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Sunlight Induced Movement of Planktonic Organisms and Their Relationships to Water Movements

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AND THEIR RELATIONSHIPS TO WATER MOVEMENTS

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ABSTRACT

Previous studies have shown the planktonic organisms of various natural water bodies to be quite sensitive to the levels of solar ultraviolet radiation incident at the water surface in summer. It has been assumed that the majority of the phytoplankton are simply carried about in the mass of the water which they inhabit with little control of their position or sunlight exposure. Photosynthetic microorganisms must strike a delicate balance with regard to solar radiation; they must obtain enough visible light for adequate photosynthesis while avoiding an excessive exposure to the injurious solar UV-B radiation.

It is proposed that the circulation in natural waters is such that organisms can "ride" the current to obtain radiation exposures approximating the average radiation level of the euphotic zone. If exposure tends to become excessive, the plankton "drops out" of the circulation into the relatively immobile thermocline region until conditions are favorable for a return to the highly illuminated surface waters. Observations with two species of aquatic plants generally confirm the proposed model.

A radiation regime where the entire population receives essentially the same exposure to sunlight could be substantially more efficient in using the available light for photosynthesis than the "static" model where it is assumed that part of the population is overly exposed and another segment continuously

dwells deep in the water in very dim light. The uniform dosage raises the potential problem that, should the average UV-B dose exceed the tolerance of the individual, virtually the entire population would be wiped out in a very short time. Perhaps such a species might gradually recover its prominence from the limited survivors or return the next season after being supplanted in its niche by other more resistant organisms.

Descriptors: Ecosystems*; Ultraviolet Radiation; Ozone; Microorganisms; Thermocline; Solar Radiation*

Identifiers: Radiation Regime

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INTRODUCTION

The sensitivity of aquatic organisms to solar UV light is such that it is apparent that shielding by overlying water is critical to the survival of various populations (Calkins, 1975, a & b, Calkins & Thordardottir, 1980, Steemann-Nielsen 1964). Although there have been proposals to predict solar UV effects based on models which assume that planktonic organisms hold a fixed depth in the water column over prolonged periods of time (Zaneveld 1975, Lorenzen 1979, Hunter et al.1982, Smith & Baker 1982), the dynamic status of the upper layers of natural water bodies is so obvious that it is clearly necessary to seek more realistic models. Furthermore, although it appears that the injury to a population which held fixed positions in the water would be greater than if mixing were assumed, i.e., it is assumed that the "static" model is conservative in its estimate of solar injury (Hunter et al.1982, Smith & Baker 1982), detailed calculations show that the extent of solar injury to populations can be much greater with mixing than in the static situation (Moeller & Calkins 1980).

Among terrestrial organisms there are many obvious ways in which both plants and animals regulate their light exposure and

their accompanying exposure to solar UV, methods which include both avoidance of exposure and modifications of the UV shielding and repair capacities of the organism itself (Brabham & Biggs 1975, Calkins 1977, Porter 1975, Barcelo & Calkins 1979, 1980a, 1980b). It is however widely assumed that planktonic organisms, the phytoplankton in particular are passively carried about in the water (Steemann-Nielsen 1964), and their exposure to light and solar UV is a series of random and haphazard events which may or may not provide the optimum radiation exposures for the benefit of the planktonic species. However, a long series of observations and measurements of the properties of aquatic organisms suggest that the planktonic populations may be much more in control of their solar exposure than is at first evident; that aquatic organisms possess subtle mechanisms which tend to produce optimum use of the available resources. If such controls are available, as will be proposed here, they suggest that an increase of solar UV exposure through ozone depletion could be far more injurious than would be predicted from the current models.

The Scaling Problem

Movements in water bodies vary from the intercontinental circulations in the oceans to microscopic movements in a rain puddle. It is not at all evident that there could be unifying patterns to the currents in waters which would have broad implications for the aquatic biota. Regarding the impact of solar

radiation, the vertical component of movements is of much greater importance than the horizontal movements. When there is no temperature (density) gradient in the water, wind generated surface currents can lead to circulations which penetrate deeply into the water body. However, a uniform density is a rare condition in most water bodies, a condition which usually arises when the water is very cold (4^0) and when solar radiation which could provide the energy for photosynthesis is at a low point in the annual cycle. At the more sunny times of the year, the sunlight which is powering the productivity of the aquatic ecosystem also warms the surface water and forms a barrier to deep circulation of surface water. Even in the largest water bodies, surface water may not penetrate downward more than a few meters or a few tens of meters before encountering a density gradient which blocks the downward flow of the warmer surface water.

Even if it is conceded that vertical movements in natural waters may be restricted in depth, it is still not evident that there could be substantial similarity of the biological impact of these movements in the oceans and in much smaller water bodies. The relationships can best be comprehended by analyzing the dependence of the important biological factors on depth and how these relate to various general types of waters.

Aside from warming the water (a factor of rather minor significance in itself, since aquatic organisms tend to tolerate a

relatively wide range of temperatures), solar radiation supplies visible light for photosynthesis and concomitantly the UV-B wavelengths 280-320 nm which are injurious. Attenuation of radiation in water can be such that many different waters behave similarly, that they "scale" identically with regard to solar radiation. Organisms can be in waters of quite different clarity, but in essentially the same radiation environment if the ratio of attenuation coefficients for visible light and UV-B radiation are the same. Figure 1 shows some of our data on attenuation of visible light and UV-B and similar data previously collected. Table 1 illustrates the ratio of attenuation coefficients from a number of Icelandic observations.

A much more extensive set of observations can be used to deduce typical values of the ratio of visible to UV-B attenuation coefficients. Figure 2 is a plot of UV-B attenuation vs. the transparency of water as measured by the Secchi disc, i.e., the depth (Z_{sd}) at which a 20 cm white disc disappears from view when lowered into a natural water body (Holms 1970, Tyler 1968). A widely used approximation estimates that visible light intensity will fall to 1% of the surface value at a depth 3 times Z_{sd}. Thus, the attenuation coefficient of visible light K_{vis} can be deduced from the observed value of Z_{sd}, i.e.:

$$I/I_0 = .01 = e^{-(K_{vis}) \times (3\ Z_{sd})} \qquad \text{Eq. (1)}$$

$$\text{or } \ln\ .01 = (-K_{vis}) \times 3\ Z_{sd} \qquad \text{Eq. (2)}$$

$$\text{and thus } \frac{1.535}{Z_{sd}} = K_{vis}$$

Figure 1.

The attenuation of visible and UV-B in various natural waters. Panel A shows the attenuation of visible (526 nm) light; open figures, and UV-B (Robertson Sensor), closed figures, at the same stations.

Panel B shows the attenuation of total solar radiation and UV-B plotted as in Panel A. Data from Kentucky Lake in Western Kentucky (Δ) and from the site of the major biological collections, the pond on the golf course at Jacobson Park, Lexington, Kentucky (∇). The ratio of $K_{visible}/K_{UV-B}$ is noted for each plot. Although one of the Icelandic marine waters shows an attenuation coefficient more than 15 times larger, the pond and clear marine water "scale" almost identically in the penetration of visible and UV-B solar radiation.
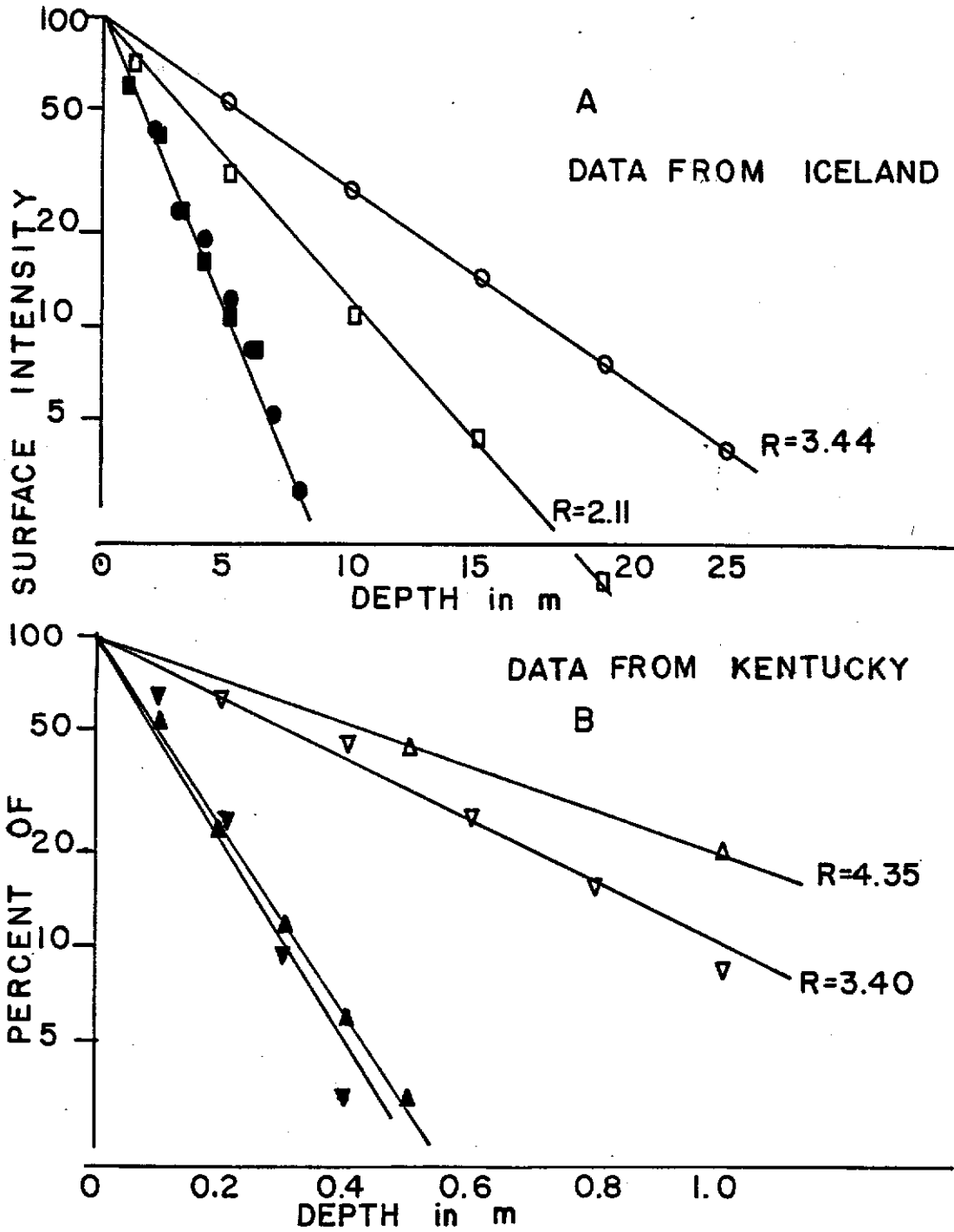
Figure 1.

Figure 2

Plots of UV-B attenuation vs. Z_{sd} for typical waters.

