W. B. Silker - 1977. The chemistry, biology and vertical flux of particulate matter from the upper 400 m of the equatorial Atlantic Ocean. Deep-Sea Res., 24: 511-548.
- Budyko, M. I. - 1974. Climate and life. Academic Press, New York, London, 508 pp.
- Degens, E. T. and P. Stoffers - 1976. Stratified waters as a key to the past. Nature, 263: 22-27.
- Denman, K. and T. Platt - 1978. Time series analysis in marine ecosystems. In Time series and ecological processes, edit. by H. L. Shugart Jr., pp.227-244. SIAM, Philadelphia.
- Eldt, R. C. 1977. Detection and examination of anthrosols by phosphate analysis. Science, 197: 1327-1333.
- Eppley, R. W. and B. J. Peterson - 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature, 282: 677-680.
- Estrada, M.- 1978. Mesoscale heterogeneities of the phytoplankton distribution in the upwelling region of N.W. Africa. In Upwelling ecosystems, edit by R. Boje and M. Tomczak, pp. 15-24. Springer, Berlin.
- Hastenrath, S. and P. J. Lamb - 1978. Heat budget Atlas of the Tropical Atlantic and Eastern Pacific Oceans. The Univ. Wisconsin Press, Madison, London, 90 charts.
- Margalef, R.- 1967. Some concepts relative to the organization of plankton. Oceanogr. Mar. Biol., Ann. Rev., 5:257-289.
- Margalef, R.- 1975 a. External factors and ecosystem stability. Schweiz. Z. Hydrol., 37: 102-117.
- Margalef, R. - 1975b. Composición y distribución del fitoplancton marino en la región de afloramiento del NW de Africa, en marzo de 1973. Res. Exp. Cient. B/O Cornide, 4 : 145-170.
- Margalef, R.- 1978a. Phytoplankton communities in upwelling areas. The example of NW Africa. Oecologia aquatica, 3: 97-132.
- Margalef, R.- 1978b. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanologica Acta, 1: 493-509.
- Margalef, R.- 1979. The organization of space. Oikos, 33: 152-159.
- Riley, G. A., H. Stommel and D. E. Bumpus - 1949. Quantitative ecology of the plankton of the Western-North Atlantic. Bull. Bingham Oceanogr. Coll., 12: 1-169.
- Sapotschnikov, V. V. -1975. Genetic components of vertical distribution of phosphorus. Trude Institute Okeanologii P.P. Shirshov, 102: 66-69.

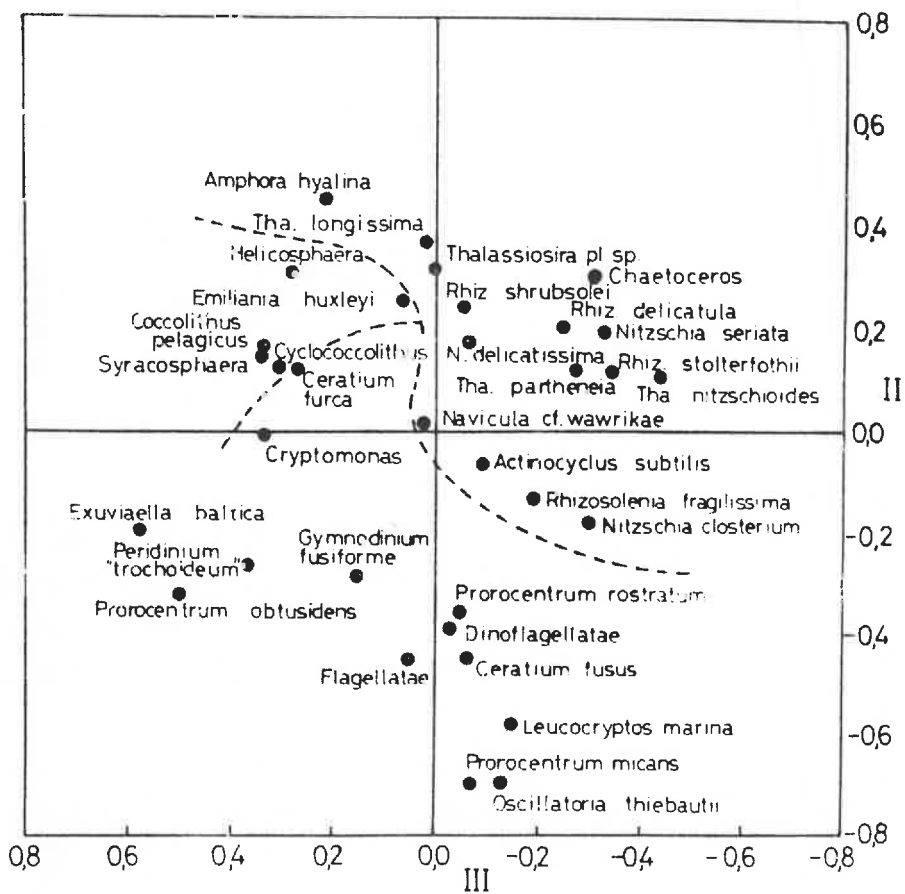


Fig. 1.- Plot of loadings of species and groups of species on the second and third principal component axes, based on correlation analysis between species and groups of species. Dashed lines separate the main taxonomic groups.

