Seasonal distribution of chlorophyll *a* in relation to physical structure in the western Irish Sea

Seasonal distribution
Chlorophyll *a*
Stratification
Irish Sea
Fronts

Distribution saisonnière
Chlorophylle *a*
Stratification
Mer d'Irlande
Fronts

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ABSTRACT

The seasonal distribution of chlorophyll *a* across a frontal region and its relation to density in the western Irish Sea have been assessed on the basis of data collected between 1980 and 1982. Over the seasonal cycle with the most complete data set (1981), frontal water was found to have significantly more chlorophyll *a* ($\bar{x}$ = 2.43 μg l^{-1}) associated with the surface layer than either the stratified ($\bar{x}$ = 1.36 μg l^{-1}) or mixed ($\bar{x}$ = 1.35 μg l^{-1}) waters. However, when chlorophyll *a* was averaged to 30 m, the influence of the front was less marked, largely due to subsurface chlorophyll *a* patches in the stratified water. Although the regions could not be distinguished at the 95% confidence level in the depth-mean results, there is some indication that the mixed ($\bar{x}$ = 1.30 μg l^{-1}) region contained less chlorophyll *a* than either the stratified ($\bar{x}$ = 1.75 μg l^{-1}) or the frontal ($\bar{x}$ = 2.17 μg l^{-1}) regions. Considerable variability was observed in the recorded values of chlorophyll *a*. However, in general, chlorophyll *a* increased in all regions soon after the onset of stratification and remained relatively high until stratification broke down in October.

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RÉSUMÉ

Distribution saisonnière de la chlorophylle *a* en relation avec la structure physique dans l'ouest de la Mer d'Irlande.

La distribution saisonnière de la chlorophylle *a* dans une région de front thermique en relation avec la densité dans l'ouest de la Mer d'Irlande, a été étudiée à partir de données recueillies entre 1980 et 1982. Lors d'un cycle saisonnier (1981) on trouve que, dans les eaux de surface, la quantité de chlorophylle *a* dans l'eau frontale (2,43 μg l^{-1}) est significativement plus élevée que dans les eaux brassées (1,35 μg l^{-1}) ou stratifiées (1,36 μg l^{-1}). Cependant, lorsque la moyenne de la chlorophylle *a* est calculée jusqu'à une profondeur de 30 m, la présence du front devient moins marquée, parce qu'on trouve des concentrations localisées de chlorophylle *a* dans l'eau stratifiée en dessous des eaux de surface. Lorsque la moyenne jusqu'à 30 m est considérée, les régions ne se distinguent plus ($P <$ 0,05). Cependant, la région brassée (1,30 μg l^{-1}) semble contenir moins de chlorophylle *a* que les régions stratifiée (1,75 μg l^{-1}) et frontalière (2,17 μg l^{-1}). Il y a une grande variabilité dans les valeurs de chlorophylle *a* observées. Cependant, en général, la concentration de la chlorophylle *a* s'élève dans toutes les régions juste après le début de la stratification et reste relativement élevée jusqu'à la fin de la stratification en octobre.

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INTRODUCTION

The shelf sea fronts are the boundary zones which separate vertically mixed and stratified waters during the summer months. Their location is controlled by a competition between buoyancy input by surface heating and tide and wind stirring (Simpson, Hunter, 1974). Their physical structure and behaviour have been extensively studied in the last decade and are now well documented (Simpson, Bowers, 1981; Simpson, 1981).

Considerable interest in recent years has been directed towards the study of biological processes in relation to frontal regions. In particular, attention has focused on the distribution of phytoplankton or chlorophyll *a* at fronts and there are a number of reports of localised patches of elevated phytoplankton biomass or chlorophyll *a* concentration in surface waters in their vicinity (*e.g.*, Beardall *et al.*, 1982; Holligan, 1979; Holligan, Harbour, 1976; Pingree *et al.*, 1975; Savidge, 1976; Seliger *et al.*, 1981; Simpson *et al.*, 1978; Simpson *et al.*, 1982; Fournier *et al.*, 1977; Fournier *et al.*, 1979).

Frontal regions are also frequently associated with rich pelagic fisheries (Fournier, 1978; Mills, Fournier, 1979; Mills, 1980) and have recently been implicated as foci for Atlantic Herring spawning grounds (Iles, Sinclair, 1982). This association with fisheries combined with the measurement of high standing stock of phytoplankton or chlorophyll *a* has led to the suggestion that frontal regions may be areas of high primary productivity. Such a hypothesis is difficult to prove, for increased biomass in a region does not necessarily imply that the production resulting in the observed standing stock occurred in that region. This may especially true in active areas such as those in the immediate vicinity of a front. Studies in which primary production rates have been estimated are difficult to interpret because the incubations leading to production estimates are carried out over short time scales, thus not taking into account diurnal fluctuations in photosynthesis. In addition, changing light environments brought about by natural water movements do not affect all species in the same way (*e.g.* Richardson *et al.*, 1983) and definition of the long-term light exposure of a single phytoplankton population in a frontal region is extremely difficult. Thus, extrapolation of results from discrete short-term incubations in order to predict primary productivity over longer time periods requires assumptions about the responses of phytoplankton to light and the long term distribution of phytoplankton which may not necessarily be valid.

