

Observations on the horizontal coherence of chlorophyll *a* and temperature

M. J. R. FASHAM* and P. R. PUGH*

(Received 12 June 1975; in revised form 26 August 1975; accepted 9 September 1975)

Abstract—Time series of chlorophyll *a* fluorescence and temperature have been obtained at a number of depths, from two widely separated areas of the North Atlantic. These data strengthen the view of Platt and his co-workers that, over space scales between 40 m and 1 km, phytoplankton behaves as a passive contaminant of fluid motion. It was found that the observed high coherence between chlorophyll *a* and temperature extended to longer wavelengths for stations observed in temperate spring bloom conditions, than for stations observed in tropical summer conditions.

Certain features of the temperature and chlorophyll *a* power spectra are discussed which suggest that, at frequencies less than the Brunt-Väisälä frequency, internal waves make a significant contribution to the spectrum. This implies that, for space scales between tens of meters and a few kilometres, improved sampling methods will be required to separate the effect of internal waves from the real spatial heterogeneity of the phytoplankton.

INTRODUCTION

It is generally accepted that the spatial distribution of phytoplankton and zooplankton, in the oceans, is usually patchy or aggregated. This has been demonstrated over a wide range of length scales, from centimetres (CASSIE, 1959) through metres (BERNHARD and RAMPI, 1965; WIEBE, 1970; FASHAM, ANGEL and ROE, 1974) to kilometres (CUSHING and TUNGATE, 1963). A number of different causal processes have been suggested to explain this patchiness (STAVN, 1971) but very few experiments have actually demonstrated any of these processes in the ocean. A number of workers (BARNES and MARSHALL, 1951; CASSIE, 1960; FASHAM, ANGEL and ROE, 1974) have demonstrated a correlation between the abundance of particular zooplankton species and temperature or salinity but this still begs the question as to the causal mechanism. Furthermore, it is unlikely that one process will explain patchiness at all length scales.

An analysis of some time series of temperature and chlorophyll *a* measurements made in the Gulf of St. Lawrence by PLATT (1972) and DENMAN and PLATT (1975) have led them to suggest that, over length scales between 10 m and

1 km, the local abundance of phytoplankton might be controlled by the physical transport process of the water and not by any dynamic behaviour of the organisms.

In parallel with this work mathematical models have recently been developed (STEELE, 1974a, c; PLATT and DENMAN, 1975) in which the effects of the horizontal turbulent diffusion of water have been added to equations representing the growth of phytoplankton and its predation by herbivores. These studies suggest that patches attributable to variable phytoplankton growth rate would only occur above a certain critical size (10 to 100 km) and that, below this critical size, patches would be dispersed by diffusion.

This parallel development of methodology and theory obviously represents an important advance in the problems of plankton patchiness. The experimental work described above was carried out at shallow depths in a coastal area, but there is no obvious reason why similar mechanisms should not occur in deeper waters. This paper describes a series of experiments to look at the distribution of chlorophyll *a* at various

*Institute of Oceanographic Sciences, Wormley, Godalming, Surrey, England.

depths in two open ocean areas of the North Atlantic.

METHODS

The experiments were carried out during two cruises of R.R.S. *Discovery* in 1974 (see Table 1 for station data). Chlorophyll *a* fluorescence was measured continuously using either a Turner Model 111 or an Aminco fluorometer supplied with water from a Flygt Model B2050 submersible pump. The fluorometer readings were calibrated at intervals by taking discrete samples from the outflow and measuring the chlorophyll *a* concentration spectrophotometrically.

The pump was suspended over the side of the ship at a depth of *ca.* 3 m and water was brought on to the deck through 30 m of 5-cm bore reinforced plastic tubing at a rate of between 150 and 185 litres min⁻¹, depending on the total length of tubing used. A small 'bleed' was taken from the centre of this tubing and passed to the fluorometer, the flow rate being adjusted to *ca.* 500 ml min⁻¹. To the suction side of the pump, various lengths, 61 to 122 m, of 5-cm bore hosing were attached, dependent on the depth to which sampling was to be carried out. The water inlet probe consisted of a cylinder of polypropylene, closed at one end, but perforated by numerous small holes. This was designed (a) to avoid the

capture of large animals; (b) to prevent any clogging of the inlet by, for example, jellyfish; and (c) to reduce the overall suction pressure (as the total area of the holes exceeded the cross-sectional area of the tubing) and thereby reduce the disturbance to the surrounding water. This device was attached to a Bissett-Berman STD (salinity-temperature-depth) probe so that it was about 0.5 m above the sensors and projected out about 1 m from the probe itself. With this arrangement, and the positioning of the water intake holes in a horizontal plane, it was hoped that the sensors would not be affected.

For these experiments an Aanderaa recording current meter was suspended on a 0.5-m strop below the STD probe, and was adjusted to record the current velocity and direction continuously. However, due to a malfunction, records were not obtained for Stas. 8517/7 and 8517/8. On analysis of the tapes the mean drift of the water past the sensors was calculated taking into account the mean ship's drift as determined by the two-component E.M. logs and satellite navigation (FASHAM, 1970).