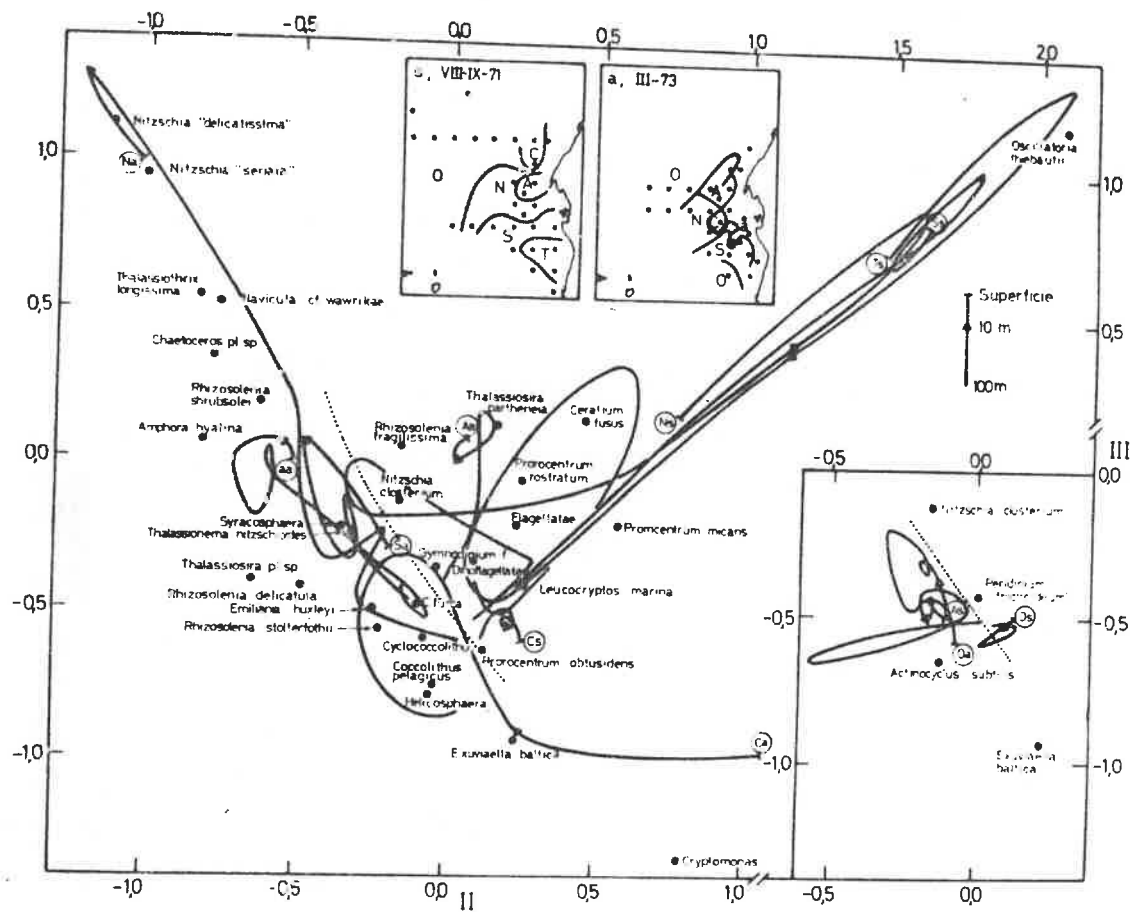
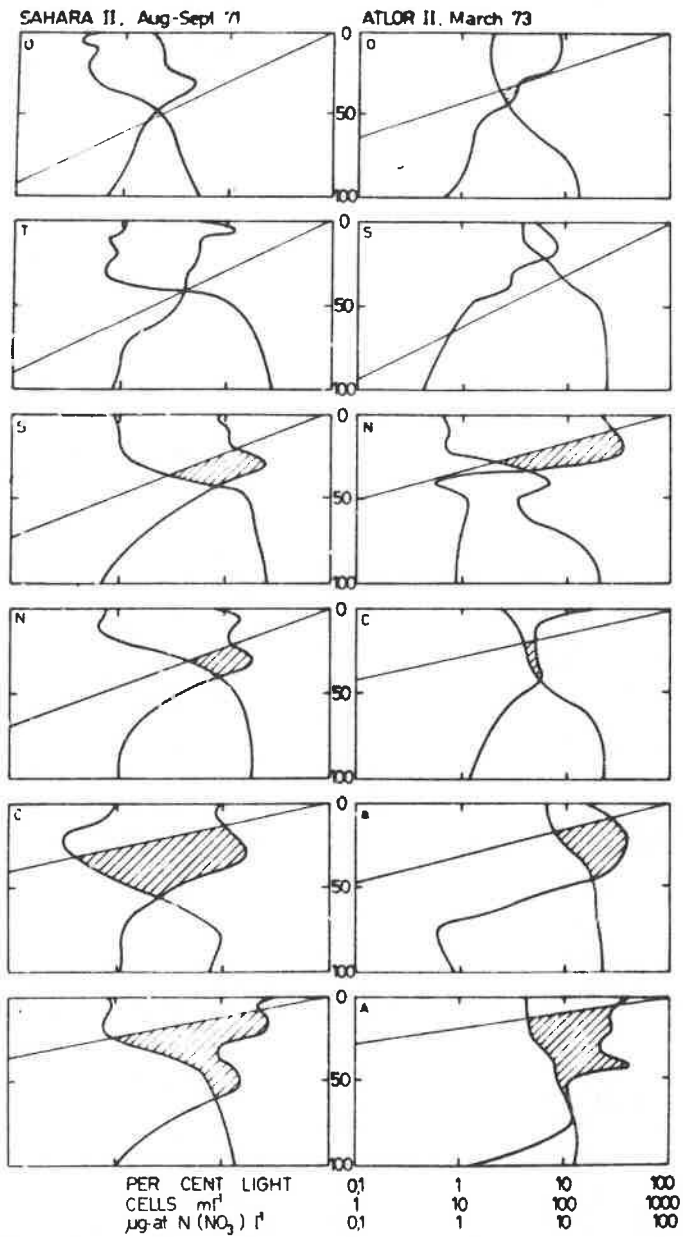
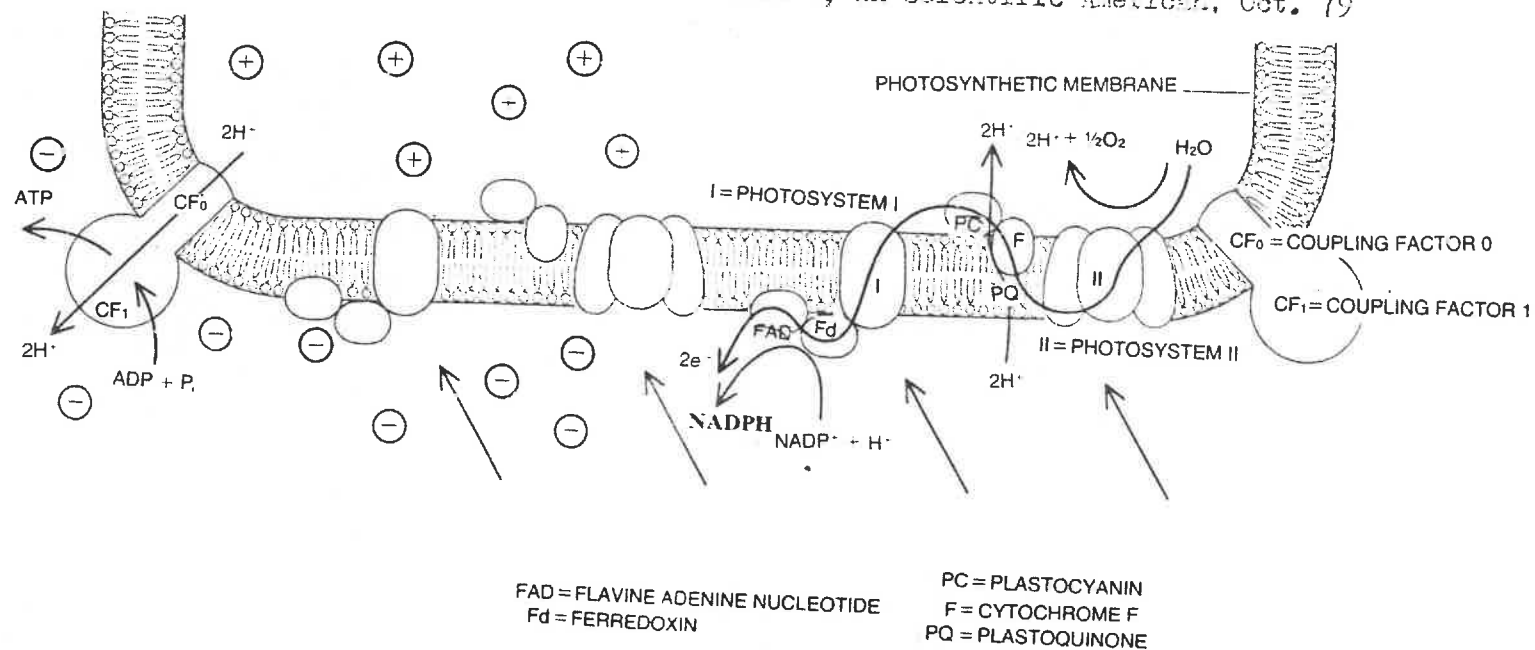


Fig. 2.- Plot of loadings of species and groups of species, and of the different depths for each region, on the second and third