Earlier reconnaissance of frontal areas by the authors suggested a large temporal variability in surface chlorophyll *a* distributions. Although the immediate frontal zone is often characterised by elevated chlorophyll *a* concentrations with respect to surrounding waters, this is by no means always the case. Published reports of biological studies on fronts are, in the main, confined to a limited number of crossings. Quite naturally, there may be a tendency to record those occasions in which there is a dramatic difference between frontal and surrounding waters; those cases in which the frontal region cannot be distinguished from surrounding waters remaining unrecorded. Therefore, a systematic approach to the study of chlorophyll *a* distributions in frontal areas is necessary to put previously reported results into perspective and to prevent any bias towards positive results.

The central aim of the work reported here is to establish whether there is any significant influence of the existence of a seasonal thermal front on surrounding chlorophyll *a* distributions. The particular front under consideration occurs in the western Irish Sea and has been the subject of detailed study since the late 1960s (Simpson, 1971). As can be seen in Figure 1, the front extends some 110 km from the southern tip of the Isle of Man to the Irish coast near Dublin. Stratified water to the NW of the front is usually separated from cooler well mixed water to the SE by a region of strong horizontal temperature gradients up to 1°C/km which is clearly visible in satellite infra-red (IR) images.

Repeated surveys were made throughout the seasonal cycle, with the intention of maintaining a sampling interval of about two weeks. However, weather conditions and constraints on ship-time forced some deviations from that plan. Occasionally, it was also possible to sample the same line of stations at intervals of 1-3 days which allowed recording of changes in chlorophyll *a* distribution over shorter time scales.

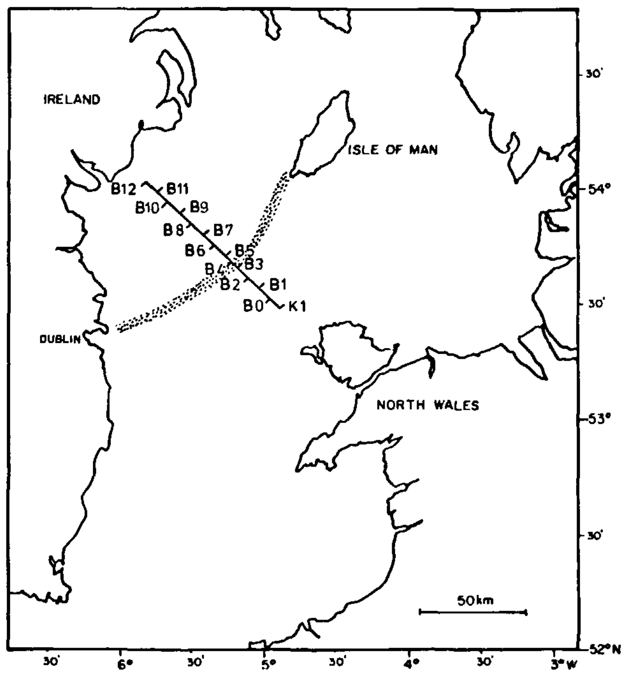

Figure 1
The Western Irish Sea and line of stations. The shaded area indicates approximate position of the front.

MATERIALS AND METHODS

Observations were made at fixed stations along a line in the western Irish Sea (Fig. 1) between April 1980 and May 1982. The orientation of the transect was normal to the average frontal position as shown by satellite IR imagery. Temperature and salinity were profiled using a Plessey 9400 CTD. Hydrocasts using standard NIO bottles were undertaken to provide calibration samples. When underway, continuous records were taken of surface temperature, conductivity and *in vivo* fluorescence (Turner Designs 10,000 R). In this paper, "surface" is taken to mean a depth of 2 m; the depth from which surface samples were collected.

In 1980, continuous profiles to 30 m were obtained using a Variosens submersible fluorometer. Due to instrument drift, a calibration was performed for each station using samples collected from 2, 10 and 20 m and assuming a linear relationship between chlorophyll *a* and $\log_{10}$ fluorescence. In 1981 and 1982, fluorescence profiles of each station were obtained by lowering a pump through the water column and directing the flow through the Turner Designs Fluorometer. The pump was held in position at 5 m intervals for a period of time sufficient to ensure accurate profiling. Fluorescence between these depths was visually monitored to guard against missing dense, vertically restricted layers of phytoplankton. Calibration samples were collected from 2, 10 and 20 m. For each cruise, a curve was fitted graphically to the calibration data (chlorophyll *a* vs. $\log_{10}$ fluorescence). Samples for chlorophyll *a* analysis were filtered onto GF/C filters and extracted in 90% Analar acetone. Chlorophyll *a* determinations with correction for phaeopigments were made spectrophotometrically after the method of Lorenzen (Strickland, Parsons, 1972) with absorption being measured on a Cecil Instruments Spectrophotometer CE 303.

RESULTS

The seasonal evolution of the physical structure in the western Irish Sea is summarised in Figure 2 *a*, which is a plot of the stratification parameter φ (J m^{-3}). This quantity is a measure of the amount of mechanical work (per unit volume) required in order to bring about complete vertical mixing (Simpson, 1981). It is derived from temperature and salinity data by the relation:

