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Studies of a larval herring (*Clupea harengus* L.) patch in the Buchan area. III. Phytoplankton distribution and primary productivity in relation to hydrographic features

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Abstract

The distributions of phytoplankton species, biomass and productivity in the Buchan area are described. Photosynthetic rate estimates, reinforced by *in vivo* fluorescence yield data indicate highest rates of production in the inshore isothermal waters and in the transitional zone separating these from an offshore stratified region. Pigment concentration estimates and plant carbon concentration estimates derived from cell plasma volume measurements indicate that phytoplankton biomass was greatest in the transitional zone. These observed distributions are attributed to an autumnal bloom stimulated by increased vertical advection causing remineralisation of the euphotic zone.

Introduction

Phytoplankton distribution and/or productivity in relation to boundary zones or 'fronts' between different water masses have been extensively studied in recent years by a number of workers.

A survey of the literature reveals a tendency to observe high chlorophyll concentrations in surface waters in the vicinity of frontal regions and, in cases where primary production has been measured, there is also often an indication of elevated photosynthetic rates occurring in frontal waters (e.g. Pingree *et al.* 1975; Holligan & Harbour 1976; Savidge 1976; Simpson *et al.* 1978; Holligan 1979; Floodgate *et al.* 1981; Seliger *et al.* 1981; Beardall *et al.* 1982; Simpson *et al.* 1982; Holligan *et al.* 1984). However, as pointed out by Richardson *et al.* (1985), most of these reported observations of increased biomass/productivity in frontal zones represent single crossings of the front and may be misleading when considering the long term production of a frontal region and surrounding waters in general. In a seasonal study of a thermal front in the Western Irish Sea, these workers observed that high

chlorophyll concentrations in the surface waters near the front were an intermittent feature of this region and that, on a number of occasions, no elevated surface chlorophyll concentrations were observed near the front. Such occasions, when a frontal zone is indistinguishable from surrounding waters are unlikely to be reported in the literature and, thus, a bias may develop which supports a general claim of high productivity in frontal zones.

Although there is no doubt that elevated chlorophyll biomass and/or increased rates of primary production occur at least intermittently in many frontal regions, the effect that this production may have on higher trophic levels is unclear. Reports of zooplankton distribution and production at fronts are relatively few and those that do exist are difficult to interpret (see Kiørboe & Johansen 1986). However, it seems likely that the duration of the occurrence of elevated phytoplankton biomass in a frontal region will dictate the importance that that patch has to secondary production in that region. In frontal areas exhibiting highly variable phytoplankton distributions, zooplankton may not be able to respond to elevated phytoplankton concentrations (see Richardson 1985). In more stable frontal zones, dense phytoplankton patches may exist long enough to stimulate zooplankton production.

Richardson *et al.* (1986) have demonstrated a direct association between the distribution of herring larvae and a thermal front off the northeast Scottish Coast. Since herring larvae are dependent on zooplankton nauplii as a food source, we are interested in investigating whether the presence of this front in any way affects zooplankton production in the area.

The purpose, then, of this study was to examine phytoplankton distribution and primary productivity in relation to copepod distribution and production (see Kiørboe & Johansen 1986) and the distribution of recently hatched herring larvae in the Aberdeen Bank area.

Materials and methods

The study was conducted onboard the RV *Dana* (Danish Fisheries Ministry) from Sept. 16-29, 1984. Details of cruise area and hydrographic data collection are given in Richardson *et al.* (1986).

Surface chlorophyll distributions were mapped by taking 5 l samples from the ship's pumped seawater supply which was run continuously throughout the cruise. These samples were immediately filtered onto Whatman GF/C filters and extracted in 90% acetone. Cells were disrupted with an ultrasonic disintegrator with care taken to prevent sample overheating. After 30-90 minutes in darkness at 5°C, samples were centrifuged and absorption read on a Perkin Elmer 554 spectrophotometer. Chlorophyll-*a* concentrations were calculated according to the Lorenzen method (Strickland & Parsons 1972).