Panel A   Oceanic waters

Panel B   Coastal waters

Panel C   Lakes

Dotted lines on Panels B and C compare the fit of lakes and coastal waters.
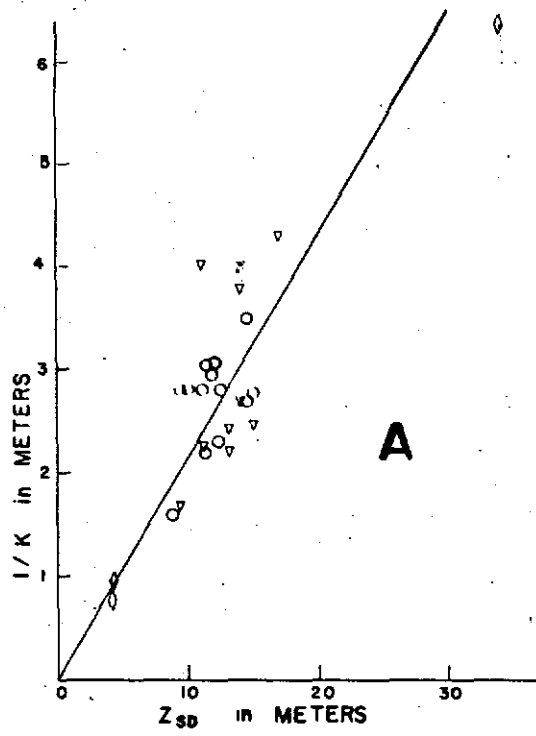
Figure 2.
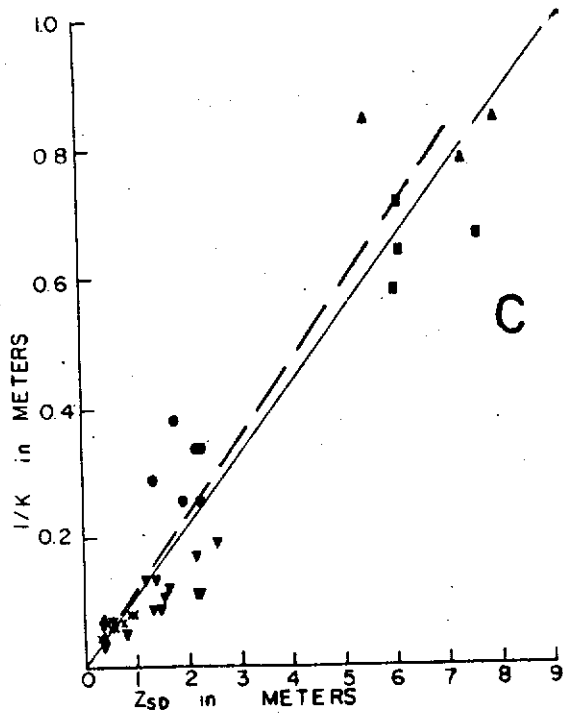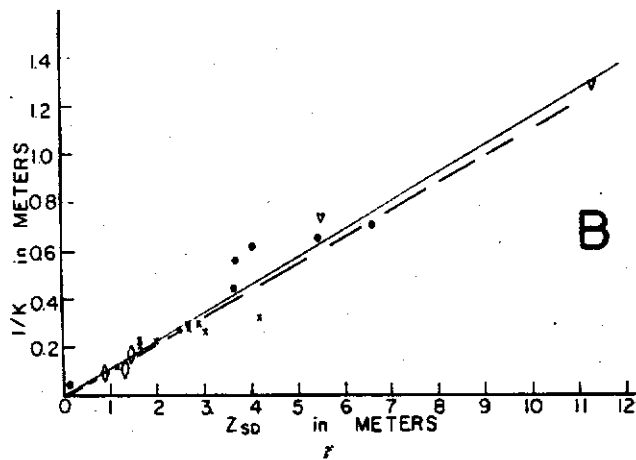
Figure 2.

TABLE 1

Typical Icelandic*		Ratios from Secchi Disc Data
Sta	Ratio $\dfrac{K_{UV-B}}{K_{vis}}$	
Iceland		
15	3.275	Typical Oceanic Waters (Fig. 2A)
16	2.81	
21	3.42	$\dfrac{K_{UV-B}}{K_{vis}} = 3.01$
22	3.58	
23	2.96	Typical Coastal Waters Fig. 2 B
24	2.74	$\dfrac{K_{UV-B}}{K_{vis}} = 5.58$
25	2.5	
33	2.88	
45	1.98**	Typical Lake Fig. 2c
54	2.19	
56	2.4	$\dfrac{K_{UV-B}}{K_{vis}} = 5.86$
64	1.58**	

*vis = 526 nm

** Waters of high productivity at the time of measurement.

Thus we find that a very large group of natural waters show values of the ratio of UV-B to visible attenuation coefficients which span a relatively narrow range (approx. 1.5-6) a fourfold difference. While a fourfold difference of attenuation coefficient will lead to very different levels of UV-B at the deeper levels, calculating the _average_ UV-B exposure in some fixed volume of water (such as the euphotic zone, i.e., the layer of water receiving 1% more of the surface irradiance) one finds that the UV-B exposure varies only by the ratio $\frac{K_{UV-B}}{K_{vis}}$. This conclusion arises from the application of the formula for average radiation exposure when the target material is well mixed. A formula for this situation, developed by Morowitz (1950) and expressed in more convenient terms by Calkins, Buckles & Moeller (1976), is given in Equation 3:

$$I_{av} = \frac{I_o}{KZ} (1-e^{-KZ}) \qquad\qquad Eq. (3)$$

where I_{av} is the average exposure, I_o is the exposure level at the surface, K is the absorption coefficient for the radiation in question and Z is the depth of the volume under examination. Exposures where the term KZ is appreciable cause the exponential term in equation 3 to become small and average exposure to depend linearly on K. Thus, it can be concluded that the average UV-B exposure in the euphotic zone of typical natural waters will only vary by a factor of 4 or less due to UV-B attenuation by the water column, freshwaters in general being better protected from UV-B than marine waters.

The foregoing argument suggests that the average UV-B exposure in the euphotic zone falls within a rather restricted range. The average exposure is only of significance when the volume is well mixed; without mixing, parcels of water at the surface and deeper in the water will receive quite different levels of exposure.

Is there any reason to believe that the depth of the mixed layer will be related to the euphotic zone? It is possible that mixing could be much deeper or shallower than the bottom of the euphotic zone. However, it should be especially noted that the barrier to vertical mixing and the euphotic zone arise from the same source, the limited penetration of solar radiation into natural waters. Photosynthetic organisms cannot grow at depths below the levels at which there is significant solar radiation and absorption of the solar radiation in the surface water blocks its mixing with the deeper, cooler water.

There is clearly case by case variation but in general it is evident that aquatic organisms in a wide variety of natural waters face much the same problem regarding obtaining visible light for photosynthesis while avoiding injurious UV-B exposure. While UV-B and visible attenuation vary in such a way as to equalize different waters, the second important factor, the rate of circulation becomes important. It is not necessary that the number of mixing cycles be the same for all situations; all that is required in order to apply the Morowitz formula to a body of water is that that organisms residing in the water pass through a number of

mixing cycles during the time of irradiation, 4 hours centering on solar noon for UV-B, 8 to 16 hours for visible light. Although much research is needed on the rate of circulation and mixing in natural waters, there is an obvious general compensation in different waters. In the oceans where the water is very clear and the euphotic zone is deep, strong winds are common and the velocity of vertical circulation will in general be high; lakes and smaller water bodies often have smaller depths to the thermocline but will also have generally lower rates of vertical circulation. In general, there is an overall scaling of effects such as to compensate for differences in transparency in natural waters and to suggest that the mechanisms which the biota of one class of water use to cope with solar UV radiation might also be significant in quite different types of water.

We have investigated a small freshwater pond in detail and from these observations a model or pattern of responses is suggested. The model which we propose also explains some observations made in the waters off Iceland and suggest that aquatic algae could employ much the same tactics to best exploit the available natural resources regardless of the location in which they reside.

THE "FERRIS WHEEL" MODEL OF PLANKTONIC MOVEMENT

Successful species inhabiting the earth must simultaneously satisfy the numerous constraints and limitations of their particular ecological niche. Phytoplankton have some particularly restrictive constraints upon their patterns of form and behavior. They must

extract their essential nutrients from very dilute solutions, the oceans or natural freshwaters, and thus a large surface to volume ratio is required, a requirement which can be met by organisms of small size (which tend to predominate among the phytoplankton). However, the large surface to volume ratio tends to make the organisms inefficient at swimming. The absolute swimming velocities of phytoplankton in general are small compared to the velocities of various currents in the epilemnion of natural waters. Many very common species such as most diatoms do not appear to be able to swim at all. On the other hand, phytoplankton are required by their nature to reside in the sunlit portions of the water column (which roughly coincides with the epilemnion) during the photosynthetically active portion of their life cycle.

It would be possible to remain at the water surface, receiving maximum possible photosynthetically active light, if an organism were sufficiently buoyant, however, those phytoplankton which have been tested were found incapable of surviving the solar UV incident on the water surface during even a single sunny summer day. (Calkins 1975a, Nachtwey 1975, Calkins & Thordardottir 1980). The small size of common phytoplankton evidently does not include enough shielding material to reduce sea level solar UV to a tolerable amount, a scheme of importance to the full-sun terrestrial plants. (Brabham and Biggs 1975) Thus, phytoplankton must use the UV shielding properties of the water column, without at the

same time removing themselves from the necessary amount of photo-synthetic light.

While the surface layers of natural waters will from time to time be calm and relatively static, the condition which predominates is that the upper layers, in particular the epilemnion, are stirred and set into complex motions, primarily by wind blowing along the water surface (see Harris and Piccinin 1977). Wind through frictional drag in the water surface can exert a force along the direction of the wind which can to some extent "pile up" water on the downwind side. However, water, unable to support a shearing force, will be set in motion in the reverse direction of the wind generated surface current. If the wind were simply a narrow jet, the return current could be along the surface. In actual water bodies little of the return current can be at the surface directly opposing the wind, so return currents below the surface are set up. Surface water must therefore sink and since in daytime the surface water is warmer and thus less dense than the deeper water, work is done by the wind.

Statement of the Model

It is proposed that phytoplanktonic organisms may use the circulation currents in the epilemnion of natural waters to control their daily average position and that the positional control results in a more or less optimal level of light for photosynthesis while the solar UV-B injury is maintained at a tolerable level.

Referring to Figure 3, it is obvious that when there is a rotation of water in the epilemnion an organism could utilize the water current to control its average position much more effectively than would be possible by direct swimming. To increase light exposure there must be an upward movement in dim light which brings the organism out of the thermocline region or hypolemnion into the circulation. The upward movement should be rather weak in order not to enter the static core of the circulation or pass the center of circulation where the particle will soon be carried downward again.

To decrease solar exposure, the organism should move downward but the downward movement would be most effective if it began when the light intensity began to diminish, thus carrying the particle out of the circulation at a point where it would not be swept back to the surface for another cycle.

The Langmuir Circulation

Although the presence of circulating currents in natural waters other than the Langmuir (1938) circulation is well established (whitecaps, Thorpe and Stubbs 1979, or thermal cells, Owen 1966), the detailed presentation of the model will be based on Langmuir circulation, a relatively well defined, common (Harris and Piccinin 1977) and extensively studied pattern of water movement, a rotation in a plane perpendicular to the wind direction. Other processes which may circulate surface water are of a more turbulent nature and difficult to model.

Figure 3

A schematic representation of the Langmuir circulation and the way phytoplankton (♀) enter and drop off the circulation to regulate their light and UV-B exposures. The Langmuir circulation is shown by a cross section in the water perpendicular to the wind motion. Water velocities are represented by arrows along the flow lines, longer arrows represent greater velocities, more numerous short arrows represent diffuse low velocity flow.
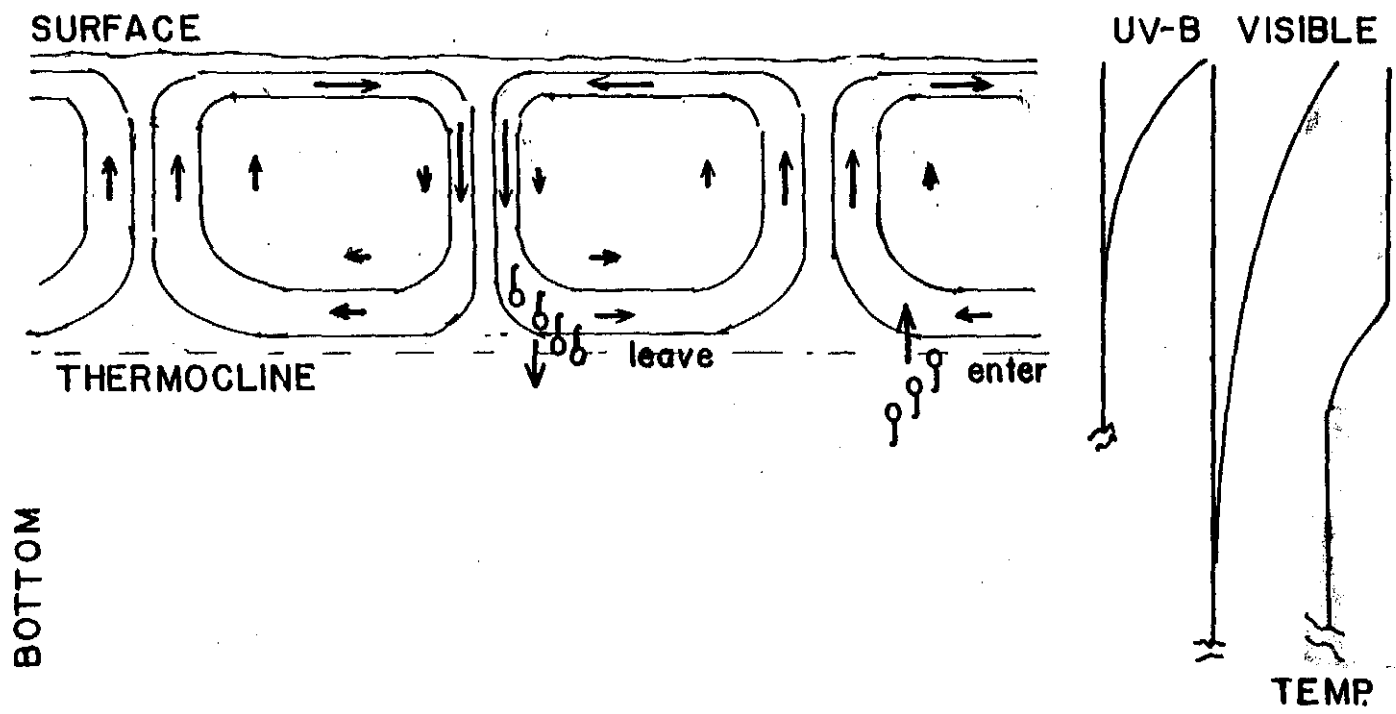
Figure 3.

