Homage to Ramon Margalef; or, Why there is such pleasure in studying nature
(J. D. Ros & N. Prat, eds.). 1991. *Oecologia aquatica*, 10: 77-94

THE RELATIONSHIP BETWEEN FUNCTIONAL ANATOMY OF LAKES AND PRIMARY PRODUCTION

JORDI CATALAN

Departament d'Ecologia. Facultat de Biologia. Universitat de Barcelona. Av. Diagonal, 645. 08028 Barcelona. Spain

Received: January 1990

SUMMARY

The morphology of a lake and exchanges of energy across its boundaries together constitute its functional anatomy. The amount and variability of primary production are related to this functional anatomy. This relationship involves preferential scales, intervals that can be characterized by non-linear functions, time delays and changes of phase. The larger the volume of reference and the sharper the boundaries, the more significant the link between functional anatomy and primary production. Dynamic physical and biological models must include the development of functions and estimation of parameters in certain characteristic intervals but must also forecast where (or when) qualitative or abrupt changes could appear. For research on intralake variability of primary production special attention should be paid to the relative duration of successive stable and unstable phases. In interlake studies, lakes having functional anatomy with features which determine sporadic ice-formation, meromixis, seasonal thermocline, etc. would show less predictable variability in primary production than lakes with a regular annual pattern. In extreme cases, low frequency fluctuations can lead to completely new biological systems.

KEY WORDS: Lake morphology, primary production, phytoplankton, hydrodynamics

INTRODUCTION

Pelagic ecosystems escape direct human perception. This has stimulated the development of conceptual aspects in the ecology of these aquatic systems to the detriment of descriptive details, which are more generously provided by benthic and terrestrial ecosystems. Human size is much smaller than lakes and oceans, and several orders of magnitude bigger than most organisms inhabiting them. As a consequence, our view of these ecosystems has been and is still highly conditioned by sampling methods, knowledge about them being based on imaginative re-creation from data given by the artificial senses of devices and analytical procedures. It is needless to go back to Ehrenberg's time; when POMEROY (1974), for instance, described the complicated marine microbial food web, the classical view of the ocean as an ecosystem started to change radically (GOLDMAN, 1988).

The main characteristic of pelagic ecosystem dynamics is the vertical segregation of the production elements. Particles sink and matter accumulates in the deepest part of the water body. Although organic matter is mineralized in the sediment or in the deepest part of the water column, nutrients remain distant from the light and from the primary producers. If the input of nutrients is not continuous in the photic zone, production is limited. Those nutrients in dark layers must be carried to the photic zone to be reincorporated with living biomass, and this transport requires energy. This mechanical energy (convective mixing, advective movement, etc.) is as important for ecosystem dynamics as energy incorporated by photosynthesis which flows internally through the food web.

Starting from this basis, the qualitative relationship between external energy and ecosystem primary production has been summarized as follows: "External energy stimulates primary production by increasing covariance between resources (light and nutrients) and primary producers (phytoplankton)" (MARGALEF, 1980). Nonetheless, it is very difficult to find a simple and general parametric equation of this relationship. MARGALEF (1978, 1980, 1989) proposed that primary production could be related to a certain power (less than unity, *ca.* 0.6) of the total available external energy. However, MARGALEF (1978) himself pointed out some limitations to the general application of such an expression.

On the one hand, the relationship has been found suitable in the ocean on annual scales (MARGALEF, 1978), but in lakes the volume of reference is much smaller, and so the role of boundaries becomes more significant or at least more apparent. Energy exchanges and morphology interact to constitute a functional anatomy of lakes. On the other hand, while the range of external energy is broad and changes according to the spatial and temporal scales, phytoplankton physiological and lifetime scales are short and stay fixed when the frame of reference is enlarged or decreased. As a consequence, the relationship between external energy and primary production may change its nature on different spatial and temporal scales.

The purpose of this paper is to present a view of lake ecosystems where functional anatomy is considered to be the main factor determining the non-anthropogenic intralake and interlake variability of primary production. The relationship involves preferential scales, time delays and non-linear relations with characteristic phase changes.

The lifetime of phytoplankton organisms is the appropriate reference for the time scales of the biological processes related to primary production of lakes (HARRIS, 1980). Physiological adaptation is the only possible answer to variable conditions in scales of less than hours, while community changes need days. Equivalence between spatial and temporal scales are determined by diffusion coefficients in the water mass. Diffusivity differs by two or three orders of magnitude between the horizontal plane and vertical dimension in lakes. With this set of scales in mind, let us consider the relationship between production and functional anatomy starting from the level of the microenvironment of a phytoplankton organism and moving on to the level of the whole lake.

THE MICROENVIRONMENT OF A PHYTOPLANKTON ORGANISM

It is very difficult for humans to imagine the microenvironment of phytoplankton and, probably as a consequence, these organisms have been considered trapped by the forces of water motion like inert bodies in a soup. But slowly a more structured and organism-dependent image of the phytoplankton world is emerging.

If we consider a time scale of seconds, we may assume that the light field during this period is nearly constant for algae and interaction between mixing and resources should involve nutrient uptake alone. The rate of nutrient uptake depends essentially on two kinds of processes: 1) those related to the uptake kinetics of each cell, which we will not consider here; and 2) those related with transport from the fluid to the cell wall. The transport depends on the nutrient gradient between the cell surface and the fluid, which generates a diffusion process.

In a turbulent environment, changes in fluid velocity occur above the Kolmogorov length (FRISCH & ORSZAY, 1990):

$$l = (\nu_k^3 / \varepsilon)^{1/4}$$

where ν_k is the kinematic viscosity (c. 10^{-6} m^2 s^{-1} at 20° C), and ε is the dissipation rate or the energy dissipated by unit mass (10^{-10}-10^{-5} J kg^{-1} s^{-1} = m^2 s^{-3}). Nowadays, the dissipation rate can be estimated directly from microestructure probes data. Its value, even during storms, rarely approaches 10^{-4} m^2 s^{-3} (DILLON & CALDWELL, 1980; IMBERGER, 1985). Thus, values of the Kolmogorov length are generally between 1 cm and 1 mm. Only in hot waters (40° C) with very strong mixing (10^{-4} m^2 s^{-3}) does one find figures of 200-500 μm.

Most phytoplankton organisms are much smaller than 1 mm, although some colonies are occasionally approximate to 1 mm (REYNOLDS *et al.*, 1987). Thus, the flow around the phytoplankton cells could be laminar, and changes in the field of the fluid velocities due to turbulent mixing may not directly affect diffusion around the cells. Only those organisms which move