principal axes in an analysis of correspondance. The inset at right has to be considered as superimposed in the corresponding place. Each line links the successive depths, from surface to 100 m, and is marked by a symbol that refers to the maps and dates in the center top.

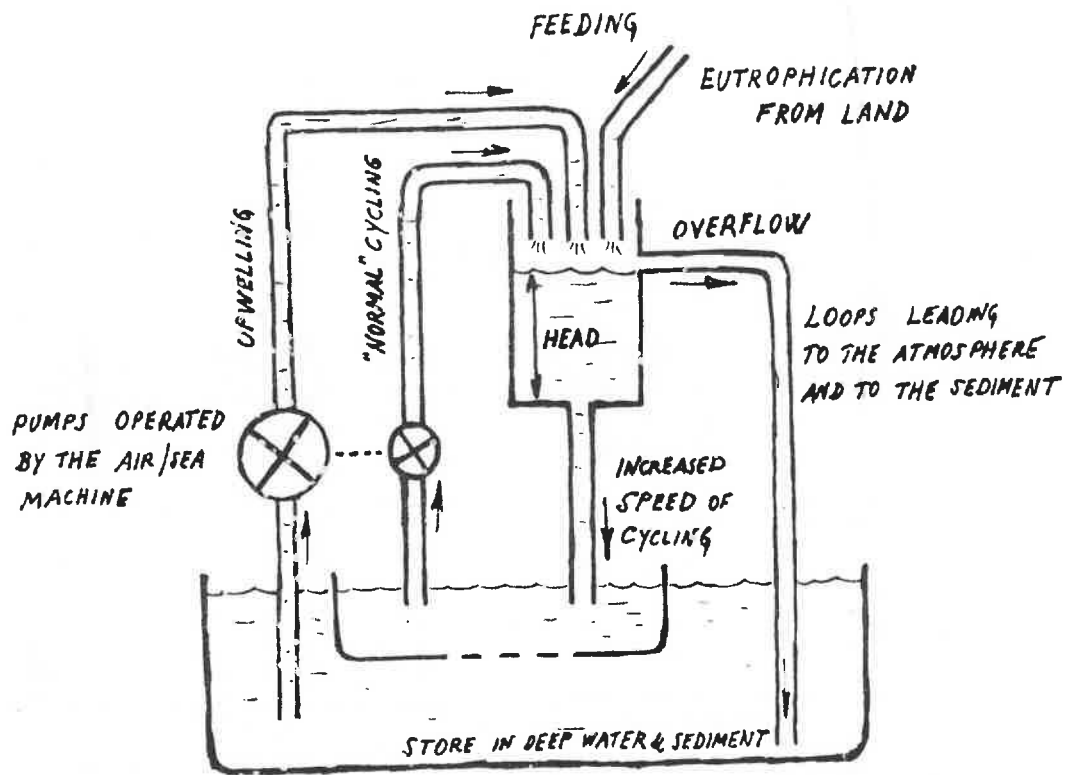


Average and characteristic profiles of the vertical distribution of light, nitrate and phytoplankton cells, in the different cruises and in the different areas. For positions see fig. 2.

