Turbulence and marine life*

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SUMMARY: The decay of the mechanical energy of waves, currents and tides generates turbulence that propagates downwards, diffuses nutrients and influences in different ways the movement of organisms. Light and turbulence combine in creating local conditions for primary production. Mechanical properties of organisms (size, shape, production of mucilages) interact under different regimes of turbulence. Turbulence is a main factor in determining the stratification of populations. Organisms manipulate turbulence with results that could have positive selection value. It is suggested that many organic constructions, like the limbs of copepods, provided with setae, rather than as filters, function as manipulators of the turbulent regimes at a small scale, in ways that increase the effectivity of feeding currents, introducing longitudinal asymmetries in the turbulent currents, in a way that could allow to speak of a "turbulence valve".

Key words: Mixing, nutrients, pelagic life, plankton, phosphorus, Redfield ratio, sinking, turbulence valve.

Turbulence consists of irregular movements of the molecules in a fluid, through which mechanical energy is transmitted and decayed. Through this mechanism, transport of heat and of materials in solution is accelerated along the respective gradients.

This appears simply enough, although a rigorous approximation to the physics of turbulence may appear rather discouraging. To the biologist, the energy involved in turbulence is obviously material and responsible for the maintenance of ecosystems. This may seem less than obvious when ecologists often have been guilty of neglecting essential energy inputs by fixation on photosynthesis and to transfers of energy delivered from it to other trophic levels. Other energy sources active on earth that contribute as well to the organization and maintenance of ecosystems have been neglected systematically, as is obvious in the case of vascular terrestrial vegetation, where energy of transpiration mediates the input and translocation of water and nutrients and quantitatively widely exceeds the energy of photosynthesis. Furthermore human civilization, besides food, uses increasing amounts of energy from many sources. Turbulent energy in aquatic environments may be relatively compared, at least, with transpiration energy in terrestrial ecosystems.

Primary producers in open waters are very small, and never build the relatively persistent structural frame of terrestrial vegetation. Phytoplankton assimilates in a top layer, usually 40-80 m thick, and the formed organic matter enters a food chain that extends to maximal depths. Turbulent energy, mostly originated by the interaction between atmosphere and water at the surface, plays an essential role in returning the nutrients from the levels and places where they tend to accumulate, chiefly in deep

water, to illuminated layers again. This role of turbulence covers wide spectra of wave length and power.

Much less energetic turbulence is unavoidably generated by the swimming of the organisms and through the feeding currents that animals generate. Here it becomes a mixed benefit, and leads both to the use of turbulence in the detection of prey and enemies, as well as to the development of ways of concealment or to the broadcast of false information, selected as it limits the probabilities of being caught. In summary, the role of turbulence in aquatic life is so important that Ambühl (1960) could write "There is no life without water, and there is no life in water without turbulence in water".

Both surroundings, the atmosphere and the water, are fluid and turbulent: Water is a practically incompressible liquid, air is a compressible gas. These disparate mechanical properties are the sources of important differences. But turbulence always sensibly accelerates transport along the gradients.

Mechanical turbulent energy is necessary to the continued life of plankton. Benthic life is capable of redirecting circulation and developing turbulence in a large scale (like in corals), but also generating, controling and using turbulence very effectively over smaller scales (Riisgard and Larsen, 1995).

Life of plankton and its dependence on turbulence provides an excellent example of how evolution gradually takes control of environmental forces. Turbulence results from (entropic) dissipation of mechanical energy that works in a fluid. Water is a barely compressible liquid of relatively high density, supports mechanically the organisms and as a solvent of exceptional properties is the carrier of materials and provides an excellent substrate for mechanical and chemical interaction among aquatic organisms (Fig. 1).

Dissolved and suspended materials diffuse or move along any gradient of decreasing concentration, from places where they are added to places where they are consumed, and turbulence accelerates the flow. In oceans and lakes, surface waves are an important source of turbulence; turbulence is generated also in internal surfaces with shear, between overlaying water masses of different density or between the water and the bottom.

Living beings are, in part, dissipative systems, and in part selforganizing systems, and turbulence in the surrounding fluids around contributes to dissipation of heat and of momentum and in special to displacement of selected molecules. Between layers of contrasting salinities, the so called "salt fingers" result from differences in the diffusivities of heat and of solutes, and create asymmetrical boundaries of peculiar properties.
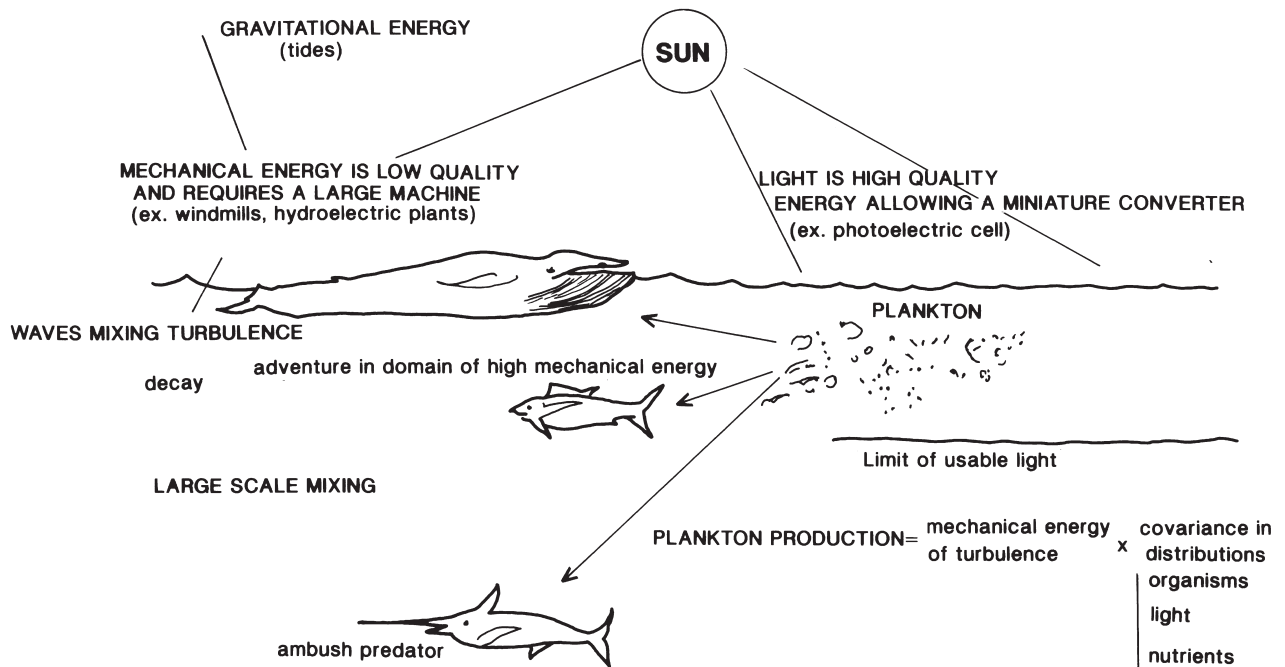

Fig. 1. – A general sketch of the interaction between light and mechanical energy in the oceanic environment.