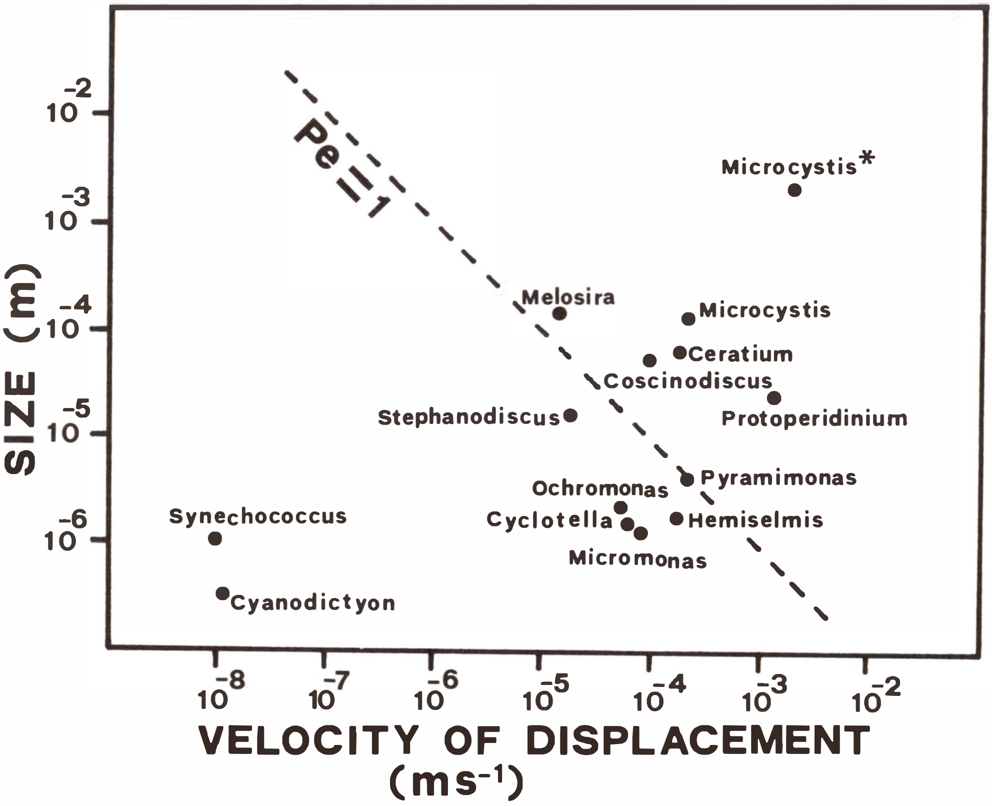

FIGURE 1. Size vs. maximum velocity of movement by sinking, floating, or swimming of some selected phytoplankton marine and freshwater species. Peclet number (Pe) = 1 divides phytoplankton into organisms depending on molecular diffusion and organisms whose movement enhances nutrient transport to the cell surface. *Synechococcus* sp., *Cyanodictyon* sp., *Stephanodiscus astraea*, *Ochromonas minima*, *Cyclotella nana*, *Micromonas pusilla*, *Hemiselmis simplex*, *Pyramimonas disomata*, *Melosira italica*, *Microcystis* sp. (*, from tropical lakes), *Ceratium tripos*, *Coscinodiscus wailesti*, *Protoperidinium quinquecorne*.

faster (large dinoflagellates, rapidly-sinking diatoms or colonies with significant excess of buoyancy) could jump from one eddy to another and, in this way, enlarge their potential dispersion or their capacity to explore space.

However, although there might be no direct effect, turbulence determines inertial delays of the organisms with respect to the fluid, implying an advective movement around the cell. Nowadays, it is not clear whether this process may be more relevant for nutrient uptake in some phytoplankton species than other ways of relative motion with respect to the fluid. The Peclet number (Pe) relates advection to molecular diffusion:

$$Pe = v\ d\ /\ D$$

where v is the organism velocity, d its size, and D the molecular diffusion (10^{-9} $m^2\ s^{-1}$). When Pe >> 1, the movement increases nutrient transport to the cell surface although there is no turbulent boundary around it (Reynolds number $v\ d\ /\ v_k < 1$). Some large flagellates and colonies of cyanophytes and diatoms reach Peclet numbers higher than 1 by swimming, quick floating or sinking movements (Fig. 1). Unfortunately, there are no data for inertial delays. MUNK & RILEY (1952) calculated the ratio between mean slippage associated with velocity changes due to turbulence and Stokes' sinking velocities for spherical cells, and they gave values of 10^{-3}-10^{-2} in normal turbulence fields and 0.3 for strong mixing. Thus, from a theoretical viewpoint, inertial delays do not seem particularly important in nutrient uptake for spherical organisms. Nonetheless, many algal forms depart significantly from sphericity and still little is known about how morphology affects their inertial delay.

From size and motion velocities phytoplankton organisms can be divided into two main sets (Fig. 1): a) those trapped by viscosity depending on molecular diffusivity, including most of the freshwater species; and b) those which can enhance nutrient flow to the cell by their self-generated motion and are big enough to reach Pe >> 1, which comprise some species relevant in the productivity of lakes (*Microcystis*, *Ceratium*, *Melosira*). After CSANADY (1986) and SPIGEL & IMBERGER (1987), the nutrient flux (NF) per unit volume can be roughly characterized as follows for spherical cells:

for Pe < 1,

$$NF\ (mol\ m^{-3}\ s^{-1}) = 12\ \ \Delta N\ D\ d^{-2};$$

for Pe > 1,

$$NF = K\ \Delta N\ D^{2/3}\ v^{1/3}\ d^{-5/3},$$

ΔN being the nutrient difference (mol m^{-3}) between the cell surface and the environment, and K an adimensional constant whose value is about 6 for Pe > 1000, differing in less than one order of magnitude for smaller Peclet numbers. In any case, nutrient flux per unit volume depends mainly on size, decreasing with it. Therefore, when dealing with spherical cells, one expects to find smaller cells in oligotrophic waters. Organisms living at Peclet numbers < 1 have no preferential flux zones around the body. For Peclet numbers > 1, the higher the number the more localized the flux zones in some parts of the organisms. This phenomenon might bring about the development of a specialized zone for uptake or for heterotrophic nutrition (GAINES & ELBRÄCHTER, 1987), which may increase cell polarity or colony differentiation.

On the millimetre scale, although much research is required to gain a realistic image of the microplankton world, the most probable conclusion seems to be that a turbulent environment has little relevance in nutrient uptake, which depends more on the individual features of the organisms. The link between functional anatomy and primary production must be sought at a higher scale.

Recently, MITCHELL *et al.* (1990) report that millimetre-sized clusters of plankton can be produced by the shear of a laminar flow across the surface of a microplankter. Additionally, above critical concentrations of 1,000 to 10,000 cells ml^{-1} these clusters can became temporarily stable, sinking as streamers of plankton-laden water with radii of one or more millimetres. The streamers can increase migratory velocities by one order of magnitude. In turbulent waters, motion by vertical eddy diffusion is greater than the swimming and sinking velocity of most phytoplankton. Nonetheless, phototaxis, negative geotaxis or gyrotaxis (on the basis of which a mechanism generating spatial heterogeneity was proposed by MITCHELL *et al*., 1990) can introduce biases in the general pattern generated by eddy diffusivity. The bias might be decisive in critical circumstances, like, for example, in phytoplankton being trapped or not on the thermocline, or as a way to accelerate phytoplankton circulation in the mixed layer which may be advantageous (MARGALEF *et al*., 1979). But these are events which became relevant on time scales higher than those considered hitherto.

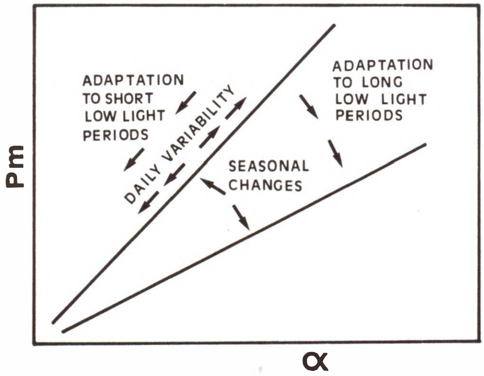

FIGURE 2. Variability in the relationship between the maximum production at light saturation (Pm) and the slope of the photosynthesis-irradiance curve in the light limited zone (α) associated with changes in light of different time scale. The light intensity that saturates the system (I_k = Pm / α) changes at larger time scales than Pm and α.