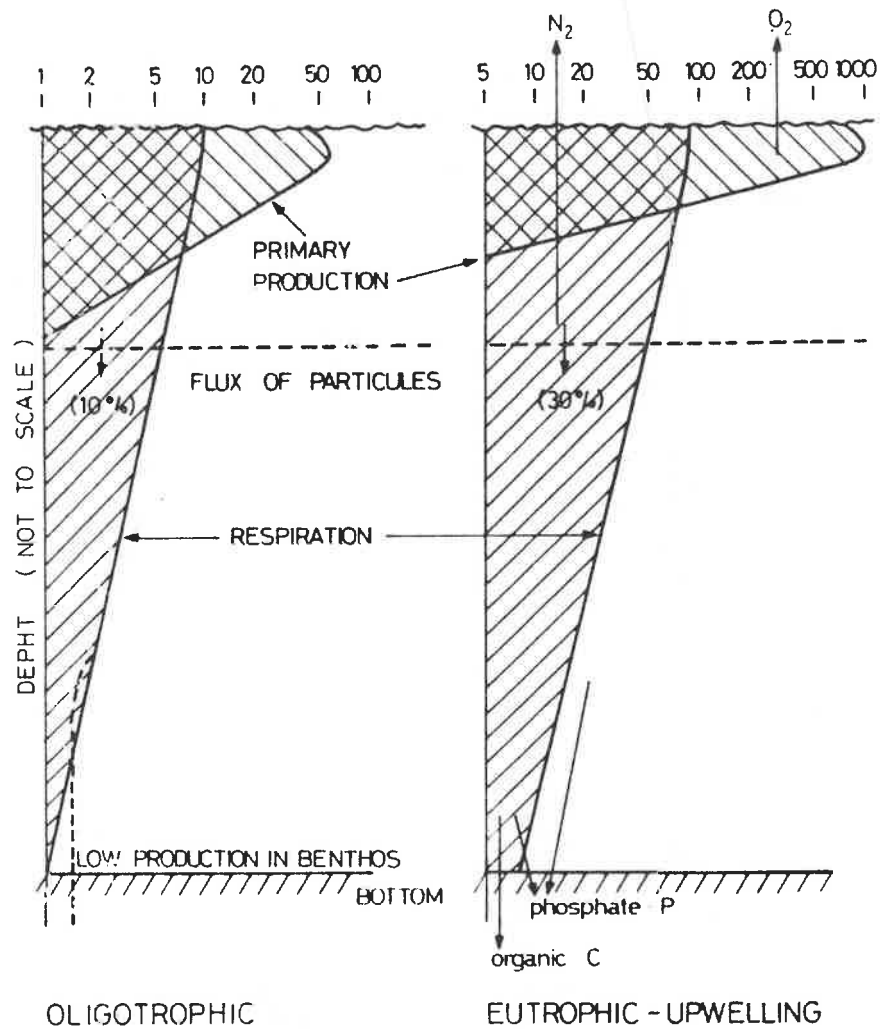
From K.R. Miller, in Scientific American, Oct. 79



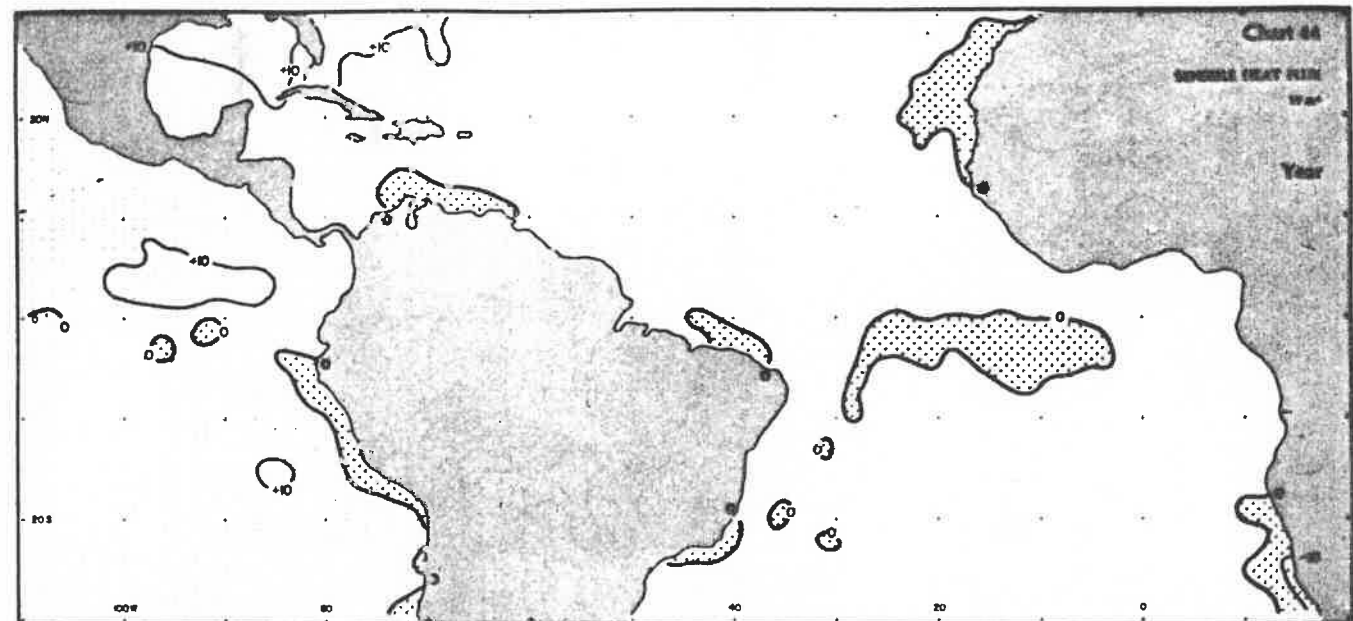
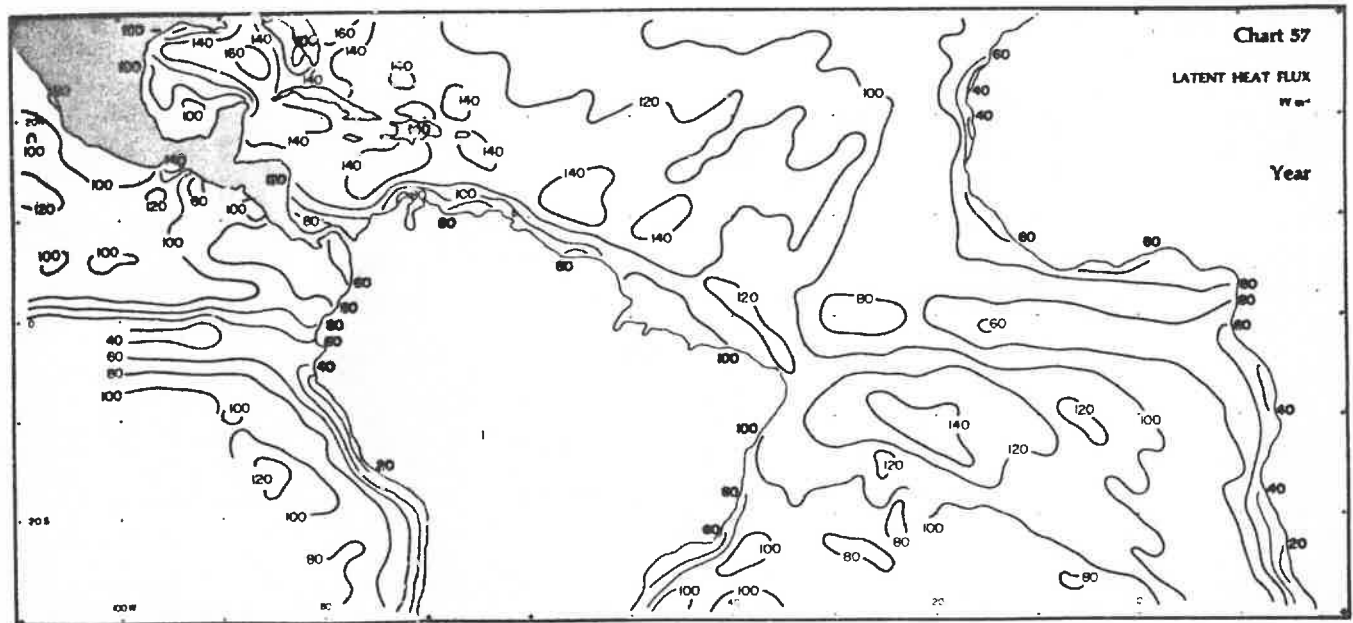
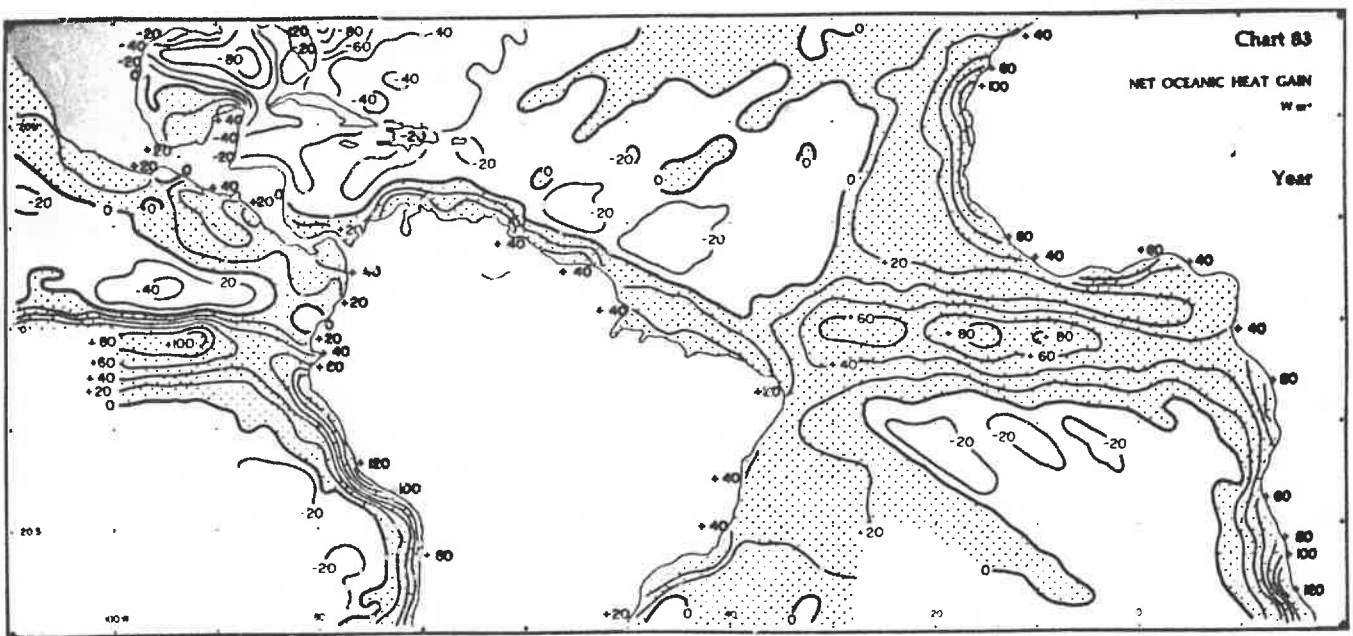
Chain of reactions powered by photons is exploited by the photosynthetic membrane inside the chloroplast to accomplish a separation of charges. NADP^+ is reduced to NADPH and ADP converted into ATP. The electrons are shuttled through an electron transport chain (involving plastoquinone, plastocyanin, photosystem I, ferredoxin and flavine adenine dinucleotide) and finally reduce NADP^+ with the aid of protons. The membranes form sacs called thylakoids. The positive charges accumulate on the inside of the membrane of the thylakoid, and the negative charges outside. Protons outflow and convert ADP into ATP. Sinking of plankton cells and of particulate organic matter in general, introduces reducing power into the deep layers.