The frequency outputs of the STD and the millivolt output of the fluorometer were sampled, usually every 1.6 s, by the shipborne IBM 1800 computer, using the standard STD sampling program. All the raw data were stored on disc,

Table 1. *Details of the experiments.*

Run	Discovery Station	Date	Position	Duration	Depth of Sensors (m)	Approx. thermocline depth (m)	Water depth (m)	Wind Speed (Knots)	Number of observations	Max. or Min. cross-correlation coefficients
1	8507/34	5.iv.74	43°52'N 12°49'W	2257-0006	25	20	4750	8-10	243	0.95
2	8507/34	6.iv.74	43°55'N 12°44'W	0021-0320	25	20	4750	8-10	456	0.85
3	8507/35	6.iv.74	43°56'N 12°42'W	0415-0615	15	20	4750	6-9	420	0.90
4	8513/5	7.v.74	42°47'N 11°55'W	2244-2350	100	10	1640	2-5	250	0.88
5	8513/7	8.v.74	42°47'N 11°57'W	0217-0455	20	10	1640	2-7	490	0.96
6	8513/8	8.v.74	42°48'N 11°58'W	0457-0711	45	10	1640	8-14	441	-0.69
7	8598/2	21.viii.74	8°39'N 23°07'W	0233-0435	50	25	5000	13-17	441	-0.79
8	8617/2	25.viii.74	8°45'N 23°00'W	0401-0602	50	20	5000	13-18	416	-0.64

N.B. The number of observations refers to the number after averaging. See text for details.

so that during subsequent analyses of the results any averaging time could be used to compensate for the response time of the fluorometer and the turbulent mixing of the water in the hosing.

The turbulent mixing factor was calculated from the diffusivity rate, having first clearly established that the flow in the hosing was turbulent. Depending on the length of tubing used, which also affected the flow rate, this mixing was calculated to occur over a distance of between 4.3 and 5.5 m, which represents a minimum response time of 2.8 to 4.5 s. These values can be less than the minimum response time of the fluorometer (PLATT, 1972). The theoretical transit time for the water through the hosing was also calculated so that the delay time between the STD and fluorometer readings could be assessed.

The experiments were carried out during periods of calm weather so as to minimize the ship's drift and its degree of rolling which, by affecting the head of water, could result in irregular flow rates. Each experiment was carried out over as long a time period as possible, consistent with the computer disc storage space. To avoid any effects of fluorescence inhibition, in shallow depths, by high light intensities (KIEFER, 1973) all the runs were made at night. Each run was usually preceded by a vertical profile of fluorescence down to *ca.* 100 m. The depth for the first three runs was chosen to be close to the seasonal thermocline, while the other runs were at a number of depths below the thermocline.

Nutrient and chlorophyll samples were collected at 10-min intervals. The values for the nutrient concentrations, however, were at the lower limit of detection and consequently have not been included here.

CALCULATIONS

The time series were analysed by calculating the power spectra of temperature and fluorescence separately, and the cross spectrum between temperature and fluorescence. The cross spectrum consists of two parts, the squared coherency and the phase, but attention in this paper will be focussed on the squared coherency. This quantity, which for brevity will usually be referred to as the

coherence, takes the value zero when there is no correlation at a given frequency between the two time series, and the value 1 when there is perfect correlation.

Before analysis samples were averaged in groups of ten to minimize aliasing problems and to allow for the response time of the sampling system. The profiles were then de-trended by subtracting a straight line joining the two end values. This method has been shown by FRANKIGNOUL (1974) to cause the least distortion to the spectral estimates. The power spectra and cross spectra were calculated using the Fast Fourier Transform and then averaging the Fourier harmonics over a given interval (JENKINS and WATTS, 1968). A constant value is often used for this interval but, if the spectrum is to be plotted on a log-log scale, this will result in a crowding of estimates at the high frequency end of the spectrum, while at low frequencies, which are often of most interest, there will only be a few points. This was avoided by starting with a low averaging interval and then gradually increasing its value for successive estimates. The sequence of intervals used in these analyses was 3, 3, 4, 5, 6, 7, 8, 10, 12, 15, 18, 22, 26, 32, 38. . . . A consequence of this method is that the confidence intervals decrease with frequency but this was not found to be a disadvantage.

Before calculating the cross spectrum between fluorescence and temperature the former profile was shifted by an amount equal to the time delay caused by pumping the water from the inlet to the fluorometer. As there was in all cases a high correlation between temperature and fluorescence, the delay could be estimated by calculating the cross-correlation function between these two quantities and observing the lag value for which this function was a maximum (or minimum in the cases where the profiles were 180° out of phase). The delay was found to be 100 and 144 s using 122 and 152 m of tubing, respectively.

RESULTS

The first six runs were taken in the southern part of the Bay of Biscay during the spring phytoplankton bloom. Vertical profiles of tem-

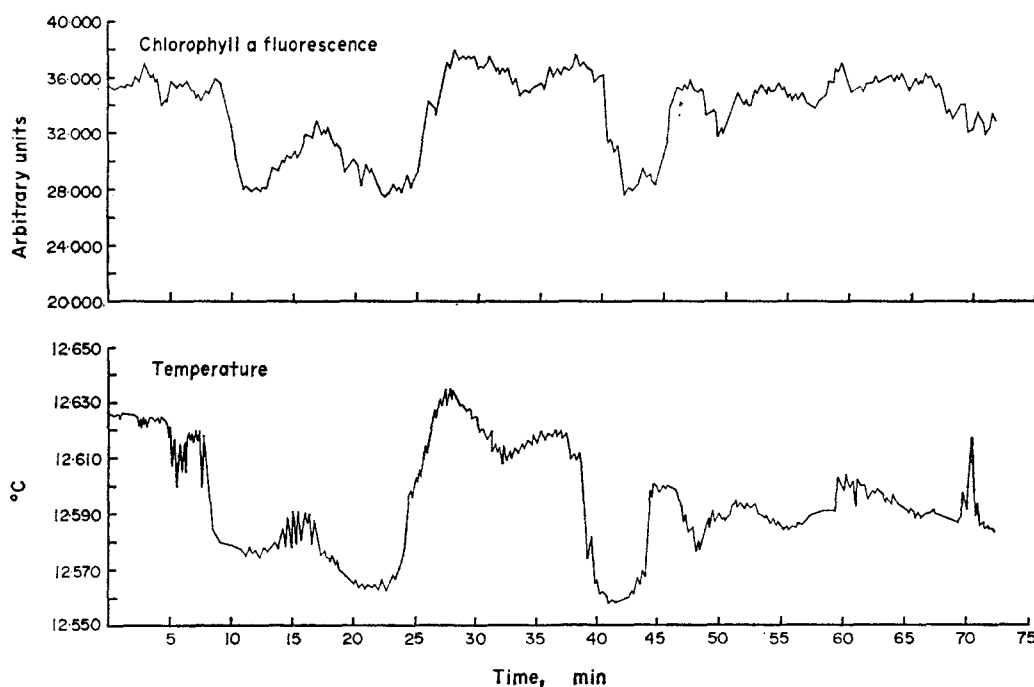


Fig. 1a. Time series of chlorophyll *a* fluorescence and temperature obtained on run 1. Sampling interval 1.6 s.