Figure 3 is a composite of some of the known properties of Langmuir circulations. Titman and Kilham (1976) model Langmuir circulations stream with a more diffuse upwelling component. Langmuir circulations will tend to mix the warmer epilemnionic water, equalizing the temperature in the epilemnion; Langmuir (1938) noted the effective deepening of the epilemnion by sustained circulation; he also notes that the circulation at the bottom of the cell is less rapid than at the surface. Stommel (1947), Langmuir (1938) and Scott et al. (1969) find a correlation of width to height of the convection cell. Stommel's (1947) observations suggest a square to flattened rectangular shape to the individual circulations. Langmuir (1938) notes that the thermocline is practically a fixed surface like the lake bottom and is not set in motion, thus limiting the Langmuir circulation to the waters over the thermocline.

Downwelling speeds of 1-2 cm/second at wind speeds of 2-4 m/sec. are typical; Langmuir observed upwelling speeds of about $\frac{1}{2}$ the downwelling velocity. If one observes surface and bottom horizontal velocities 1/5 the vertical velocity, then time to complete one cycle can be computed. If the epilemnion were 1 m deep, a particle would make a complete traverse in about 10-20 min. Thus, an organism entrained in a shallow Langmuir circulation might make many cycles in a day. If the cell were 5 meters on a side the circulation would require 1 to 2 hours per cycle at minimum wind speed; at higher wind velocities the cycle time would be reduced.

Harris and Picinnin (1977) calculate cycle times to be somewhat shorter than the calculations noted above. When the cycle time is small compared to the delivery time of solar radiation (8 to 16 hours per day for visible and approximately 4 hours centering on noon for solar UV-B), then it is reasonable to assume solar radiation exposure equals the average exposure in the mixed layer, which can be calculated using the Morowitz (1950) formula (equation 3) and the optical parameters of the water.

The Biological Component of Control of Radiation Exposure

An aquatic organism which can move through the water has the potential for modifying the solar radiation exposure it receives. The organism's control of solar exposure will obviously depend on its capacity to move, i.e., orientation and vertical and horizontal motions. It is not so obvious that to effectively control solar exposure requires a capacity to gather and process information about the exterior environment which can then be used to properly direct the motions. A planktonic algae a few microns in diameter will be carried along with the water motion and will receive only a very limited number of clues to its progressions through space. Such an organism could not "swim against the current" to avoid being swept down by the converging component of a Langmuir cell because being carried, even in rapid movement, by a parcel of water is in no way different from standing motionless in a stationary parcel of water.

To swim at random would be as likely to accelerate the submergence as to retard it. Chemical (including nutrient) and thermal gradients in the epilemnion are likely to be very small and erratic and to offer little information for orientation when there are currents and turbulent mixing in the surface layers.

In contrast to horizontal positioning information, there are at least two reliable clues for control of vertical orientation, gravity and sunlight. Differences in density and/or hydrodynamic resistance can orient an assymetrical organism, once oriented the organism may swim upward or downward as the situation requires. Even simpler, if an organism can control its buoyant density over a sufficient range, it can move upward or downward relative to the parcel of water in which it is carried. There is an extensive literature on buoyant changes in planktonic algae (Smayda 1970, Burns and Rosa 1980).

Downwelling solar radiation in aquatic systems is always much more intense than upwelling (Jerlov 1968), thus providing an orientation cue. Many planktonic organisms demonstrate phototaxis, often of a very complex nature (Forward 1976). It would be immaterial whether the algae oriented its vertical motion by light or gravity, the critical point is that given the right stimulus for vertical motion algae can respond by motion in the proper direction.

The essence of the biological control system requires two responses. When solar radiation is insufficient the algae moves upward, when solar radiation is excessive the algae move downward. It is obvious that a positively buoyant (or upward swimming) algae will move upward until it enters the circulation in the epilemnion. Likewise, it is obvious that a negatively buoyant or downward swim-

ming algae will be very likely to drop out of the circulation when it is swept over the stationary thermocline. In the thermocline or hypolemnion there would be little chance of a negatively buoyant organism reentering the circulation since the temperature (density) gradient blocks the downward penetration of the Langmuir cell.

We cannot, at this time, offer evidence regarding the mechanism by which the small upward and downward movements are generated; we will present data suggesting our modeling of the near surface events is correct. Evidence will be noted that various algae move upward in dim light and become negatively buoyant after UV-B (and intense visible) exposure as is postulated in the model.

METHODS

In the course of this project we have made both field observations and conducted laboratory experiments. The description of methods will be divided into two broad categories, physical methods which primarily includes various kinds of measurements using physical instrumentation and biological methods which focuses on techniques for collecting, culturing and observing living organisms.

We have obtained data on total incident solar radiation and wind velocity from the Agricultural Engineering Department of the University of Kentucky who maintain a continuously recording station for these observations.

The most difficult problem in environmental solar UV research is expressing the incident solar UV radiation in proper units which

express the biological potency of the radiation flux. It is accepted that the injurious capacity of solar UV (per photon) varies by a factor of more than 1000, the shorter components near 300 nm being the more effective while photons of wavelengths from 340 nm to 400 are of relatively low potency. The exact shape of the "action spectra" for wavelengths from 360 to the shortwave limit of sunlight (approx. 295 nm) is of great biological significance and current interest (Calkins & Barcelo 1980, Calkins and Barcelo 1982, Caldwell 1982). It is clearly improper to base the interpretation of solar UV effects on ecosystems on the simple physical flux of solar UV radiation. We rely on the Robertson-Berger meter to measure solar ultraviolet radiation with a weighting factor which simulates typical biological responses (Berger 1976, Calkins, Buckles & Moeller 1976. The Robertson-Berger meter has been found to compensate for substantial changes in spectral distribution of UV-B in a number of aquatic organisms (Calkins & Barcelo 1982); it also has been shown to be an appropriate instrument for measurement of attenuation of solar UV-B in natural waters (Smith and Calkins 1976).

Sampling: During a preceeding project it was observed that there were unexplained fluctuations in the total numbers of organisms which would be inferred to be present in a water column of defined volume. A special sampler was designed to alleviate this problem. The sampler was essentially a

brass tube which could be rapidly dropped into the water, reaching from the surface to bottom. The column was then subdivided by gates and each segment collected for the determination of the number of organisms present. Although some data were taken by this means, the operation of the gates proved more difficult than anticipated and most data was collected as was done previously; a sample bottle was filled at preselected depths in the water. In previous work and in the Volvox studies the sample bottle was filled from shore using a long rod and a float to establish sample depth. Where there is a gradual slope from the shore, it is very difficult to sample accurately. For the majority of the work reported here (the Cerratium studies), a small inflatable raft was used and samples collected directly under the raft, a much easier and more accurate procedure.

Biological Procedures

The quantitative work reported here used two naturally occurring species of aquatic plants, the colonial algae Volvox and the dynoflagellate Cerratium. Samples were collected at various times and depths. Sets of samples were either returned to the laboratory or carried to a small building on the site (The Golf Course at Jacobson Park, Lexington, Kentucky) where the samples were scored using low power michroscopes to count the numbers of organisms present. Samples were kept cool between collection and scoring and there was no evidence that the subject organisms either died or

multiplied in the interval between collection and counting. Sample sizes, usually 1-10 ml, which would contain 10-100 organisms per sample were chosen, but when the organisms were scarce or had moved away from that part of the water column, fewer than the desired number might be found in the sample volume. The samples were not concentrated for counting by filtration or other means.

A number of laboratory experiments were performed; however, we were not successful in growing either the Volvox or Cerratium in the laboratory and without large numbers of experimental organisms to work with it was not possible to obtain clear and reproducible results. The qualitative behavior observed in the laboratory will be noted, but our quantitative results are essentially field observations.

FIELD OBSERVATIONS

Volvox: Volvox were found in sufficient density for position analysis in the early spring of 1981. This organism was samples in an area of the pond where the bottom was at 40 cm. Figure 4 shows the movement in relation to incoming solar UV (▲). Beginning from a relatively even distribution in early morning, there is a pronounced downward movement with a heavy accumulation on the bottom (▼), but the bottom accumulation lags the light by about two hours and lasts until about 10:30 p.m. when a relatively uniform distribution is restored.

Figure 5 shows the movement of Volvox in April. On the April day the movement away from the surface is much more prompt and

Figure 4

The movements of <u>Volvox</u> during a February day. The percent
of the total population found at each of 5 locations is plotted
for a 24 hour period; surface (O), 10 cm (∇), 20 cm (▯) 30 cm
30 cm and 40 cm (bottom) (▼). The number of Robertson meter
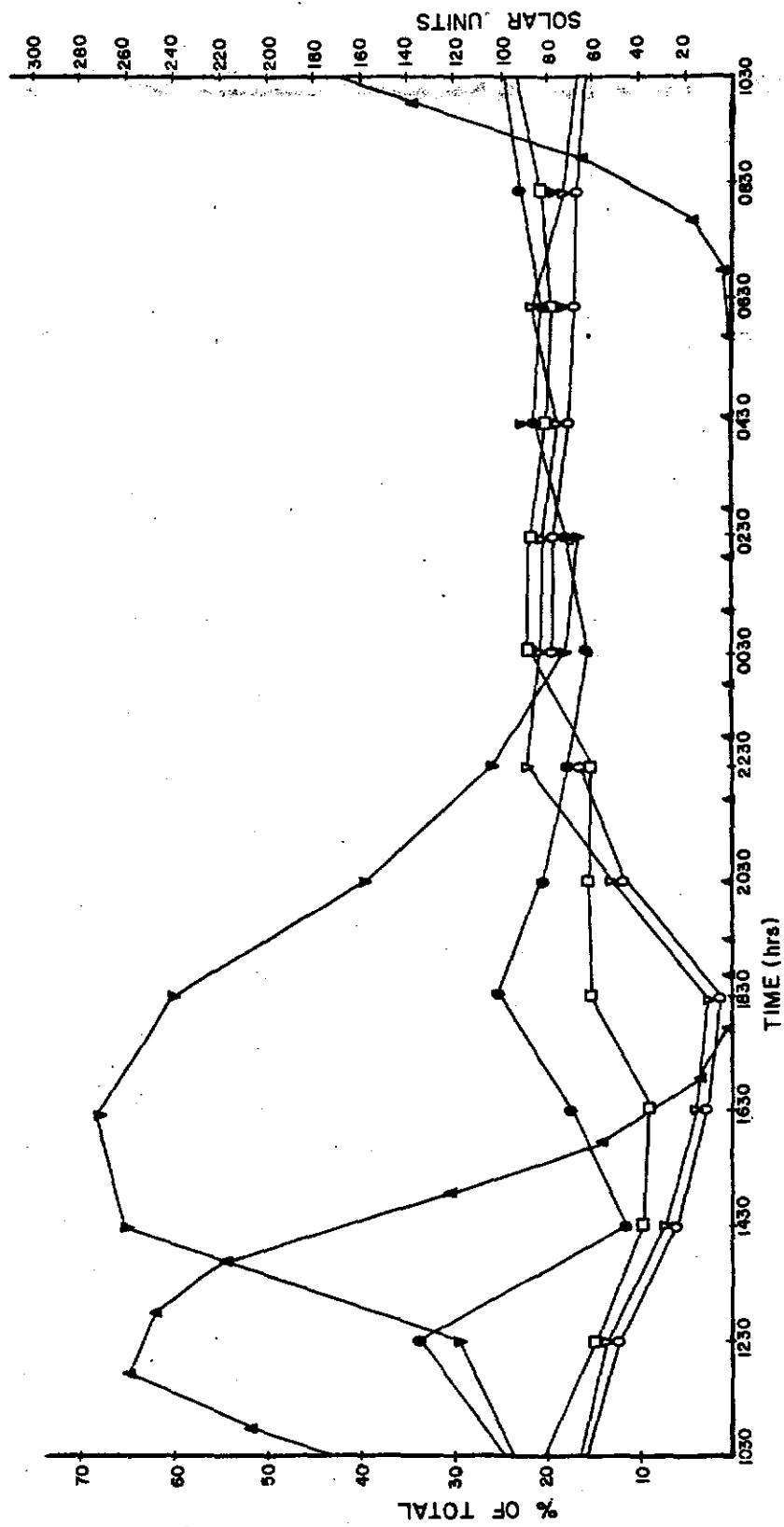counts (▲) per half hour is indicated on the "Solar Unit" scale

