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Life-forms of phytoplankton as survival alternatives in an unstable environment

Life-forms
Phytoplankton
Turbulence
Diatoms
Dinoflagellates
Types biologiques
Phytoplancton
Turbulence
Diatomées
Dinoflagellés

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ABSTRACT

The different life-forms observed in phytoplankton are functionally interpreted as adaptations to survival in an unstable and turbulent environment. In comparison with terrestrial and benthic plants, the primary producers in phytoplankton are small, of rapid turnover and expendable; this is the result of evolution under conditions of automatic and passive exploitation, where grazing may be only secondary. Any atom is more likely to travel downwards when in a particle than in solution, and the most likely final situation in a completely stagnant environment would be one of segregation between light (on top) and nutrients (in depth). Stability and local diversification on different scales may be interpreted in the same manner. The combination of sedimentation with turbulence or variance in the components of velocity is believed to be the most important factor in the biology of phytoplankton. Consequently, the best predictor of primary production and of dominant life-forms in phytoplankton is the available external energy, on which advection and turbulence depend. This factor overrules more detailed models using light and nutrients as most relevant parameters, and based on laboratory experiments. Energy controls transportation, although the motility of organisms also contributes to the vertical organization of the ecosystem. The amount of energy exchanged and degraded per unit of surface also finds expression in the horizontal dimension of the structures that may be studied as approximatively closed systems with reference to the cycle of matter. Comparative analysis of different life-forms and their relation to the properties of the environment leads to an ordination along a main sequence, from fertile and turbulent water to exhausted and stratified environments. Populations selected under such diverging conditions range typically from diatoms to dinoflagellates. This correspondence is explained with the help of the model of Riley *et al.* (1949), which may be further developed in different ways. Fresh waters considerably expand the niche space of phytoplankton over the area of specially enriched water, and in such conditions cells enveloped in mucilage are frequent in a life-form not altogether absent in marine phytoplankton. Interpretation of such covers in terms of selection is not completely satisfactory, but mucilaginous envelopes of this type retard absorption and act as a feedback mechanism of population control. It is possible to balance in a single expression environmental factors and properties of the organisms, in such a way that probability of survival might be inferred from some performance index computed on such variables.

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RÉSUMÉ

Les types biologiques du phytoplancton, considérés comme des alternatives de survie dans un milieu instable

Les caractéristiques des différents types biologiques reconnaissables dans le phytoplancton sont interprétées fonctionnellement comme des adaptations à la survie dans un milieu essentiellement instable, turbulent. Contrairement aux producteurs primaires terrestres et benthiques, les algues du plancton sont petites, à renouvellement rapide, et subissent des pertes inévitables, dans lesquelles l'effet des animaux ne vient qu'en seconde place. Tout élément chimique a une plus grande probabilité de migrer vers le fond s'il est associé à une particule que s'il est un des constituants d'une substance dissoute; en conséquence, la situation finale la plus probable est une dissociation entre la lumière (couches supérieures) et les éléments nutritifs (accumulés dans les couches profondes). Le même processus, responsable du ralentissement des cycles et de la stabilisation, peut se moduler avec plus de détail. La probabilité de sédimentation, combinée avec la variance des composantes des vitesses dans les différentes dimensions, est regardée comme le principal facteur qui régit la biologie du phytoplancton. L'énergie externe dont la dégradation nourrit l'advection et la turbulence, permet la meilleure prédiction de la production primaire et des types biologiques qui survivent. L'énergie échangée définit aussi la dimension horizontale des structures qui peuvent être étudiées comme des systèmes relativement clos en ce qui concerne la matière. L'énergie externe contrôle le transport, mais le mouvement propre des organismes contribue aussi à l'organisation verticale de l'écosystème. Les modèles détaillés de la biologie du phytoplancton, basés sur les effets, étudiés au laboratoire, de la lumière et de la concentration en sels nutritifs ont leur utilité; leur possibilité d'application pratique est cependant limitée en raison du rôle prépondérant des mouvements de l'eau. L'analyse des rapports entre les propriétés du milieu et les types biologiques permet de reconnaître une séquence principale qui va des eaux fertiles et turbulentes aux eaux pauvres et stratifiées et correspond à un classement des organismes, dont les formes typiques extrêmes sont, respectivement, les diatomées et les dinoflagellés à cellule aplatie. Leur morphologie s'explique fonctionnellement sur la base du modèle de Riley *et al.* (1949) qui peut être un point de départ utile. Le phytoplancton des eaux douces montre un enrichissement de types biologiques dans les milieux spécialement concentrés en éléments nutritifs. Un type biologique caractéristique qui, quoique rare, ne manque pas dans le milieu marin, possède des enveloppes mucilagineuses, diversement interprétées, mais qui certainement ont pour effet de ralentir l'absorption des éléments nutritifs, et peuvent représenter ainsi un mécanisme de régulation des populations. Il est possible d'unir dans une seule expression des paramètres concernant les organismes et d'autres caractérisant leur milieu, de façon à pondérer un indice total, exprimant la probabilité de persistance de la combinaison envisagée dans chaque cas.

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INTRODUCTION

The purpose of this paper is to examine the selection processes leading to different life-forms of phytoplankton, as alternative strategies for survival. In plankton ecosystems, the survival of populations is the result of a temporary equilibrium between success in remaining afloat and inevitable sinking. This process will be examined in broad terms with reference to marine phytoplankton, with frequent utilization of hints and clues provided by the study of freshwater communities. This is a subject of general ecology that requires some excursions in peripheral fields. Such ancillary material, unless referenced, is based on Margalef (1974 *b*).

Horn (1971, p. 123) writes that "the most productive community would be an infinitude of layers of sparse and microscopic leaves with no non productive supporting tissue. Phytoplankton in turbulent water form such a community ". But is this really so? Terrestrial ecosystems are in fact, on the average, three times more productive per unit surface than aquatic systems. This is a natural consequence of the "bottomless" (eu)photic layer in water.

The basic, built in limitation in primary production, valid for the entire biosphere, lies in the ratio between the number of molecules of chlorophyll and the number of centres of reaction in the chloroplast. A comparable dead end appears at another level of organization in terrestrial plants, in the form of constructional limitations in the section of transport tissue. In practice, an upper limit of productivity is set by the self shading effect of chlorophyll. An optical density of 2, that is, the absorption of 99% of the incident light, is achieved by little more than 300 mg of chlorophyll per square metre, that is, by a single sheet of leaves on land, by the equivalent of a single layer or of a few layers of cells in water. On earth, the ratio between the extension of leaves (maximal section) and the surface of soil on which the vegetation stands is, on the average, 4.3 (Lieth and Whittaker, 1975), and this means that the amount of available chlorophyll is four times that which can be effectively operating. The concentration of chlorophyll in plankton rarely attains the limit of optical density 2; the most commonly observed concentrations are between 5 and 100 mg/m^2.

Organization of the phytoplankton community is related to the extinction of light in water. Terrestrial vegetation grows at the bottom of the atmosphere; aquatic vegetation in the top layers of water. The distribution of phytoplankton chlorophyll could be compared against an ideal distribution that optimizes the absorption of light by the plants, taking into account other causes of extinction by water and miscellaneous dissolved and suspended materials. If (chl) is the concentration of chlorophyll, k' its absoption per unit concentration, and K the optical density of other absorbing materials, the effectivity in the use of light is related to the ratio

$$\frac{k'(\mathrm{chl})}{k'(\mathrm{chl})+\mathrm{K}}.$$

This is straightforward simple reasoning, and converges with the usual approach to the estimate of the actual use of light (Lorenzen, 1972). In consequence, the best use of light would be obtained through the concentration of chlorophyll as close as possible to the surface, using most of light before any extinction due to materials alien to the organisms. It may be conceived that neuston and pleuston would compete successfully with phytoplankton. In freshwater, compact neuston with *Chlamydomonas* or *Euglena* may contain as much as 100 mg of chlorophyll per square metre. But neuston is an exceptional community, developing under the uncommon combination of high nutrient supply and no turbulence. As a general rule scarcity of nutrients and high turbulence decide the issue, with the result that photosynthetic neuston is rare, and almost absent in marine water. Pleuston composed of macrophytes has certain advantages associated with the use of atmospheric CO_2 and the availability of extra nutrients through vertical roots sinking in the water. Opportunist and expansive communities of pleuston are becoming a nuisance in disturbed or stressed fresh-water environments in warm countries.

The air/water interface being out of question, and most of the bottom lying in the dark, a substantial proportion of the primary producers of aquatic ecosystems are suspended inside the photic zone, defined as the stratum where light is not inferior to 1% of light at surface. This is the basis of several substantial differences between plankton and terrestrial (and benthic) ecosystems (Table 1).

The remark on the neuston communities above mentioned that it is rare for high nutrient concentration and perfectly calm water to exist simultaneously. "Structural" constraints of this type in the organization of ecosystems are often disregarded, perhaps because they are less amenable to experimental research in the laboratory. I believe that our understanding of plankton biology suffers much from in consequence, and I will try to make this clear below.