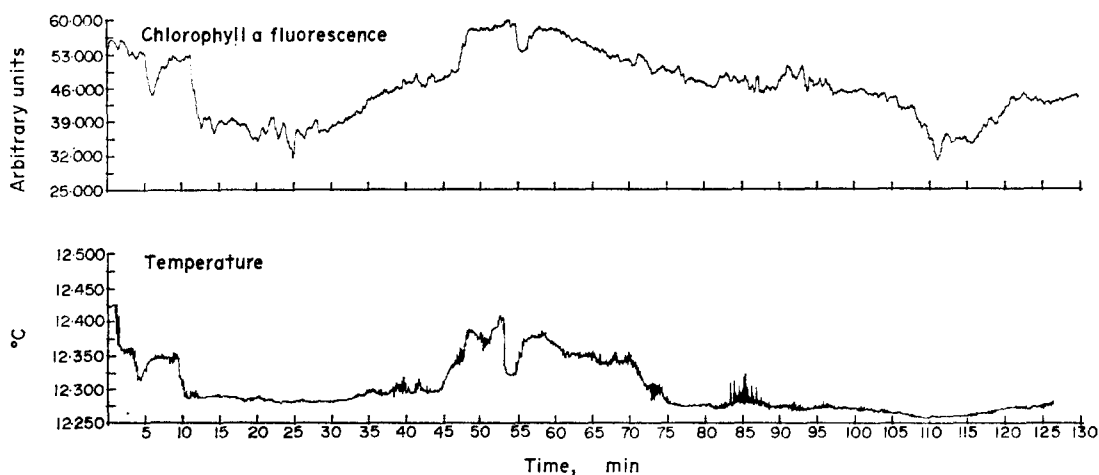


Fig. 1b. Time series of chlorophyll *a* fluorescence and temperature obtained on run 2. Sampling interval 1.6 s.

perature and salinity taken during this period showed that the seasonal thermocline was in the process of formation and was sometimes partially stabilized in calm conditions. The temperature difference across the thermocline was small, usually of the order of 0.1 to 0.5°C. In

contrast, the last two runs were made in the tropics in the presence of a permanent thermocline with a temperature difference of 3 to 4°C. In addition, the mean phytoplankton abundance was about two orders of magnitude less than that in the Bay of Biscay.

The salinity records for all runs were considerably affected by spikes which made them unsuitable for spectral analysis and so only temperature and chlorophyll *a* profiles were analysed. Figure 1a shows the sampled values of temperature and chlorophyll *a* fluorescence for run 1. It is immediately apparent that, despite the small variation in temperature, there is an obvious positive correlation between temperature and fluorescence. As another example the data from run 2 have been plotted in Fig. 1b. In this case the overall correlation is not so high (see Table 1), and also a visual inspection suggests that the degree of correlation varies throughout the run, being highest in the middle and lowest at either end. The rest of the runs show very similar features.

The temperature and fluorescence power

spectra for run 1 are plotted in Fig. 2 and, as would be expected from Fig. 1a, they are similar in form. The slope of both graphs is slightly steeper than -2 and both have a noticeable peak at about 7 cycles h^{-1} . A prominent signal having a period of this order is obviously present in Fig. 1a. These features were also present in the power spectra for runs 2 and 3. The squared coherencies between temperature and fluorescence for runs 1 to 3 (Fig. 3) show significantly non-zero values for frequencies between 1 and 40 cycles h^{-1} , while at higher frequencies the coherence drops to zero. In addition runs 2 and 3 show a peak in coherence at about the same frequency (6–7 cycles h^{-1}) for which there were peaks on the power spectra of temperature and fluorescence.

The mean current velocity during run 6 was 35 cm s^{-1} ; this value has been used to calculate