Figure 4.

coordinated with the light. The algae do not move to the bottom, but there is also a strong movement away from the 10 cm level which correlated with the solar maximum.

Considering the low level of solar UV incident in February and that 30 cm of water will reduce the incident intensity by a factor of 10, it is difficult to interpret the movement to the bottom as being required for protection from UV damage; however, it should be noted that the killing of coliform bacteria by solar UV at low temperatures appeared to be much more effective than at higher temperatures (Calkins, Buckles & Moeller 1976). The movements observed in April are more nearly the movements anticipated to protect organisms from UV-B injury.

More extensive observations of Volvox were planned, but the algae disappeared from the regular collections at this site requiring a new subject organism to be selected.

Cerratium: The photosynthetic organisms in the collection changed sharply in early summer. The predominant organisms were extremely small flagellated algae (nanoplankton) which were too small and difficult to identify to be useful for collection of positioning data. Beginning in July 1981, a small variety of the dynoflagellate Cerratium was observed in the collections. This organism, although quite small, is very distinctive in morphology and easily identified and counted in the collections.

The Cerratium collections were all made from the raft. The level of water in the pond varied somewhat, the depth ranging from

Figure 5

    The movement of a population of <u>Volvox</u> sampled in April.
The symbols are as in Figure 4: surface (O) 10 cm (∇), 20 cm (▢),
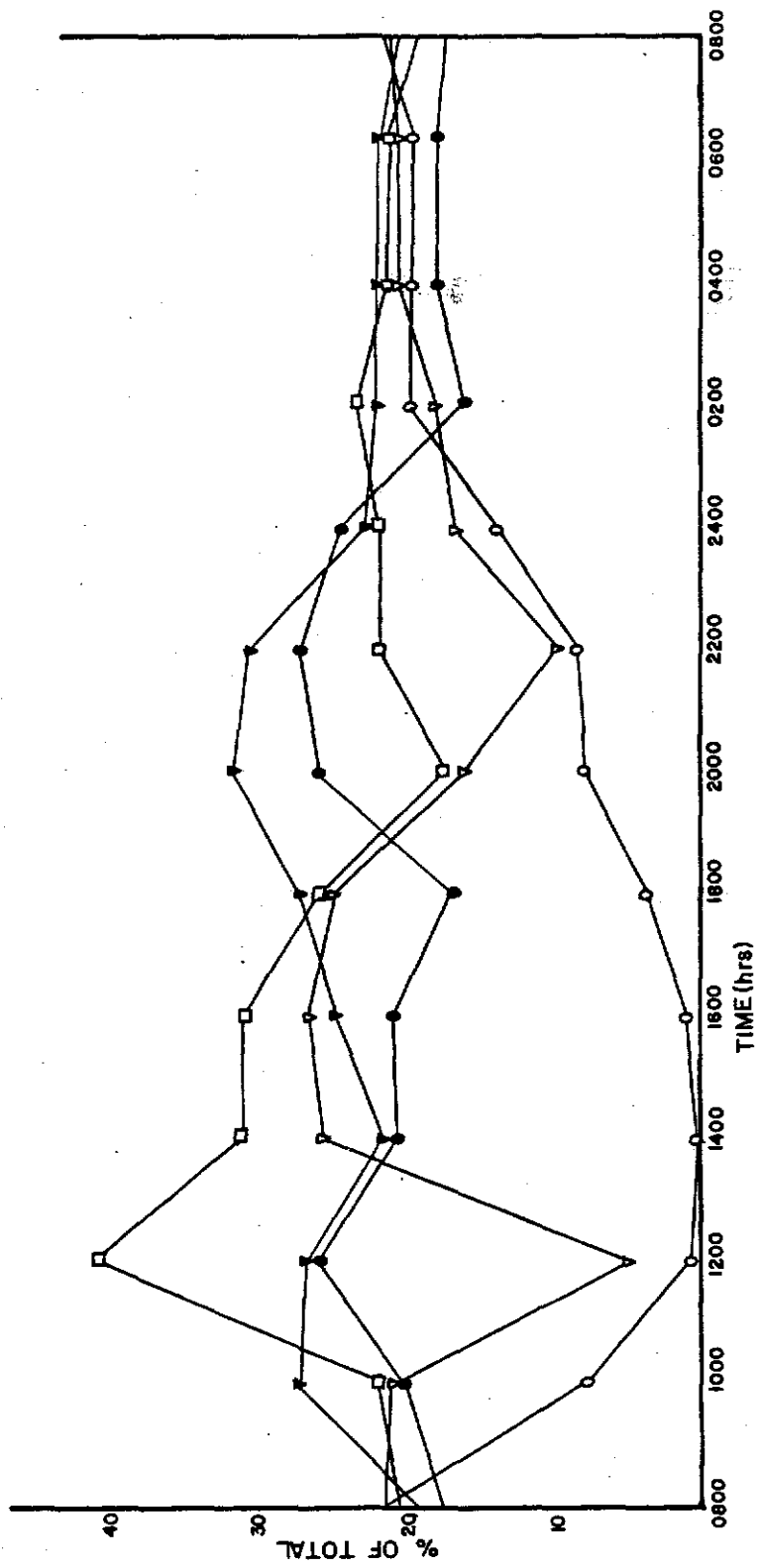30 cm (●) bottom, 40 cm (▼).

Figure 5.

112.5 - 100 cm. The bottom was soft mud and care was used not to stick the collection bottle into the mud and render the sample uncountable by collecting too much mud.

Figures 6 - 12 show the vertical positioning behavior of Cerratium as related to a number of parameters which could influence the distribution of the organism. The night data are pooled in Figure 6. The complete temperature series was only observed once among these collections and was found to be quite uniform. Although there is some variability, the night observations show an essentially uniform distribution of organisms with no clear trend of movement.

The observations at 6:30 and 8:30 in the morning were plotted together (Fig. 7). Very little light has arrived at the time of these observations; the water temperature is almost uniform from top to bottom and only the beginnings of distribution changes are evident. In all cases there is some upward movement from the bottom although it tends to be small and erratic. By 10:30 a.m. (shown in Figure 8) a strong pattern of movement is evident. There is an upward movement in all cases except the observations on 8/7, a day which was quite windy, but for which the wind data was unavailable (NA). (Note the uniform temperature throughout the pond at this collection.) The profiles of these collections 7/22, 7/23, and 8/4 are very similar and tend to be approximately equal above 75 cm. The wind is relatively high on 7/22 and 7/23. The 8/10 and 8/12 profiles are similar with pronounced peaks of concentration around 50 cm (just below the thermocline on 8/12) and the wind was light on these days.

Figure 6

The vertical distribution of _Cerratium_, night collections in 1981.

The upper two panels show the vertical distribution of organisms and the water temperature profile; temperature and concentrations are indicated by the corresponding symbols: 21:30 on 7/29 (O), 22:30 on 7/22 (∇), 1:30 on 7/30 (□), 2:30 on 7/23 (●), 4:30 on 8/4, 4:30 on 8/7 (◼), and 5:30 on 7/30 (△). The corresponding wind speeds are indicated, the data for 4:30 on 8/7 (◼), and 5:30 on 7/30 (▲). The corresponding wind speeds are indicated, the data for 4:30 on 8/7 was not available. The bottom 2 panels indicate the incident UV-B in "solar units" equalling 400 Robertson counts; total radiation in Langleys is indicated. Both the daily cumulative and hourly rate of solar radiation are indicated; naturally only cumulative values are plotted in Figure 6.
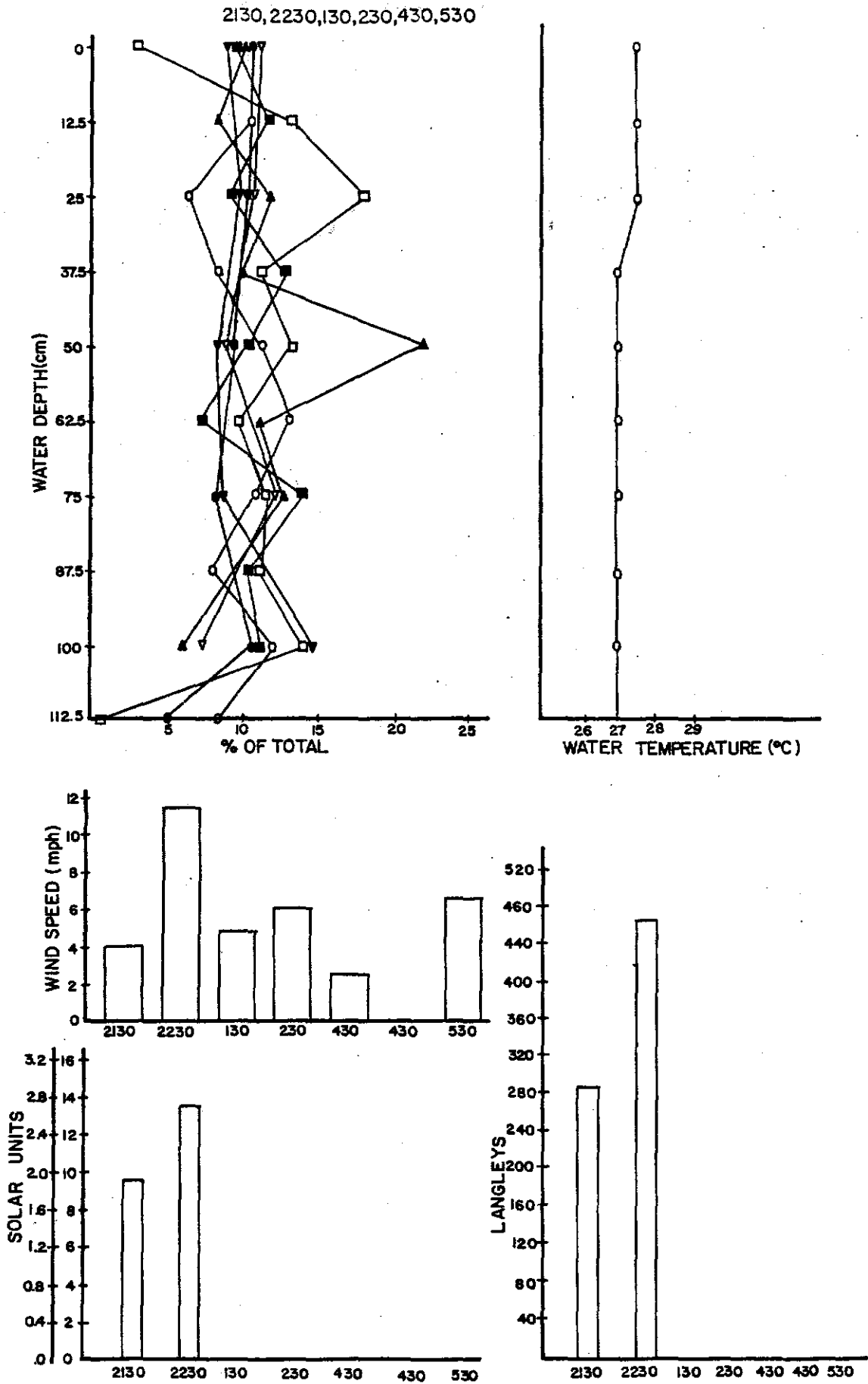
Figure 6.