Turbulent oscillations cover a wide scale of size, in an irregularly hierarchical pattern as expressed by the few rhymed lines attributed to L. F. Richardson and repeated *ad nauseam*: "Big swirls have little swirls that prey on their velocity, and little swirls have lesser swirls and so on ... to viscosity". Viscosity, the tendency of molecules to adhere together sets a limit to turbulence; it depends on the nature of the fluid and on conditions like temperature.

The decay of energy in the production of irregular movements has been rationalized through several theoretical models that imagine the way trajectories modify with the passage of time, down to molecular level. From its molecular composition alone, at "regular" temperatures, water would be expected to behave as a gas; but it is a liquid, because its molecules are more densely packed than a preliminary theoretical approach could predict, held together in small groups by secondary hydrogen bridges. The average size of each one of such molecular clusters depends on temperature and perhaps also on other conditions. This is not without consequences for the degree of hydration of living matter and certainly also in the dependence of viscosity and turbulence from temperature.

Adequate observations of small motions require tracers and become difficult and even impossible at the smallest scale, and some of the accepted assumptions have been acquired in a deductive and probably incorrect way. Only the recent development of sophisticated equipment apt to collect and analyze large amounts of information about movements of the fluids over small scales of time and of space, keep a promise of empirical progress (Imberger, l994).

In stationary situations in which decay is compensated by a constant input of energy - that might come, eventually, from surface waves - , the local spectra of turbulence may remain relatively constant for a while. The supplied energy may come with orbital movements of water, such as those generated by the waves raised by wind in the surface, which momentum propagates downwards. The spectra of the movements of small parcels of water shift over time and space, periods may split and movements that formerly were regular end in confused turbulence. On average, wavelengths and amplitudes decrease and frequencies may go up, in a genuinely irreversible and entropic process, in which a wide spectrum of motion is alway present. Trains of waves can reflect and meet again and interfere among them, being out of phase, after travelling dif-

ferent paths. The prevailing notions for explaining observed or supposed regularities have been based on analogy and dimensional analysis. It was expected that chaos might provide a complementary conceptual frame. Indeed, one of the pioneers of the science of chaos, Lorenz (1963), got a start into chaos theory through the consideration of thermal turbulent convection in the atmosphere.

Indeed, chaotic behaviour has been observed or suspected in nature or in experiments, since Reynolds (1883), who studied flow by means of streaks of colored fluid interspersed in a stream, and in different situations. There is a particular value of the mean velocity of the fluid, that depends on the diameter of the pipe or of the channel, and, of course, on the nature of the fluid, below which the flow is smooth ("not chaotic") and disturbances are rapidly obliterated. If speed goes up, the flow becomes increasingly sensitive to disturbances, however small, and for higher speeds the rectilinear regime breaks down completely. Energy is drained from the larger scales of motion to smaller scales, until viscosity of the fluid sets a limit. Viscosity is, indeed, one fundamental property, characterizing the "fluid machine of turbulence".

It was inferred from Reynolds that the "upper critical velocity", separating the smooth rectilinear flow from the aparition of eddies and generalization of flow irregularities, could be related to the kinematic coefficient of viscosity (ν, of dimension L^2T^{-1}). The diameter of the pipe, multiplied by the flow speed and divided by the coefficient of kinematic viscosity, yields a dimensionless number, the Reynolds' number, *Re*, expression of the ratio of the inertial to the viscous forces, with a critical value around 1000; above such value, flow is perceived as turbulent. The coefficient of kinematic viscosity is temperature dependent (it decreases with increasing temperature). In experiments with water, viscosity can be easily increased by cooling or adding mucilage.

An analogous and parallel measure of the behaviour expressed by the Reynolds' number, and going under the same name, has been adapted to characterize the expected regularities in the movement of free particles or mobile organisms immersed in a fluid: this particular form of the Reynolds number is made equal to VL/ν or $\rho VL/\mu$. V is speed in cm s^{-1} and ν is the coefficient of kinematic viscosity, of dimension cm^2 s^{-1}, its unit being the stokes; μ is the coefficient of dynamic viscosity, of dimensions g cm^{-1} s^{-1}, the unit being the poise; $\nu\rho=\mu$ (ρ stands for

density). This practical Reynolds' number is below 0.1 for a phytoplankton cell that sinks slowly in water, and half a million or more for a swimming fish. In these examples, laminar flow is supposed to brake the supply of nutrients to the phytoplankton, and turbulent flow, in which eddies absorb much energy, will surely slow down the potential speed of the fish. For convenience in particular applications, it might be acceptable to compute analogous Reynolds' numbers on the distances between the radii in any filtration device, or, in particular situations, with reference to the definite thickness of a liquid layer.

A, a symbol for *Austausch,* the German word for exchange, is used for actually observed speeds in the turbulent transmission or diffusion of heat, salinity, or momentum (specified adding to A the appropriate subindex, θ, s, v), and has the same dimensions as dynamic viscosity, μ. As expected, its numerical values when refering to properties with no return, like heat and motion, are larger than values refering to properties in which transmission happens both ways, with partial return, like in the forwarding of salts, gases and nutrients in solution. Most frequent actual values at sea go from much less than 1 g cm^{-1} s^{-1} in the well stratified water during the warm season, to 3-50, in the same units, in agitated waters; these numbers refer to the vertical direction. Water stratification by density makes horizontal diffusion much easier, as less energy is involved in effective mixing along the horizontal plane. *Austausch* numbers, A_x, refered to the horizontal are often 100-1000 times larger than those mesured along the vertical (A_z).

SCALES OF INTERACTION BETWEEN TURBULENCE AND PLANKTON

Turbulent mixing in oceans and lakes, principally under the action of wind, brings back nutrients to the surface and restarts the cycle. The work done can be appreciated in different ways. If, to begin with, the water was stratified by density, large scale mixing raises the center of gravity along the vertical. Work done is equal to the product of the total mass M by the vertical distance between the two consecutive positions of the center of gravity (E) and the acceleration of gravity (g). This total work, gME, replaces nutrients to the illuminated layers, allowing biological production to proceed. This is an example of large scale mixing (Fig. 2).

A much larger fraction of available energy is usually dissipated just in mixing over small and smaller distances, although the biological results may be as significant as in the precedent example of large scale mixing. The wave spectrum of turbulence shifts naturally along time towards shorter wavelengths, and dissipates and practically would stop if no more momentum were injected. If A_z is the value of "Austausch" along the vertical, and dV/dz the change of sinking speed along the vertical, the vertical diffusion of mechanical energy will be $A_z(dV/dz)^2$. The irreversible dispersal or diffusion of mechanical energy and temperature is unavoidable and in absolute value is higher (more increase of entropy) than diffusion of materials in solution, because a fraction of such materials can always and eventually travel back, a feat that is not possible concerning heat (heat cannot flow from a cold to a warmer body) or momentum. In consequence, as already stated, vertical diffusivity for movement is higher than vertical diffusivity for nutrients, and in the sea, the ratio A_z/A_m, or A_v/A_m, with reference to the vertical axis z, may be between 5 and 50. One conclusion is that turbulent diffusion is somewhat parsimonious or not as effective as it would be desirable, in the task of supporting the fertility of the top levels of the seas, by replenishing them with nutrients from below.