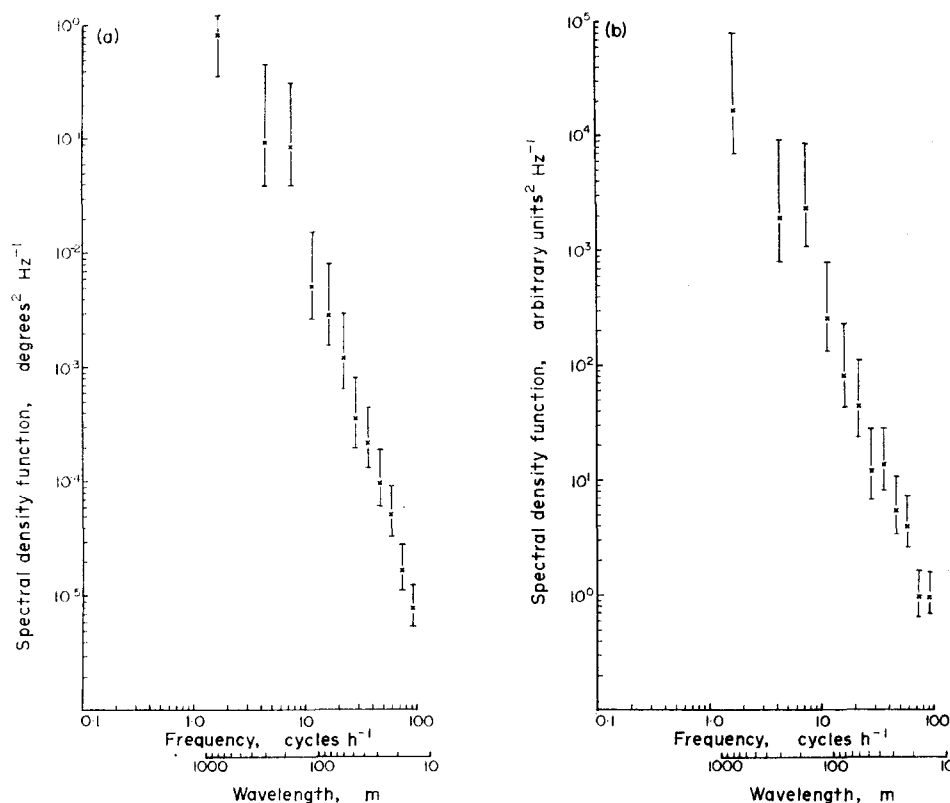


Fig. 2. Spectral density function of temperature (a) and chlorophyll *a* fluorescence (b) for run 1. Confidence intervals are at the 95% level.

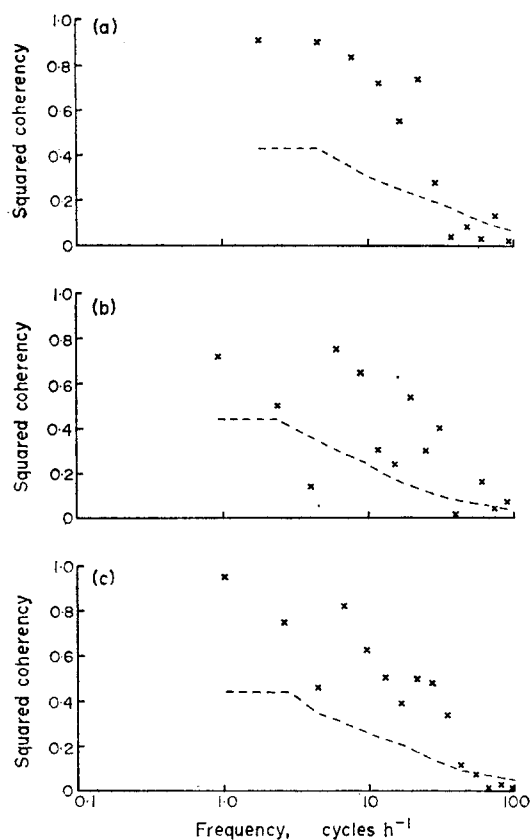


Fig. 3. Squared coherency between temperature and chlorophyll *a* fluorescence for runs 1 to 3 (a to c). The dotted line indicates the 95% confidence interval assuming the true coherency to be zero.

the space scale on Fig. 2, using the frozen turbulence approximation. It is difficult to confirm the validity of this approximation in any particular case and so these space scales should be treated with some caution. However, they probably give fair indications of orders of magnitude.

The second group of runs (4 to 6) were taken in approximately the same area but about one month later. Despite the fact that run 4 was deeper than any of the other runs, there are more similarities between this run and 5 and 6 than between 5 and 6 and the other five runs. The power spectra for run 6 only has been shown (Fig. 4), the spectra for the other two runs being very similar. The slopes of both spectra are close to -2 and, in contrast to the previous runs, there are no prominent peaks. Furthermore, the

squared coherencies (Fig. 5) drop below the 95% significance level at much lower frequencies than for the previous runs. This is most marked on run 6, while runs 4 and 5 do have some high coherencies in the range 10 to 50 cycles h^{-1} . It will be noted (Table 1) that the cross correlation function for run 5 was positive while for run 6, taken shortly after, it was negative.

Runs 7 and 8 were made in the tropics in the presence of a strong thermocline. In both cases temperature and fluorescence were negatively correlated. The power spectra for run 8 (Fig. 6) show marked similarities to the first three runs in having a prominent low frequency peak (in this case at about 5 cycles h^{-1}) and a high frequency slope steeper than -2 . The squared coherencies (Fig. 7) are also similar to the first three runs, except in one respect. They differ in that the coherence at the lowest frequency drops below the 95% significance level. The mean current velocities for runs 7 and 8 were 80 and 58 $cm\ s^{-1}$ respectively and these values were used to obtain the space scales in Fig. 6.

DISCUSSION

The coherence between temperature and chlorophyll *a* fluorescence described above supports PLATT's (1972) conjecture that over certain space scales the chlorophyll *a* concentration behaves as a passive contaminant of the fluid motion of water. During the writing of this paper, Dr. T. Platt kindly provided us with proof copies of his group's latest work on this topic (DENMAN and PLATT, 1975) in which they have also calculated squared coherencies between temperature and fluorescence and their results agree broadly with the results presented in this paper. This agreement is especially interesting in that our experiments were made at a number of depths in deep ocean areas while the experiments of Denman and Platt were all carried out in the top 10 m in shallow coastal regions.

The main features of the power spectra were the peak at the low frequency end followed by a tailing off at a slope (on the log-log scale) of -2 or steeper. In comparing our data with those of DENMAN and PLATT (1975) the peaks in our