DIURNAL MIXED LAYER

At a scale of meters, minutes and hours, turbulent and advective processes in the water body can move phytoplankton populations up and down in a resource gradient. In a mixing layer, nutrient distribution will tend to be at least as homogenous as the distribution of organisms and therefore algae move up and down in an environment where light is the most variable resource. In this case, the link between external energy and primary production is related to the cost of adaptation of the phytoplankton to the light field.

Phytoplankton photoadaptation involves several processes which require different periods (HARRIS, 1980). Change in the fluorescence yield is the quickest response to changes in light intensity, taking minutes and serving as an emergency exit. On an hourly scale, photoadaptation results in changes in photosynthetic behaviour, which is commonly characterized by photosynthesis *vs.* irradiance curves (P-I). These curves have been characterized by several expressions (i.e. STEELE, 1962; HERRON & MAUZERAL, 1972; JASSBY & PLATT, 1976; PLATT *et al*., 1980). Usual parameters are α, which is the slope of the curve in the light-limited zone; Pm, the maximum production at light saturation; and I_k, light intensity at Pm, which is equal to the quotient of Pm and α. Although α and Pm are apparently independent, it has been proved that α and Pm change proportionally to keep I_k constant during short periods of changes in irradiance and during diurnal light variations (HARDING *et. al*., 1987). I_k changes seasonally or during prolonged low-light periods (Fig. 2). At the biochemical level, it represents a change in the size of the photosynthetic units: if I_k decreases, light-harvesting pigments increase more than reaction centres. Therefore, changes in pigment composition, or in pigments with respect to other cell components (carbon, carbohydrates, etc.), also take some days. Eventually, if physiological or structural cell changes cannot deal with the variation in resources, growth is modified.

The ratio between adaptation time and mixing time determines which type of adaptation is possible. If mixing time is higher than adaptation time, the organism must adapt to the mean value of the light field; if not, phytoplankton can adapt to each new light intensity.

The transition from autumn overturn to mid-winter in a high mountain lake, when the lake is covered by ice and snow, well illustrates the relation between mixing time and photosynthetical adaptation in several regimes of mixing and light levels. Figure 3 shows changes in photosynthetic parameters in Lake Redó (Pyrenees) during the winter (CAMARERO *et al.*, in prep.). During overturn the phytoplankton is distributed more or less homogeneously along the vertical axis (Fig. 3a). Nonetheless, there is a clear differentiation between Pm near the surface and Pm below a depth of 15 m. However I_k, which requires a longer adaptation time, is quite similar for phytoplankton populations at any depth, and its value corresponds to mid-depth light intensity (25 m). This means that during autumn overturn in Lake Redó, the mixing time of phytoplankton is shorter than the time of I_k adaptation and

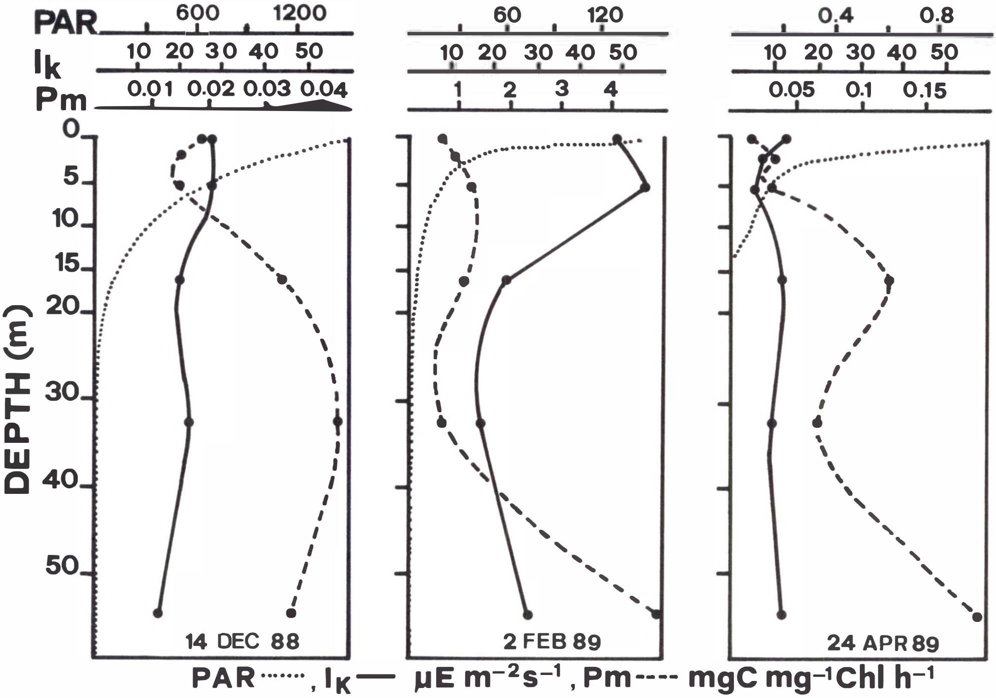

FIGURE 3. Photoadaptation in Lake Redó (Pyrenees) during 1988-89 winter. During the ice-free period (A) vertical mixing did not allow I_k differentiation and phytoplankton was adapted to mean depth irradiance. During the ice-covered period with little snow (B) I_k variability followed light values, time of mixing was larger than time of adaptation. When more snow was accumulated in the cover (C), phytoplankton was not able to adapt its I_k to the very low irradiance.

longer than the time of Pm adaptation; α changes parallel to Pm. During overturn, the mixing time of heat has been estimated to be less than an hour (CATALAN, 1988). For phytoplankton, it is likely to be longer, but less than a day. When ice forms on the lake surface, turbulent mixing reduces markedly and, as a consequence, Ik differentiation is possible (Fig. 3 b). Then snow accumulates and the light penetration goes down to very low levels (Fig. 3 c). Adaptation reaches its limit and I_k becomes homogeneous and very low throughout the water column again. I_k does not reach the values of light in the water column and so it seems impossible for these algae to be able to adapt to such low light levels.

Any characterization of phytoplankton photoresponse to a variable light field must involve a historical perspective. On a scale of days, the effect upon primary production of a sudden change of light (because of snow accumulation, or water rise or deepening, for instance) would differ depending on the phase of growth of the algae population. Not only is the mean light field important, but the variance of the light environment is also significant during the growth phase. Photosynthetic measurements showed that algae grown under steady illumination had higher photosynthetic efficiency (α) and capacity (Pm) when incubated under steady or little-fluctuating light (0.1 Hz). However, algae grown under highly-fluctuating light had higher photosynthetic efficiency and capacity than those grown under steady illumination, when incubated under 1.0 and 10.0 Hz light (QUÉGINER & LEGENDRE, 1986).

Although, as pointed out above, the relation between mixing time and adaptation time determines whether phytoplankton adapt to the mean light environment or follow light variation, it is not clear how photoadaptation relates to system net primary production. We may hold that an adaptation process would be energetically cheaper the longer it takes to happen, thus explaining the substitution of one photoadaptation mechanism for another. However, maximization of system primary production is not necessarily the main aim of phytoplankton cellular regulation.

Seasonal primary production dynamics may be understood as an accumulation of short-time events. At the scale of months, a statistical link between primary production and external energy may easily arise from the high weight that relatively few productive events, occurring when mixing breaks some nutricline, have in the statistical analysis. The coefficient of the power relations between primary production and external energy (MARGALEF, 1978) could be an indicator of the relative abundance of productive and unproductive mixing events. However, the relationship can appear confusing when we compare the spectra of mixing events from different lakes and the variability of primary production at each intensity.