In experimental ecology, the reactions of an organism or of a population to different intensities or concentrations of each of the factors under test are observed. The factor may be declared to be important if there is a significant correspondence between any quantitative expression of the factor and the way the population behaves. Such experiments are common in the study of factors which are easy to identify and to measure, such as temperature, salinity, or concentration of selected nutrients. The reactivity of organisms to such factors may have a genetic basis and may shift and evolve. Even closely related stocks of certain organisms can behave quite differently in response to such variables as temperature and nutrient concentration. Any description of the yearly cycle of phytoplankton in relation to the annual change of temperature and light would appear to make sense. Spring species grow well at moderate temperatures and high light intensity; some weeks later we may find more species that do well at high temperature and high light intensity, and so on. But, such a shift in the requirements of successively developing species does not explain the annual cycle. It is only natural that the genotypes adjust to produce such fine tuning; but without denying the relevance of such adaptations, it may be suspected that the composition of the communities, considering the functional morphology of the species, might be controlled by other factors, such as mechanical energy of water or turbulence.

WATER MOVEMENT CONTROLS PLANKTON COMMUNITIES

In my opinion, the characteristics of planktonic organisms that do not change easily, as far as the morphological, mechanical and general physiological properties of the cells are concerned, are less sensitive to temperature, salinity and shades of light, and much more dependent on turbulence and general nutrient availability.

Phytoplankton appears as a community which is poorly controlled from inside. Plankton contains nothing comparable with the well-structured transport system found in a forest, with fungi, roots, wood and leaves. In natural plankton, control is still entirely in the physical environment, in the mobile structure of water masses, with cells of circulation and eddies of every size. It is significant that all projects for the mass cultivation of unicellular algae end with the proposal to construct a "technological tree", complete with supply pipes, pum-

Table 1
A comparison between plankton and terrestrial ecosystems.

Properties compared	Plankton	Terrestrial ecosystems
Size of primary producers	Small	Large
Turnover of primary producers	Rapid	Slow
Maximum amount of chlorophyll	350 mg/m² (in fact, much less)	4 x 350 mg/m²
Main factor of selection operating on plants	Passive sinking or indiscriminate grazing	Competition for light, avoidance of animals
Ratio animal biomass/plant biomass	High	Low
Control of transportation by	Physical environment or animals	Plants
Detritic pathway	Important	Very important
Dependence on external energy	Total, except perhaps in patchiness	Tendency to control microclimate

ping units, illumination devices including mirrors, and so on.

I have myself been guilty of according too much importance to grazing, biochemical interaction, and other phenomena playing among organisms, as causes of succession. It now seems to me that the sequence of populations is basically controlled by the physical environment, by advection and turbulence. Any appearence of regularity along succession would be the result of an orderly shift in the way environmental control is excercised, as turbulence dissipates.

A model of plankton in stratified water is based on the fact that an atom goes down with a non-vanishing probability and at a higher speed when it is in the body of an organism, or is part of any other particle, than when it is in solution. As the thickness of the photic zone is limited, the system organizes itself along the axis defined by distribution and operation of light and gravity. The result is a slowing down of turnover, expressed by

$$\int_0^z f(\mathrm{N}, \mathrm{T}, (\mathrm{chl}), \ldots)\, dz \Big/ \int_0^z \mathrm{B}\, dz \rightarrow \text{minimum},$$

where N, T, (chl), ... stand for the factors of production, and B stands for the biomass. Decreased production is a natural consequence of segregation in the distribution of the factors of production. Finally, where there is light, no nutrients are left, and where nutrients remains, there is no light.

Such a description of the slowing down of the average turnover in a bounded system may be understood in terms of the probability of occurrence of the different states of the system. Left to its own resources, the system would shift in the direction of more likely states. Not only may the value of the precedent expression be expected to decrease in time, but also the rate at which it changes. Such a rate of change would reach zero when the supply of nutrients upwards depended exclusively on physical diffusion. In this final state, no further net downward migration of biogenic non conservative elements out of the photic zone would occur.

The above expression and the principles embodied therein are of very general application. Studies in lakes and reservoirs provide evidence that the slowing down of turnover is observed. In systems under stress (upwelling areas, eutrophic lakes), the same trend finds another expression in the expulsion from the system, and across its boundaries (atmosphere/water, water/sediment), of a fraction of the materials involved in the cycles. Oxygen and nitrogen escape to the atmosphere, organic carbon and phosphorus are incorporated in the sediment. After stress is discontinued, they may partially return.

ACTIVE VERTICAL TRANSPORT

The fundamental mechanism operating in ecosystems of open water is based on the acceleration of particles relative to atoms, ions and molecules in solution. Particles move vertically in a passive manner, but living particles, organisms, can move actively, using a fraction of the solar energy collected in photosynthesis.

In passive phytoplankton and inanimate seston, accelerations and decelerations in the sinking speed explain some of the observed patterns of stratification or differences in vertical distribution. Particulate material may accumulate just in or below the layers where sinking speed slows down, for example in colder layers. The number of particles per unit volume decreases at a greater depth in still water, the remaining particles may collide and adhere physically, and the aggregates thus formed sink more rapidly (McCave, 1975). Acceleration of particles by compaction in their descent may result in a relatively empty water, the material and its nutritive value being conserved for the bottom. Such a mechanism helps to explain the distribution and density of deep sea benthos.

Active transport is important because it may alter the common pattern of passively sinking particulate material. A fraction of the energy of primary production is used by phytoplankton in circulating. Flagellate cells manage to maintain an appropriate level of light, and limit the loss of cells from the photic zone, if the water is not too turbulent. True migration along short vertical distances has been observed in a number of dinoflagellate species, as well as in other motile algae, both in the sea and in freshwater. If division of phytoplankton cells occurs in the dark and is more likely in the cells that have been more illuminated before, changes in numbers along the vertical may simulate the results of vertical migration. Migratory phytoplankton approach the surface during light hours. Dinoflagellates are supposed to assimilate nutrients in deeper water and then move up towards light. This would mean the use of photosynthesis energy in the return to the photic zone of a fraction of nutrients lost in the general process of sedimentation. Flagella are perhaps more important in the function of the destruction of gradients in the water bathing the cells. The maintenance of an appropriate motility is the result of an evolutionary process based on the selection of individuals, but motility is decisive only in relatively calm water, and might be less relevant to survival in turbulent water.

The migration of zooplankton accelerates the downwards transport, since animals tend to excrete at a deeper level than the level at which they feed. Moreover, fecal pellets of copepods sink much faster than uncompacted detritus. The fact that vertical migration accounts for 2-20% of the metabolism of zooplankton suggests that migration is of relevance to the survival of the species. Such investment of energy would be difficult to understand otherwise. But it is difficult to determine a process of selection leading to the development of migratory behaviour. It would appear that once the appropriate place for feeding is located it would be better for the animals to remain in that place.

The migration of zooplankton redistributes more uniformly over the ecosystem the patchy primary production of the photic zone. Again, it is difficult to visualize a mechanism of selection arriving at such result. Hardy's hypothesis of the "seven-league boots" afforded by migration to zooplankton, accepts that through migration, zooplankton is able to exploit better the productive zones. If the extent of vertical migration is related to light, in water which is more productive and less transparent, the levels between which migration extends would be expected to remain closer to the surface, a smaller horizontal extension would be exploited (Isaacs *et al.*, 1974) and patchiness would perhaps remain higher. Some of the models developed for the study of vehicular traffic (Prifogine and Herman, 1971) may be of application in the study of the generation of the patterns of vertical distribution and, in particular, of the dynamic waves that characterize the distribution of migrating animals.

Predator pressure has often been accepted as a partial explanation. If animals remain during the light hours in deep and dark water, they are less conspicuous to eventual predators. But for predators, mechanical clues may be more important than optical ones. Moreover, predators travel up and down with their prey. Better metabolic conditions may also be accepted as a basis for selection (McLaren, 1963), since animals feed at a high temperature and assimilate, rest and excrete at a lower temperature. A fluctuating temperature such as that which migrating animals should encounter along their path can have an accelerating effect on metabolism. It may be equivalent to a constant temperature higher than the actual temperature averaged over the range of its variation (Hagstrum and Hagstrum, 1970; Hagstrum and Leach, 1973; Halbach, 1973; Pattee, 1975). This rule is not general, however, and significant departures have been observed.

Once the whole migratory circus has started, a selection mechanism can come into effect. The migrants of a given level or belonging to a certain relay feed preferentially on those migrants of the upper layer that are lagging behind in their own migration, and give off to upper trophic levels the feeble or lazy individuals that do not migrate up fast enough. Zooplankton in migration comprises a complex of populations, some of which react directly to the light while others are governed rather by internal rhythms, making the whole system perhaps more exploratively interactive, and capable of attaining some measure of stability and regularity.

From the point of view of this paper, a most relevant question is the incidence of migration on the turnover speed of the pelagic ecosystem. Does migration work in a manner similar to the process of slowing down based on the differential speeds of diffusion and sinking of particles, or does it operate in an opposite way? It appears out of question that the major effect of vertical migration in zooplankton is a definitive slowing down of the general turnover of biogenic elements. It cannot be denied that animals play an important part in the local recycling of nutrients, and nutrients can be injected by animals in spots where they would otherwise remain at a lower concentration. But this effect does not detract from the overall consequences, which are important for the understanding of the biology of phytoplankton. Different species play their game against the background provided by such general trend.