The path described by a freely suspended organism does not exclude randomness, in a degree that depends on turbulence and on the capacity of the organism to orient itself in relation to light, to gravity, and any other possible cue or stimulus, and to control its own speed and trajectory in relation with them. A simple approach is to suppose a random walk and to subdivide it into small steps. The expected lineal distance between both endpoints (D) separed by N steps of length L is $D=LN^k$, where k expresses a fractal property; k=1 for a straight path, k→0 in a path that keeps turning around inside a small volume. Intermediate values are expected in the normal aquatic environments and they depend on turbulence. The non uniformity of turbulence, as well as the directionality of external stimuli (light, gravity) make clear that movements along the vertical may be and usually are much more internally influenced or determined than drifting around along an horizontal plane, which is characterized by higher values for turbulence and by the lack of directional stimuli. The fractal walk in this example is supposed to be

Minimal extension necessary
to mobilize auxiliar energy

1   10   100 km

1% of effective radiation

Primary production mW m^{-2}

200
100
50
20
10
5

Primary production g C m^{-2} year^{-1}

2000
1000
500
200
100
50

1% of e.r.

1   10   100 1000mWm^{-2}

Auxiliary energy used to
enchance primary production

SUN

Atmosphere/hydrosphere
interaction

Light used in
primary production

Auxiliary energy
appear invested ★

Units of equal degree of closure

★Mostly in transport

O$_2$ N$_2$

★Transport + mixing

★Mostly in mixing
(small scale turbulence)

← output
pattern

amplification
of
discontinuity

← uniform
input

x.y.z models

P C

dV$_z$/dx ≠0

A$_z$ =2 - 50

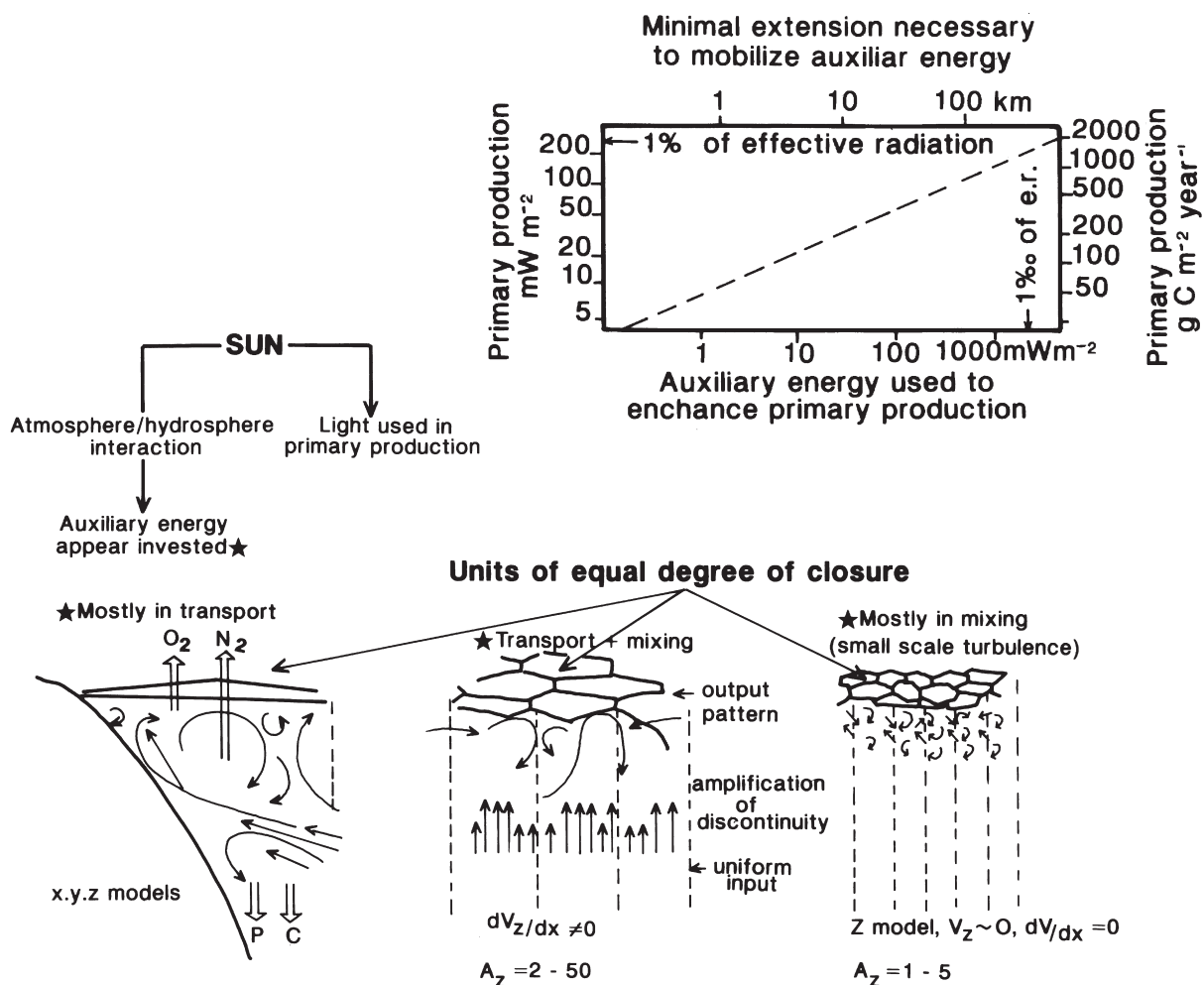Z model, V$_z$∼O, dV/dx =0

A$_z$ =1 - 5

FIG. 2. – Schematic representation of typical oceanic situations in function of vertical flow and of turbulence. Energy involved in upwelling of deep water or in simple mixing of water enhances primary production, in a degree proportional to the supplied extra energy. In the lower part of the figure, input of energy is assumed to increase from right to left (Redraw from Margalef, 1974 and Watt, 1973).

decomposed in relation to the three dimensions: $k^2 = k_x^2 + k_y^2 + k_z^2$. This approach is useful to introduce the analysis of vertical migration, and helps to understand the random shifts in the horizontal plane that are associated with such migration.

Oceanographers and biologists are impatient with and critical of the current theoretical models and expect much from expansion of empirical research in the field (Lazier and Mann, 1989). Turbulence (or non turbulence) close to small solid bodies is expected to take the form of laminar shear. The existence and metabolism of very small creatures poses many problems to fluid dynamics, real or imaginary. The image of tiny things of 1-2 μm swimming happily and confidently, is always haunting to the observer.

Electrical charges of the membrane (eventually pushing the cells along the environmental gradients of electrical potential) might influence neg-atively the aggregation of assimilating cells into food balls. Experimentally, small living organisms can be displaced electrophoretically between electrodes with a speed that is also related to the intensity with which they assimilate. One question poses itself: would filter-feeding be more effective at night, when electrical charges in the surface of autotrophic organisms may be supposed to drop?