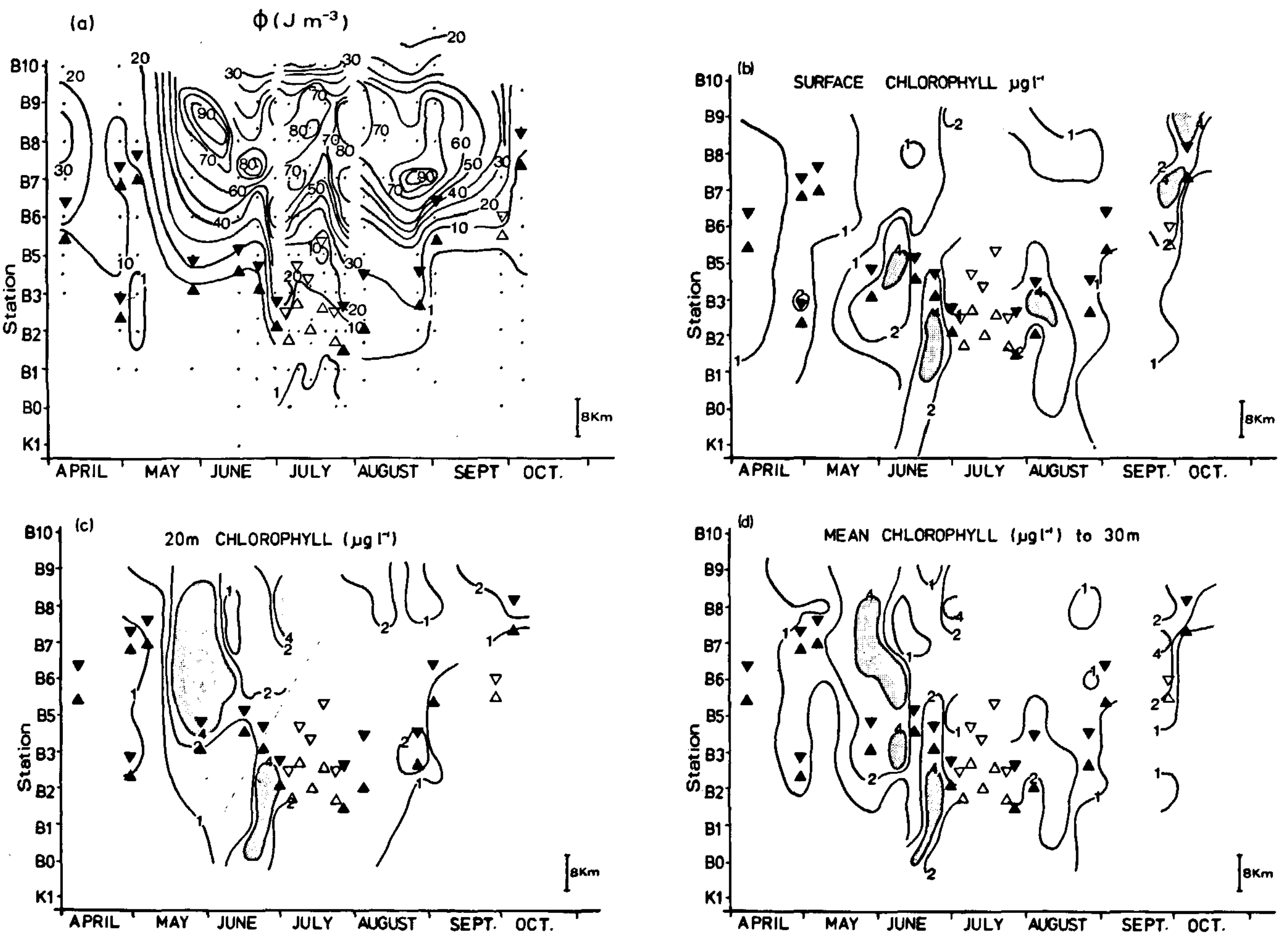

Figure 2

Time series of the distribution of stratification and chlorophyll a *along the line of stations: a) the stratification parameter φ for 1981 and July 1980; b) surface chlorophyll* a*, 1981; c) chlorophyll* a *at 20 m, 1981; d) chlorophyll* a *averaged over depth (to 30 m) 1981* ▼ *indicates the surface frontal area;* Δ *indicates that stratification was present but that there was no surface temperature gradient.*

$$\varphi = 1/h \int_{-h}^{0} (\bar{\rho} - \rho)\, gz dz; \; \bar{\rho} = 1/h \int_{-h}^{0} \rho \, dz,$$

where ρ = density (kg m^{-3}), g = gravitational acceleration = 9.81 m/s^{-1}, z = depth (m), and h = bottom depth (m). The data for July were collected in 1980, and the rest in 1981. The lack of data for the month of July in 1981 was due to the unavailability of the ship. Also marked in this figure are the frontal areas for each of the cruises. In most cases, the frontal area was determined from the vertical contour plots of temperature; in some cases from those of density. When only surface data were available, the surface temperature records were used to determine the frontal position. The frontal area was defined as the area where the isotherms corresponding to the seasonal thermocline (*i.e.* excluding very shallow transient thermoclines) reach the surface, or failing that, the bottom. For the cases when only surface data were available, the frontal area was chosen as the area of strongest horizontal gradient in surface temperature. There is a visual association between the frontal area and the φ = 10 J m^{-3} contour.

The initial stratification apparent in early April 1981 decreased to the order of 10 J m^{-3} or less over the whole section following a major storm on April 24th and 25 th. As stratification became re-established in early May, the front moved rapidly to the south-east. It then remained more or less stationary close to stations B3-B5 for the period of May to September after which it rapidly retreated. Nearly all of the stratification arises from temperature differences, except in early April, when salinity differences have been found to make a dominant contribution. This haline effect was apparent in most of the early season observations in the western Irish Sea and also in the results of Slinn (1974).