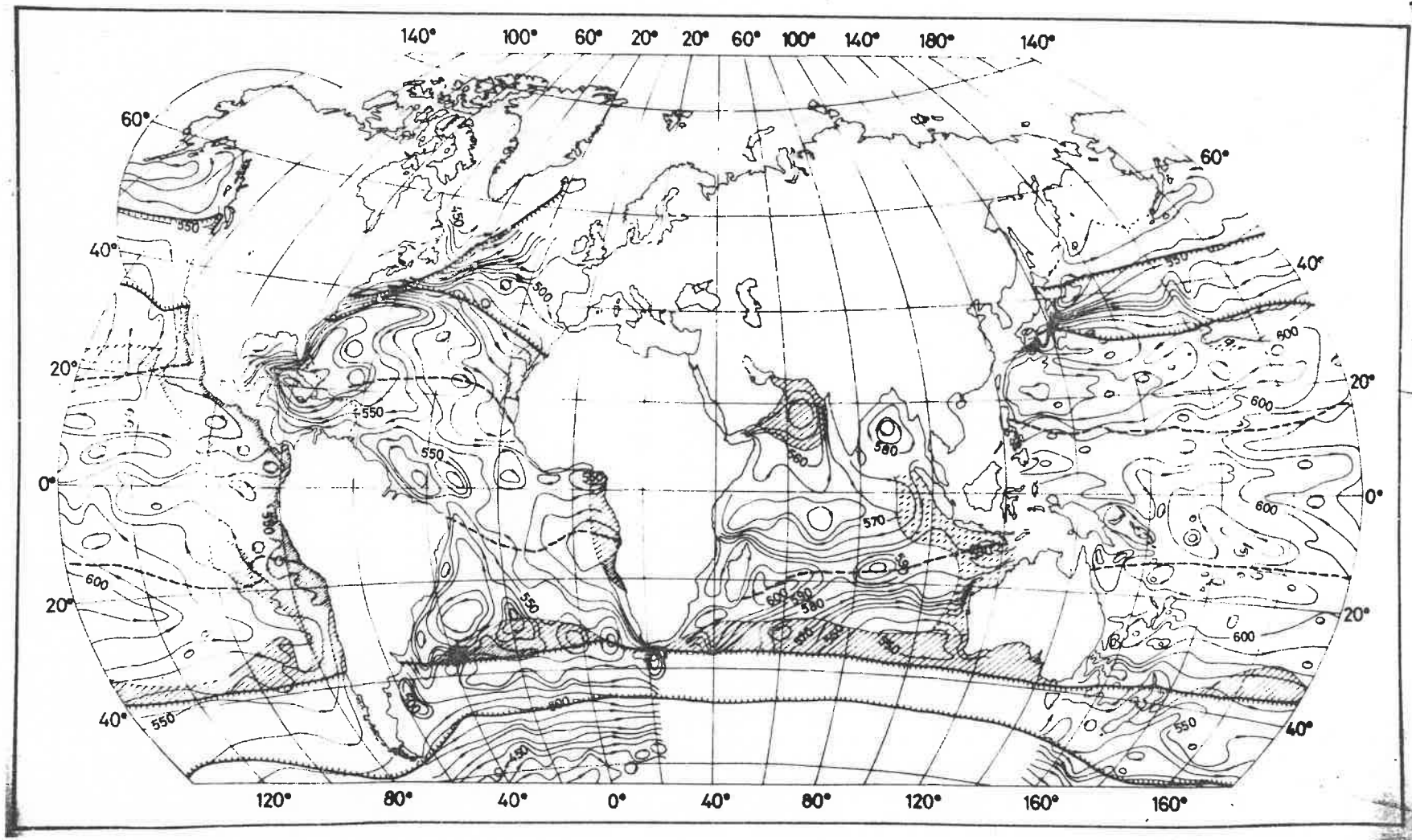
HYDRAULIC MODEL OF A FORCED ECOSYSTEM
 A RUBE GOLDBERG APPROACH TO MODELLING



Vertical distributions of primary production and of respiration in idealized oligotrophic and eutrophic systems. In the eutrophic system a larger proportion of the particulated organic matter is transported to deep water and is incompletely recycled. The eutrophic system has an output of elements to neighboring compartments.



Yearly net oceanic heat gain and yearly fluxes of latent heat and sensible heat, in watts per square meter. From Hastenrath and Lamb (1978).



Dynamic topography of the 0 db over the 1500 db surface, and faunistic and biogeographic regions of the oceans. The most productive areas are shaded. Dashed lines mark the boundaries of a tropical region. From Byrkov, Neuman and Beklemishev, in Beklemishev (1969. Ecology and Biogeography of the open Ocean, "Nauka", Moscow).