On the basis of theoretical constructions, including dimensional analysis, a decay of turbulent energy over small spaces is commonly supposed to follow a law of a -5/3 power. This is discussed in other companion contributions, and for a biologist one of the most important unresolved question may be the possibility of having intermittences left, that is, small volumes at rest, which could serve perfectly as spaces where agregation of mucilages might easily happen.

This supposed basic spectrum might be expanded over to larger scales in an attempt to comprise in the same broad pattern, the clumping or patchiness that is revealed in most statistical studies on the large scale distribution of plankton organisms. The particular reasons for the distributions are rarely clear. Anyway, a previous logarithmic transformation of the original concentration of organisms simplifies the analysis and the presentation of distributions in terms of numbers of cells or concentrations of pigments, along transects from a moving ship. On an arithmetic scale, such transects would show a "mountain range" profile, compatible, when projected on an horizontal plane, with discontinuous high density patches dispersed over a less populated background extension that tend to coalesce into a continuous reticulum. Considerable expectations have been placed on the adoption of generalized spectral distributions in ecology (Platt and Denman, 1975). But it would be hard to believe that an identical power rule holds over very large areas, as local hydrodynamic accidents upset continously the assumption of uniform turbulence. The only valuable general conclusion is that these and many other considerations that assume only the uniformity of ratios and slopes may provide reasons for a generalized use of logarithmic transformation of organism concentrations.

Natural distributions extend over space and time and always are the outcome of changes asymmetrical in space - discontinuous patches over a reticulated main ground - and irreversible in time, alternating gradually and often slowly increasing with catastrophic drops. Indeed plankton dynamics and the resulting plankton distributions, expressed over time and space, fit reasonably well with the I/F noise generation and distribution, with an inverse and logarithmic relationship between the intensity of disturbance (measured by the energy involved) or the size of the resulting "patch" of plankton (I) - that provide an expression of the energy involved - and the frequency (F) with which patches or disturbances of a defined class occur.

Such distributions are consistent with the existence of small areas that are energy rich, developing strong turbulence, biologically very active or very productive, and not necessarily persistent (although often they develop repeatedly in the same places), always contrasting and set against surfaces increasing in extension as they become less and less productive and comprise water masses that are more stratified or less turbulent.

Heterogeneity, often refered as patchiness, at all the scales is real in plankton distributions and, as assumed in precedent comments, consists in spaces with high plankton density relatively discontinuous and included in a network or background with a lower density of life and less turbulent water. Several mechanisms account for their ocurrence, among them the one described by Levin and Segel (l976). One of them concerns primary irregular distribution of small eddies in response to wind; over any large area, asymmetry is introduced by composition of random eddies with the rotation of Earth, as deep-water ascends and fertilizes the center of such cyclonic eddies that exceed a minimal size, thus generating a set of discontinuous spots characterized by high productivity under local upwellings, in contrast with the anticyclonic gyres which centers may be descending and anyway remain less distinct and often less productive or contain organisms that are more adapted to survive in sinking water masses. Also, anticyclonic eddies might blend together more easily than cyclonic ones.

Most of above considerations converge in making it likely that more turbulent and biologically more productive patches may lie enclosed in a sort of low turbulence reticulum. Such patterns, with different scales and different intensities, are expected to manifest themselves in most sections available for spectral analysis (Platt and Denman, 1975). Observation from space is opening new possibilities for obtaining evidence, much needed to validate or to refute the significance of the mechanisms refered to, and the repetitions down to the smallest scales, apt to accomodate the so called "microbial loop".

For application at very small scales, mixing length (I) refers to the theoretical length of the average path followed by any small parcel of water until it is assimilated and adopts the momentum of the surrounding fluid. From the basic relation

$$\rho[I(dV/dz)]^2 = A_v(dV/dz)$$

one gets

$$I = (A_v/[\rho(dV/dz)])^{1/2}$$

where ρ is density of water. The concept of mixing length might be helpful to understand plankton biology, at millimetric scales, between 0.5 and 10 mm, if the actual structure of turbulence, with intermittencies or not, were known, and adopted in the right way to improve this expression.

If the distances between recognizable or tagged particles were measured in a continuous way, they would be found not constant and usually increasing. If their mutual distances increase exponentially and indefinitely along time, the powers in the functions that describe succesive positions may be assimilated to exponents or numbers of Lyapunov, that appear to have a useful meaning in different ecological contexts; for instance in relation to changes in the numerical importance of populations of coexisting species. Besides, Lyapunov exponents are often associated with chaotic behavior of the evolving turbulent systems.

PLANKTON BIOLOGY
IN RELATION TO
LARGE SCALE TURBULENCE

Most work done on turbulence is disordered and irreversible, and has to be written down in the account of entropy - the dissipative part of the ecological machine. The speed of degradation of energy in turbulence increases with temperature. Viscosity of water opposes turbulence, but viscosity is effective only over small distances. In the open sea, turbulence is a part of a vast dissipative matrix, and contributes to feed the self-organizative systems in it: the living organisms of plankton. Vertical organization is better developed and preserved when turbulence is low and close to the twilight zone, that is also an actual store of biodiversity, that behaves like the seed bank of a forest. It is sustained and enriched by the results of the successive blooms in the more turbulent levels of the photic zone. Thus, dynamics of diversity becomes associated with distribution of turbulence and acceleration, and the preservation of genetic biodiversity happens mostly in less turbulent environments, including sediments.

Energy, most of it from wind, sets water in motion. Total work is reflected in the vertical shift upwards (E) of the center of gravity of the water column when gradients of stratification decrease. This increases potential gravitatory energy, and turbulence energy is added in the amount of $A_z(dV/dz)^2$ per unit volume. The symbol g is the acceleration of gravity, dV/dz is the vertical gradient of current speed, A_v is turbulent viscosity and A_z is turbulent diffusivity. $A_v(dV/dz)^2$ is larger than gEA_z. Strong vertical gradients in horizontal speed and A_x appear associated with thermoclines and other density gradients.

Viscosity is a function of temperature; at 30°C viscosity is approximatively half, and at 75° one fourth, of its value at zero degrees. In consequence, at higher temperature, water has more capacity to contain small scale turbulence. Hydrostatic pressure is less important as a modifying factor.

In oceans and lakes there is a competitive course between penetration of turbulence and penetration of light, from which issue many important aspects of physical and chemical stratification and production. This is very clear when comparing (1) the fluid system of open water with (2) an algal mat or stromatolite in which high viscosity (mucilage) dampens the turbulence and places the sharp chemical boundaries inside a narrow band. Biochemical gradients as expressed in redox potentials may be in ratios up to one to a million in the respective situations (plankton:algal mats). Many other valuable generalizations on these aspects, that obviously are related to the origins and fundamental constraints on the process of organization of the biosphere, are ameanable to experimental approach.

The first quantitative approximations to population dynamics and to the study of interactions between populations of different species (demographers: Lotka, Volterra) ignored space. Indeed, space was introduced in the ecological models by marine biologists, as a consequence of their wish to take into account sinking organisms in more or less turbulent water. In part it was the consideration of turbulence that made ecologists think about the need to improve the early and traditional Lotka-Volterra models.