In 1980 and 1982, the spring phytoplankton increase appeared first in the stratified region and seemed closely related to the onset of stratification. Chlorophyll *a* was not homogeneously distributed in the water column but concentrated in the upper 20 m. Figure 3 shows results obtained between 13th and 16th April, 1982. In general, chlorophyll *a* determinations indicated maximal concentrations in the stratified water of about 10 times those in the isothermal water. At this time the surface to bottom σ_t difference was about 0.4. The same pattern was observed on April 17th, 1980; surface fluorescence and chlorophyll *a* determinations indicated chlorophyll *a* values within the stratified water of at least one order of magnitude higher than in the isothermal water. At this time the surface to bottom σ_t difference did not exceed 0.3.

In 1981, this pattern was not observed and the first markedly elevated chlorophyll *a* concentrations were recorded in late May as a localised thermocline patch. This patch is not considered to represent a spring outburst owing to its subsurface position in the water column and late date. Nor is it considered to represent the remnants of a surface bloom which had sunk out of the surface water. This assertion is based on our failure to detect appreciable concentrations of phaeopigments in the thermocline phytoplankton population, and on unpublished data (Heath, pers. comm.) which suggest that the dominant algal species present at 17 m divided more rapidly at that depth than when transferred to a higher position in the water column.

It is possible that a short-period "bloom" in 1981 occurred in the surface waters and went undetected during the 19 day interval between our samplings. However, the "bloom" itself may also have been shorter or less intense than in the other years studied due to the breakdown of the incipient stratification, which was present in early April, by an episode of very strong wind mixing on April 24th. Restratification began on May 1st and was firmly established by May 10th, 1981. The disappearance of stratification and its re-establishment was recorded by instruments moored at station B8 (thermistor chains and current meters fitted with temperature, conductivity and pressure sensors).

Figure 2 *b* represents surface chlorophyll *a* distributions across the Irish Sea from April to October 1981. On nearly all of the sampling occasions, the highest recorded values for surface chlorophyll *a* occurred in the vicinity of the front. These patches were recorded on both sides of the front.

Figure 2 *c* illustrates the chlorophyll *a* distribution at 20 m throughout this same period. The front no longer appears as important as a focal point for chlorophyll *a* distribution and there is evidence of subsurface chlorophyll *a* patches in the stratified water from the end of May. These occurred at intervals throughout the summer months. The sub-

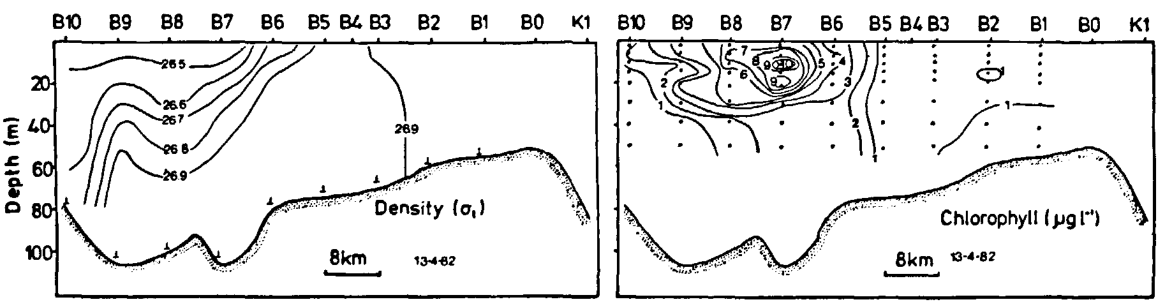

Figure 3
Density (σ_t) and chlorophyll a *vertical section for April 13, 1982. The symbol ⊥ marks the depth to which the CTD was lowered.*

surface patch observed at the end of May included chlorophyll *a* values (17 μg l^{-1}) which exceeded any recorded at the surface throughout the year.

In the western Irish Sea, where the light attenuation coefficient ranges from 0.1 m^{-1} to 0.3 m^{-1} and the depth of the surface mixed layer seldom exceeds 20 m during spring and summer (Lavín, Sherwin, 1984), the most important contribution to water column photosynthesis will be made by organisms in the upper 30 m. While in the mixed water the surface chlorophyll *a* may be representative of the chlorophyll *a* concentration in the water column, this is not the case in the stratified water. Therefore, the average chlorophyll *a* concentration in the upper 30 m is better suited to examine the overall influence of the front on the distribution of chlorophyll *a*. Figure 2 *d* shows this influence to be relatively weak by comparison with the effect on the surface distributions of chlorophyll *a* (Fig. 2 *b*). The variability in this vertically averaged picture emphasises the dangers of trying to draw general conclusions from a single transect of a frontal zone.

A selection of vertical plane section data from the various surveys in 1981 is shown in Figure 4. These plots were selected to illustrate all the major features of seasonal chlorophyll *a* distribution. In almost all examples, there is some evidence of subsurface chlorophyll *a* maxima closely associated with the maximum vertical density gradient. The exceptions are the cruises at the beginning and the end of the period of stratification. The most pronounced and extensive subsurface chlorophyll *a* peak recorded occurred at the end of May (Fig. 4 *b*). This chlorophyll *a* peak was dominated by *Rhizosolenia delicatula*. At this time no *R. delicatula* was observed in the mixed water.

A prominent feature of the June survey (Fig. 4 *c*) was a maximum of chlorophyll *a* of up to 4 μg l^{-1} occurring in the mixed water. The dominant species in this phytoplankton assemblage was *R. delicatula*; the same species that had dominated the subsurface maximum in the stratified water on the 28th of May. Although it is interesting to note the disappearance of a thermocline population of *R. delicatula* and the appearance of this organism in mixed water no firm link can be established between the two temporally and spatially separated diatom patches on the basis of the data.