There are different sources of mixing energy: wind action, inflows and outflows, heat exchange, etc. Each of them has particular characteristics: 1) wind has an immediate and local effect, followed by inertial arrangements when it ceases which may vary greatly from lake to lake, depending on morphology. 2) Inflow and outflow generate advection, which determines a clear directional spatial differentiation. Inflow differs from other external sources of energy in carrying nutrients and organic matter from outside the system. Inflow magnitude, and nutrient and matter concentration depend on the watershed features and thus the functional anatomy of lakes extends to the catchment area. 3) Finally, input of energy in the form of heat produces the mixing action with some delay - that is, when the heat is lost by the system sometime later. Its role has to be considered on a higher time scale. Hence, convection has a strong seasonal influence in most lakes. As an immediate effect, positive heat flux partially compensates for wind action.

Inputs of energy generally occur near the lake surface, so understanding the behaviour of the mixed layer near the surface is a first step in the matching of phytoplankton adaptation to physical processes on short-time scales. The daily behaviour of the mixed layer, integrated by rhythmic events and probabilistic fluctuations, determines the episodes of primary production, the integration of which will cause the seasonal and annual fluctuations.

The behaviour of the diurnal mixed layer can be typified by employing a series of dimensionless numbers and characteristic lengths (IMBERGER, 1985). For instance, a useful ratio showing functional anatomy at this scale is the Wedderburn number (PATTERSON *et al.*, 1984), whose magnitude determines the deepening regime of the mixed layer (SPIGEL & IMBERGER, 1980) (Fig. 4).

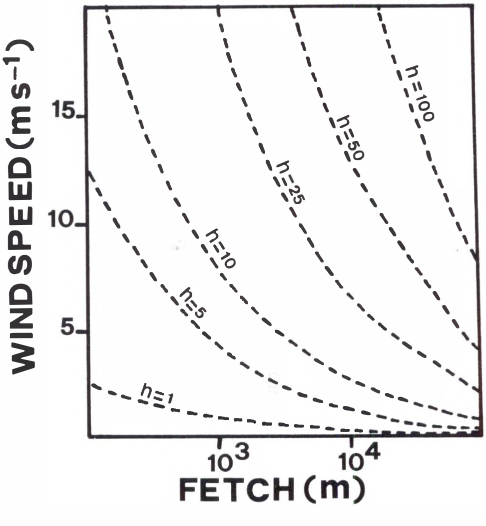

FIGURE 4. Given a particular density differential ($\Delta\sigma$) in a two layer water body, the efficiency of a wind action in altering the stratification depends on the geometry of the upper layer and time of response on the geometry of the basin (H,L). In the figure, wind speed (v), fetch (L), and thermocline depth (h) are plotted for Wedderburn number = 1, which means severe mixing, for a $\Delta\sigma = 0.08119$ (that is, a 1° C temperature differential in the range of about 10° C). $W = (g\ \Delta\sigma\ h / (\sigma_a C_d v^2)) / (h/L)$, where g is the acceleration due to gravity, σ_a the air density, and C_d a drag coefficient. Time of response is given by $t = (2L / (g\ \Delta\sigma/\sigma_0 (H-h)/H)^{1/2}) / 4$).

Based on a two-layer rectangular cavity with densities of σ_0 and $\sigma_0 + \Delta\sigma$, the Wedderburn number represents the ratio between surface wind stress and the pressure gradient resulting from the slope of the interface (the maximum baroclinic pressure force). It is a Richardson number with an aspect ratio. W = 1 corresponds to the interface surfacing at the upwind end, where vertical mixing is enhanced, and the upwelled water is redistributed horizontally by advection. Rapid deepening accompanies the large interface displacements, and complete mixing may occur during a single wind episode. W > 10 indicates that mixing effects are much more relevant in the vertical dimension - there is no share production at the interface, and wind action and convection determine all mixing processes at the interface.

Another interesting property of the mixed layer is the ratio between wind-induced mixing velocity and penetrative convection velocity. This relationship has been traditionally expressed as the Monin-Obukov length (IMBERGER, 1985). For a net surface heat input, it represents the depth scale over which wind stirring approximately balances the rate of gain of potential energy from the surface heating. For a heat loss, it represents the depth of the mixed layer influenced by wind stirring.

The next step is to characterize how phytoplankton biology matches those patterns of mixing described by dimensionless numbers and characteristic length: how and when entrainment of nutrients or particles to the diurnal mixed layer occurs; what are the delays between the physical and biological processes; etc.

An early approach was the relation between primary production and the quotient between photic depth and mixing depth (SVERDRUP, 1953). Obviously, if phytoplankton remains outside the photic zone part of the time during mixing, primary production will decrease; although this is not always the case if the mixing depth represents the frontal zone where water richer in nutrients is entrained from a non-mixed layer. Both photic zone and mixed layer change during the day and from day to day, and they are not independent. The mixed layer depends on light absorption in the water column, and light absorption on phytoplankton growth, which in turn depends on the ratio between photic depth and mixing depth. The buoyancy characteristics of phytoplankton species involved and the pattern of daily variability of the mixing layer may determine competitive advantages for some species (SPIGEL & IMBERGER, 1987).

On the other hand, it is not easy to define the depth of the photic zone in relation to the light field. The depth of the photic zone has often been underestimated. One cannot talk of compensation depth in general, but for each cell. Some algae can grow at very low light levels. It is not rare for oligotrophic lakes to present production maxima at depths at which light is between 1 and 0.1% of the subsurface irradiance. Moreover, experiments carried out at very low light levels suggest that the energy required to sustain a cell may vary with growth rate (GIBSON, 1987). Thus, compensation depth requires a dynamic definition. In general, the models available require a shift to more dynamic approaches where both mixing processes and phytoplankton adaptability are compared at the appropriate scales. Since compensation depth is not general, but depends on the species and even on the status of the individuals, this is a mechanism for succession. At the base of the photic zone, the spatial segregation of species may increase and different species could develop successively.

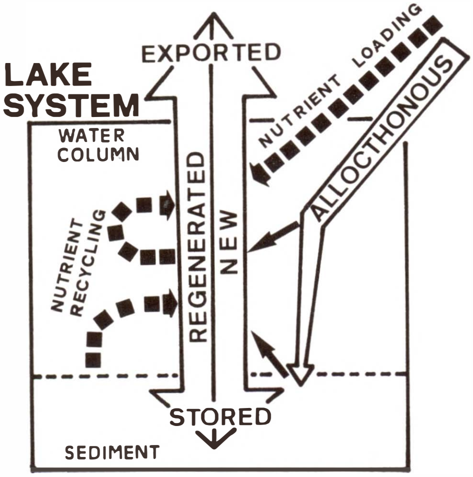

FIGURE 5. Lake production can be partitioned according to the inlake or outlake origin of nutrients (regenerated and new production, respectively), and according to its destination (exported or stored). For a given nutrient loading the relative importance of each fraction would depend on lake functional anatomy. Allocthonous (imported) production contributes to new production but with delay respect to its entrance to the system.

A compensation depth can be considered for the whole ecosystem. SMETACEK & PASSOW (1990) have pointed out the significance of grazing and heterotrophs in modifying the phototroph compensation depth in the oceans. Nonetheless, in many lakes, sediments are as relevant as open water biomass in determining the lake respiration centre of gravity (CATALAN, in press).

THE LAKE AS A SYSTEM

The primary production of lakes can be divided conceptually by considering the origin of the supporting nutrients (Fig. 5). Two components can be distinguished: new and regenerated production. The conceptual idea of DUGDALE & GOERING (1967) for the photic zone of the oceans can be stated for a lake as follows (AXLER *et al*., 1982): new production is based on external loading of nutrients; and regenerated production is based on in-lake recycled nutrients. Sediments are considered part of the whole lake ecosystem. Notice that if this definition of new and regenerated production for the lakes were applied to the ocean considered as a "sole big lake", most of the new production measured today would have to be understood as regenerated. The partition between new and regenerated is always relative and depends on the definition of the "box" of reference.