A sensible reversal of the trend to retard the turnover of phytoplankton in the pelagic ecosystem would require animals feeding in the depth and excreting close to the surface. Animals adopting such behaviour could be named "superprudent predators" and are probably as real as the Loch Ness monsters. Perhaps some specialized predator feeding at the end of long trophic chains, such as the sperm whale, comes close to the idea of what a superprudent predator should be. But we do not know if sperm whales defecate closer to the surface than the level at which they feed. At all events, a very complex behaviour, implying much information, is involved, and organisms at the end of long trophic chains contribute less in quantitative terms to the overall budget of the ecosystem. Other candidates for the title of superprudent predators might be the larval midges and other insects that transport organic matter from the deep benthos to the surface and out of water, and flamingos and other birds, feeding at the bottom of water and stirring the mud.

Its would appear that a significant reversal of the general trend to be produced by an animal would require the tapping of some source of external energy, i. e., non-endometabolic energy. Man has such sources of energy and can recycle effectively and work against the slowing down of natural cycles. The migration of biogenic elements out of the photic zone in the pelagic environment is paralleled in the case of man by what are perceived as illnesses of cul-de-sacs in transport, exemplified by erosion and displacement of soils and by pollution. Naïve and exploitative man behaves like zooplankton.

EXTERNAL ENERGY

Although human activity, and perhaps of other animals as well, could accelerate or regulate recycling, this would require more energy than is available on a metabolic basis. All heterotrophs, animals and bacteria, tend to work against a sustained productivity and for a slowing down of the cycles. Natural ecosystems, however, never run down to the limit and the actual return of nutrients, when achieved, is not determined by organisms, but by a more effective agent, by external energy supplied to the system. External energy is a convenient expression for energy that does not go through the photosynthetic path and the trophic food chain, but which is being degraded as the result of interaction between the atmosphere and the hydrosphere. Such energy is made available to the ecosystem, and in the ecosystem is managed according to the structure that the system has already attained.

Only in recent times have ecologists become fully aware of the importance of such external energy. This awareness has probably come from considering the meaning of exometabolic energy in human life and civilization, specially in energy subsidized agriculture. There is a wide range of inputs of energy that support production in aquatic ecosystems. The two most important are in the form of turbulence generated and spread from the surface, or else in upwelling.

In a double logarithmic plot of yield against the external energy involved in production, it appears that both agriculture on land and plankton production in oceans and lakes follow the same pattern (Fig. 1 upper right). The energy involved in supplying nutrients to the photic zone in aquatic environments is difficult to estimate. This is a tentative approach in an almost unexplored field. The relation between primary production and available external energy cannot be linear or logarithmic throughout, because excess energy cannot be managed by the system. It would lead to a situation similar to the repeated weekly turning over of the soil of a field. The excess of energy would not permit the growth of any crop. An analogous situation has been reported at sea, where and when strong mixing drives a large proportion of the phytoplankton out of the photic stratum. This effect has been studied by Gran, Sverdrup and other authors long ago, and its expression has been formalized as a rule stating that mixing depth cannot exceed a certain multiple of the compensation depth, before growth of phytoplankton is expected to proceed.

Considering only the range in which the log/log relation is reasonably linear and fitting tentative data, there is a difference between plankton and agriculture in the position of the line of regression, because the computation of the subsidy of energy to agriculture does not include the energy involved in rain, and in the natural transport of nutrients that is associated with erosion of rocks and soil. But if such energy, which is hard to estimate, were included, it seems that the general pattern might be comparable.

Important differences exist between aquatic epicontinental and marine systems. History and different opportunities for evolution might explain the taxonomic differences. Physiognomic differences in the composition of phytoplankton may be related to ordinary differences in the ranges of the values of turbulence and of nutrient concentration. What factors are most important in the distinction between fresh-water and marine environments, between lakes and oceans ? Probably more relevant than the concentration of sodium chloride is the effect of the rotation of the Earth, which generates completely different conditions of advection and of mixing. In the lakes of the temperate zone, the thermic cycle causes periodic instability, and allows a vertical mixing paid for with the energy afforded by wind, with recycling of the biogenic elements in a vertical column, *in situ*. The mechanism operating in the oceans is different. Nutrients that have accumulated in deep water rise in places far away of from the sites of sinking. The fact that sinkings areas may be segregated from upwelling areas implies an important horizontal transport.

Faced with the overwhelming importance of circulation and turbulence, a careful consideration of the niceties of light distribution and of kinetics of absorption of nutrients may appear irrelevant. The ecosystem, in fact, is driven or controlled by external forces and any modest simulation of the orders of magnitude involved in the phenomena shows, at least, how immaterial is the choice among the different models of dependence of production on light and nutrients. Primary production appears simply as a function of the external energy supplied to the system and degraded in it.

There are ways of computing such energy, and in different textbooks (for example, Budyko, 1974) and papers, maps have been published showing the amount of energy degraded in different areas of the ocean as a result of thermal exchange and transport. In maps representing the energy that travels through the surface, the absolute figure is more important than the direction. It is remarkable to note how well some maps of the exchanged energy match the distribution of the values of primary production over the same areas.

Figures of the energy exchanged in the surface of the sea have been variously estimated. Many of the produced values fall between 300 and 500 cal/cm^2/day, or 10 and 16 kcal/cm^2/month, or between 150 and 250 W/m^2. These values are rather high, and associated with above average primary production. Figures are much lower in the major areas of the oceans (Bowden, 1975; Clark *et al.*, 1974; Reed and Halpern, 1975). The decay of available potential energy in eddies separed from the Gulf Stream has been estimated at 0.1-0.4 W/m^2 (Cheney and Richardson, 1976) and estimates of the tidal energy dispersed on the surface of the shelf fall from the same range to 10 W/m^2. In upwelling areas and for short periods, it would appear that values close to 1 000 W/m^2 may be obtained. Such regimes can be supported only by the funnelling of energy to do work in one spot.

The figures above must then be compared with following ones. The solar constant is 1 390 W/m^2. Average evaporation, world-wide, uses a power of 78 W/m^2; evapotranspiration, in tropical forests, is of the order of 150 W/m^2. The power used by human civilization attains locally relatively high figures, as 4.2 W/m^2 in the Ruhr valley and 630 W/m^2 (still half the value of the solar constant) in Manhattan (Koblet and Stumm, 1974).

The power really involved in enhancing primary production is, of course, only a fraction of the total power dissipated in a given place, and may amount to less than one per cent of that total. But the local dissipation of energy sets an upper limit.

Difficulties arising at this stage of attempting estimates, are related to the spatial or mechanical organization of the process of dissipation of energy. The capacity to do work is concentrated, and very energy intensive processes, like upwelling, occur in restricted areas. This leads to the consideration of the water masses as parts of machines that perform work.

In any thermodynamic consideration of the biosphere it is not correct to take only into account the energy that enters the ecosystem at the level of the photosynthesis and circulates in the form of energy associated to chemical bonds. It is necessary, as well, to consider external energy, although it may be difficult to decide the fraction of such energy that has to be included in the budget of the ecosystem. In any case, one feels relieved of the duty of providing exact estimates of primary production, since the boundaries between internal and external energy are somewhat vague in the regulation of productivity, and the total amount of power driving the ecosystem is impossible to estimate precisely.

Auxiliary or external energy works in different ways. The turbulence caused by wind and waves propagates towards deeper layers, and becomes effective for the productivity of phytoplankton especially at the level where it bites on water with a high concentration of accumulated nutrients. When this happens, primary production is enhanced deep down in the photic zone, and not at the surface, as perhaps would be expected if the main controlling role were attributed to light. Or else the work is done in the transport of large volumes, and the most effective direction is upwards, in upwelling. Recent years have witnessed the awakening of a considerable interest in the upwelling areas (several symposia and expeditions, the Coastal Upwelling Ecosystems Analysis (CUEA) as a part of the International Decade of Ocean Exploration, etc.). Although it is not possible in this paper to review all the relevant work in this area, a few considerations on infrequently discussed aspects are necessary.

Assuming an excess yearly rainfall of 40 cm in the Southern Polar region, a world upwelling of 8 cm per year may be anticipated (Assaf, 1975). Accepting a concentration of nutrients in deep water correlative of 1 µg-at P/1, the resulting influx would hardly improve over the influx due to physical diffusion, and primary production would remain below 1 g C/m^2 year, with some allowance made for recycling in the photic zone, a very small fraction of the actual production indeed. Upwelling in particular areas is several hundred times more intense, leading to values of primary production above 500 g C/m^2 year. Nutrients are injected into the photic zone by mixing, and here recycle. Averaged over large surfaces the input may be small or negligible, but local production is maintained by the mixing of water and recycling over the steep gradient at the boundary of the photic zone. The work done in displacing water is always the best predictor of primary production.

In regions where upwelling takes place, the vertical components of speed of water vary from place to place and from time to time, and the resulting instability become organized in cells of circulation because of the need for continuity. Small eddies find accommodation between large eddies. Particular size ranges in the power spectrum of turbulence may carry a disproportionately large fraction of the energy. In the horizontal plane, a particularly interesting cell size might be expected where centrifugal force and Coriolis acceleration are comparable.

The external energy may do work moving the water along a path (advection) or shifting it back and forth (turbulence). Horizontal or vertical net transport may be important in moving phytoplankton or in introducing nutrients. Turbulence appears as a key factor in other situations. Available energy is better used, in terms of enhancing primary production, in advection than in turbulence. Advection energy is of higher quality, turbulence is its decay.