Figure 7

Various observations of the vertical distribution of <u>Cerratium</u> at 6:30 and 8:30 a.m. plotted as in Figure 6.

Symbols - 6:30 on 7/23 (0), 6:30 on 8/4 (▽), 6:30 on 8/7 (▢), 6:30 on 8/12 (●), 8:30 on 8/7 (▼) 8:30 on 8/12 (■); the wind velocity at 6:30 and 8:30 on 8/7 was not available. Right hand bars indicate accumulated solar radiation, left hand member of pairs indicates rate during the hour previous to collection.
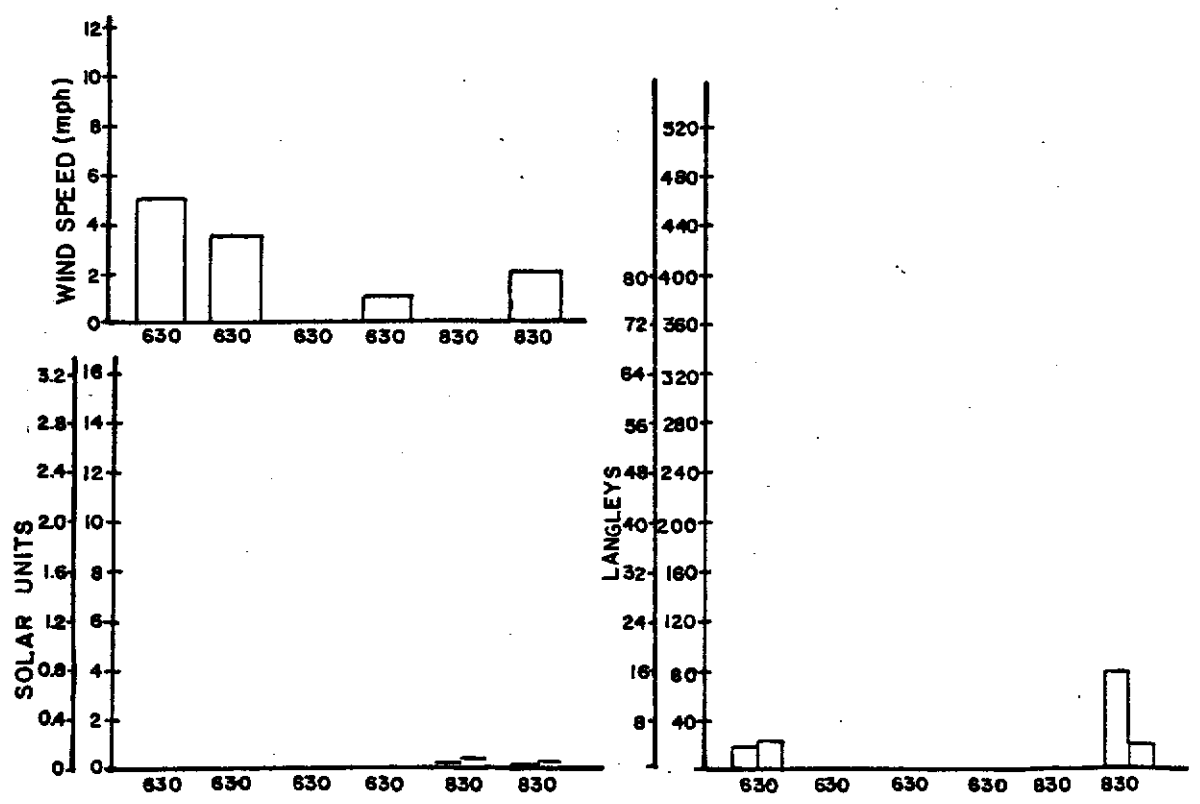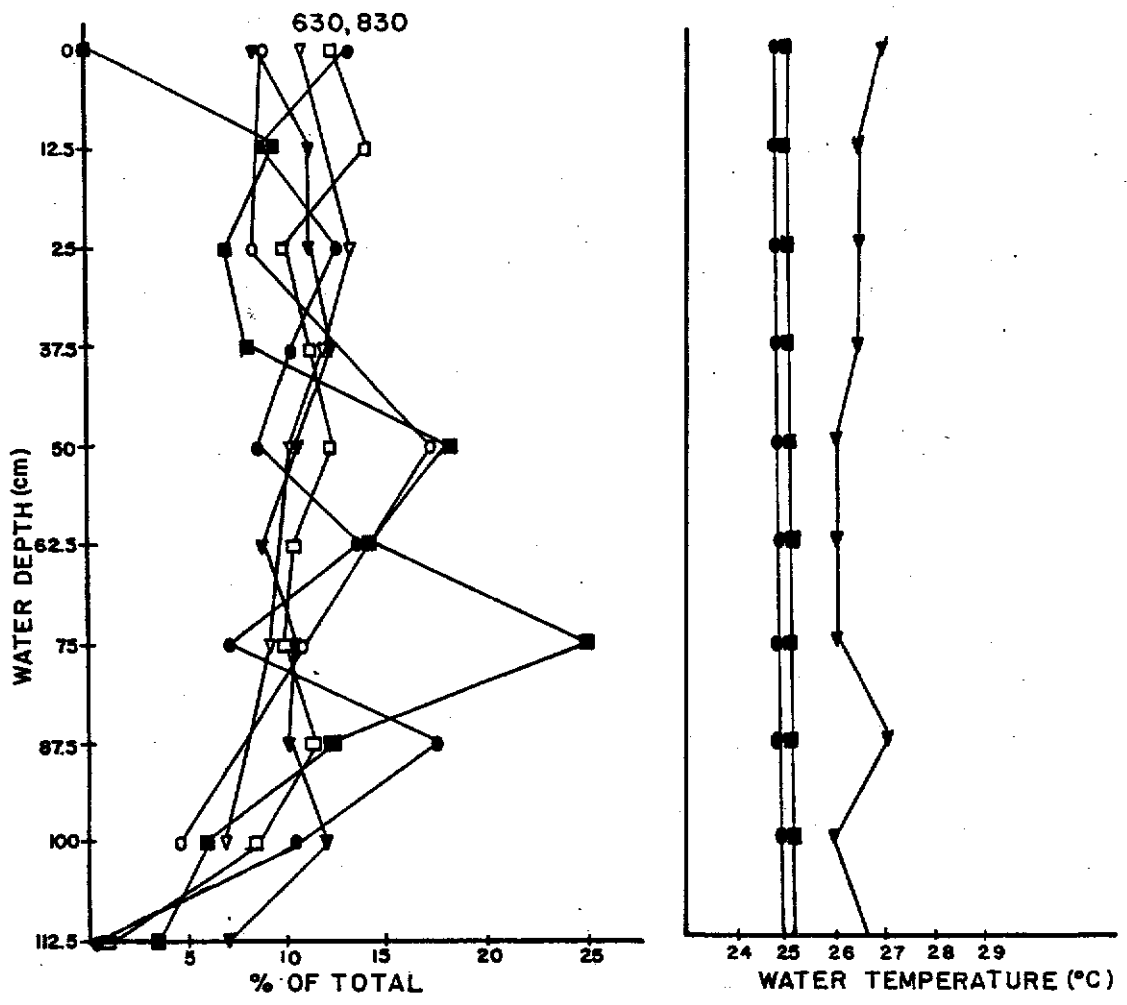
Figure 7.

Figure 8

The vertical distribution of <u>Cerratium</u> collected at 10:30 a.m. on various days.

Symbols indicate date of collection - 7/22 (●), 7/23 (▼), 8/4 (■), 8/7 (O) 8/10 (◘), 8/12 (∇), wind data was not available for 8/7, but it was a very windy day; paired bars in the lower panel indicate hourly rate (left) and cumulative (right) solar UV-B and total solar radiation.
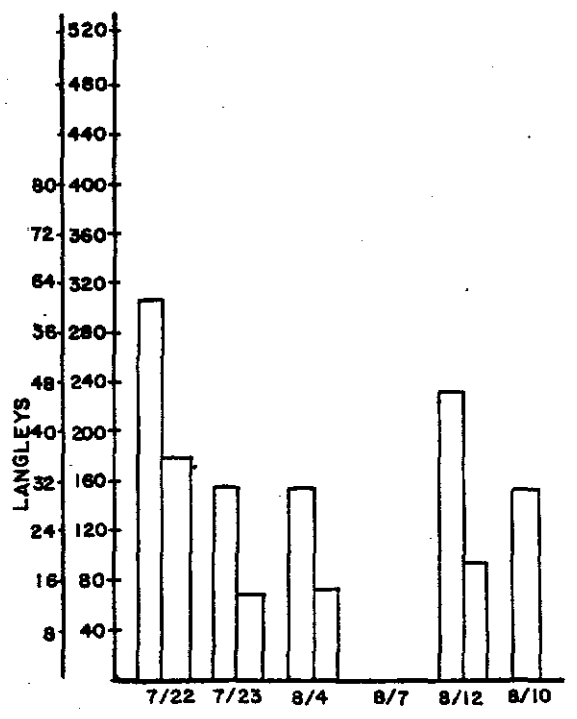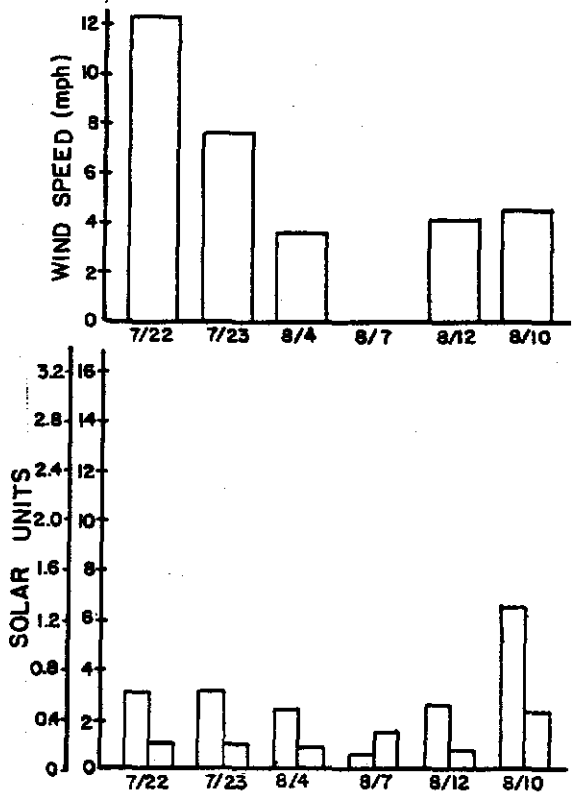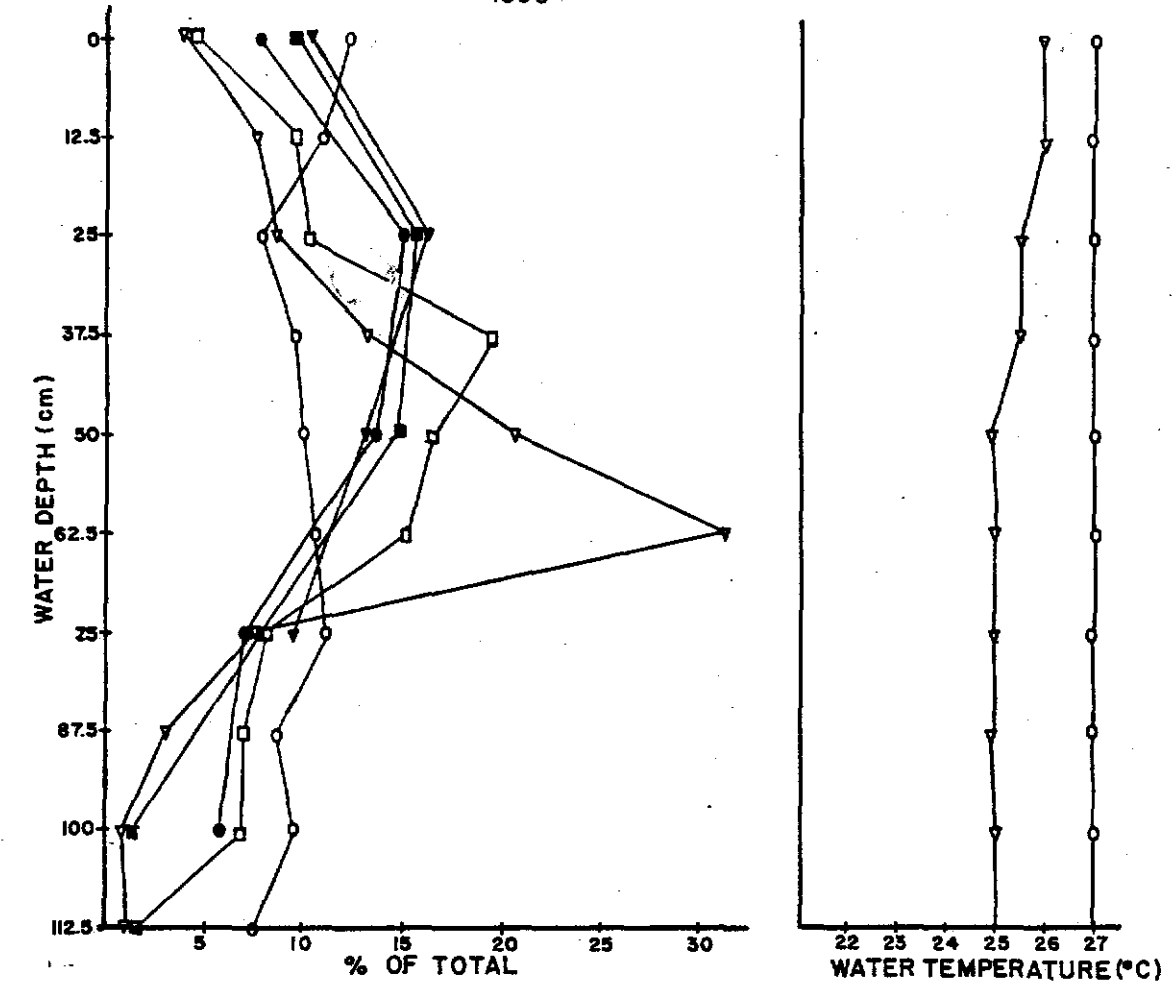
Figure 8.