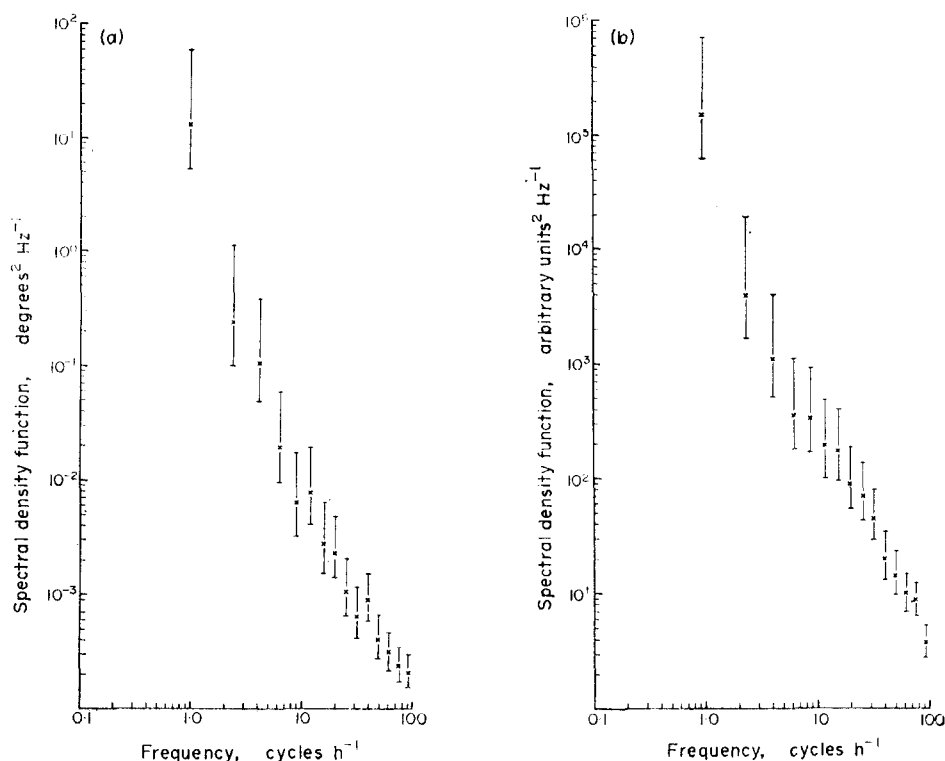


Fig. 4. Spectral density function of temperature (a) and chlorophyll *a* fluorescence (b) for run 6.

spectra can probably be identified with the 'Knee' referred to by them, at which their spectra showed a change of slope. In fact a number of their spectra do show a peak at this point although they do not refer to it. Denman and Platt state that this 'Knee' usually occurs at a wavelength of 100 m while in our case the peak was found at wavelengths of 200 to 400 m (see Figs. 2 and 6). In view of the assumptions of the frozen turbulence approximation this can be considered good agreement.

Many attempts have been made to explain the form of the power spectra for the fluid motion of the water (or some passive contaminant of it such as temperature) in terms of hypothetical properties of this motion. This task is complicated by the fact that different physical processes may dominate in different frequency ranges (KITAYGORODSKIY, MIROPLO'SKIY and Filyushkin, 1973). For instance throughout the inertial sub-range the Kolmogorov theory of locally isotropic

turbulence predicts a $-5/3$ power law relating the energy density to frequency. In his first paper, PLATT (1972) suggested that his chlorophyll spectrum obeyed a $-5/3$ law while admitting that the assumptions of local isotropy were unlikely to be valid over the frequency range covered by the experiment. However, OKUBO (1972) stated that other theories of turbulence have been postulated that do not require the isotropy assumption.

In an area of large density gradients, such as the thermocline, internal waves are a likely contributor to the power spectrum for frequencies less than the Brunt-Väisälä (B-V) frequency. Indeed, ARMSTRONG and LAFOND (1966) observed a high correlation between temperature and nitrate, silicate and transparency from continuous samples at a depth of 9 m off the coast of California. They attributed this correlation to internal waves propagating along the thermocline which was itself a horizontal boundary between two

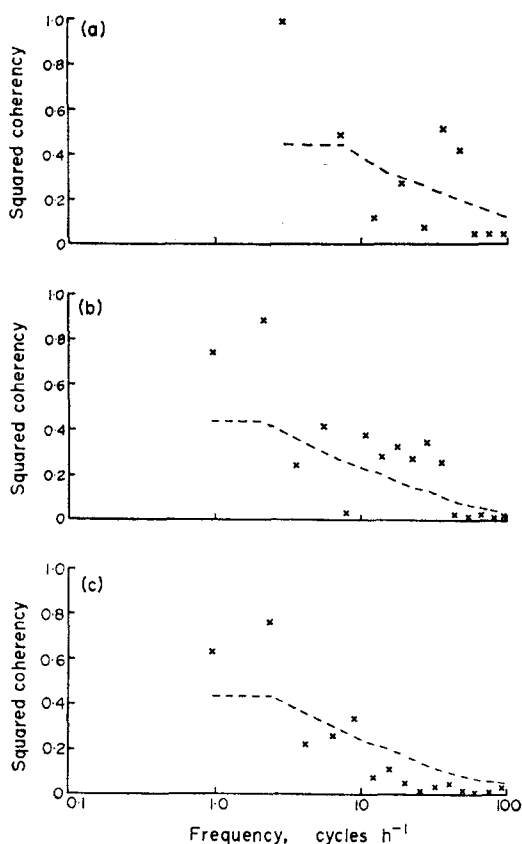


Fig. 5. Squared coherency between temperature and chlorophyll *a* fluorescence for runs 4 to 6 (a to c).

layers of different chemical properties. They did not carry out a spectral analysis but the dominant period was of the order of 10 to 20 min, which is similar to that observed in the present data.

GARRETT and MUNK (1972, 1975) have developed a semi-empirical model to describe the spectrum of internal waves in wave number and frequency space. This model predicts a -2 power law for frequencies between the inertial frequency and the local B-V frequency. However, PHILLIPS (1971) has shown that, if the vertical structure consists of uniform layers separated by thin sheets of high temperature and density gradient (WOODS and FOSBERRY, 1966; OSBORN and COX, 1972), then observations obtained from a temperature sensor fixed at one depth will produce a -2 power law for the spectrum irrespective of the underlying motions of the water.