Primary production can be proportional to a certain power k, less than unity, of the available external energy E, as in $P = f.E^k$. An appropriate expression has to be more complicated, to destroy the monotony of P and make it decrease again for very high values of E, if water is deep. Also, k must be related to the way the total energy E_t is plit in a part associated to transport or advection (E_v) and a part being degraded already in form of turbulence (E_a). A spectrum of both fractions, or a plot of their ratio (which requires some decision about the computation of a residual velocity) against size of structure will help to understand the conditions of survival of phytoplankton. The ratio E_v/E_a varies with the volume of reference in a way that certainly must be relevant for the biology of phytoplankton, and certain relations may be conjectured that maximize the positive effect of external energy on production. Analogous considerations are relevant on a smaller scale in the theory of reactors and chemostats, where flow and mixing can be controlled separately. These considerations are admittedly sketchy, and suffer from the general lack of connection between the rigorous concepts of mechanics and the hypotheses of the biologist.

The real situations are complex. Offshore, all the energy exchanged in a column of water may dissipate as turbulence or mixing over a small range (Fig. 1), and the

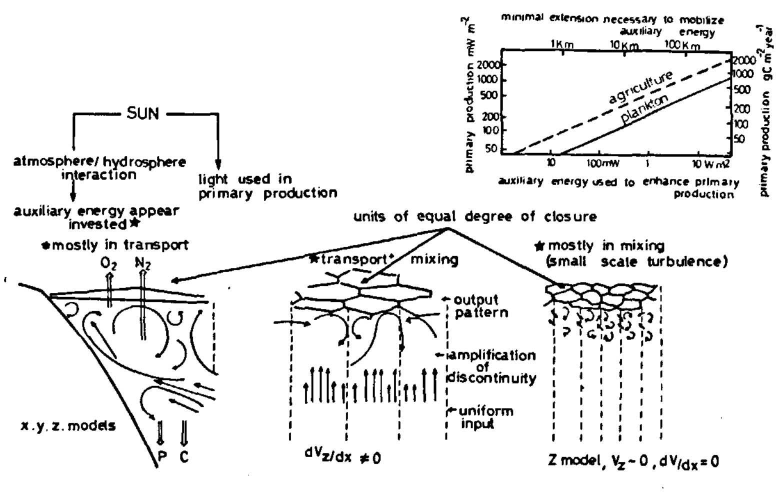

Figure 1

The amount of energy invested in transport and turbulence is basic to the determination of primary production in marine ecosystems. Upwelling ecosystems (left) use much energy, have an important horizontal transport and cannot be properly modelled with reference to a small section. In them, a number of elements (O, N, C, P) are involved in loops cycling outside the system. Ecosystems depending on less energy degrade most of it in turbulence, primary production is low, and can be modelled as narrow cylinders or prisms (right). Upper right, dependence of primary production on auxiliary energy, tentative values, from Margalef (1974 *a*) *and Watt* (1973).

whole ecosystem can be modelled as a set of adjacent water columns, with almost no exchange or with symmetrical exchange among them. In such situation, the model for a single prism or column is representative of the model for a large set of columns. In other words, a conceptual model with a reasonable degree of closure can be constructed over a small section, or referred to a small area of the surface of the sea.

The coastal upwelling system is representative of an actual situation differing largely from the precedent. It is obviously impossible to create a closed model in what concerns the cycle of nutrients when referring to a small extension of the surface of the sea, because nutrients come with deep water from a great distance, and the synthesized organic matter is dispersed around the spots of intensive upwelling in a more or less centrifugal manner. In such areas, a considerable amount of the available energy is spent in eddies of large size, or in promoting general circulation, as well as in accelerating wind. Contrary to what is often stated in a too general manner, in many situations, upwelling drives wind and not the converse.

For the understanding of the biology of plankton it is necessary to know how eddies break down, according to their size, and how the net vertical flow organizes circulation cells. The injection of nutrients in the top layers of the upwelling systems is rather small, but the top layers keep circulating, and elements recycle in them faster than in other places and therefore less efficiently. The net result is a supersaturation of oxygen close to the surface, developing what can be called the "oxygen valve", because it causes a net loss of oxygen to the atmosphere. Heterotrophic activity is intense in the core of discontinuous pockets or lenses of water, with oxygen depletion and denitrification. Accordingly, nitrogen joins oxygen in escaping towards the atmosphere. The development of secondary loops in the circulation of nitrogen and oxygen between water and atmosphere, as well a other loops with the sediment involving organic carbon, phosphorus and metals, is a characteristic of all ecosystems subjected to stress.

Meteorology does not attempt to provide a detailed description of convection clouds, but the general situation or overall pattern of which the clouds are a part may be quantified. Local weather is more difficult to describe than climate. Oceanography can provide descriptions valid on a large scale, but we know much less about the details of hydrographic structure. Such knowledge is more relevant for understanding the life of plankton than the detailed structure of the cumulus clouds is for the study of terrestrial ecosystems. We require some sensible approach to the conception of small eddies between large eddies, the detailed structure of turbulence, which forms the background where plankton develops.

Physical considerations make it impossible to accept an uniform distribution of energy, or an uniform upwelling. Somehow water has to escape horizontally at the surface, and achieve a wide range of speeds, with important local differences in transport. Energy is progressively degraded in creating surface turbulence. As a consequence, even if the global result were predictable, depending only of the rate of injection of nutrients into the photic zone, the small details of the distribution can, at best, be described only with difficulty, and prediction is altogether impossible. We find here, in another form, a problem that also plagues ecologists in other fields, apparently as remote as the composition of clays and of humic substances. Where the amount of energy left is small, the situation is more diversified, any trend for a change is no longer obvious, and the stability of the different possible states is indifferent. There is a basic difference between a vertical upwards directed flow of predictable effect, and the rich detail associated with the structures at a small scale that characterize the final stages in the process of degradation of energy. There are thermodynamical reasons for this, but that is small consolation.

FUNCTIONAL MORPHOLOGY OF PHYTOPLANKTON. THE MAIN SEQUENCE

The actual distribution of phytoplankton populations is the result of interaction between the life cycles of a great number of species and the selective properties of an environment, which differs from place to place and from time to time. In a tentative approach, ideal categories, designated as "life-forms", can be conceived as the expression of adaptation syndromes of organisms to certain recurrent patterns of selective factors. I have chosen as principal factors those related to the supply of external energy, i.e., supply of nutrients and decaying turbulence.

The traditional approach of Raunkjaer (1934) to the concept of life-forms in large plants, as an expression of their adaptation to climate and, particularly, to its fluctuations, kindled some interest among planktonologists. However, most of the attempts to classify plankton in groups based on simple morphology (disks, chains, stars, needles, etc.) are better forgotten. Munk and Riley (1952) later showed the possible relevance of shape in relation with sinking and with the absorption of nutrients.

A number of points related to the use of nutrients and growth, grazing and sedimentation form the background for the distinction of life-forms, have to be considered separately and then blended together, as embodied in units of evolution.

The effectivity in the use of light has been made proportional to the ratio between the amount of chlorophyll and the total amount of absorbing materials, in the photic zone. Empirically, this model cannot be proved less accurate than the apparently more sophisticated ways of integrating the available light that are of common use (Bannister, 1974; Steele, 1962; Talling, 1971).

The actual rate of increase of a population, r, as defined by the expression $dN/dt = rN$, is usually related to the concentration of a limiting substrate or nutrient, S, and to a maximal rate, r_{max}, through the expression of Michaelis-Menten

$$r = r_{max}\frac{S}{S+K_s},$$

where K_s is a constant. This and r_{max} define a curve that relates r to S.

Besides, other expressions are available for the same purpose, and might provide a better adjustment to empirical data. The Verhulst-Pearl equation used in population dynamics in one of them. It may be combined with Michaelis-Menten expression in a single equation (Margalef, 1974 *b*) that includes both the effect of the consumption of nutrients and the consequence of the increase of the population under study, if it is convenient to kept them apart, as it might be if the cells produce some inhibitor of growth.

All these expressions are descriptions of a law of diminishing returns. Accepting as the most simple the first formula, the effect of a number of different limiting factors may be interactive or multiplicative, or else the control goes to the factor closer to its minimum (Droop, 1973, 1974), and then we should have

$$r = r_{max}\min_{i=1}\left\{\frac{S_i}{S_i+K_i}\right\}.$$

Light has already been considered, and temperature is usually entered in some form based on the Arrhenius expression, but may be of secondary importance.

Grazing by animals can be accepted as a constant risk, proportional to the density, Z, of animal populations (gZ). If distributions are heterogeneous in space and animals are particularly motile, more complicated expressions may be proposed, and some of them may simplify to gZ^k, where k is higher than unity if animals are particularly motile and efficient. It may be assumed that g has its maximal values for small and medium size cells, disconnected and with ordinary surface, and that g is lower for cells difficult to handle, bulky, with setae or with mucilaginous covers, connected in large colonies, with special or toxic membranes. The final determining factor has to be the way the animal species detect their food and get hold of it.

Phytoplankton contains from 0.2 to 1.2 mg of dry matter per cubic millimetre of volume. Largest values are reported for thick shelled diatoms (*Melosira granulata*, a fresh water species) and also in green unicellular algae. Reported values of density of cells fall between 1.01 and 1.45, with some exceptional figures as high as 2.1. At high temperatures, cells contain less water and their density is higher, as shown by the majority of the available data. Gas vacuoles (cyanophyceae), fat (*Botryococcus*) and liquid vacuoles poor in salts (large marine diatoms and some dinoflagellates) contribute to a decrease of density or increase the buoyancy.