Gordon A. Riley provided an important and most welcome stimulus, and in several contributions - especially in a joint paper with Stommel and Bumpus (1949) - presented and justified a wise and stimulating model. Here are sketched: a) the expression originated by Riley, and below, b) a recent version of it in more modern and proper notation, that substantially embodies the same concepts (Delhez *et al*., 1993), but tries not to be limited to a single column of water. Sinking relates to the first derivative of vertical distribution and turbulence tends to take out secondary irregularities and relates to the second derivative.

a)

$$dN/dt = rN - gNZ - V\,dN/dz + A\,d^2N/dz^2$$

| total changes | | cell division | | consumption by zooplankton | | sinking | | turbulent diffusion |

proper Lotka and Volterra dynamics

N = phytoplankton
r = rate of increase
g = grazing by animals
V = vertical speed
A = turbulent diffusion
z = vertical dimension

b)

$$\delta y/\delta t = Q^y - \nabla (\underline{v}\, y) - \nabla\, \tilde{\underline{\Phi}}^{\,y}$$

y = state variable
t = time
$\underline{v}$ = velocity vector
Q^y = rate of production-destruction of y
∇ = three-dimensional nabla operator
$\tilde{\underline{\Phi}}^{\,y}$ = turbulent flux of y

Turbulent exchange (A, Φ) disperses and redistributes the populations, contributing to recolonize a space in which population density might be driven down by sinking. Simultaneously, mixing at all scales, brings back nutrients to the illuminated layers. The equilibrium conditions shift continuously and intensity of turbulence in combination with penetration of light may become decisive in this respect. Its role is defined also by depth, down to which surface waters mix vertically, a depth that in shallow shores is limited, a condition helped very much in evolving from the preliminary approximations (Gran and Braarud, 1935) to the present model.

The same basic assumptions were suggestive (Margalef, l978) of the important role of terms of the form A ($[d^2S/dx^2] + [d^2B/dx^2]$) that could be interpreted as the product of turbulence (*Austausch*, A) by an expression of the covariance between different factors of production, like biomass (B) and substrate or nutrient concentration (S). This hint suggested the need to look more closely at possibly relevant literature for further inspiration and it was found that von Smoluchovski (1918), working with colloidal systems, was led to accept that reaction speed depends both on the local diffusivity or turbulence (A) and on the overlap or covariance in the spatial distribution of available potential reactants (C) [See also Kelzer (1982) and Kopelman (1988)]. In its tentative adaptation to ecosystems, the expression of such points of view could produce:

production (P) = energy of mixing *Austausch* turbulence × covariance in the distribution of factors of production

Light cannot be displaced by mechanical work (by turbulence) and belongs to an independent frame. Light or any analog of it was not relevant in the problem that von Smoluchovski (1918) wanted to attack.

Simple derivation in relation to time yields an abridged suitable description of ecological succession:

$$dP/dt = C\,(dA/dt) + A\,(dC/dt)$$

All these models allow subdivision into smaller compartments in a way that might show also if, and how, the concepts of new production and recycled production can be separated.

In very general terms, these different approaches turn around the basic concept of systems in which (turbulent) diffusion, including sinking, and reactions (primary production, grazing), are determinant. In the same group comes the KISS model (Skellam, l951; Kierstead and Slobodkin, 1953), and it surprises the aquatic ecologist to see that even the developers of the theory of dissipative systems (Nicolis and Prigogine, 1989) never refer to attempts from physicists and oceanographers, made known between 1918 and 1949 and oriented to deal with this very general problem of self-organization and pattern formation based on diffusion and reaction. Instead they hint only at Turing (1952) as a most distinguished precedent.

SHAPE AND SIZE AS PASSIVE ADAPTATIONS TO SURVIVAL IN TURBULENT ENVIRONMENTS

The consideration and analysis of the presumptive evolutionary play between nutrient absorption, swimming and environmental turbulence becomes fascinating (Margalef, 1978). Passive sedimentation of phytoplankton is an always present risk, as it takes cells out of the photic zone towards situations of likely poor illumination, although, it can bring the cells in contact with water enriched in nutrients. In the presence of moderate and high turbulence, swimming adaptations such as are only possible in very small organisms, cannot matter much anyway. The problem is how to compensate the losses that sedimentation causes in the populations through an increased input of the nutrients enhanced by turbulence, that would allow the populations to increase at a rate capable of compensating and even exceed the loss of cells suffered. Non-motile

x

diatoms thrive frequently under turbulent conditions, as well as coccolithophorids that have lost functional flagella and are, besides, lested by calcareous coccoliths. All these organisms and many others are rather heavy and naturally may tend to sink; in turbulent water such abilities could not make a serious difference. But in stratified and less turbulent water it pays to invest energy in swimming and so to be able to position the cells in the most favourable situations, an optimization that could be useless in turbulent water. Intensity of mixing and nutrient supply in the photic layers are decisive factors.

Turbulence, assuring renewal of the layers of water in contact with phytoplankton cells, and often associated with larger scale water movements, becomes a critical factor in the selection and evolution of the species. Size and shape of cells determine the surface/volume ratio. Organisms in the size class of approximately 1 μm should become prisoners of viscosity and their potential opportunities to assimilate and multiply are perhaps more restricted than was imagined at the time of the discovery of the richness and ubiquity of picoplankton.

For sizes above those of bacteria and small cyanophytes, the relations between size and shape of the cells and colonies, and viscosity, turbulence and nutritive capacity of water have attracted the attention of several authors (Munk and Riley, 1952; Gavis, 1976; Margalef, 1983; Lazier and Mann, 1989, and many others). In an open and creative approach, Gavis (1976) combines several likely components of fitness under a compound index P, without dimensions, that may be taken as a measure of the prospective evolutionary success of any strain or lineage. Thus, competition between stocks or species might depend on shape, size, nutritional efficiency, etc., that is, on the different factors that enter in the computation of the said index.

Rearrangement of the terms in the original Gavis (1976) expression results in:

$$P = K'(K_s/V_{max}) \times (d\o) \times [A+(1/2)\o V]$$

| kinetics | size and shape | environment |

K'   =   constant
d   =   size
A   =   turbulence, $cm^2 s^{-1}$
K_s, V_{max} =   constants that refer to absorption kinetics
$\o$ =   coefficient of shape:
                 =1 for the sphere
                 <1 for other shapes
V   =   sinking speed

The persistence of a population depends on properties of the organisms in relation to environment qualities, supply of nutrients, and mechanical forces in the environment responsible for turbulence. A general conclusion might be (Carlson, 1962) that even with an efficient motility, it is possible to improve the conditions of nutrition through adaptation or manipulation of properties of the environment. There is a speed range in which benefits may top the energy investment. Improvement seems always possible along some definable evolutionary paths.