The noon collections (Fig. 9) were made at low wind periods and show a very similar positioning pattern. The _Cerratia_ have positioned themselves at the lower end of the thermocline. They have moved away from the bottom, but are also avoiding the surface. At this time of maximum solar UV, the bulk of the population is 50 cm deep where the UV-B would be attenuated by a factor of 30.

The midafternoon collection (Fig. 10) shows two patterns of distribution. The low wind observations (8/4, 8/10, 8/12) show much the same pattern as the noon collection, a very large peak of distribution at an intermediate level in the water column. The peak distribution has moved upward to about 37.5 cm (attenuation of approx. 15). The thermal profile for these three days suggests a stable situation without mixing. The two observations when the wind was stronger (7/22, 7/23) show evidence that the _Cerratium_ was more mixed or somehow more evenly distributed in the surface waters. The 7/23 data suggests a well mixed surface layer overlying a stationary bottom layer; the 7/22 are similar but show a low density point at 25 cm which could be the core of the circulation where few organisms might collect.

The 1630 collection (Fig. 11 was again a collection from low wind days. The temperature gradients no mixing; there is a slight upward movement in the distributions of organisms. By 1830 (Fig. 12) some mixing of surface waters is evident in the temperature profiles for 8/10 and 8/12; on 8/4 the warm layer shows a constant decrease in temperature to 75 cm (the level absorbing approx. 80%

Figure 9.

The vertical distribution of <u>Cerratium</u> plotted as in Figures 6-8.
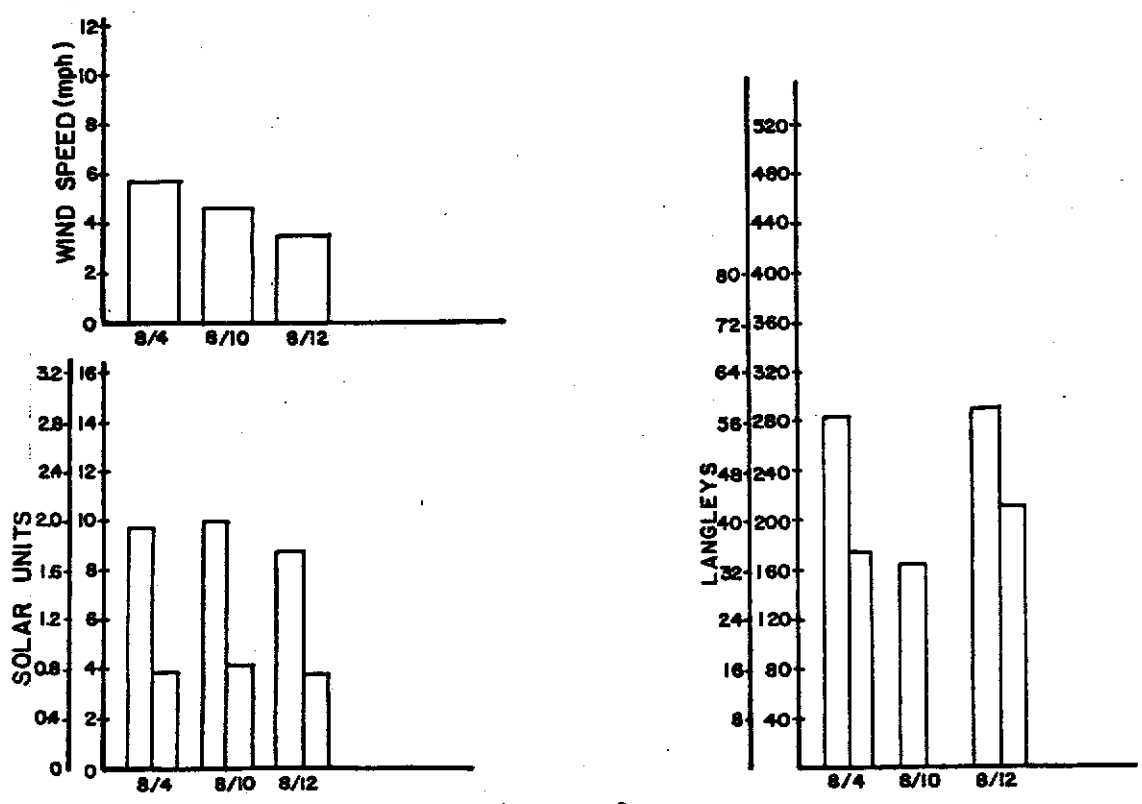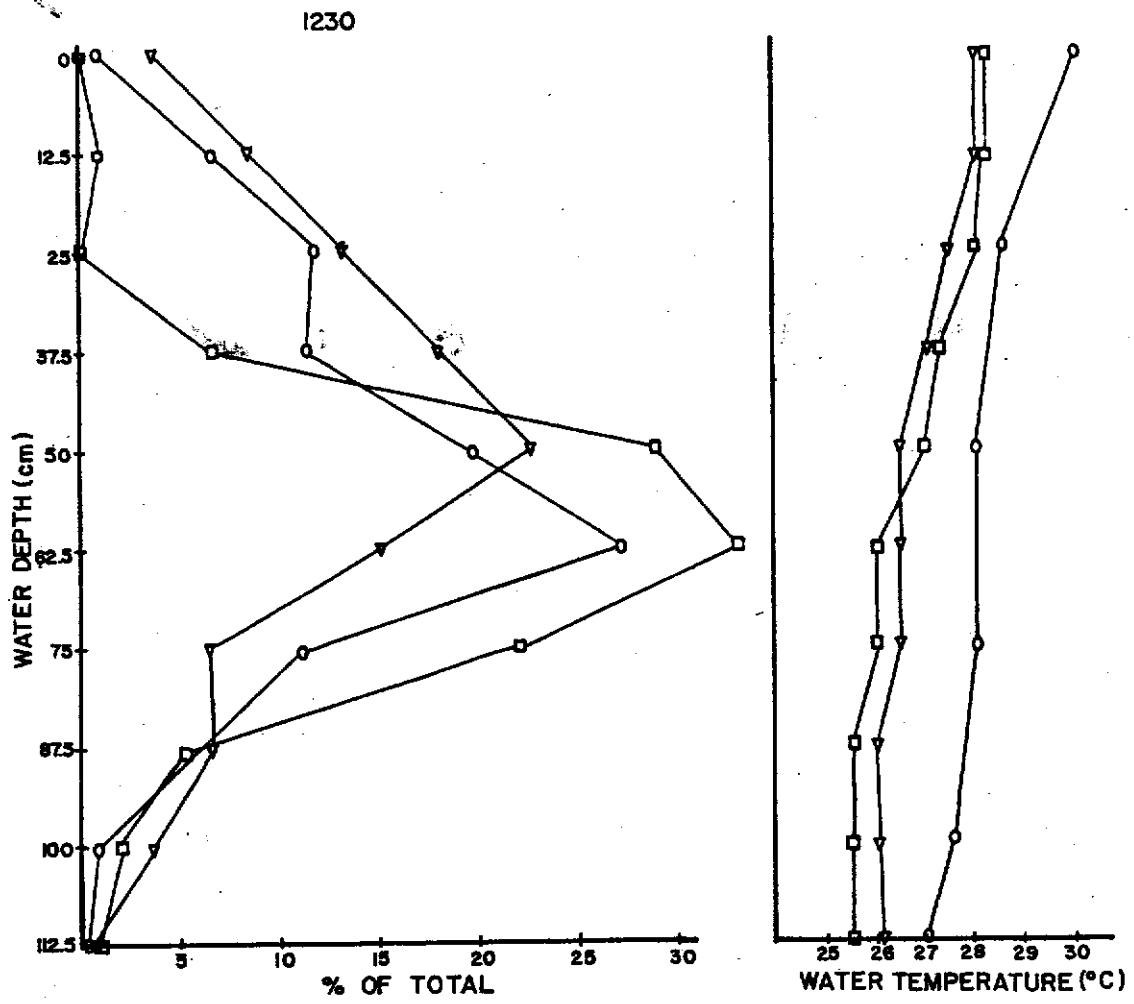
Symbols indicate 8/4 (0) 8/10 (∇) and 8/12 (□).

Figure 9.

Figure 10

The distribution of _Cerratia_ at 14:30 on several days, plotted as in Figures 6-9.