The simplest theory concerning sedimentation speed of passive organisms is based on the Stokes (1851) model, which gives the final speed (V) of a spherical particle of radius r and density ρ falling through a liquid of density ρ' and viscosity m; g is the acceleration of gravity,

$$V = (2/9)\,gr^2(\rho-\rho')/m.$$

For a viscosity of 10 mPo, normal in water at 20°C and 1 000 mb, and an excess density $(\rho-\rho') = 0.02$, the final velocity for bodies 10 µm across, would be 4 mm/h; for bodies of 100 µm diameter, 400 mm/h. If the excess density is 0.05, we would have, respectively, 10 and 1 000 mm/h. Most observations on the sinking speed of phytoplankton fall in the range between 1 and 100 mm/h. Large departures from Stokes expression have to be expected, due to the influence of shape, and to the fact that the surface of the cell has special properties, electrical and others, that attract layers of water or introduce other effects changing the applicability of the simple model based on perfect viscosity. In other words, there is a structured viscosity in the water layers close to the membrane. Such viscosity and its changes have been disregarded in dealing with filter feeding of zooplankton and its seasonal variations in speed and efficiency.

Attention has been accorded to the cell size, in part as a reflection on the fact that a major part of phytoplankton is made of small cells, and also because of theoretical considerations. In water rich in nutrients, small cells with a high ratio of surface area to volume, may multiply faster than larger cells; but in oligotrophic water a high S/V ratio may be essential to keep a minimal rate of absorption. Although small will be always beautiful, large size wins if environmental conditions do not fluctuate too much.

Ostwald (1902) introduced a coefficient to take into account the shape. The simplest approach is to make such a coefficient a measure of the deviation of the surface relative to the surface of a sphaerical body of the same volume. The ratio surface/volume, S/V, decreases as the cell increases in size, as the inverse of a linear dimension. Any shape departing from sphaericity enlarges the relative surface. For a number of phytoplankton species, the ratio between actual surface and the surface of a sphaerical body of the same volume is between 1 and 1.1 for rounded cells, increasing to 1.5 for elongated cells and to 2 or 3 for more thin and needlelike organisms. The ratio may be higher in organisms with hornlike expansions of the body, and is significant in terms of absorption and nutrition, if cytoplasm extends inside such appendages. It is assumed that horns of *Ceratium* and bristles of *Chaetoceros*, at least in species that contain chromatophors (as *Ch. brevis*), increase the surface of absorption of the cell. Allometric change of shape of cells inside a population, and related to the size of individual cells, usually restricts the range of variation in the ratio surface/volume (Lund, 1945; Margalef, 1953, 1974 *b*).

The sedimentation of passive phytoplankton has been assumed to be effective in the absorption of nutrients, as resulting in continuous change of the water in contact with the cell. In addition to cell shape, the manner of sinking in the water has been considered important, for instance, do needle-like cells sink vertically or horizontally or does curvature of cells or the way they are linked together in colonies influence somehow the sinking movement and the renewal of water around the cells (Munk, Riley, 1952; Gavis, 1976; Canelli, Fuhs, 1976). The last named authors propose a way to introduce relative flow in a general expression, according to the same general law of diminishing returns

$$r = r_{\max}\frac{\text{flow}}{\text{flow}+\text{K}}.$$

We may now proceed to the discussion of the dependence of the different life-forms of phytoplankton on nutrient supply and turbulence. I accept them as the most important factors shaping the cells through evolution, and the only reason for proceeding to a functional interpretation of morphology. Input of nutrients is usually associated with turbulence. In consequence, the number of independent variables and of realized combinations (niches) is reduced. Thus, the set of strategies available to phytoplankton is simplified, in the sense that species adapted to a high concentration of nutrients (adaptation revealed by the values of $v_{\max}$ and K_s, parameters of the function of assimilation) are adapted, as well, to a higher turbulence. Such is the case for many non motile species, such as diatoms. Species adapted to thrive and persist under low concentration of nutrients may also be manifestedly adapted to a low turbulence, which allows and even requires some motility from the part of the organisms. The dinoflagellates provide excellent examples. Their life strategies may correlate with a certain degree of heterotrophy and the development of defence mechanisms against grazers or predators.

The rate of increase, related to the amount of nutrients and light, is countered by a probability of being driven out of the photic zone, or of being eaten by animals. Different strategies leading to survival must be predicted, according to the general organization of the ecosystem. They have to be considered in probabilistic terms.

Not all the cells sink at the same speed; some travel faster than average, others lag behind, and depending on the turbulence of water, it may ever happen that a fraction of the population will in fact occupy a higher level than at the start. Successive distributions may thus be related to turbulence and statistical properties of the distributions used as a measure of turbulence. If all the population is at the same depth at time t_1, and at time t_2 the population is distributed with a variance s^2 around the same average depth, the coefficient of eddy diffusion A is related to s as

$$\frac{1}{2}s^2 = \text{A}(t_2 - t_1).$$

This expression results from the expressions of diffusion and of the normal distribution, and dimensionally is correct. Length is the dimension of s, and A (Austausch) has the dimension L^2T^{-1}. In speaking loosely of turbulence in relation to the biology of cells, the coefficient of eddy diffusion A is probably the best reference, but other ways to express the process of mixing are possible, such as the one used in Table 2.

The coefficients of eddy diffusion actually usually form a vertical gradient, and there may moreover be a residual sinking speed V, so that the assumed symmetrical distribution of cells at both sides of the origin is never realized, and the model becomes more complicated. Variance in the paths of migration, and values of the coefficients of eddy diffusion are different according to the dimensions of space.

All the differential models used today run to the generalized expression of Riley *et al.* (1949) of the form

$$\underset{(A)}{d\text{N}/dt} = \underset{(B)}{r\text{N}} - \underset{(C)}{g\text{NZ}} - \underset{(D)}{\text{V}\frac{d\text{N}}{dz}} + \underset{(E)}{\text{A}\frac{d^2\text{N}}{dz^2}}$$

(A), local change; (B), increase; (C), grazing; (D), sinking; (E), dispersal.

N, phytoplankton population; r, rate of increase; g, rate of grazing; Z, population of grazers; V, vertical (sinking) speed; A, coefficient of eddy or turbulent diffusion; z, vertical axis;

Regulation in a system is related to the relative dependences of inputs and outputs on the contents of the system. There is always a feeble regulation, since the

Table 2

Simple programme for simulation of phytoplankton populations, used in the preparation of Figure 4. Successive values are obtained by iteration ($N_{t+1} = N_t + \Delta N$).

Layer	Population density	Concentration of nutrients	Grazing coefficient
1	N_1	M_1	G_1
2	N_2	M_2	G_2
3	N_3	M_4	G_3
4	N_4	M_4	G_4

Sedimentation

$N_4 = N_3S$
$N_3 = N_3(1 - S) + N_2S$
$N_2 = N_2(1 - S) + N_1S$
$N_1 = N_1(1 - S)$

Turbulence

$N_1 = N_1(1 - (A/(1 - A))) + N_2A + N_3A^2 + N_4A^3$
$N_2 = N_2(1 - (2A/(1 - A))) + N_1A + N_3A + N_4A^2$
$N_3 = N_3(1 - (2A/(1 - A))) + N_1A^2 + N_2A + N_4A$
$N_4 = N_4(1 - (2A/(1 - A))) + N_1A^3 + N_2A^2 + N_3A$

Multiplication

$R_1 = \exp(V_m(M_1/(M_1 + K_m))(N_1/(N_1 + K_1)))$
$R_2 = \exp(V_m(M_2/(M_2 + K_m))(N_2/(N_1 + N_2 + 2K_1)))$
$R_3 = \exp(V_m(M_3/(M_3 + K_m))(N_3/(N_1 + N_2 + N_3 + 3K_1)))$

Consumption and mixing of nutrients

$M_1 = M_1 - BN_1(R_1 - 1) + A(M_2 - M_1)$
$M_2 = M_2 - BN_2(R_2 - 1) + A(M_3 - M_2)$
$M_3 = M_3 - BN_3(R_3 - 1) + A(M_4 - M_3)$
$M_4 = M_4$

Actual multiplication and grazing

$N_1 = N_1R_1(1 - G_1)$
$N_2 = N_2R_2(1 - G_2)$
$N_3 = N_3R_3(1 - G_3)$
$N_4 = N_4(1 - G_4)$

S, sedimentation; A, turbulence; V_m, K_n, kinetic constants in dependence on nutrients; K_1, constant in dependence on light; B, nutrient contents of cells;

output is more dependent on the contents than the input. No contents, no output. A plankton composed by swimming dinoflagellates is more regulated from inside than a plankton made by free sinking diatoms. The fact that the output is highly dependent on gradients (that is, on organization of space) is a valuable hint that organization and regulation of plankton populations cannot be disconnected from the consideration of space.

According to Riley *et al.* (1949) a stationary population can be maintained only if

$$V^2 < 4A(r - gZ).$$

In consequence, the population is maintained if the net rate of increase ($r - gZ = a$), a function of nutrient supply, light, and population density of grazers, keeps a certain proportion with the sinking speed of cells and with the turbulence of water. Combining two precedent expressions and taking one unit period of time, it may be seen that the net rate of increase, a, is related to the variability of the trajectory downwards of the cells

$$s^2 = 2A, \qquad V^2 \lesseqgtr 4Aa, \qquad (s/V)^2 \geqq 1/2a.$$

Survival of the population may be achieved if the different relevant parameters combine in such a way that they result in a minimum value of a characteristic parameter. So many factors are involved that, at the present stage, it is almost hopeless to expect a correct expression. But the idea of finding a means of describing how different properties of an organism, in interaction with properties of the environment, combine and produce a score, an expression of the probability of survival, is certainly sound.