Nutrients for new production can enter the system in a mineralized form or as part of imported organic matter. The latter portion determines the heterotrophic level of the system, and introduces a time delay in the use of elements brought in by the inflow. Delay depends both on the specific properties of the system and on the nature of the organic matter.

In a homogenous territory, nutrient loading is related to watershed size (SCHINDLER, 1971), and to catchment physiography. In a given watershed, external energy, in the form of precipitation and water flow, probably has less influence on average nutrient loading than on its seasonal variability.

On the other hand, matter produced in the system, after cycling in the water column several times - or with no cycling - is eventually stored in the sediments or exported through the outflow or through organism-mediated transport (for example, Chironomidae emergence). Work done by external energy is useful, as regenerated primary production, when it results in the transport of nutrients from a zone where stored production is mineralized to the photic layer. The functional anatomy of lakes can be viewed as an apparatus capturing energy, just as we conceive of the photosynthetic apparatus or of the plant morphology capturing photons. As in the photosynthetic process, the efficiency of the conversion of the energy reaching the system into production depends on a first component of physical nature (functional anatomy) and a second component of biochemical nature (metabolic biological processes which generate gradients and adaptative physiological processes). Functional anatomy determines the potential to produce, but biochemistry regulates the efficiency in the use of this potential. For instance, mixing events of the same magnitude which occur too often will have different results in incorporating nutrients to the productive zone if the periodicity is shorter than mineralizing time. This is a little investigated subject that would be important in understanding the variability of lakes that base their production in the regenerated portion. Recovery of the stored production into regenerated production has an efficiency that depends on the biogeochemistry in the sediments but also on time between storing and mixing episodes.

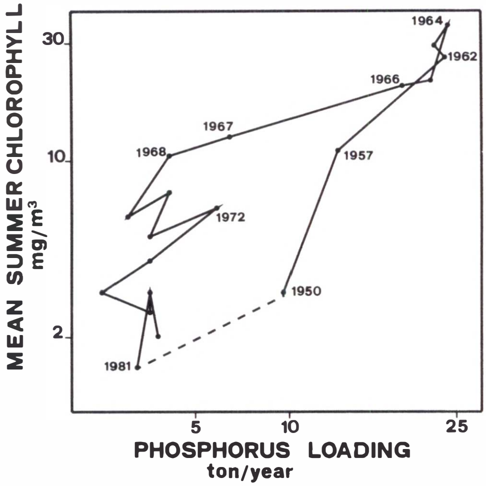

FIGURE 6. Trajectory followed by Lake Washington during its eutrophication and regeneration phases in the space defined by nutrient loading (intensive magnitude) and mean chlorophyll in surface samples for July and August (extensive magnitude). Area defined by the trajectory might depend on the functional anatomy of the lake (Data after EDMONDSON, 1985).

For theoretical limnology and lake management it is important to understand how the functional anatomy of lakes influences the division of primary production into the several types mentioned above. For instance, eutrophied lakes do not follow the same trajectory during recovery as during eutrophication, in terms of pairs of nutrient loading and phytoplankton biomass (Fig. 6). The shape and size of the area between the two trajectories depend on the functional anatomy of the particular lake. In theory, if more energy is available for mixing, production is kept at a higher level (ALONSO, 1989a,b) and the system loses and stores less material, hence the trajectories back and forth would be more similar.

Morphological characteristics of lakes and their biological production have long been related. THIENEMANN (1928) already pointed out that oligotrophy is associated with lake depth. FEE (1979) found that the variability of primary production in some lakes of the Experimental Lake Area (Canada) strongly correlated with the ratio between the area of epilimnetic sediments (Ae) and the volume of the epilimnion (Ve), but had little relation with the nutrient loading, except when the lakes had been artificially eutrophied. The ratio Ae/Ve is equivalent to the ratio between the probability of retention of a particle in the epilimnion and the mean depth of that epilimnion. In other words, the nearer a compartment where nutrient recycling occurs to the photic zone the higher the production. In general, the external loading to the lake is scaled to catchment size, the nutrients received are diluted according to the lake volume (SCHINDLER, 1971) and, finally, increased depth represents a higher dilution of nutrients recycled in the deepest part of the lake (MARGALEF, 1983).

This view of the relationship between production and lake morphology does not give sufficient emphasis to the role of mechanical energy as a necessary link between them. The relationship between morphology and production is usually established in rough terms on an annual time scale; the significance of external energy could be easily understood on a seasonal or even on a daily level.

The relationship between primary production and morphology and physical regimes of lakes is not monotone. A series of "switchers", "multipliers" and "accumulators" have their particular configuration in each lake. This determines the characteristics of the link between external energy driving the system and the dynamics of lake primary production on seasonal and annual scales. In the relation between temperature and water properties, two particular points represent qualitative changes in the relationship between the functional anatomy of lakes and primary production. These are the maximum density point (*ca.* 4^{o} C in pure water) and the freezing point. When these temperatures are reached in a lake, there is a qualitative change in the effect of different external energy sources.

Radiation induces convective mixing until the water reaches 4^{o} C, then the water increases in buoyancy and partially withstands wind action. Heat introduced in the lake represents a potential energy which will do its work later. Hence, going above 4^{o} C will bring about a time delay in the relationship between external energy and primary production, but it also implies an accumulation of energy which will act in a shorter time. In large bodies like the ocean, this occurs spatially: energy accumulates in large areas and is given back to the atmosphere as sensible heat plus latent heat locally (upwelling zones). When the lake cools below 4^{o} C, convective mixing by heat loss stops and radiation again has a direct effect as a mixing agent. Therefore, in a typology of lake variability the relative length of the periods below and above 4^{o} C would be important.

Formation of surface ice has several implications for lake production and the external energy relationship. The best known are its insulating and light-reducing effects, especially if snow accumulates on the top (CATALAN, 1989). But there is another, less obvious effect of the formation of ice. Cover formation opens the possibility of integrating precipitation events for a long period and concentrate their effect on lake production when the cover thaws. Lakes receiving the same winter precipitation in their watershed might show different fluctuations in spring production depending on whether they freeze or not. An interesting example has recently been given by GOLDMAN *et al.* (1989), comparing primary production variability in Lake Tahoe and Castle Lake. The extreme production fluctuations in Castle Lake correlate with El Niño events but not the extreme fluctuations of Lake Tahoe, although they are both at a similar latitude. It seems that Castle Lake reflects El Niño-induced variability in precipitation because it freezes and, therefore, integrates in its cover the snowfalls throughout the winter, whereas Lake Tahoe because of its size does not freeze and the effect of the precipitation increase or decrease is diluted during the year.

In Castle Lake, the higher the snow accumulation during winter the lower the spring production. The exact mechanism involved in this relationship is unclear. In Lake Redó in the Pyrenees the same seems to occur, although data are much more scarce. In this lake, production depends on nutrient inputs from sediments situated below 25 m and particularly 40 m deep. The thicker the snowpack the slower the thawing of the lake cover and the shorter the period of spring isothermy. As a consequence, convective mixing action upon fine sediments is also shorter during spring, and nutrient input lower. A similar mechanism may occur in Castle Lake, because persistence of the cover during thaw implies a more stratified flow of melting water, and, thus, delays action upon deep fine sediment. This phenomenon introduces variability in the primary production series of these lakes because their total production depends more on the regenerated portion than on the new portion. Probably, the larger the nutrient loading, implying a relative increase in new production, the lower the relative effect of lake cover in annual production fluctuations, unless other mechanisms appear.