It would seem, therefore, that little can be deduced from the slope of the power spectra. However, the small peak at the low frequency end of the spectra does perhaps deserve more attention. This peak has been observed in temperature spectra by a number of workers studying internal waves (BRISCOE, 1974; PINKEL, 1974; CAIRNS, 1975) and was found to occur at a frequency close to the local B-V frequency. In our case it was not possible to measure the local B-V frequency during the experiment but for runs 7 and 8 vertical STD profiles were made immediately preceding the main experiment and these produced B-V frequencies in the range 5 to 10 cycles h⁻¹ which agrees favourably with the frequency of the peaks in the temperature and chlorophyll power spectra. It is interesting to note that CAIRNS (1975) used the Garrett and Munk model to simulate the peak observed in his temperature spectra and suggested that an internal wave with six modes was adequate to fit the data.

The probable presence of internal waves must be taken into account when interpreting the cross spectra between temperature and fluorescence. The coherencies for runs 2, 3 and 7, 8 (Figs. 3 and 7) all show peaks in coherence at the same frequency as the peaks in the individual power spectra of temperature and fluorescence. This fact is consistent with the presence of internal waves, given that there is some correlation between the vertical profiles of temperature and fluorescence. The cross correlation coefficients (Table 1) show that, taking the profiles as a whole, temperature and fluorescence can be either positively or negatively correlated. This will obviously depend on whether the vertical gradients of temperature and fluorescence against depth have the same or different signs. The first case will probably be the most common, but fluorescence profiles similar to Fig. 8 are often observed and in this case the sign of the correlation will depend on the sampling depth. Runs 5 and 6 provide an example of this.

The cross spectra for runs 1, 2, 3, 7 and 8 all show coherencies significantly greater than zero at frequencies between the B-V frequency and about 40 to 50 cycles h⁻¹. Thereafter the coherence drops below the 95% level. This high coherence

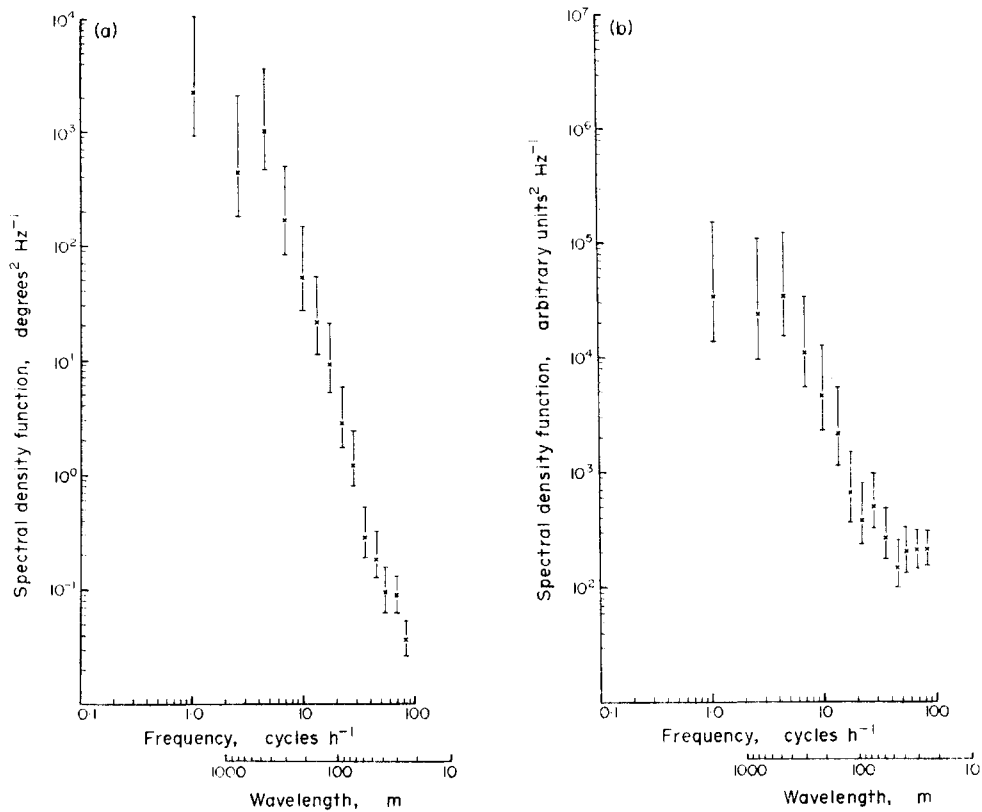


Fig. 6. Spectral density function of temperature (a) and chlorophyll *a* fluorescence (b) for run 8.

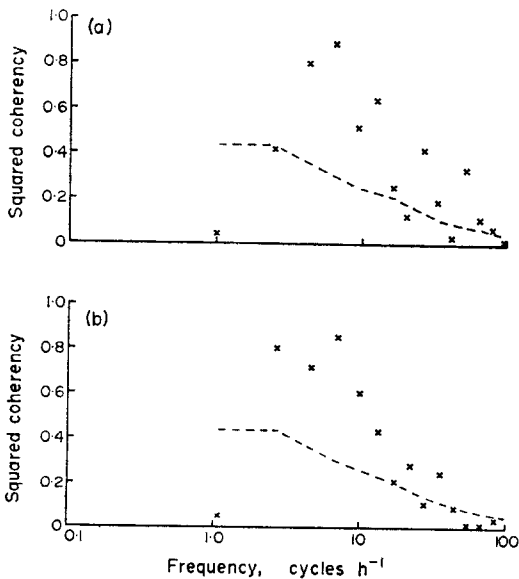


Fig. 7. Squared coherency between temperature and chlorophyll *a* fluorescence for runs 7 and 8 (a and b).

at frequencies above the B-V frequency could be caused either by horizontal turbulent motions or by contamination, caused by the internal waves, from small-scale vertical structures possessing high correlations between temperature and fluorescence. The present experiment is unable to distinguish these two processes.