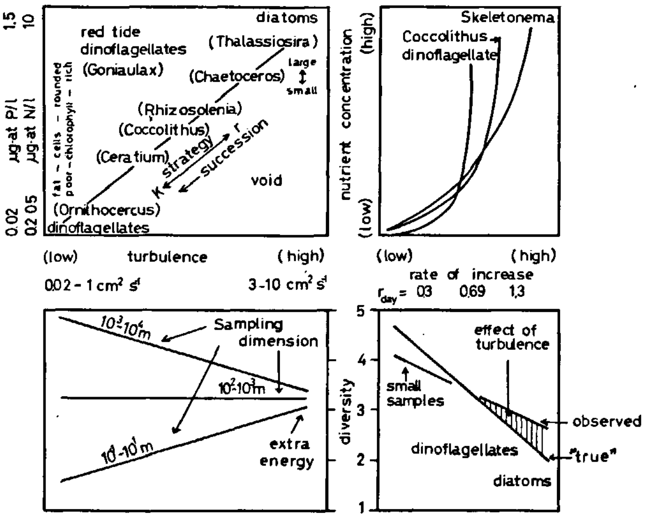

Figure 2

The main strategies in phytoplankton. A tentative plot of the principal life-forms, with examples. In the core graph (upper left) examples of the different life-forms are placed in an ecological space defined by concentration of nutrients and by the coefficient of vertical eddy diffusivity. These properties are reflected separately on the immediate graphs, that represent rates of increase in relation to nutrient concentration (upper right) and diversity at different scales in function of turbulence (lower left). Finally, rate of increase and diversity are tentatively related in the lower right corner.

Different species can achieve the same score, or standard, combining different strategies. Evolution of phytoplankton might be related in a most important way with the exploitation of the many available possibilities. Although according to standard ecological theory, strategies would quite often be divergent. But strategies are imposed in a considerable measure by the physical properties of the environment.

In turbulent water, a population can maintain itself if the rate of increase covers both grazing and the loss of cells towards lower layers, loss resulting from the combined effects of sedimentation and diffusion (Kierstead, Slobodkin, 1953; Platt *et al.*, 1977). Turbulence causes some cells actually to move upwards, and if their multiplication can reconstruct the whole initial population, survival is assured. This may happen frequently, as turbulence is associated with inflow of nutrients. But if turbulence is excessive, most of the population disperses out of the photic zone (Sverdrup, 1953). In water of low turbulence, non-motile cells sink fatally and the population disappears. In such an environment it pays the organism to invest some energy in swimming around, and it helps if the species are well defended against animals. On the other hand, motility would be useless in an environment with "large grained" turbulence.

Matrices of transition provide a practical way of presenting and developing this model. Ashby (1956) proposed a matrix of probability of change of level with reference to an hypothetical population of insects moving over the bank of a river; the same procedure was considered later by myself (1962) and by Lerman *et al.* (1974). The matrix expresses the probability for an element to leave a certain compartment and to be found in another compartment in the next unit of time. The effects of both, sinking and turbulence, are easily visualized. Turbulence appears as a noise added in the transmission along time of the information content of the populations. Turbulence is an analogue of drift in genetics. Both blurr the boundaries in spatial scenarios where competition would be expected to produce sharper limits. Such a matrix is multiplied by another matrix with a single column, giving the rates of multiplication of the cells at each level (Fig. 3). The model can be complicated or subdivided at will.

$$\underbrace{\left|\begin{array}{ccccccc} & a & b & c & d & e & f \\ a & . & . & . & . & . & . \\ b & 1 & . & . & . & . & . \\ c & . & 1 & . & . & . & . \\ d & . & . & 1 & . & . & . \\ e & . & . & . & 1 & . & . \\ f & . & . & . & . & 1 & . \end{array}\right|}_{\text{sinking}} \times \underbrace{\left|\begin{array}{ccccccc} & a & b & c & d & e & f \\ a & 0.8 & 0.2 & . & . & . & . \\ b & 0.2 & 0.6 & 0.2 & . & . & . \\ c & . & 0.2 & 0.6 & 0.2 & . & . \\ d & . & . & 0.2 & 0.6 & 0.2 & . \\ e & . & . & . & 0.2 & 0.6 & 0.2 \\ f & . & . & . & . & 0.2 & 0.8 \end{array}\right|}_{\text{turbulence}} \times \underbrace{\left|\begin{array}{cc} a & 3 \\ b & 2 \\ c & 2 \\ d & 1 \\ e & 1 \\ f & . \end{array}\right|}_{\text{multiplication}}$$

Figure 3

Representation of the dynamics of a planktonic population by the product of three matrices of probability of transition, from one layer to the next, or of change inside the same layer (increase). Layers a to f, from the surface to depth.

A simulation using realistic parameters for different sorts of idealized organisms, and different environmental conditions, starting always with an uniform distribution spanning four strata, provides some matter for further thought (Table 2; Fig. 4).

It is obvious that the result of competition between different life-forms will be different according to external conditions. Diatoms will become dominant in turbulent water rich in nutrients, and dinoflagellates will constitute the bulk of the population in stratified water, poor in nutrients. Interaction between species would be more effective or more predictable in conditions of low turbulence. This agrees with the actual distributions observed in nature. The model shows also why a population of rather low density has to be expected just below the surface, not as a consequence of some detrimental effect of radiation that anyways is not excluded, but as a simple statistical consequence of the combination of sinking and turbulence. The phytoplankton maxima in relatively deep water, so common in nature, can also be nicely reproduced. The model is not dimensional, and thickness of strata and intervals of time can be selected as convenient.

In the model discussed so far, turbulence and diffusion refer to the vertical dimension. The average value of the coefficient of eddy diffusion in the top layers of the oceans is about 0.4 cm²/s, which can be taken as a dividing limit. Diatoms are predominant in regions of high turbulence, in the range from 2 to 100 cm²/s; dinoflagellates in the range of 0.02 to 1 cm²/s. In an horizontal dimension, coefficients are several orders of dimensions higher. They are relevant in the explanation of patchiness. However, as expected, heterogeneity of planktonic populations is more intense in the vertical than in any horizontal dimension.

The shape of the curves describing rate of increase against concentration of nutrients (Fig. 2) for the different species, is consistent with the model and explains succession as the nutrients are used (Eppley, 1970). Regular succession runs parallel to consumption of nutrients and to the decay of turbulence. In the organisms living in stratified water of low turbulence, like large dinoflagellates, the renewal of the water bathing the cell is as important as keeping afloat. This explains why in the dinoflagellates the flagellum that makes the cell rotate on its long axis is stronger and attached, and surely does more work than the flagellum that propels the cell. The flattening of the cell, with increased resistence to turning around, combines with the development of the transverse flagellar apparatus. Both characters appear to be locked in a course of seemingly counteracting adaptations (Taylor, 1971; Margalef, 1974 *b*). The final result is an increase of the flow of water that washes the cell.

What can be called the "main sequence" in the spectrum of adaptations of phytoplankton, combines the mechanical needs of remaining afloat, with nutrient kinetics, and may be a path often followed in the course of succession. An axis describing the relative importance of $r - K$ strategies can be superimposed on it.

The picture can be completed by examining briefly the situations characterized by low nutrients and high turbulence and the reciprocal. The area of high turbulence and low or moderate nutrient concentration in

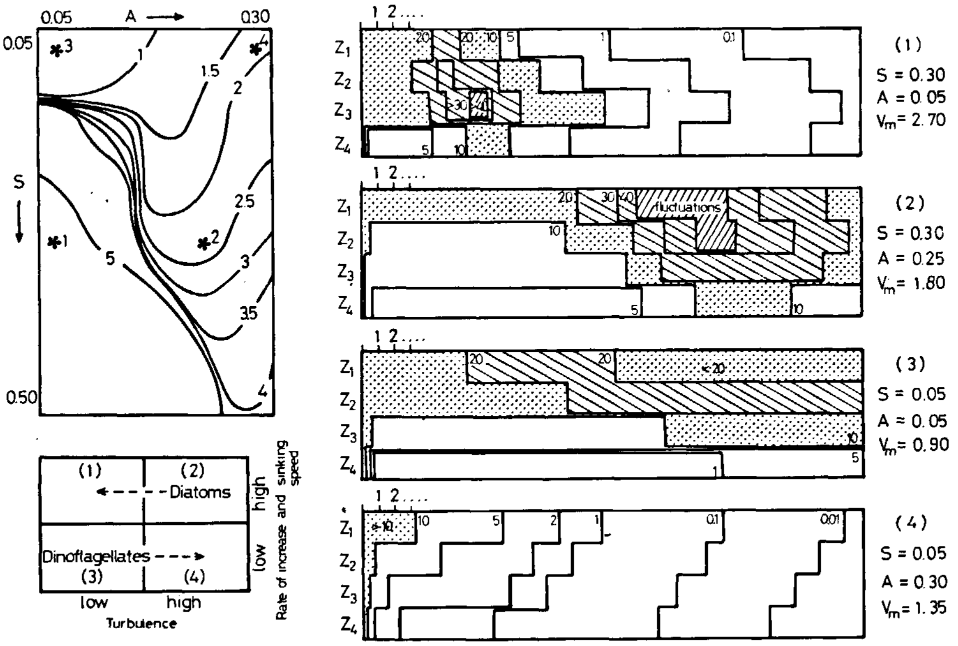

Figure 4

Results of simulations based on model and program of Table 2. Constants, $B=1.2$, $G_1=0.07$, $G_2=0.08$, $G_3=0.10$, $G_4=0.12$, $K_1=25$. $K_m=9$, $M_4=100$. *Initial values,* $N_1=N_2=N_3=N_4=10$, $M_1=M_2=M_3=50$, $M_4=100$. *Iterations* 1, 2, ... *up to* 30, *with four levels.* Z_1 *to* Z_4, *using the stated values of variables* S, A, *and* V_m *(right). Upper left, minimum values of* V_m *for indefinite persistence of populations under different combinations of* S *and* A *(stars are the points of simulations presented in detail at right). Lower left, projection on the diagram of Figure* 2. (1) *and* (2) *are diatoms,* (3) *and* (4) *are dinoflagellates;* (2) *and* (4) *are turbulent environments.*