Symbols indicate - 7/22 (0), 7/23 (∇), 8/4 (▯), 8/10 (●), 8/12 (▼).
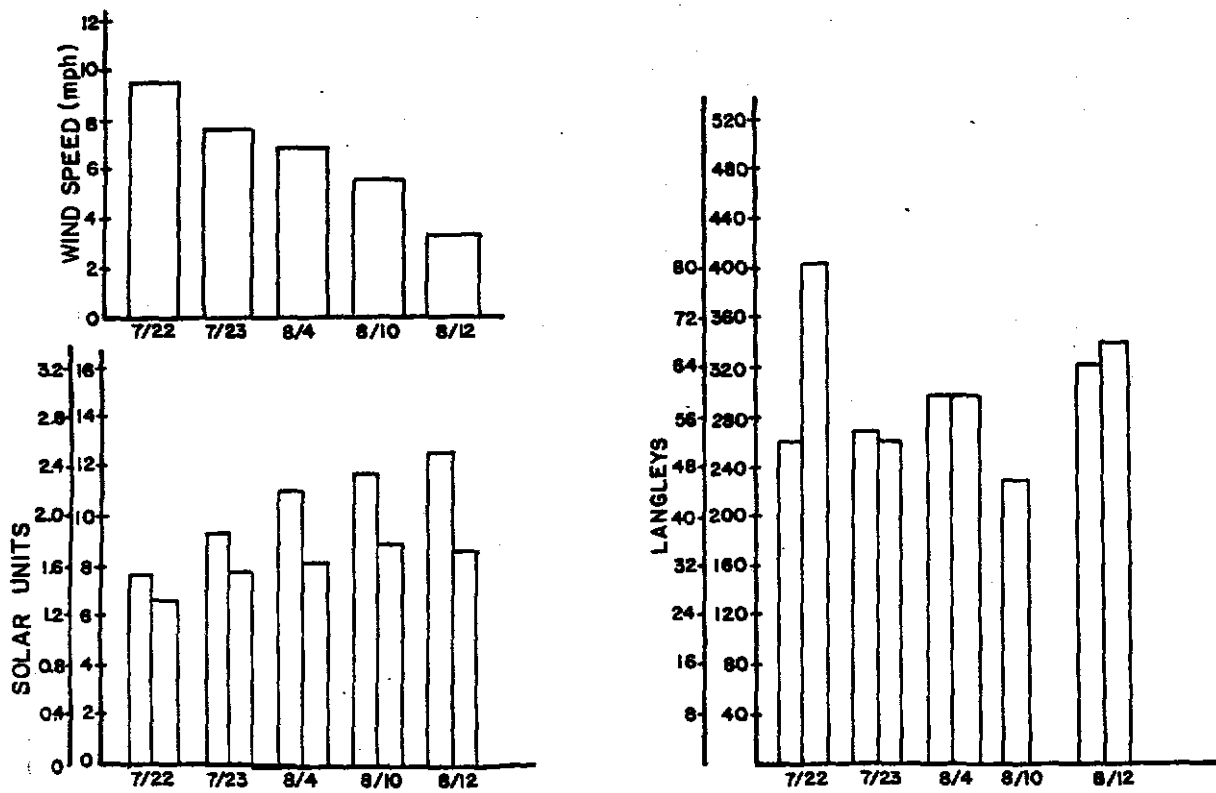
Figure 10.
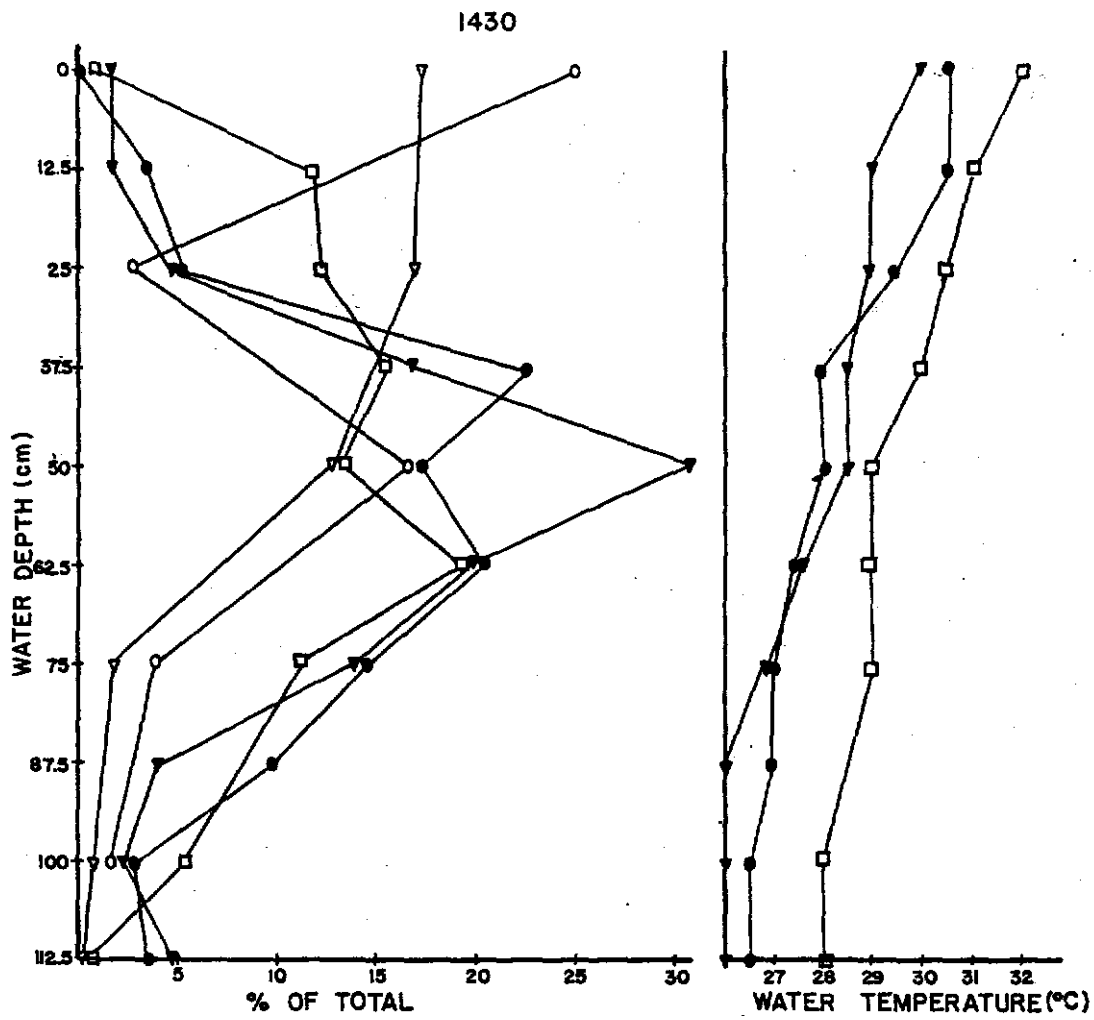
Figure 11

Vertical distribution profiles of <u>Cerratium</u> collected at 16:30 plotted as in Figures 6-10.

Symbols indicate collections on 8/4 (0) 8/10 (▯), 8/12 (∇).
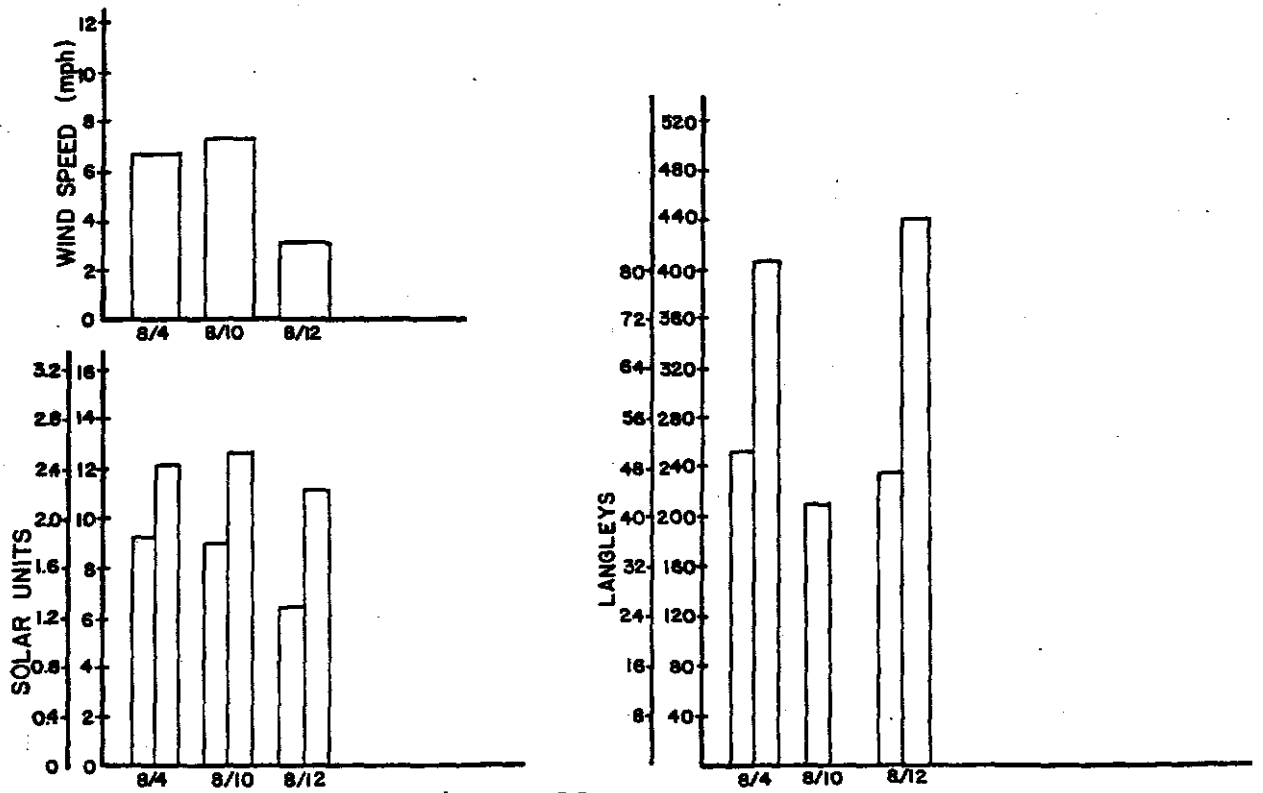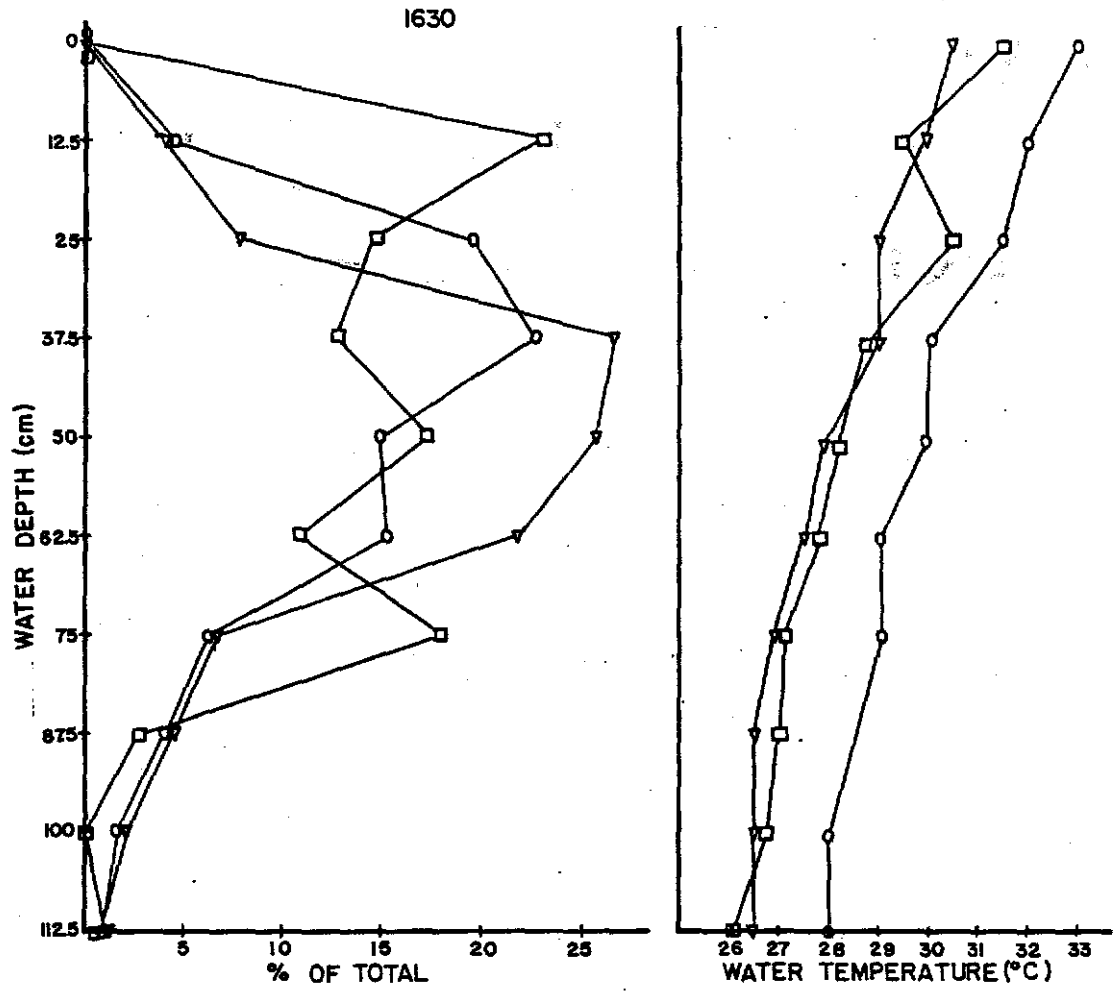
Figure 11.