During the autumnal overturn, there appeared to be a resurgence of chlorophyll *a* (Fig. 4 *f*) in the very weakly stratified water around station B8 while concentrations of chlorophyll *a* over most of the rest of the section were < 1 μg l^{-1}.

Variations on a shorter time scale can be seen from data collected in July, 1980 (Fig. 5). The physical structure remained unchanged for most of the month, with notably weak surface temperature gradients. Increased heating after the 24th enhanced the definition of the surface front. The chlorophyll *a* distribution, however, exhibited marked changes. On the 8th (Fig. 5 *a*), a subsurface peak was present from station B5 to B6. On the 11th (Fig. 5 *b*), the maximum was found in the surface layer and thermocline of stations B4 to B6. On the 24th and 28th (Fig. 5 *c* and 5 *d*), it was the well mixed water that contained the largest concentrations of chlorophyll *a*.

The chlorophyll *a* data collected between July 1980 and May 1982 have been summarised, in Figure 6, in an effort to ascertain whether significant differences can be detected between the average values of chlorophyll *a* present over a season in stratified, frontal and mixed waters of the western Irish Sea. The assignment of stations to stratified, frontal and mixed regions was made according to the position of the frontal area as defined above. Figure 6 *a* shows the variation of the chlorophyll *a* concentration at a depth of 2 m. Only in the surface water of the stratified region was there indication that the data fit the classical model of Cushing (1959) of a spring bloom, summer trough, autumn bloom of phytoplankton in temperate waters (Fig. 6 *a*). In mixed and frontal water, chlorophyll *a* peaks occurred intermittently throughout the period of stratification. Figure 6 *a* suggests more chlorophyll *a* in frontal surface water than in mixed or stratified waters during the period of stratification.

The mean chlorophyll *a* concentration to 30 m is presented in Figure 6 *b*. In all three regions, the mean chlorophyll *a* values in the upper 30 m were observed to rise from low values in early April and to remain above winter concentrations until late autumn. The "spring/autumn" phytoplankton bloom sequence suggested by chlorophyll *a* distributions in the surface of the stratified region was not as obvious in the integrated water column result since we dot not consider the May-June peak in chlorophyll *a* concentration in the stratified water to represent a spring outburst.

The temporal displacement of the peaks of chlorophyll *a* concentration recorded in the three regions in early summer, 1981 can also be seen in Figure 6 *b*. There were no data on algal species present in the frontal region on June 9th. However, the May 28th peak in the stratified water and the June 15th peak in the mixed water both consisted of *R. delicatula*. As stressed earlier, there were no data to link the two populations but the occurrence of a chlorophyll *a* patch of such magnitude in frontal waters between the sightings of the two *R. delicatula* patches is intriguing.

Averaging over time of the most complete annual data set (1981) yields a seasonal mean chlorophyll *a* concentration for stations representing stratified, mixed and frontal waters. An analysis of variance for unbalanced data (Table 1) of the surface values shows that the frontal region contained significantly more chlorophyll *a* than either the mixed or stratified regions ($P < 0.05$). Average chlorophyll *a* in the surface stratified water was 1.36 μg l^{-1}, in the surface mixed water 1.35 μg l^{-1} and in the surface frontal water 2.43 μg l^{-1}.