the right under corner of the principal graph in Figure 2 is typified by the case of a mixing depth much thicker than the compensation depth. It is a limiting situation of minimal production and extreme dispersal of populations and strong stochastic component in their taxonomic assemblage.

The combination of high nutrient concentration with low turbulence is found only, in the sea, in transitory situations, or when there is some border condition, such as inflow from the land. Such an unusual combination might represent a sort of illness, not completely ironed out by evolution, since it produces the red tides that may end in catastrophe, with the collapse of many populations, including the causal species. The bulk of such populations is made up of swimming forms (dinoflagellates) and their cells are less flattened and richer in chlorophyll than the dinoflagellates of the regular end of the main sequence.

A MORE DETAILED LOOK AT THE RANGE OF AVAILABLE STRATEGIES

In developing the approach of Riley, Stommel and Bumpus, the conclusion was reached that organisms survive only if they can match a number of requirements. Different parameters can be combined to produce an indicator, and its value can be supposed to determine whether the organisms succeed of fail.

Gavis (1976) has actualized and completed the work of Riley and coworkers, developing a new expression, in which parameters relevant in the ecology of plankton, combine to produce a dimensionless number (P′), which must exceed a certain value to warrant the survival of the populations.

Following expression is the product of the equations (4) and (11) from Gavis (1976), with some changes in the lettering

$$P' = (C\,df\,AK_s/v_{max})(1 + dV/2A)$$

K_s, v_{max}, kinetic constants; A, turbulent diffusion; *d*, a characteristic dimension; *f*, coefficient of form, maximum = 1 for a sphere; C, a constant; V, vertical speed (sinking).
This expression can be rearranged and presented as

$$P' = C\underset{(A)}{(K_s/v_{max})}\underset{(B)}{(df)}\underset{(C)}{(A + 1/2\,dV)}$$

(A), kinetics of nutrition; (B), morphology; (C) physical environment.

The contents of the three brackets can combine in different ways and produce about the same value of P′. Growth and morphology are involved in coping with the constraints imposed by the physical environment. Inside each bracket a compensating effect can be expected as well. Values of K and v_{max} are positively correlated. Small cells are sphaerical, larger cells are characterized by a smaller value of the coefficient of form. This coefficient of form is negatively correlated with the relative surface of the cell that has been used before in these pages. Concerning the last bracket, it is obvious that turbulence and sinking speed compensate each other.

The number of available strategies can still be larger than implied in the last paragraphs. Long expansions of the cell body or bristles *(Chaetoceros, Ceratium)* help to keep the cells joined in chains or flakes of several millimetres, or are associated with other structures or secretions which serve the same purpose. Consequently, the cell *(Ceratium carriense, C. massiliense)* or the colony *(Chaetoceros, Rhizosolenia stolterfothii)* is anchored in eddies that are one order of magnitude larger than the single cell, in a way that smaller eddies closer to the cell can wash its surface and increase absorption. The following analogies may explain how this works: a small particle is subjected to Brownian movement, a larger particle receives many impacts and does not move. A small boat dances on the waves, a large ship is washed by the waves.

The smallness of the Reynolds numbers that are obtained as applicable to phytoplankton, reveal that at its order of magnitude, viscosity may be more significant than flow. But the whole theory of Munk and Riley and their followers accepts the importance of the flow of water over the cell in enhancing absorption, and direct proof (Canelli and Fuhs, 1976) confirms the relevance of flow over viscosity. At any rate the theory that the size of the colonies of plankton organisms can help to utilize differentially the separate ranges of the spectrum of turbulence, might afford a partial explanation of the common occurrence of several species of the same genus. Such congeneric clusters *(Ceratium azoricum* and *C. carriense, Chaetoceros danicus* and *Ch. decipiens, Rhizosolenia robusta* and *Rh. stolterfothii)* belong, actually, to different systems of eddies and to different ecological niches, if one chooses this way of expression. Each species filters out some segment in the whole spectrum of turbulence of the water, and competition between species is alleviated, as far as the parts of the spectrum relevant for each one of the species are not coincident. A careful study of the smaller range in the spectrum of turbulence would be rewarding (Denman, Platt, 1976).

Coccolithophorids contain plates of calcium carbonate, and are expected to have an increased sinking speed. Moreover, their flagella are rarely functional, at least in cultures. We do not know if this handicap is compensated by some scavenging of important nutrients in the mineral deposit of the coccoliths.

Buoyancy as a consequence of gas, fat or aquaeus vacuoles adds another niche dimension. Large dinoflagellates such as *Ceratium* can actually eat bacteria and small diatoms and are rarely consumed by animals. They are like the species sitting at the top of food chains. In very fertile (upwelled) water, another life-form is found, characterized by the accumulation of mucilage or of threadlike secretions around the cells. It is typified by diatoms as *Thalassiosira (Th. partenea, Th. subtilis)* and *Chaetoceros (Ch. socialis, Ch. radians)* and by other chrysophytes *(Phaeocystis).*

MARINE AND FRESH WATER PHYTOPLANKTON

Traditionally, fresh water phytoplankton has been seen as quite different from the marine phytoplankton. With the exception of some cyanophyceae, and euryhaline continental species that develop or survive in seas of low salinity, like the Baltic, there are no common species. But the differences in the representation of the main phyletic groups and in the relative development of the different adaptations to a suspended existence have been overplayed. Most of the differences are due to the much larger dimension of the "ecological space" in the epicontinental waters. The fresh water environment offers more realizable niches for the evolution of plankton species.

Continental waters offer a wider spectrum of possibilities. Turbulence is often lower and nutrient concentration is usually higher, sometimes exceedingly higher, than in the sea. This difference is the result of an intensive coupling between land and freshwater. Limnologists are usually fond of an ordination of the ecosystems along the axis oligotrophy-eutrophy. Marine ecosystems are, in general, oligotrophic, in the sense that production is low, turnover is slow, and the cycle of matter is contained in the marine environment proper. Only upwelling systems develop mechanisms essentially similar to those operating in the eutrophic lakes, involving a loop with the atmosphere (O, N) and another with the sediment (organic C, P, Fe, Mn).

On the whole, conditions prevailing in the oceans are almost covered by the diagram of Figure 2. If properties of the fresh water environment and composition of its plankton are plotted on the same graph, there is a good correspondence between both sets of communities. In fresh water and under relatively high turbulence we have diatoms (*Asterionella, Melosira, Fragilaria*); in intermediate situations and more or less in the place of the coccolithophoridae, there is *Dinobryon*, with cells inside bell shaped cups that confer them special hydrodynamic properties; and *Ceratium hirundinella* appears as a vicariant of the common marine dinoflagellates. But in fresh water there are no such extreme forms as *Ornithocercus* or *Histioneis*, that represent a peculiar line of evolution exclusive of extremely oligotrophic marine regions. The place of the "red tide" dinoflagellates is covered by *Peridinium cinctum* and related species, as well as by the euglenophyta (a genus of this group, *Eutreptiella*, participates in marine red tides), volvocales and representatives of other groups. Volvocales and some fresh water species of *Gymnodinium* have mucilaginous covers.

In the ecological chart of the plankton of Figure 2, the area that is almost exclusive of fresh water starts at the top of the figure, where nutrient concentration is high, and along a line where most organisms excrete abundant organic material, including some organisms of upwelled marine water, as noted before.

Excretion in soluble form of part of the assimilated carbon is a common feature of algal cells. Its amount is variable and is subjected to environmental regulation. Byerrum and Benson (1975) showed that excretion by a dinoflagellate was positively correlated with ammonia concentration in water. If results of such experiments are generalizable, possible interactions between plants, animals, and bacteria could be anticipated. Plants tend to use ammonia over nitrate, and in taking ammonia out of the environment might protect themselves from further loss of organic matter. A rather important amount of excretion is to be expected in most freshwater environments, and perhaps more if water is deficient in some essential nutrients, although not in carbon and in other nutrients. Homoptera feeding on plant juices rich in sugar, but deficient in necessary elements, give off an abundant organic secretion and are perhaps comparable to the mucilage producing phytoplankton.