The data from runs 4, 5 and 6 showed some differences from the other runs. The coherence for runs 4 and 5 dropped below the 95% level at a number of frequencies less than 40 cycles h⁻¹, while for run 6 the coherence was only significantly greater than zero at frequencies less than 3 cycles h⁻¹. The absence of any peaks in the power spectra for these runs suggests that the loss of coherence may be related to a reduction in the amplitude of internal waves. If this is true it again suggests that a large amount of the coherence for frequencies up to 50 cycles h⁻¹ shown during the other runs may be caused by internal waves.

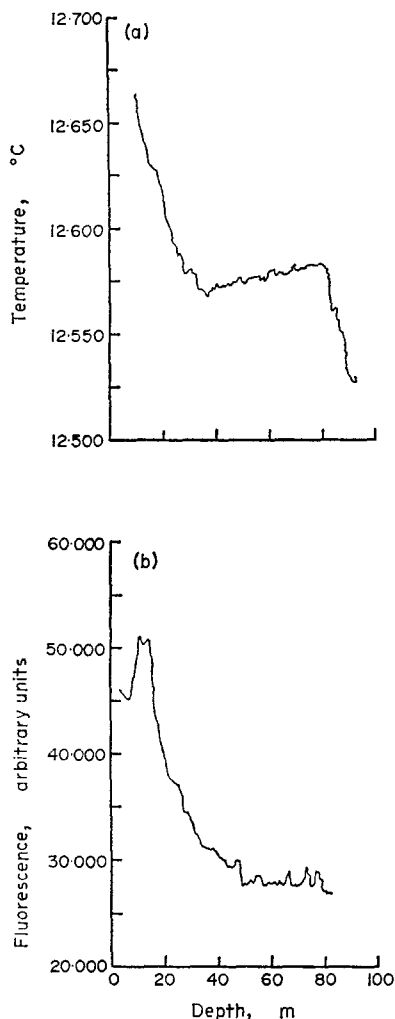


Fig. 8. Depth profiles of temperature (a) and chlorophyll *a* fluorescence (b) taken just before run 4.

If we now consider the coherence at frequencies less than the local B-V frequency, then the data show an interesting difference between the Bay of Biscay results and those for the tropical area. The former showed no drop in coherence at low frequencies (space scales greater than 1 km, assuming the frozen turbulence approximation) while the data from the tropics did show a drop. This latter result was also obtained by Denman and Platt using a towed pumping device and they interpret this in terms of the critical path size referred to in the introduction. Thus for space scales above this critical size areal differences in

the growth rate of phytoplankton will not be damped out by horizontal diffusion and this will result in a drop in coherence between temperature and fluorescence. Furthermore, the presence of internal waves should not affect this conclusion as the horizontal space scales involved are much longer than any possible amplitude of the internal waves, bearing in mind the depths of the thermocline (Table 1). We can thus conclude that the critical path size was smaller in stable tropical conditions than in the temperate spring bloom. WROBLEWSKI, O'BRIEN and PLATT (1975) have used scale analysis to derive a formula for the critical length, L_c , viz.

$$L_c = 2\pi \left(\frac{D}{b - R_m \lambda} \right)^{\frac{1}{2}},$$

where D is the eddy diffusivity, b the phytoplankton growth rate, R_m the herbivore maximum grazing rate and λ is the Ivlev constant. A large value for the critical length (L_c) can, therefore, be caused either by a large eddy diffusivity or by phytoplankton growth being in balance with herbivore grazing. PLATT and DENMAN (1975) and STEELE (1974b) suggest that the latter effect may be common in the open seas, especially following the spring bloom. However, the large values for critical length in the Bay of Biscay were observed *during* the spring bloom. It is, of course, possible that the differences between the two areas may be due to local differences in the eddy diffusivity. If measurements of eddy diffusivity could be made, then experiments of this sort could be used to test the mathematical theories of critical length.

It has been suggested above that in regions of a large temperature gradient, such as a thermocline, internal waves will make a significant contribution to the power spectrum for frequencies less than the local B-V frequency. KAMYKOWSKI (1974) has stated that given a uniform distribution of organisms above the thermocline, then an internal wave propagating along this thermocline will cause aggregations above the troughs of the wave. This conclusion appears to be erroneous as although the vertical to horizontal dimensions of an area of water change during the passage of

the wave, as stated by Kamykowski, the density of organisms per unit area remains the same. However, if there is a vertical gradient of organism density then internal waves will create an apparent horizontal patchiness as discussed above. In this case, the peak in the chlorophyll *a* spectrum in the region of the B-V frequency may be reflected as a dominant wavelength in the size of these aggregations. In this respect it may be significant that, using the Longhurst-Hardy net, FASHAM, ANGEL and ROE (1974) found that at 500-m depth the horizontal dimensions of copepod and ostracod patches did not vary greatly between species. The mean patch size was 200 ± 86 m which is of the same order of magnitude as the wavelength at the peaks in the chlorophyll spectra, although the latter data were obtained at depths of 20 to 50 m.

One conclusion to be derived from this is that for studies of plankton patchiness at length scales between about a few tens of metres and the critical wavelength (say 1 km), a sampling method is required that can separate patchiness caused by internal waves from true spatial heterogeneity. DENMAN and PLATT (1975) suggested using a towed 'Bat-fish' which could oscillate over a depth range of 10 m giving one cycle for every 100 m horizontal displacement. However, the results of the present work suggest that (depending on the local B-V frequency) this might cause aliasing problems due to the presence of internal wave energy at that wavelength. A more foolproof experimental design might be obtained by attaching an *in situ* fluorometer to an isotherm following device such as described by LAFOND (1962) or CAIRNS (1975).

Acknowledgements—We would like to thank the Oceanography Departments of the Universities of Liverpool and Southampton for the loan of their fluorometers, and Miss P. A. KIRKPATRICK for drawing the diagrams.