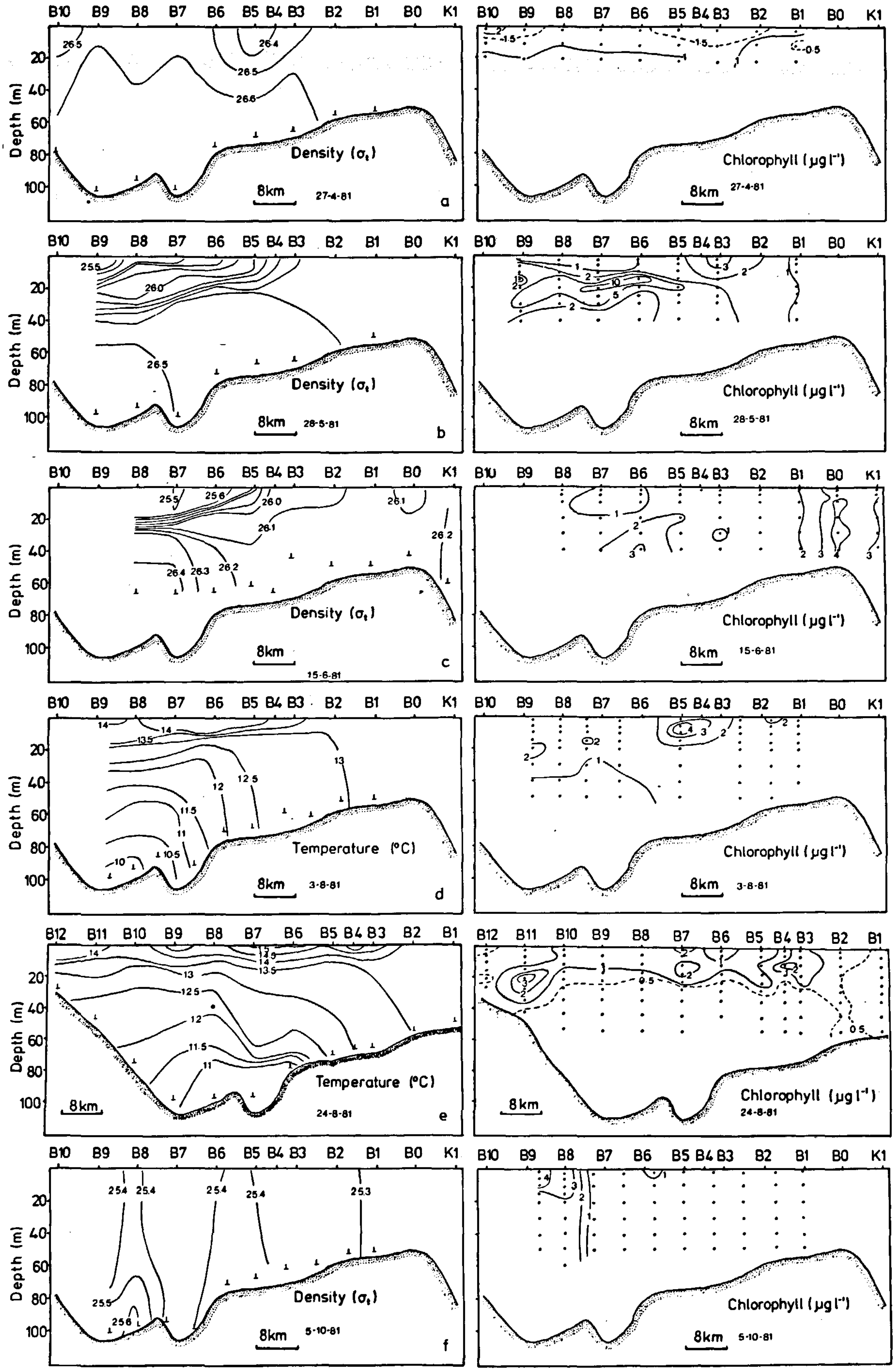

Figure 4

A selection of vertical sections of chlorophyll a *and density (or temperature, when σ_t was not available) along the line of stations over the period April-October, 1981. The chosen increment in temperature is approximately equivalent to the increment in σ_t.*

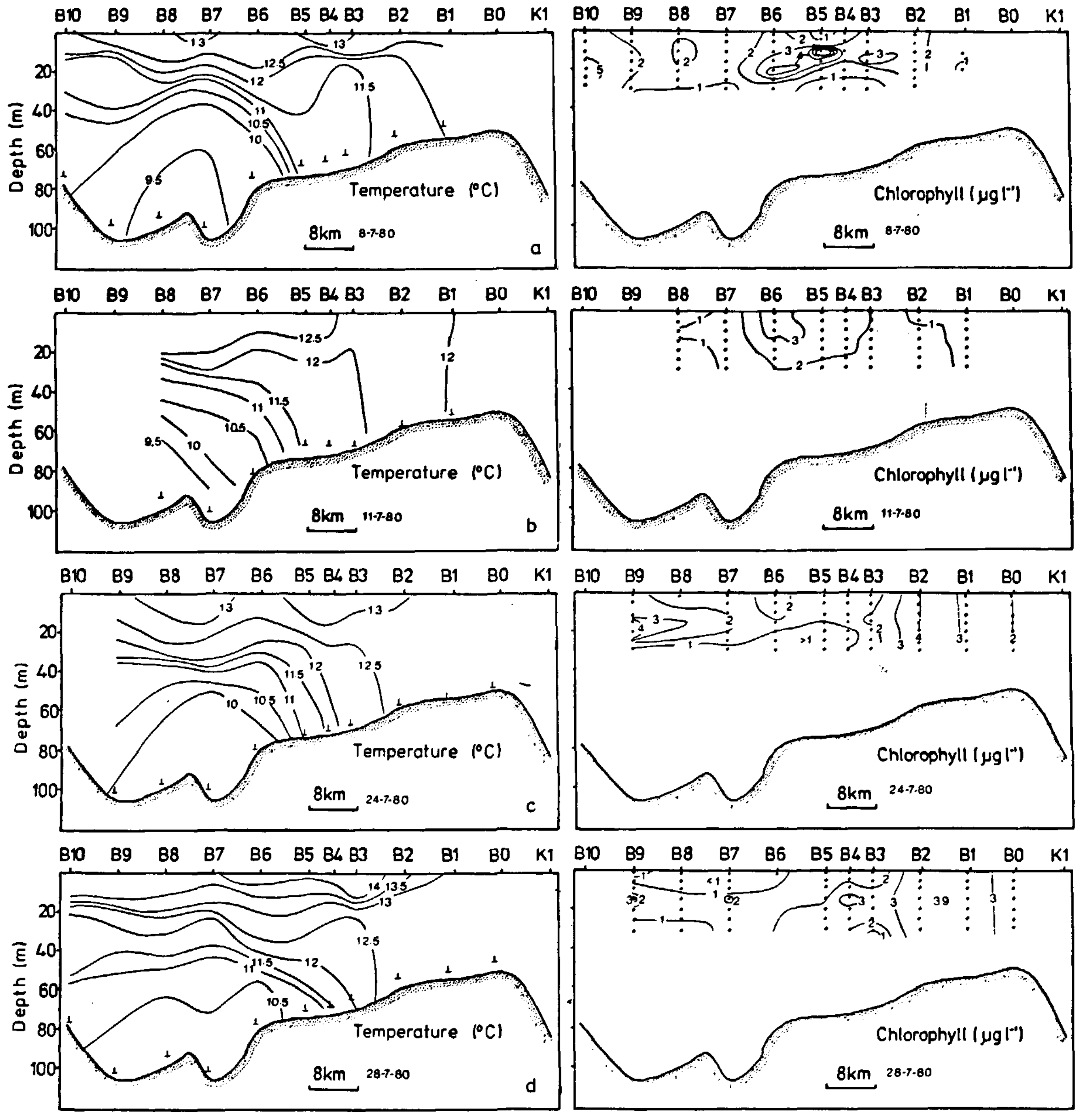

Figure 5

Vertical sections of temperature and chlorophyll a *obtained between the 8th and the 28th of July, 1980.*