Lazier and Mann (1989) argue, very reasonably, that turbulence over small scales is not well understood, and that anyways, active movement or sinking of the cells may be more important; conversely, turbulence may erode away the so called microzones (Mitchell *et al.*, 1985), with accumulated excreta that may give support to "microbial loops". There are known instances of accelerated growth under the influence of increased turbulence, introduced in the cultures in the form of bubbling (Aguilera *et al.*, 1994). But not much descriptive information is available on the mechanics of motion of small flagellates (Melkonian, l992), and the nature and eventual help provided by the flow close to the cells is barely known. Coanoflagellates and other peculiar types of organisms pose other unanswered questions. Diverging solutions (strategies) might have been adopted in the evolution of many kinds of small flagellates and of dinoflagellates.

Dinoflagellates possess an undulating flagellum sunk in the girdle that keeps the cells turning, often working against the resistance opposed by the flattening of the whole cell or by the expansions or outgrowths added to the cell body, that also is often strongly asymmetrical: the necessary result of such construction principles is to have an accelerated flow of water over the cell body, that surely improves the chances for absorption. An interesting design includes a small cell body and long appendages that extend over a large space and may anchor the cell in a relatively fixed position agaánts smaller turbulent eddies that "wash" the surface of the cells (*Ceratium vultur, C. trichoceros, Ceratocorys horrida, Triposolenia, Amphisolenia, Dinophysis miles, Thalassiothrix longissima, T. antarctica, Chaetoceros, Bacteriastrum,* etc.).

The correspondence between the hydrographic conditions prevailing in the different seasons of the year and the syndromes of adaptation of the organisms most frequent under such situations,
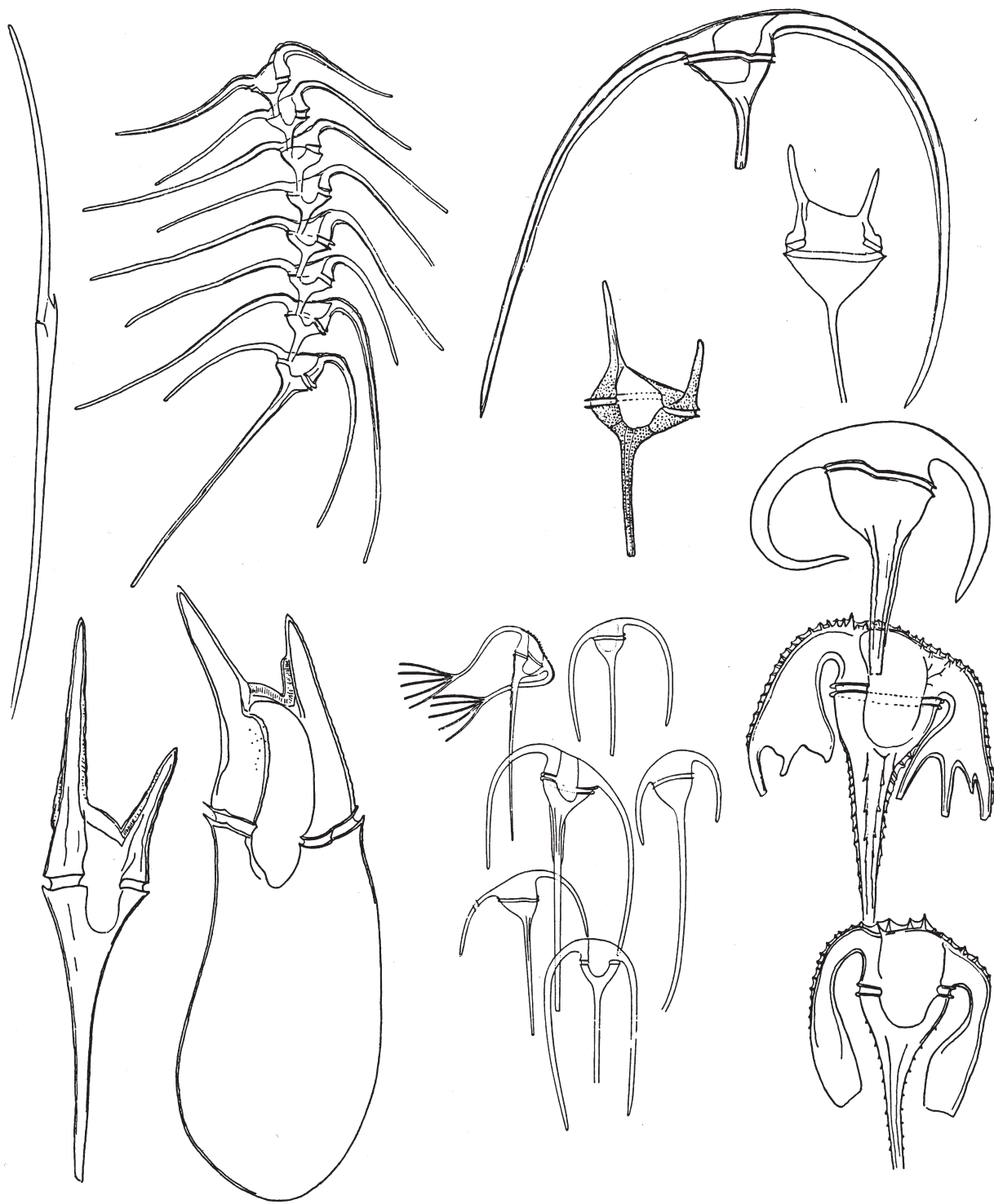
FIG. 3. – Examples of shapes in planktonic dinophytes that increase cell surface washing, even in conditions of low turbulence.

helps to explain one important part of the seasonal dynamics of phytoplankton (Margalef, 1978). Turbulence, *Austausch,* may play, thus, a principal role in the alternative dominance of diatoms or dinoflagellates.

THE ROLE OF SECRETIONS IN THE WAY TO THE OBLITERATION OF TURBULENCE

Sheets of mucilage that cover the cells of phytoplankton, and that have been excreted by them,

increase the viscosity of water so much that positive consequences of turbulence must become strongly dampened by the mucilaginous cover. Mucilaginous sheets are common around small aquatic organisms, and not only in algae of different groups, chiefly in fresh-water, but also around ciliates (*Ophrydium*) and rotifers *(Collotheca, Conochilus). Phaeocystis,* and species and forms of *Chaetoceros, Thalassiosira, Nitzschia,* and a few others often appear surrounded by jelly-like covers. In the polar oceans, comparable secretions are common around the organisms of the pack, initially submerged in a brine that can be enriched in nutrients, after the separation of grains of solid ice. Such organisms, mostly diatoms, may appear, consequently, covered by, and included in, a reticulum of water made more consistent by mucilage, as clearly observed in samples collected in the Antarctic by Marc Steyaert in the fifties. Such samples were preserved in alcohol, which led to the coagulation of the mucilaginous reticulum surrounding and enclosing the cells.

It would seem that the presence of such mucilaginous sheets would limit diffusion, although it is known that bacteria can move faster through liquids made more viscous by long molecules, and that some kinds of molecules can travel faster than usual due to the support provided by polysaccharides.

Surficial mucilaginous secretions over the body of larger animals, like fishes, could help to iron out the irregularities that generate turbulence and absorb momentum. An equivalent adaptation operating in a larger scale is the flexibility and easy accomodation of the surface of larger animals, a positively selected feature that reduces resistence encountered in cruising through fluids. Such properties are well known in the skins of cetacea and are provided by the soft feathers over the body of birds.