Solar heating introduces buoyancy stabilization of the water column. The kinetic energy introduced by wind action is usually insufficient to overcome the potential energy inherent in the stratification in some periods of the year. Episodic events and accumulation of results lead to the division of the summer water column into compartments. Particularly interesting is the relationship between the trophic state and this compartmentalization. Oligotrophic lakes present deep chlorophyll maxima which are usually below the thermocline, in the upper hypolimnion, where light is between 1 and 0.1 % of surface and where pseudo-eddy diffusivities incorporating the effects of all the mechanisms which result in vertical transport are higher than in the thermocline itself (QUAY *et al.*, 1980; CATALAN, 1988). Turbulence is active in the surface mixed layer, hypolimnion is largely quiescent with internal waves. Seiching and shear in the upper hypolimnion favour intrusions from the boundaries into the interior. These intrusions represent a nutrient transport which feeds the phytoplankton development far from the surface. Furthermore, waves and tilt of the thermocline can temporally increase light availability to the phytoplankton situated near the compensation depth. In these fertilization mechanisms of deep chlorophyll development, special attention should be paid to the relationship between the depth of the thermocline and the depth of sub-basins or low slope boundaries. Fine materials can accumulate here as sources of nutrients and of reductor power which may be horizontally transported.

A shift to new system characteristics during seasonal dynamics or a eutrophication process occurs when the deep chlorophyll maximum crosses the thermocline and the lake splits into a productive epilimnion and a respiratory hypolimnion.

The dynamics of lacustrine pelagic systems, probably due to the influence of open water oceanography, are usually treated with little attention to the boundaries: infinity is supposed to be quite near. However, boundaries are fundamental in lakes, because mixing upon them occurs at scales much closer to phytoplankton scales than in the ocean. The main nutrient deposits in lakes are sediments. Recycling of nutrients takes place in fine sediments (< 6 μm particles), where there is both more organic matter and higher water content. Therefore, factors determining in-lake sediment distribution are important elements of the functional anatomy of the lake. The main factors are slope, inflow and wind action.

Slope may cause sedimentary material to move. HÅKANSON (1977) established that fine sediments do not accumulate on slopes > 14%, and that below 4% slope has no effect. Therefore, the steeper the slopes and the deeper the lake, the higher the seasonal variability of regenerated production, because pumping of nutrients from the sediment is concentrated in shorter periods of the year or only occurs from year to year (meromixis).

River influence generally decreases logarithmically from the mouth, although it is difficult to establish where river action ceases to control bottom dynamics and wind action begins to dominate (HÅKANSON, 1982). Within areas dominated by wind action, three main zones can be distinguished (HÅKANSON, 1977): accumulation areas, where fine materials are continuously being deposited; transportation areas, where periods of accumulation are interrupted by shorter periods of transportation; and, finally, areas of erosion where there is no deposition of fine materials. These areas are highly determined by lake morphology. Only in shallow lakes can wind-induced waves transfer energy directly to the lake bed. HILTON (1985) proposes that wind energy causes redistribution of the semifluid material (gyttja, for instance) down to a depth of at least one wavelength of the wind-driven waves (SMITH, 1975). Then a boundary can be calculated delimiting lakes with quite a different productive response to wind.

Another mechanism causing sediment redistribution and implying a net transport towards the deepest parts of the lake is intermittent complete mixing (ICM; HILTON, 1985). During overturn, a fairly constant concentration of particles occurs in the water column. When quiescent conditions follow, the mass of particulate material that settles at any point in the lake is directly proportional to the depth of the overlying water. The turbulent levels reached in the water column determine the relevance of intermittent complete mixing. In large deep lakes, it is unlikely that an efficient mix of resuspended particles occurs and, therefore, the significance of the ICM is greater in medium size lakes (< 6 km^2). It is interesting to note the dual role of external energy in ICM lakes. On the one hand, it contributes to the concentration of materials, especially organic matter, in the deepest part of the lake, thus increasing the distance between the gravity centre of primary production and the gravity centre of respiration. On the other hand, it stimulates regenerated production by accelerating diffusion of nutrients. This dual role may contribute to the splitting of the annual cycle into periods of different contribution of new and regenerated production to global production; and, especially in oligotrophic lakes, it contributes to increasing seasonal variability in primary production and dependence from one productive period to the next.

Lake compartments and water density singularities determine the existence of interfaces (spatial and temporal) between phases of appreciably different turbulent kinetic energy. These sharp transitions from high to low levels of turbulence have been called "ergoclines" by LEGENDRE & DEMERS (1985). Processes near or around ergoclines are usually determinant of aquatic ecosystem dynamics. Functional anatomy can also be seen as a set of ergoclines.

In spatial ergoclines, both phases coexist and interact through the interface in the course of time. Examples are summer stratification, thermal bars, marine fronts, etc. In temporal ergoclines, the two phases do not coexist and the interface is ephemeral in relation to the duration of the phases, for instance, formation of the thermocline, lake freezing, etc. The whole ecosystem crosses the interface at the same time and therefore transport or exploitation processes from one phase to the other have an abstract sense.

It is important to consider the interface position relative to the light-gravity axis. Obviously, asymmetry between the two phases is higher when the interface is orthogonal to the light-gravity axis, which is the case of most spatial lacustrine ergoclines. However, in large lakes frontal systems parallel to the light-gravity axis may develop, and thermal bars may occur near the shore line even in small lakes (IVEY, 1983).

The interface between a mixed phase and a stable phase can represent merely a boundary between two states, or it may be an active front where turbulence erodes a nutricline whose origin is in the previous compartmentalization of lake biological activity. This latter case corresponds to the classical deepening of the thermocline or the resuspension of sediments, for instance, and results in a higher production of the mixed phase because of the exclusion of one of the reactants (light) from the stable phase.

When the interface does not represent an obvious rupture of a nutricline, biomass maxima usually occur on the stabilized side of the interface. This is intuitively understood when the ergocline is the boundary between water and a solid (rock, sediment, etc.). When the ergocline is

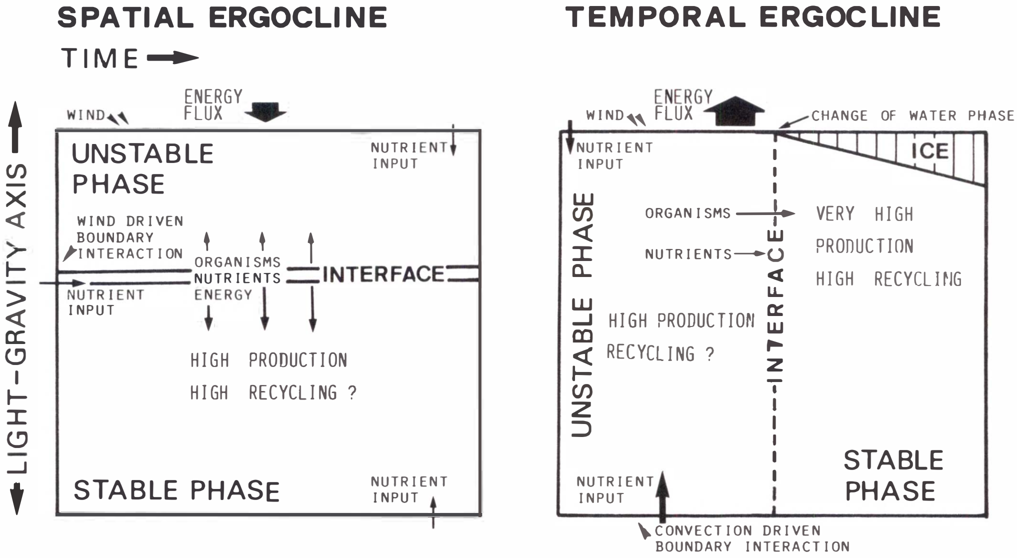

FIGURE 7. Many oligotrophic high-mountain lakes present two chlorophyll maxima associated with two different ergoclines: a summer deep chlorophyll maximum (SDCM) usually develops in the stable phase of the vertically stratified lake just below the thermocline; and a chlorophyll maximum under ice (CMUI) often develops when lake freezes. The temporal ergocline is thought to be an archetypal example (CATALAN & CAMARERO, 1991) for the case that maximum of phytoplankton biomass on the stable phase of the ergocline does not depend on an accumulation process but depends rather on an increase of productivity induced by the sudden change of phase of the system, from a turbulent to a stable environment, without any apparent parallel increase of nutrient input in the system, but with a more efficient and quick recycling.