If the secretion accumulates faster than it dissolves, it becomes visible in the form of covers and sheets, making quite common in fresh water a situation that in the marine environment appears only in borderline cases (for example, *Thalassiosira*). It may be supposed that the presence of mucilaginous material against the cell should have on absorption an effect opposite to that of movement in naked cells; in other words, it must act as a brake on growth. It is in fact a self-regulating brake, with feedback: the more nutrients, the more jelly, more shielding, less absorption, decrease in production of mucilage, enhanced absorption, and so on. Of course, different environmental factors such as bacterial populations, calcium concentration, etc., can change the compacity of the cover and its readiness to dissolve.

Different adaptive interpretations of the presence of mucilaginous covers have been proposed. Because a single enzyme may make the difference between secretion of soluble organic matter and accumulation of longer molecules in a jellylike cover, it is reasonable to look for factors of selection. The mucilaginous covers have been viewed as enhancing buoyancy, or as mechanical and chemical defenses against predators. The chemical aspect has been stressed by Porter (1976), who reported that algae envelopped in mucilaginous covers resist better the digestive action of animals and passed through the digestive tract of grazers not only relatively unharmed, but even having had the possibility of extracting precious nutrients from the gut of the animals that ingested them.

The supposed braking effect mentioned before suggests another dependence that might be important at the level of the ecosystem. An abundant mucilaginous secretion can be visualized as a mechanism that prevents crashes like those occurring in "red water" outbreaks, and converts the "illness" into a regular process, through a sert of population control. The chemical composition of the mucilaginous covers is probably different according to the season, although the available data refer only to benthic species.

Blue green algae are common in fresh water, but very rare in marine plankton. The presence of gas vacuoles is assumed to represent an adaptation to float, and accumulation of cells in the surface of water bodies is an advantage from the point of view of utilization of light. But such distribution often anticipates catastrophe, as in red tides. Nitrogen fixing blue greens are common in fresh water (*Anabaena, Aphanizomenon,* etc.) and their occurrence can be easily explained by the importance of the nitrogen loop between water and atmosphere, in freshwater ecosystems under stress. A similar situation in the marine environment would be expected only around the upwelling areas and in other places where there is denitrification. Actually, the marine floating symbiosis of *Oscillatoria (Trichodesmium)* with bacteria and fungi, able to fix nitrogen, has been reported most often from areas not far from upwelling regions.

The chemical composition of sea water is more uniform than the epicontinental waters. The different nature of rocks and soil, the interaction between water, soil and terrestrial vegetation, provide a larger spectrum of possibilities. Not only the common nutrients, but oligo-elements are also involved, with some general properties such as alkalinity and total mineral content, pH and presence of organic matter, also playing a role. The great number of species found in freshwater plankton, belonging to quite different taxonomic groups, as well as the notable seasonal and local variability of fresh water plankton may find a partial explanation in the diversified chemical composition of inland waters.

MIXING AND THE "GRAIN" OF PLANKTONIC COMMUNITIES

Turbulence is a selective factor in local communities. It is also a factor in mixing neighboring pockets of water that could harbor different or divergent populations. When Hutchinson (1961) pondered the apparently excessive diversity of the plankton samples, he hinted at mixing ocurring in nature or as a result of collecting the samples, as well as commenting on the multiplicity of available niches. There is no reason for wondering now. We have seen that the possibilities for carving a living are many, affording ample possibility for ecological segregation, whatever this means (see also Richerson *et al.*, 1970).

Intensive sampling over a 2×2 mile block (Margalef, 1969) has shown how well the pattern of mixing is reflected in the spectra of diversity. In a spot with more turbulent water, close to the breaking of internal waves, a relatively dense population of diatoms developed. Diversity was apparently excessive at the lowest end of the spectrum, that is, over very small volumes, but as the sampled volume increased, diversity did not increase very much. On the contrary, where water was stratified, density of populations was lower, dinoflagellates were predominant, and the diversity spectrum was steep. That is, diversity was low in small volumes, but increased steadily when the sample was enlarged by adding new parcels of water. This shows that, along the main sequence of plankton life-forms, there is *also* a difference in the spatial structure of populations as described by diversity spectra. The tentative relationship is sketched on Figure 2, below.

The coexistence of similar species of phytoplankton, even of species belonging to the same genus, is no longer puzzling. I have examined recently (Margalef, 1974 *a*) the association between congeneric species in two genera common in the marine plankton *(Chaetoceros* and *Ceratium),* both in the Mediterranean and in the Caribbean. In the case of *Ceratium* the hypothesis of random and independent distribution is enough to explain any association detected between congeneric species. Population density is low, population dynamics is slow, so not much interaction exists inside the volume of one sample. *Chaetoceros* exhibits a different pattern of distribution, with a higher degree of association between species in the genus. The distribution of *Chaetoceros* can be explained assuming that samples without *Chaetoceros* fall in two groups. Samples that actually fall outside of the statistical universe relevant for the distribution of *Chaetoceros,* samples in which *Chaetoceros* should not be expected to occur, and samples that belong to that universe, with a high probability of occurrence of each species and no segregation among them. The conditions that would be expected to lead to a monotonous plankton, produce as well intensive mixing and local accumulation of opportunistic forms that contribute to an exaggerated diversity. But the different species of *Chaetoceros* when in an environment of decaying turbulence, associate with different sizes of eddies and belong, in fact, to different niches.

Grazing pressure tends to be indiscriminate on non-motile cells and in turbulent water. However, motile organisms in water of low turbulence can also be tracked and captured by diversified macrophagous animals, which are more evolved in their divergent specialization. This is simply another instance of ecological asymmetry in the main sequence of life-forms.

The subtle equilibrium between intensity of mixing and degree of allowed segregation can be viewed as well from another angle. The whole planktonic ecosystem is an example of stabilization of this kind. Where there is light, there are no nutrients, and where the nutrients are, there is no light. The same can be said about other factors and with reference to a smaller range. This can be reasoned also from the model of Riley, *et al.* (1949):

$$dB/dt = rB - V'(dB/dx) + A'(d^2B/dx^2)$$

B, biomass (may allow internal cycling); S, substrate or nutrient concentration; V, V′, speed along x; A, A′, turbulent diffusion; V′, A′, refer to organisms; V, A, refer to water and nutrients; $A = A' + a$, $V = V' + v$; k, extinction of light; x, z, coordinate axes; r, rate of increase; F = a function of depth and extinction coefficient.

The biological change can be made proportional to the consumption of nutrients and its supply to the photic zone

$$rB = (-V(dS/dx) + A(d^2S/dx^2))(1 - F(k, z)).$$

where F (k, z) is related to the intensity of light. Because I consider this factor to be immaterial for the continuation of the argument, so it is set equal to zero, which results in

$$\begin{aligned} \mathrm{d}B/dt = & -V(dS/dx) + A(d^2S/dx^2) \\ & -(V-v)(dB/dx) + (A-a)(d^2B/dx^2) \end{aligned}$$

and rearranging

$$\begin{aligned} \underbrace{\underset{(A)}{dB/dt} + \underset{(B)}{V'(dB/dx)}}_{(C)} &= \underset{(D)}{V(dS/dx)} \\ &\quad + \underset{(E)}{A((d^2S/dx^2)+(d^2B/dx^2))} \\ &\quad - \underset{(F)}{a(d^2B/dx^2)} \end{aligned}$$

(A), net increase; (B), loss of cells; (C), production; (D), use of nutrients (flow); (E), effect of the lack of conformity in distribution of nutrients and plants (covariance); (F), effect of anchoring cells in large eddies or lagging behind.

This model is sketchy and very primitive, and its purpose is only to suggest other possible ways of considering the pelagic environment. The term $A((d^2S/dx^2) + (d^2B/dx^2))$ might be the starting point of another way to consider the spatial organization of ecosystems. It shows the effect of having coincident or not coincident peaks in the overlapping and interacting distributions, on the dynamic nature of the system. The final, stable situation, would be to have all things segregated and the system stopped (nutrients is one layer, light in the other). The sum of second derivatives appears multiplied by the coefficient of turbulent diffusion. A strong turbulence, moreover, has to lead to a coincidence of the distributions, with a maximum covariance.

It is clear that the term (turbulence × covariance in distributions) has to have a spectral expression, that is, the space to which it refers has to be specified, and according to space, its value should change. It represents, in short, a spectrum of organization, combining in some way, the spectra of turbulence and of diversity.

The same reasoning can be applied to the consideration of the interaction between phytoplankton and zooplankton, that produce expressions of the same form. It is also possible to derive expressions including nutrients, phytoplankton and zooplankton and to consider organization not only in one, but in the three dimensions of space. The most interesting term contains always an expression of the overlap of the interacting elements, multiplied by a measure of the turbulence of the environment.

The last term should represent the effect of organisms that filter out some sections of the spectrum of turbulence, such as the *Chaetoceros* that form colonies of large size, or the organisms that remain attached to the walls in a chemostat.

The predictable equilibrium in an ocean at rest would be an extremely low primary production and a low biomass. Almost everything particulate is expected to sink eventually, and a perfect segregation in the ranges of operation of limiting factors should be achieved. All of this would occur on a rather small scale. However, over a larger space, degradation of energy on the Earth affords power to work many mechanisms that oppose final stabilization. The game has been going on for so long now that biomass and production are incredibly diversfied, and not as low as simple thermodynamic considerations would predict. I would like to stress that the decay of the external energy has been one of the main agents of selection, leading to the evolution of many like-forms in phytoplankton.

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