In the first stages of production and accumulation of mucilages in water, probably some relation has to be found with the availability of spaces at relative rest, or of intermittency in turbulence. Any speculative model about eventual organization of movements in turbulence and their changes along a process of decay, should accomodate eventual submodels accounting for the availability of spaces at relative rest, where mucilage accretes with more facility. But the acceptance of spaces at rest could pose some difficulties for the general acceptance of the models of turbulence in the style of Kolmogorov.

The most simple explanation for the presence of mucilaginous covers is that carbon assimilation continues when there is light, even if the more limitant nutrients (chiefly P) are not available. Under such conditions, cells do not multiply, but long molecules of carbon compounds are given off. Coccolithophorids, in equivalent situations, that is, under high availability of calcium carbonate, fabricate and throw away an extra number of coccoliths.

If such explanations hold, it makes sense to view the secretion of mucilage, in the first place, as a sort of "birth control device", in the sense that mucilaginous sheets slow down diffusion - from turbulent to slow lineal diffusion regime. The extruded organic molecules, that contain carbon molecules might be analogous to the excess sugar excreted by aphids and other homoptera when feeding on plant juices that contain "an excess" of carbon compounds. As there is apparently no brake to stop photosynthesis completely, assimilation of carbon compounds continues to run, mainly during the long days and in shallow environments, like in North Sea or in the northern part of the Adriatic during the summer (Martin *et al.*, 1995; Mingazzini and Thake, l995). In general, presence of mucilages is associated with highly productive conditions, often a consequence of human impact. In summary it seems reasonable to associate production of mucilages with exhaustion of phosphate and rapidly increasing light availability - longer days, shallow waters.

Perhaps one can find a valid analogy in many terrestrial plants of arid places. In summer, these plants continue to assimilate carbon, which they give off in molecules of terpenes and isoprene. Perhaps also an analogy can be made in growing wood that is cheap because it is poor in chemical elements others than C, O, H. It is stated that isoprene production alone may siphon off 2% of the carbon fixed by photosynthesis in terrestrial plant communities (Mlot, l995). As in such situations fires may be encouraged, it seems a bit difficult to find an utilitary explanation, except in the sense of destroying competitors, inflicting on them damage more important or more definitive than on oneself. In other situations, compounds that do not contain essential nutrients, like saponins, may have a value of defence and one cannot but remember spit-bugs, surrounded by a watery fluid rendered viscous by saponins, and well populated by microorganisms of many species.

Evolutive adoption of a precise shape and size may increase survival of plankton under defined conditions and, inside a group, may open the possibilities for ecological segregation among different species. The cells and colonies of the species of *Chaetoceros*, *Bacteriastrum* and *Corethron,* according to the length

and disposition of bristles, operating in environments that show a wide spectrum of turbulence, anchor and turn with eddies of larger or of smaller size, according to the dimension subtended by the appendages, and this may be the origin of ecological segregation. We know related species with the same null or small locomotory activity, that actually belong to different "ecological niches", and some of them, like the coccolithophorids mentioned in a precedent paragraph, have flagella, but often make no use of them.

An illustrative image of segregation in function of the extension of the space used to anchor the cell or the colony can be obtained visualizing and comparing a small boat that dances above the waves, and a large ship that is washed by the same waves, and equating them with what happens with small rounded cells and, respectively, with organisms that subtend a larger volume, relatively anchored in its water, through long and rigid expansions (like *Ceratium trichoceros*); the appendices do not hinder the results of turbulence that wash the surface of the central part of the cell. Also the expansions of a few *Ceratia* (*C. platyceros, C. ranipes*) provide large absorption surfaces, either for light (the first named species) or for nutrients (the second one). Without doubt, the relation between the spectrum of turbulence in water and the way an organism with its appendices is anchored in the water may start or encourage ecological segregation and evolutionary divergence, that perhaps was effective in the case of the two last reported species of *Ceratium*.

THE INTERPLAY BETWEEN STRATIFICATION, NUTRIENTS, LIGHT AND TURBULENCE

In microbial mats and stromatolites, illuminated structures are thin and dense, with high absorption of light, and often a great part of the overlying water is immobilized by mucilages, an indication that absorption of C, N and extrusion of their compounds continue, even in the practical absence of elements allowing for cell division (mostly phosphorus). The strong gradient of redox potential, associated with a gradient in nutrient availability, is close to the surface. A few mm below starts the reducing zone, where heterotrophic prokaryota dominate. This situation contrasts with that described for water bodies, where penetration of light and of important turbulence determine less sharp structures in liquid and turbulent water, that extend over a vertical range of decameters. Changes in illumination and in vertical mixing, these in function of (wind) turbulence and variable thermal stratification, define production and distribution of organisms.

Take the Western Mediterranean as an example. The most productive layer, where photosyntetic pigments are concentrated (although rarely above 1 mg chlorophyll per cubic meter) is found between 40 and 60 m depth. Phosphorus is the limiting element, and its concentration above this level is extremely low, down to undetectable. It is rapidly used, and starving cells tend to sink. The cycle maintained by zooplankton consumption and return in the top layers is not much effective and does not counteract seriously the losses due to net sedimentation.

In marine pelagic biology there is often question of the Redfield ratio, that refers to the ordinary (atomic) relations between the basic elements C:N:P in the body of the planktonic organisms. Its accepted value is 106:16:1, or expressed in total relative weights as 100:17:2.4. Evolution of seaweeds and of terrestrial plants has included a sensible increase of the carbon fraction that is incorporated in the support and transport structures.

Phosphate seems to be always the limiting element, although for about 30 years, oceanographers have inexplicably forgotten it and centered attention on N, of which water contains an extra large supply in form of dissolved dinitrogen gas, that is available to cyanobacteria or cyanophytes. One reason to prefer N was perhaps its protean behavior that facilitates the study of different paths of regeneration, but the result has been to impair seriously the study of marine productivity. The reserve of phosphate, practically all as orthophosphate, is considerable (more than 40 mg P m^{-3} below 1000 m; in the Mediterranean less than one half of such concentration, about 15 mg P m^{-3}), but in the photic layer the concentration of available phosphorus, organic plus inorganic, is much lower and necessarily limiting.

The ratio N:P in Western Mediterranean water is a bit above the current proportions elsewhere and, in consequence, only exceptionally, nitrogen may be limiting. One characteristic shared with the Caribbean, parts of the Pacific Ocean, and probably in other extensive areas that so far have been poorly examined from this point of view, is the presence of an almost continuous layer rich in nitrite (NO_2^-), just below the limit of penetration of light of usable intensity and above the top of sensible concentrations of phosphorus. Myself and my former student Dolors Blasco (1971) have developed an interpretation of this layer (concentrations 0.2-0.5 μM N) in

the sense that it might result from the activity of phytoplankton cells as they sink to a level in which cells are still able to reduce available nitrate to nitrite, but in which light is insufficient to allow reduction and assimilation of nitrogen compounds to proceed. The cells would let nitrogen escape, now in the form of nitrite, which remains in solution in the environmental water, forming a continuous layer. This layer may show some discontinuities or openings, as well as differences in its depth, a topography that seems to be related to the horizontal distributions of the intensity of the operative agents (vertical movements, mixing, availability of phosphorus).