between two water phases, biomass maximum on the stable phase may occur due to accumulation from production in the unstable phase or to the occurrence of a production maximum on the stabilized side itself. Unless the latter option is associated with a nutrient gradient, it is difficult to understand. Nonetheless, some oligotrophic lakes provide examples where higher production seems to occur in the stable phase. CATALAN & CAMARERO (1991) suggest that this is the case in the summer deep chlorophyll maximum and in the chlorophyll maximum under ice after freezing which some high-mountain lakes present (Fig. 7). Factors suggested as contributing to the higher production in the stable phase are: 1) more efficient phytoplankton growth in a dim and stable light regime in very low nutrient environments; and 2) higher *in situ* recycling in the low turbulence phase. This higher efficiency in recycling in the less turbulent environment could be an adaptative strategy developed among plankton to conserve essential elements in the system (SMETACEK, 1985; SMETACEK & POLLEHNE, 1986). On a microscale, greater recycling means more interaction between autotrophs and microheterotrophs, but it is difficult to imagine any relation between microorganism interactions and the microstructure of the environment as stated at the beginning of this paper. The higher production in the stable phase is relatively ephemeral because there is hardly any input of nutrients. Additionally, it may be insignificant in quantitative terms with respect to the ergoclines where mixing acts upon a nutrient gradient.

The succession of mixing and stratification periods in lakes has been recognized as one of the most useful criteria for lake typology (HUTCHINSON, 1957). Temporal transitions from stable to unstable phases represent changes in the lake compartments and the breaking of biologically induced gradients by external energy. Transitions range from annual to semidiurnal and sometimes shorter time scales. For instance, the classical seasonal changes of the structure of the water column of the dimictic lakes of the temperate zone (freezing, isothermy, stratification, isothermy) occur daily in tropical high mountain lakes. At first sight it seems that, the more frequent the succession of stable and unstable phases, the higher the variance of production and also the higher the mean annual production. However, frequency in phase succession probably has a range that better matches biological processes (LEGENDRE *et al.*, 1986). Higher frequencies would not allow enough time for the development of significant chemical and biological gradients, while shorter frequencies would favour the definitive exclusion of some elements from the system. In a dimictic lake, for instance, two productive periods (spring and autumn) and two mineralizing periods (summer and winter stratification) can usually be recognized. It will be interesting to see the results of a study of the relation between the relative duration of the stable and unstable phases and the magnitude of the productive periods from a long-term series of data.

CONCLUSION

Work done by external energy is more efficient when both anisotropy and sharpness of the boundaries of the volume of reference increase, and also when the time scale includes more variability in energy exchange across the air-water interface. Therefore, the relevance of external energy in primary production should be investigated at the level of the whole lake and on time scales much greater than the microorganisms' life span.

Understanding the link between functional anatomy and primary production in detail demands a parallel development of dynamic physical and biological models, which will probably take some time. Nonetheless, at annual scales and for inter-lake comparison, it is noteworthy that many characteristics of functional anatomy are related to lake size and profile. How primary production variability changes with size for a constant latitude, or how it changes with latitude for a constant size may be relatively easily investigated, both empirically, in district lakes such as in areas of Canada, and theoretically, by physical models including simple biological processes. In my view, in inter-system studies, special attention should be paid to localizing qualitative functional changes such as the characteristics which determine the ice formation, thermocline persistence, the appearance of Coriolis effect, and formation of frontal structures in the mixed layer (IMBERGER & PARKER, 1985), for instance. For intra-lake variability research, the relative duration of successive stable and unstable phases could be significant. The relationships between different components of the functional anatomy and primary production of lakes are non-linear. Therefore, the relations should be monotone in some intervals but points where the relationship changes qualitatively or abruptly should also appear. The recognition of these situations might be more significant than characterization of monotone intervals. Lakes with functional anatomy with characteristics near any of these singular points might present more unpredictable variability in primary production, and in extreme cases, low frequency fluctuations can conduct them to completely new biological systems (SCHINDLER & COMITA, 1972).

ACKNOWLEDGMENTS

Margalef has the quality to fascinate the audience in his lectures, because of his interdisciplinary views, encyclopedic knowledge and intuition, but also because of the enthusiasm and even tenderness with which he talks about organisms. I wonder how much of my addiction to plankton research and ecology responds to these irrational stimuli.

Several friends kindly read an early draft of this paper: Quico Sabater, Quique Ballesteros, Ramon Margalef, Josep Anton Morguí and Miquel Alonso; their suggestions were always useful.

REFERENCES

ALONSO, M. 1989a. Temperature increase effects on zooplankton structure in a cooling reservoir. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, 33: 503-511.

ALONSO, M. 1989b. Els efectes de les centrals nuclears sobre les aigües continentals. *Revista de Catalunya*, 26: 47-59.

AXLER, R. P., GERSBERG, R. M. & GOLDMAN, C. R. 1982. Inorganic nitrogen assimilation in a subalpine lake. *Limnol. Oceanogr.*, 27: 53-65.

CAMARERO, L., LATASA, M., JAUME, D. & CATALAN, J. in prep. Changes in photoadaptation during the formation of the ice and snow cover in a deep mountain lake.

CATALAN, J. 1988. Physical properties of the environment relevant to the pelagic ecosystem of a deep high-mountain lake (Estany Redó, Central Pyrenees). *Oecol. aquat.*, 9: 89-123.

CATALAN, J. 1989. The winter cover of a high-mountain Mediterranean lake (Estany Redó, Pyrenees). *Water Resour. Res.*, 25: 519-527.

CATALAN, J. in press. Evolution of dissolved and particulate matter during the ice-covered period in a deep high-mountain lake. *Can. J. Fish. Aquat. Sci.*

CATALAN, J. & CAMARERO, L. 1991. Ergoclines and biological processes in high-mountain lakes: similarities between the summer stratification and the ice-forming period in Lake Redó (Pyrenees). *Verh. Internat. Verein. Limnol.*, 24: 1011-1015

CSANADY, G. T. 1986. Mass transfer to and from small particles in the sea. *Limnol. Oceanogr.*, 31: 237-248.

DILLON, T. M. & CALDWELL, D. R. 1980. The Batchellor spectrum and dissipation in the upper ocean. *J. Geophys. Res.*, 85: 1910-1916.

DUGDALE, R. C. & GOERING, J. J. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnol. Oceanogr.*, 12: 196-206.

EDMONDSON, W. T. 1985. *Recovery of Lake Washington from eutrophication. Proceedings of the International Congress on Lakes pollution and recovery.* Rome 15th-18th April. European water pollution control association.

FEE, E. J. 1979. A relation between lake morphometry and primary productivity and its use in interpreting whole lake eutrophication experiments. *Limnol. Oceanogr.*, 24: 401-406.