Table 1

Summary of the analysis of variance for surface measurements of chlorophyll a. *The analysis of variance was modified to show the significance of the differences in average chlorophyll* a *concentration between the three regions (stratified, frontal and mixed). The table shows that there is a significant (95%) difference between the three regions. Further analysis showed that this difference was due to the significant (95%) difference between the stratified and frontal regions, and between the frontal and mixed regons. There was no significant difference between the stratified and the mixed regions.*

y-variate: chlorophyll A (surface)

	Residual		Change			
TERMS	Degrees of freedom (DF)	Sum of squares (SS)	Degrees of freedom (DF)	Sum of squares (SS)	Mean Change	Variance Ratio
Initial model constant	130	157.0281	*	*		
Modifications to model	130	157.0281	0	0.0000	*	
+ cruise	116	123.7809	14	33.2472	2.3748	6.11
+ region	114	107.0574	2	16.7235	8.3617	21.52
+ cruise. region	88	34.1874	26	72.8700	2.8027	7.21

** Denominator of ratio is (RES.SS/RES.DF) from line above = 0.3885.

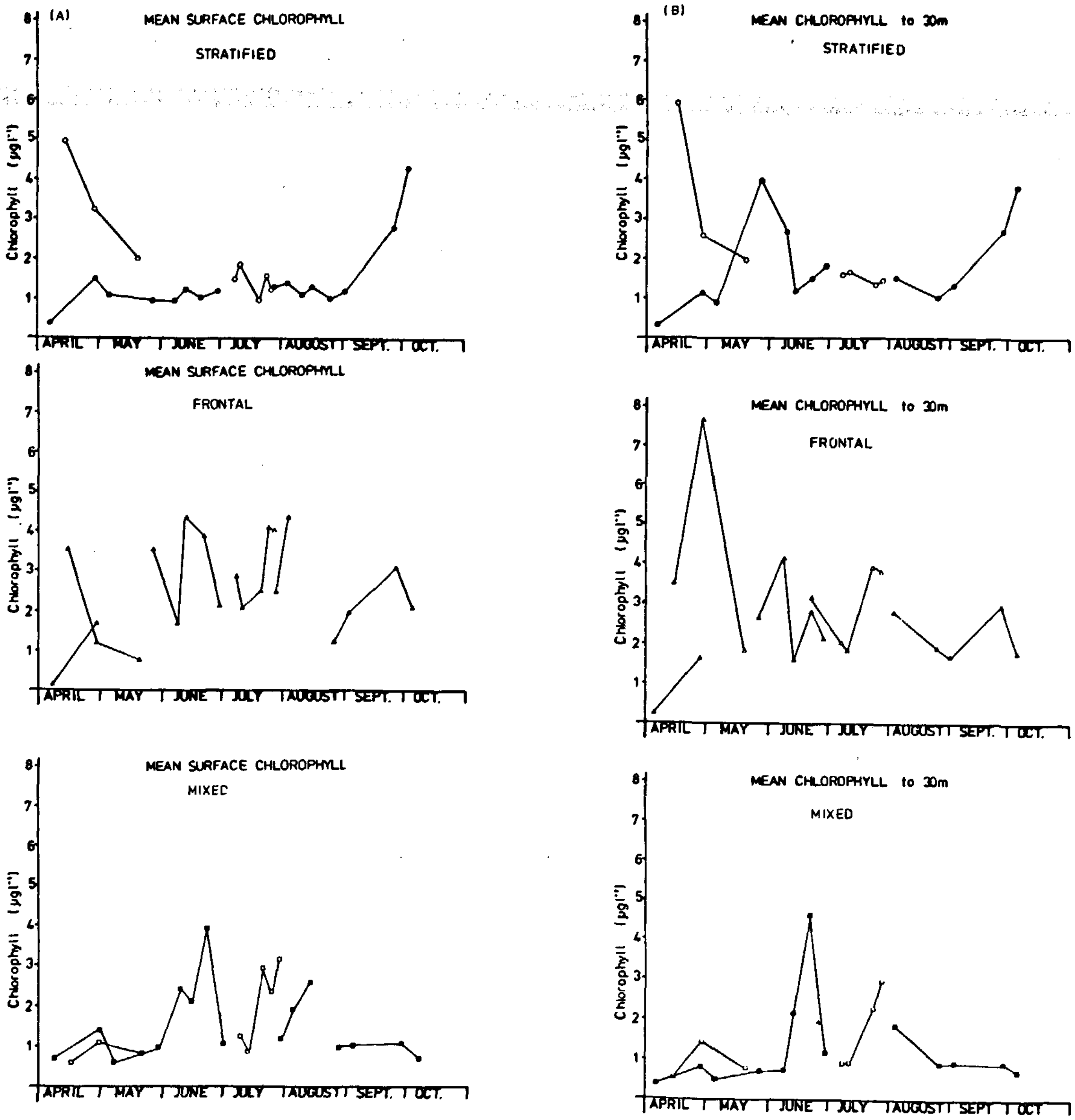

Figure 6
Time series of chlorophyll a *concentration in the stratified, frontal, and mixed regions of the western Irish Sea: a) 2 m below the surface; b) in the upper 30 m. Full symbols used for 1981 data. Open symbols for data collected in July 1980 and April-May 1982.*

In contrast, the analysis of variance of the chlorophyll *a* present in the upper 30 m in 1981 (Table 2) indicates that there is no significant difference between the three regions at the 95% confidence level. However, the frontal and the mixed regions can be distinguished at the 90% confidence level. The average values are $\bar{x} = 1.75$ µg l^{-1} for the stratified, $\bar{x} = 2.17$ µg l^{-1} for the frontal water and $\bar{x} = 1.30$ µg l^{-1} for the mixed water.