Ascending movements of water, mostly along the Western coasts of the main continents, allow nutrients accumulated in deep water to cross the limit of light sufficient for plant life and enter the photic zone, accelerating the process of primary production in the top layers. With this aspect we rejoin one of the most studied aspects of the biological oceanography, the upwelling areas that support important fisheries (Mann and Lazier, l99l and an extensive literature).

THE MANIPULATION OF TURBULENCE

Turbulence has conditioned evolution, and evolution has found ways to adapt to turbulence and even to manipulate it artfully. Some of the established relations are notorious and particularized. I will never forget an elegant presentation by Prof. Okubo - including a mathematical description of the mechanics involved - about the reproductive behavior of a species of fish. After the female has spawned her eggs, the male, in the apparent possession of a complete if unconscious knowledge and control of hydrodynamics, extrudes a jet of sperm that, with the help of perfect moves of body and fins, take the form of a rotating torus in a position that might optimize success in fertilization. Natural selection has often succeeded in combining structural contraptions and appropriate forms of behavior in the field of turbulence, subjected to the general laws of hydrodynamics of water.

This may concern what is known as bioconvection. Excellent examples are provided not only by the generation of Bénard cells by swimming cells (or flying midges and mosquitos) or by the construction and use of quasi-exosomatic devices by many tube and case dwelling organisms, among which pelagic tunicates excel.

By swimming, an organism introduces deformations and turbulence in the surrounding water. The water absorbs a large fraction of the energy involved and often a trail of eddies is generated. Evolution has led to body shapes that presumably minimize the loss of locomotive energy in feeding such eddies that, moreover, may be undesirable, as they surely could provide signals to eventual predators. More generally, selection may led to the development of adaptations that allow interpretations of the turbulent trails in the sense of crypsis (played down or misguiding in direction) or of aposematism (exaggerated and menacing).

It has been accepted that evolution has led to the gradual development of mechanically appropriated profiles, through at least two selective pressures… (1) the convenience to adopt a shape and a surface quality that minimizes energy invested in swimming - fishes, already mentioned; and (2) in damping down or redirecting advertising trails, that might attract predators. The study of the body shape of fishes provides excellent examples of optimization. In smaller organisms, 0.1-2 mm, for relatively high speeds (>1 cm s^{-1}), Reynolds' numbers fall in the turbulent region on which our interest is centered, and in this domain viscosity might work against renewal of the most close layers of water, a condition that would seem not the best for the continuity of absorption and of life. The very reasonable considerations of Lazier and Mann (1989) point out that present appreciation of such limitations might be mistaken.

There have undoubtably existed and continue to operate a large number of trade-offs related to shape and viscosity and concerning the relations between evolution, defence and competition. The techniques of *Schlieren* show how movement of the legs of copepods often leave a trail that forms an angle with the actual trajectory of the body, which posterior part migh help to erase or to confound trails, and such may be the main or one of the functions of the furca. On the opposite or receiving end, there is the constant selection pressure on predators to improve quality of pressure detectors and analyzers, and one exceptional example of such devices is the sword of an extraordinary creature, the sword-fish (*Xiphias gladius*) .

POSSIBLE ORGANIZATION OF HETEROGENEOUS REGIMES OF TURBULENCE OVER SMALL SCALES

One particular mechanism that has been relatively overlooked, probably because its reality and efficiency have to be more convincingly proved, could

receive the name of "the turbulence valve". Its reality has to be ascertained and confirmed and its biological importance quantified, but it is likely that in different forms is present in many groups of organisms, and among them in many representative of benthos.

Imagine a small channel prepared for hydrodynamic experiments. Water with small particles in suspension -eventually food particles- flows freely in an approximately laminar regime, between two linearizing filters. If turbulence is mechanically injected in the flow, as it may be through irregular pieces of flexible plastic material, kept freely swinging in the current, the flow losses linearity and particles may deviate in their trajectories and concentrate in definite spaces under lower turbulence and slower flow, close or in relation with the large scale irregular conditions of turbulence that have been created. The particles are not driven away with the same speed or by eventual accelerated veins of flow originated in the new dynamic regime, so that densified clouds "make time" in selected volumes of the experimental chamber. I do not know of any formal and adequate study of the dynamic lineal or turbulent processes involved that could be available or forthcoming. Such experiments might provide an access to a new or complementary interpretation of many complicated biological structures of unknown meaning.

Imagine water carrying particles (food algae) in suspension that flows in an approximatively laminar regime through some filter consisting of limbs with segments, setae and setulae, making a first mobile barrier of the feeding system of a small creature. Food particles move without difficulty (they are smaller than the spaces between setae or radii) in laminar regime through the limbs or setae. If, after crossing the first barrier, turbulence is mechanically injected or generated in the suspension, it might happen that the laminar flow forward, through another filter, or backwards through the same filter recently crossed in a regime of laminar flow, cannot allow the passage of the particles in suspension, that are thus separated. That would mean that particles, in the flow now made more turbulent, do not pass so easily between radii and in consequence a majority of the particles slow down or are retained and placed in a situation in which they fall under the influence of some other hydraulic or perhaps mechanical structures that, after concentration, might lead to their final ingestion by the master organism, equiped after a long evolution with all the contraptions necessary for the feat.

Obviously, controlled currents around the body of worms and crustaceans - perhaps less frequently around other animals - are legion. That such a feat is not unlikely seems obvious after the observation of films on the movements of the mouth parts of copepods and trying to extrapolate the meaning of experiments in small hydrodynamic channels. Such a "turbulence valve" seems to be, I believe, possible and acceptable, although I do not find it accepted and much less adequately - that is, hydrodynamically - described in the literature available to me.

Another reason for assuming tentatively the effectiveness of this "turbulence valve", or any other equivalent contraption, appears when sighting the films purporting to demonstrate the feeding activities in tethered copepods. They show in general an unbelievably low rate of effective captures, even taking into account the slow speed of projection, inconsistent with the observation of the guts of "wild" animals, or with the measures of their metabolism and with the theoretical amount of food necessary to keep them alive, and even with the usual estimates of the volumes of water swept clear. This is an argument that may carry some weight in favour of exploring neglected ways.

It is easy to anticipate some of the basic features that such a valve of turbulence should have in different animals - most of them, but not all of them presumably arthropods and worms - that generate laminar flows in water, then turn the flows turbulent, and the food particles in suspension seem to find spontaneously the way to the mouth or to some traveling band of mucus; in such situations very few of the potential parcels of food travel back and escape.

I recognize that there might be some difficulties in accepting that a relatively linear and parallel flow of water with suspended particles goes rapidly, without slowing noticeably, or perhaps ever slightly accelerating a bit, through one external barrier of setae with setulae, only to be retained easily against the same or similar barriers in inverse trajectories when flow has been made turbulent. More work is, of course, required to clarify the subject or fully accept this suggestion.

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