Figure 12

The vertical distribution of <u>Cerratium</u> collected at 18:30 on various days plotted as in Figures 6-11.

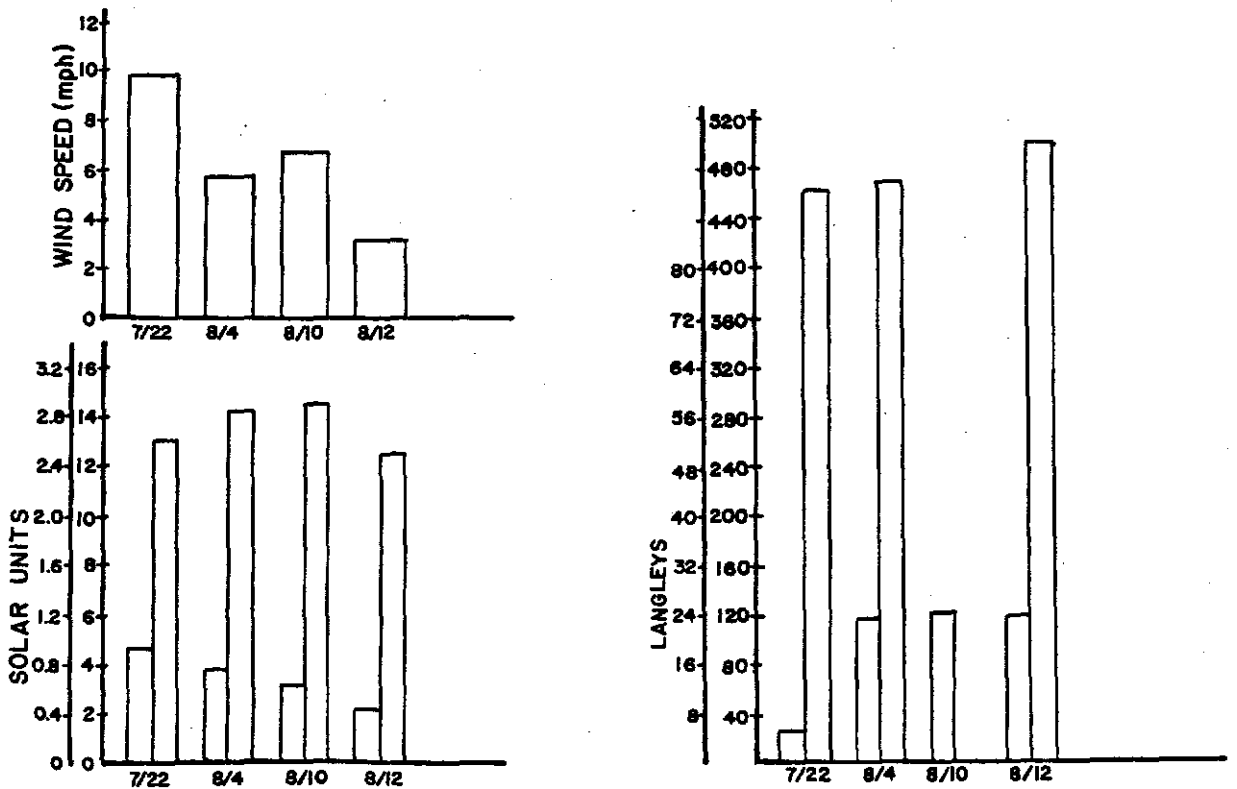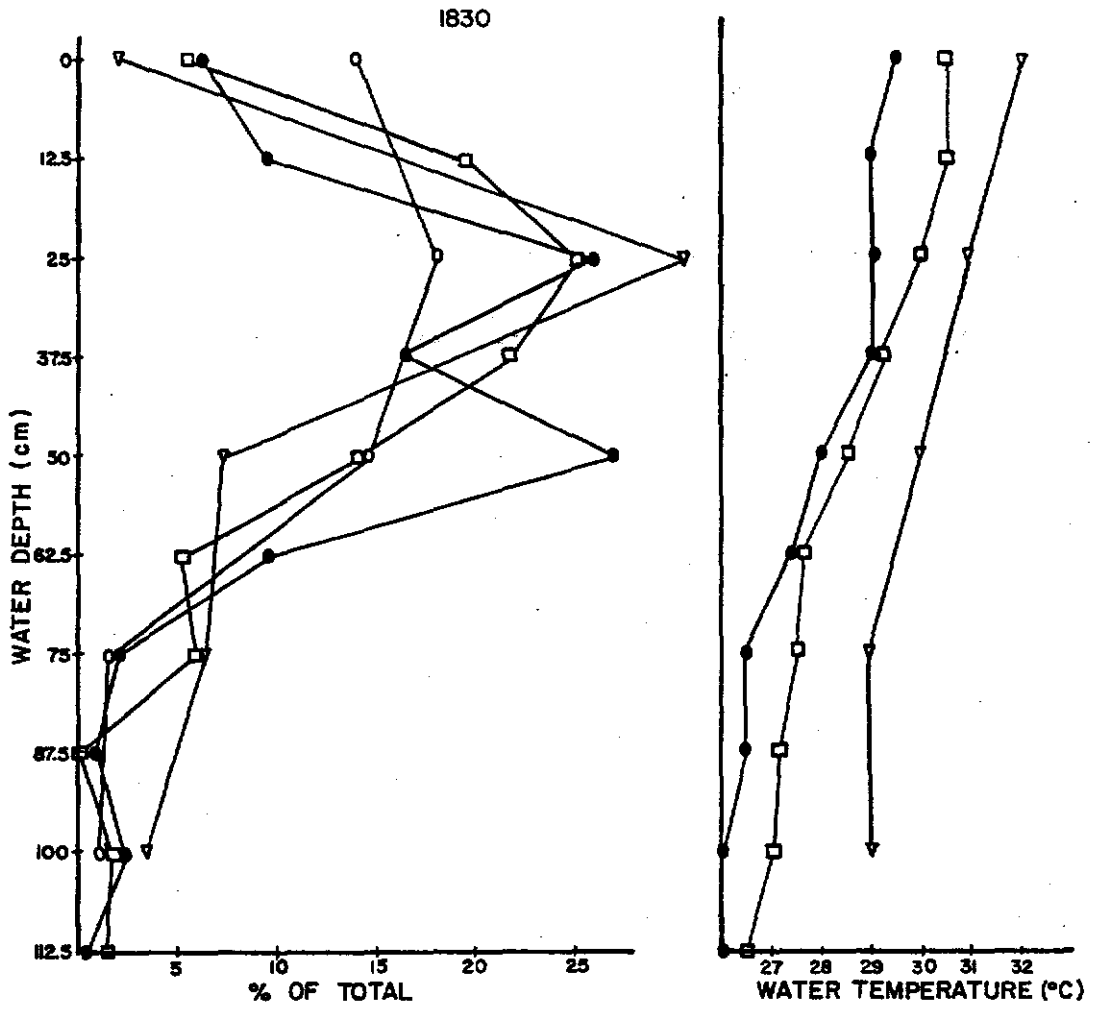Symbols indicate the date of collection 7/22 (0), 8/4 (∇), 8/10 (□), 8/12 (●).

Figure 12.

of the total incident radiation). When there is no evidence of stirring (8/4) there is a very sharp peak of population distribution which has now moved up to 25 cm below the surface. The two collections where the temperature profiles indicate mixing also show much broader distribution of the Cerratium population and the 8/12 collection shows a large peak at 50 cm, just below the level where the thermal profile indicates mixing. The 7/22 collection and wind data indicate a possibly mixed upper layer but the detailed temperature profile was not taken with the collection.

Small water bodies, such as the pond where our data was collected do not normally retain a temperature gradient overnight in summer. When the sun sets, the warm pond surface begins to radiate heat and cool producing an unstable surface of higher density which sinks and mixes. We observed a remarkably rapid mixing after sundown and uniform temperature was established with a matter of 2 to 4 hours (data not shown). As indicated in Figures 4, 5 and 6, uniform distributions of both Volvox and Cerratium prevailed through the night and various forms of stratification developed only after significant solar radiation was incident.

General Comments: The phytoplankton reported here show distinctly different distributions than the zooplankton previously noted (Barcelo and Calkins, 1979, 1980b) which moved downward from a uniform distribution, but in strong light showed no upward tendency at any time. Many factors were not recognized as important until the field data were analyzed, at a time when the project runs near its scheduled termination data. Much more relevant data could now be collected if the project were continuing,

but unfortunately this is often the case in research; a substantial amount of extraneous work must be done just to recognize the approach one should make to solving the problem. We did not recognize the value of detailed temperature profiles until late in the project. Also, we observed that windy days produced relatively uniform distributions and therefore we collected primarily on calm sunny days. We do not know the fraction of summer days where the pond would be essentially uniformly mixed throughout the day. From Fig. 1 and Fig. 3 the average UV-B exposure in our test pond equals $I_0/6$ or about 3.7 SU on a typical sunny summer day. The average visible incident (computed from Fig. 1) would be $I_0/2$ and for a typical sunny summer day would equal about 200 Langleys.

Inferences From the Field Observations:

1) Small water bodies reach a uniform temperature each night due to surface radiation cooling which then permits wind generated mixing. Consequently, the plankton tend to become uniformly distributed overnight.

2) Early morning light induces an upward movement in the phytoplankton.

3) Solar heating tends to stabilize the water column. Very strong wind will mix the entire water, but winds beginning after stabilization will form a mixed upper layer.

4) Intense solar radiation (the UV-B component appearing to be particularly efficient) moves planktonic organisms downward.

5) Without mixing, the distribution of phytoplankton will move upward after solar noon.

6) Under the most common conditions, partial or total mixing, the entire phytoplankton population will receive the same exposure to both solar UV-B and photosynthetically active light.

7) The UV-B exposure which the entire population receives under mixed conditions constitutes a significant fraction of the maximum tolerable dose.

Implications in Relation to Comprehension of the Ecological Role of Solar UV and Prediction of the Effects of Ozone Depletion

The ecological consequences of solar UV-B according to static model of the euphotic zone divide populations into two classes:

1) A surface layer of organisms which are wiped out by solar UV and 2) below this layer a protected population which is in no way impacted by solar UV. Such a model, although it is the primary way in which aquatic systems have been modeled is clearly unrealistic. If the assumed conditions existed in real waters the surface populations would disappear in a day or two and only the deep protected population would exist. The fact that mixing occurs each night would tend to make the calculated average dosage applicable over periods of the order of a week or more; furthermore, it is rare that some mixing does not occur each day, even aside from the movements of the organisms themselves.

The model assuming mixing predicts a population in which all numbers receive the same levels of visible light (which produces much more effective photosynthesis) and UV-B. From the shape of

the dose-response relationships most frequently observed (the threshold or "shouldered" type) for aquatic organisms, Calkins 1975a, it is implied that the entire population is protected from UV-B effect at the present level. However, the uniformity of dosage in the population and the proximity of the present exposures to the maximum tolerable dosage implies that relatively small increases in UV-B levels could throw the entire population beyond its tolerance limit and it would disappear from the water body and be supplanted by a more resistant species. The succession of species in various waters is well known and solar UV-B is clearly present in sufficient amounts to play a role in some cases.

When organisms are able to drop out of the circulation upon reaching the limit of their UV-B tolerance their survival will be protected, but likewise the visible light will be less fully utilized and the productivity of the waters will decline. Knowing the ratio of K_{UV}/K_{vis} permits a calculation of the loss of primary productivity which would accompany any given increase in UV-B flux. The impact on freshwaters would not be as drastic as the marine situation where K_{UV-B} more nearly equals K_{vis}, however, even the more productive freshwaters would suffer some reductions in primary photosynthesis, a possible ecological consequence of even modest (5-10%) increases in UV-B.

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