REFERENCES

- ARMSTRONG F. A. J. and E. C. LAFOND (1966) Chemical nutrient concentrations and their relationship to internal waves and turbidity off Southern California. *Limnology and Oceanography*, **11**, 538–547.
- BARNES H. and S. M. MARSHALL (1951) On the variability of replicate plankton samples and some applications of 'contagious' series to the statistical distribution of catches over restricted periods. *Journal of the Marine Biological Association of the United Kingdom*, **30**, 233–263.
- BERNHARD M. and L. RAMPI (1965) Horizontal micro-distribution of marine phytoplankton in the Ligurian Sea. *Botanica Gothoburgensia*, **3**, 13–24.
- BRISCOE M. G. (1974) Internal wave coherences from a Tri-mooring (IWEX). *Transactions. American Geophysical Union*, **55**, 291.
- CAIRNS J. L. (1975) Internal wave measurements from a midwater float. *Journal of Geophysical Research*, **80**, 299–306.
- CASSIE R. M. (1959) Microdistribution of plankton. *New Zealand Journal of Science and Technology*, **2**, 398–409.
- CASSIE R. M. (1960) Factors influencing the distribution pattern of plankton in the mixing zone between oceanic and harbour waters. *New Zealand Journal of Science and Technology*, **3**, 26–50.
- CUSHING D. H. and D. S. TUNGATE (1963) Studies on a *Calanus* patch I. The identification of a *Calanus* patch. *Journal of the Marine Biological Association of the United Kingdom*, **43**, 327–337.
- DENMAN K. L. and T. PLATT (1975) Coherences in the horizontal distributions of phytoplankton and temperature in the upper ocean. *Mémoires de la Société royale des sciences de Liège*, 6th series, **8**, 19–30.
- FASHAM M. J. R. (1970) The use of a shipborne computer for navigation. In: *Electronic engineering in ocean technology*, D. G. TUCKER, editor. *I.E.R.E. Conference Proceedings*, **19**, 259–270.
- FASHAM M. J. R., M. V. ANGEL and H. S. J. ROE (1974) An investigation of the spatial pattern of zooplankton using the Hardy-Longhurst plankton recorder. *Journal of Experimental Marine Biology and Ecology*, **16**, 93–112.
- FRANKIGNOUL C. (1974) A cautionary note on the spectral analysis of short internal wave records. *Journal of Geophysical Research*, **79**, 3459–3462.
- GARRETT C. J. R. and W. H. MUNK (1972) Space-time scales of internal waves. *Geophysical Fluid Dynamics*, **3**, 225–264.
- GARRETT C. J. R. and W. H. MUNK (1975) Space-time scales of internal waves: a progress report. *Journal of Geophysical Research*, **80**, 291–298.
- JENKINS G. M. and D. G. WATTS (1968) *Spectral analysis and its applications*, Holden-Day, 525 pp.
- KAMYKOWSKI D. (1974) Possible interactions between phytoplankton and semi-diurnal internal tides. *Journal of Marine Research*, **32**, 67–89.
- KIEFER D. A. (1973) Chlorophyll *a* fluorescence in marine centric diatoms: responses of chloroplasts to light and nutrient stress. *Marine Biology*, **23**, 39–46.
- KITAYGORODSKIY S. A., YU. Z. MIROPOL'SKIY and B. N. FILYUSHKIN (1973) Use of ocean temperature fluctuation data to distinguish internal waves from turbulence. *Izvestiya. Atmospheric and Oceanic Physics*, **9**, 272–292.

- LAFOND E. C. (1962) Internal waves. Part I. In: *The sea*, Vol. 1, M. N. HILL, editor, Interscience, pp. 731-735.
- OKUBO A. (1972) Some speculations on oceanic diffusion diagrams. *Rapport et procès-verbaux des réunions. Conseil permanent international pour l'exploration de la mer*, **167**, 77-85.
- OSBORN T. R. and C. S. COX (1972) Oceanic fine structure. *Geophysical Fluid Dynamics*, **3**, 321-345.
- PLATT T. (1972) Local phytoplankton abundance and turbulence. *Deep-Sea Research*, **19**, 183-187.
- PLATT T. and K. L. DENMAN (1975) A general equation for the mesoscale distribution of phytoplankton in the sea. *Mémoires de la Société royale des sciences de Liège*, 6th series, **8**, 31-42.
- PHILLIPS O. M. (1971) On spectra measured in an undulating layered medium. *Journal of Physical Oceanography*, **1**, 1-6.
- PINKEL R. (1974) Upper ocean internal wave measurements from FLIP. *Transactions. American Geophysical Union*, **55**, 291.
- STAVN R. H. (1971) The horizontal-vertical distribution hypothesis: Langmuir circulations and *Daphnia* distributions. *Limnology and Oceanography*, **16**, 453-466.
- STEELE J. H. (1974a) Stability of plankton ecosystems. In: *Ecological stability*, M. B. USHER and M. H. WILLIAMSON, editors, Chapman & Hall, pp. 179-192.
- STEELE J. H. (1974b) *The structure of marine ecosystems*, Blackwell Scientific Publications, 128 pp.
- STEELE J. H. (1974c) Spatial heterogeneity and population stability. *Nature, London*, **248**, 83.
- WIEBE P. H. (1970) Small-scale spatial distribution in oceanic zooplankton. *Limnology and Oceanography*, **15**, 205-217.
- WOODS J. D. and G. G. FOSBERRY (1966) Observations of the behaviour of the thermocline and transient stratifications in the sea made visible by dye markers. In: *Malta '65*, J. N. LYTHGOE and J. D. WOODS, editors, Underwater Association for Malta 1965, pp. 31-36.
- WROBLEWSKI J. S., J. J. O'BRIEN and T. PLATT (1975) On the physical and biological scales of phytoplankton patchiness in the ocean. *Mémoires de la Société royale des sciences de Liège*, 6th series, **8**, 43-57.