DISCUSSION AND CONCLUSIONS

Many other studies in which localised surface chlorophyll *a* patches have been recorded in the vicinity of fronts have been based on single frontal crossings or a number of crossings made over a short time scale. It has not been possible to extend such observations to the seasonal distribution of chlorophyll *a* across any given front. This study represents 21 crossings of a front in the western Irish Sea and we conclude that over the entire season of thermal stratification, the mean chlorophyll *a* concentration in surface waters was highest near the front as compared with mixed and stratified waters. However, the chlorophyll *a* concentration in surface frontal waters was not consistently high during the summer months. Discrete patches could be identified in this region. Since chlorophyll *a* determinations provided only an approximation of phytoplankton biomass present at any given time and no indication of growth or photosynthetic rates, the patches of high chlorophyll *a* concentration in surface frontal waters could not be interpreted as evidence of increased "production" in frontal regions.

It may be argued that elevated values of chlorophyll *a* in surface water near the front suggest enchanced phytoplankton accumulation through growth or other processes at the front. The same argument should also then be applied to the thermocline, where the highest concentrations of chlorophyll *a* recorded throughout the entire season were encountered in peaks at depths of 15-20 m. These peaks were observed intermittently throughout the period of stratification. Although values of chlorophyll *a* in the surface water of the stratified region were lower over the season than in the frontal region, the difference between the regions disappeared when the chlorophyll *a* concentrations of the upper 30 m were considered, due to the inclusion of the subsurface chlorophyll *a* peaks.

The substantial contribution to the mean chlorophyll *a* concentration of the water column made by these subsurface peaks is important in the light of the current interest in remote sensing of chlorophyll *a*. Satellite scanners, such as CZCS, would not have detected these chlorophyll *a* concentrations. Values of the attenuation coefficient calculated from irradiance profiles in these waters suggest that the depths from which the scanners receive information would be of the order 3-10 m. Thus, remotely sensed data could lead to the erroneous conclusion that chlorophyll *a* in this area was concentrated in the frontal region.

In 1980 and 1982, substantial spring phytoplankton outbursts were noted in the surface stratified water soon after water column stratification became established. This observation conforms with results obtained by Pingree *et al.*, (1976) in the Celtic Sea. The end of the period of stratification may also be important in seasonal chlorophyll *a* distribution patterns in the western Irish Sea. In October 1981, after the autumnal overturn had started, weak stratification existed only at stations B8 and B9. These same stations showed high chlorophyll *a* values in the surface water (Fig. 4 *f*) while all other stations at this time were recording winter values of chlorophyll *a*.

During the summer months, chlorophyll *a* values in the surface water of the stratified region were low (Fig. 6 *a*). Thus, it was only in the surface water of the stratified region that chlorophyll *a* distributions appeared to follow the classical seasonal model of phytoplankton development used to describe temperate coastal waters (Cushing, 1959). Although the intermittency in standing stock levels observed in the data obscures the definition of any simple seasonal pattern in chlorophyll *a* distributions, the average chlorophyll *a* concentration in the upper 30 m (Fig. 6 *b*) suggests that chlorophyll *a* values over the entire study region increased soon after the onset of stratification and remained elevated until the autumnal breakdown of stratification.

The results presented here have established differences between the annual means of chlorophyll *a* present in the mixed, frontal, and stratified waters in the western Irish Sea. When surface waters only were considered, the frontal region contained significantly more chlorophyll *a* over an annual cycle than stratified or mixed waters. When chlorophyll *a* in the water column (to 30 m) was considered, the three regions were indistinguishable from each other at the 95% confidence level. However, there was a suggestion of more chlorophyll *a* in the stratified and frontal waters than in the mixed water. The contrast between the surface and the vertically integrated result is, perhaps, the most significant conclusion in that it puts a different perspective on previously reported results and should serve to focus future discussion on the relationship between physical and biological processes occurring in this and other frontal regions.

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Table 2

Summary of the analysis of variance for average chlorophyll a *concentration in the upper 30 m. The analysis of variance was modified to show the significance of the differences in average chlorophyll* a *concentration between the three regions (stratified, frontal and mixed). The table shows that the three regions are indistinguishable at the 95% confidence level. At the 90% confidence level, the frontal and the mixed regions can be distinguished.*

y-variate: chlorophyll A (averaged to 30 m)

	Residual		Change			
TERMS	Degrees of freedom (DF)	Sum of squares (SS)	Degrees of freedom (DF)	Sum of squares (SS)	Mean Change	Variance Ratio
Initial model constant	122	193.3566	*	*		
Modifications to model	122	193.3566	0	0.0000	*	
+ cruise	106	134.9555	16	58.4010	3.6501	4.06
+ region	104	129.0381	2	5.9174	2.9587	3.29
+ cruise. region	78	70.0445	26	58.9937	2.2690	2.53

** Denominator of ratio is (RES.SS/RES.DF) from line above = 0.8980.

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