FRISCH, U. & ORSZAY, S. A. 1990. Turbulence: challenges for theory and experiment. *Physics today,* 43: 24-33.

GAINES, G. & ELBRÄCHTER, M. 1987. Heterotrophic nutrition. In: *The Biology of Dinoflagellates.* (F.J.R. Taylor, ed.): 168-224. Blackwell. Oxford.

GIBSON, C. E. 1987. Adaptations in *Oscillatoria redekei* at very slow growth rates - changes in growth efficiency and phycobilin complement. *Br. Phycol. J.*; 22: 187-191.

GOLDMAN, J. C. 1988. Spatial and temporal discontinuities of biological processes in pelagic surface waters. In: *Toward a theory on biological-physical interactions in the world ocean.* (B.J. Rothschild, ed.): 273-296. Kluwer. Dordrecht

GOLDMAN, C. R., JASSBY, A. & POWELL, T. 1989. Interannual fluctuation in primary production: meteorological forcing at two subalpine lakes. *Limnol. Oceanogr.*, 34: 310-323.

HÅKANSON, L. 1977. The influences of wind, fetch, and water depth on the distribution of sediments in Lake Vänern, Sweden. *Can. J. Earth. Sci.,* 14: 397-412.

HÅKANSON, L. 1982. Bottom dynamics in lakes. *Hydrobiologia,* 91: 9-22.

HARDING, L. W. Jr., FISHER, T. T., Jr. & TYLER, M. A. 1987. Adaptive responses of photosynthesis in phytoplankton: specificity to time-scale of change in light. *Biological Oceanogr.*, 4: 403-437.

HARRIS, G. P. 1980. Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, models and management. *Can. J. Fish. Aquat. Sci.,* 37: 877-900.

HERRON, H. A. & MAUZERAL, D. 1972. Development of photosynthesis in greening mutant of *Chlorella* and an analysis of the light saturation curve. *Plant Physiol.*, 50: 141-148.

HILTON, J. 1985. A conceptual framework for predicting the occurrence of sediment focusing and sediment redistribution in small lakes. *Limnol. Oceanogr.*, 30: 1131-1143.

HUTCHINSON, G. E. 1957. 1957. *A treatise on limnology.* Wiley. New York.

IMBERGER, J. 1985. The diurnal mixed layer. *Limnol. Oceanogr.*, 30: 737-770.

IMBERGER, J. & PARKER, G. 1985. Mixed layer dynamics in a lake exposed to a spatially variable wind field. *Limnol. Oceanogr.*, 30: 473-488.

IVEY, G.N. 1983. Experiments on convection near the temperature of maximum density and their application. In: *Proceedings of the 8th Australasian Fluid Mechanics Conference.* 2A4-2A6. University of Newcastle.

JASSBY, A. D. & PLATT, T. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. *Limnol. Oceanogr.*, 21: 540-547.

LEGENDRE, L. & DEMERS, S. 1985. Auxiliary energy, ergoclines and aquatic biological production. *Naturaliste can. (Rev. ecol. Syst.),* 112: 5-14.

LEGENDRE, L., DEMERS, S. & LEFAIVRE, D. 1986. Biological production at marine ergoclines. In: *Marine interfaces ecohydrodynamics.*: (J.C.J. Nihoul, ed.): 1-29. Elsevier. Amsterdam.

MARGALEF, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol. Acta*, 1: 493-509.

MARGALEF, R. 1980. *La Biosfera. entre la termodinámica y el juego.* Omega. Barcelona.

MARGALEF, R. 1983. *Limnología.* Omega. Barcelona.

MARGALEF, R. 1989. Le plancton: survivre et s'organiser dans un fluide mobile. In: *Océanologie actualité et prospective.*: (M. Denis, ed.): 170-183. Centre d'Océanologie de Marseille. Marseille.

MARGALEF, R. ESTRADA, M. & BLASCO, D. 1979. Functional morphology of organisms involved in red tides, as adapted to decaying turbulence. In: *Toxic dinoflagellates blooms.* (D.L. Taylor & H.H. Seliger, eds.): 89-94. Elsevier. North Holland. New York.

MITCHELL, J. G., OKUBO, A., FUHRMAN, J. A. 1990. Gyrotaxis as a new mechanism for generating spatial heterogeneity and migration in microplankton. *Limnol. Oceanogr.*, 35: 123-129.

MUNK, W. H. & RILEY, G. A. 1952. Absorption of nutrients by aquatic plants. *J. mar. Res.* 11: 215-240.

PATTERSON, J.C., HAMBLIN, P.F. & IMBERGER, J. 1984. Classification and dynamic simulation of the vertical density structure of lakes. *Limnol. Oceanogr.*, 29: 845-861.

PLATT, T., GALLEGOS, C. L. & HARRISON, W. G. 1980. Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *J. mar. Res.*, 38: 687-708.

POMEROY, L. R. 1974. The ocean's food web, a changing paradigm. *BioScience,* 24: 499-504.

QUAY, P. D., BROECKER, M. S., HESSLEIN, R. H. & SCHINDLER, D. W. 1980. Vertical diffusion rates determined by tritium tracer experiments in the thermocline and hypolimnion of two lakes. *Limnol. Oceanogr.*, 25: 201-218.

QUÉGUINER, B. & LEGENDRE, L. 1986. Phytoplankton photosynthetic adaptation to high frequency light fluctuations simulating those induced by sea surface waves. *Mar. Biol.*, 90: 483-491.

REYNOLDS, C. S. 1984. *The ecology of freshwater phytoplankton.* Cambridge University Press. Cambridge.

REYNOLDS, C. S., OLIVER, R. L. & WALSBY, A. E. 1987. Cyanobacterial dominance: the role of buoyancy regulation in dynamic lake environments. *N. Z. J. Mar. Freshwat. Res.*, 21: 379-390.

SCHINDLER, D. W. 1971. A hypothesis to explain differences and similarities among lakes in the Experimental Lake Area, Northwestern Ontario. *J. Fish. Res. Bd. Canada*, 28: 295-301.

SCHINDLER, D. W. & COMITA, G. W. 1972. The dependence of primary production upon physical and chemical factors in a small senescing lake, including the effects of complete winter oxygen depletion. *Arch. Hydrobiol.*, 69: 413-451.

SMETACEK, V. 1985. Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. *Mar. Biol.*, 84: 239-251.

SMETACEK, V. & PASSOW, U. 1990. Spring bloom initiation and Sverdrup's critical-depth model. *Limnol. Oceanogr.*, 35: 228-234.

SMETACEK, V. & POLLEHNE, F. 1986. Nutrient cycling in pelagic systems: a reappraisal of the conceptual framework. *Ophelia*, 26: 401-428.

SPIGEL, R. H. & IMBERGER, J. 1980. The classification of mixed-layer dynamics in lakes of small to medium size. *J. Physic. Oceanogr.*, 10: 1104-1120.

SPIGEL, R. H. & IMBERGER, J. 1987. Mixing processes relevant to phytoplankton dynamics in lakes. *N. Z. J. Mar. Freshwat. Res.*, 21: 361-367.

SMITH, I. R. 1975. *Turbulence in lakes and rivers.* Freshwater Biological Association. Ambleside.

STEELE, J. H. 1962. Environmental control of photosynthesis in the sea. *Limnol. Oceanogr.*, 7: 137-150.

SVERDRUP, H. U. 1953. On conditions for the vernal blooming of phytoplankton. *J. Cons. Cons. Int. Explor. Mer.*, 18: 287-295.

THIENEMANN, A. 1928. Der Sauerstoff im eutrophen und oligotrophen See. *Die Binnengewaser*, 4. Schweizerbart. Stuttgart.