During transect studies where it was necessary to obtain a vertical profile of chlorophyll distributions, chlorophyll-*a* fluorescence was recorded using a Q instruments fluorometer. This fluorometer and a submersible pump were attached to the CTD unit. Data from the CTD and fluorometer were recorded every 0.5 s. Calibration of the fluorometer was performed at every transect station by pumping

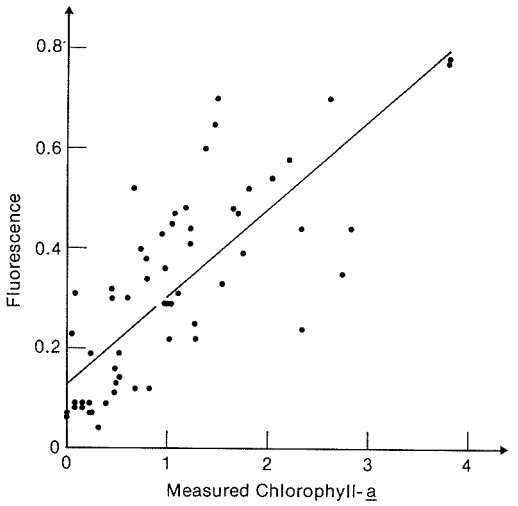

Fig. 1. Relationship between fluorescence and extracted chlorophyll determinations. data from all calibration stations and depth are included.

discrete water samples from a number of depths for chlorophyll determination. The combined calibration data from all stations exhibited a high degree of variability in the relationship between fluorescence and extracted chlorophyll determinations (Fig. 1). It was clearly necessary to eliminate some of this variability in order to produce a useful calibration.

No relationship was found between residuals from the linear regression model describing these data and either the time of day or the sampling depth. However, when the data from each station were pooled to produce station-specific calibrations, the coefficients of these relationships were found to be highly correlated with the water column stratification as described by the surface-bottom temperature difference ΔT (see Richardson *et al.* 1986). This observation was used to generate a calibration equation incorporating both the measured fluorescence (F) and ΔT.

At each station:

$$\text{Chl}a = mF + c$$

where Chl$a$ is the concentration of chlorophyll-a (mg/m^3) and m and c are linear regression coefficients. Values for m and c, as well as the correlation coefficient of the calibration line for each station, are shown in Table 1. In all but 3 cases, the resulting calibration accounted for more than 60% of the variance ($r^2 > 0.6$). In the exceptional cases (stations 152, 154 and 160), the range of chlorophyll concentrations encountered down the water column was too small to allow a meaningful relationship to be determined.

The relationships between the coefficients (m and c) *and* ΔT are shown in Fig. 2. Variation in c was small in comparison to the range of chlorophyll-a concentrations encountered during the survey and c was only weakly correlated with ΔT

Table 1. Chlorophyll *a* (mg/m^3) = *m*. (fluorescence) + *c*.

Station no.	Date	Range of Chl*a*	*m*	*c*	r^2	ΔT
30	17/9	0.16-1.00	2.39	0.03	0.53	3.9
32	17/9	0.08-1.70	3.76	−0.12	0.98	2.9
34	17/9	0.16-2.20	2.98	−0.03	0.86	2.4
36	17/9	0.16-2.74	4.23	0.13	0.74	1.2
38	17/9	0.47-3.80	4.98	0.01	1.00	0.4
40	17/9	0.47-2.34	5.60	0.18	0.71	0.3
152	23/9	0.97-1.28	−2.29	1.70	0.29	0
154	23/9	0.45-1.11	0.20	0.76	0.0004	0
156	23/9	0.08-2.04	2.97	0.14	0.77	0.8
158	23/9	0.00-1.23	2.42	−0.12	0.62	1.9
160	23/9	0.00-0.24	0.81	−0.04	0.41	3.9
162	23/9	0.08-1.04	1.93	−0.09	0.83	3.6

($r^2 = 0.4$). There was no evidence of any relationship between survey date and residuals from the fitted relationship

$$c = 0.11 - 0.05\Delta T.$$

The coefficient, *m*, was highly correlated with ΔT. Here, however, the relationship was clearly survey-specific. Residuals from a relationship describing the pooled data were highly correlated with survey date. The relationships between *m* and ΔT for each survey were:

17/9/84 $m = 5.42 - 0.77\Delta T$ $r^2 = 0.86$
23/9/84 $m = 3.48 - 0.57\Delta T$ $r^2 = 0.83$

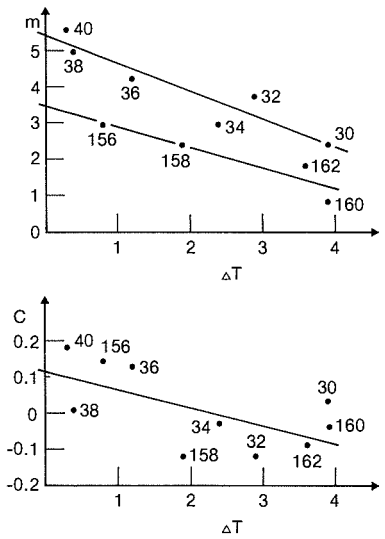

Fig. 2. Coefficients from the regression of fluorescence upon chlorophyll *a* for individual transect stations plotted as a function of ΔT. Station numbers are given in the figure.

These relationships were incorporated into a multivariate calibration of the fluorometer of the form:

$$\text{Chl}a = (a - b\Delta T)\ F + (p - q\Delta T)$$

where a, b, p and q are coefficients of the relationship between m and c and ΔT, respectively. The resulting calibration equations for each survey were:

$$17/9/84 \quad (5.42 - 0.77\Delta T)\ F + (0.11 - 0.05\Delta T)$$
$$23/9/84 \quad (3.48 - 0.57\Delta T)\ F + (0.11 - 0.05\Delta T)$$

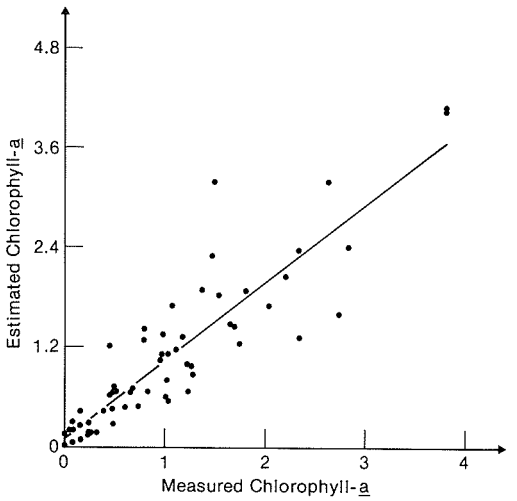

Fig. 3. 'Corrected' fluorescence determined chlorophyll *a* concentrations plotted as a function of determined chlorophyll *a* concentrations.

Fig. 3 shows the measured concentrations of Chl*a* in the calibration samples and the estimated concentrations determined using the fluorometer calibrations. Comparison of linear regression models fitted to these data and to the original fluorescence and measured pigment concentrations, indicates that the calibration method achieved a considerable reduction in the scatter around the fitted relationships (original data, $r = 0.79$, variance ratio = 100 on 1 and 64 degrees of freedom; calibrated data, $r = 0.90$, variance ratio = 267 on 1 and 64 degrees of freedom).

Primary productivity determinations were made at alternate stations along the transect lines. As the temperature profiles indicated that the depth of the surface mixed layer was at least 30 m at all stations, phytoplankton samples from 15 m were chosen as being roughly representative of the algae in the upper water column. Water was collected using a 1.5 l sampler. Immediately upon collection, water samples were filtered through a 200 μm mesh to remove large zooplankters and transferred to 25 ml pyrex glass stoppered bottles. $^{14}CO_2$ (4 μ Ci) was added to each bottle and incubations carried out at 0, 12, 30, 40, 70, 160 and 320 μmole photons $\cdot m^{-2} \cdot s^{-1}$. Details of incubations and sample treatment are given in Richardson (1985).

Samples for chlorophyll determinations were taken at every station/depth where primary productivity determinations were made. The light extinction coefficient,

k, (Jerlov 1968) was determined at every primary productivity station using a Q Instruments Quantameter.

Quench corrected counts associated with samples were converted to μg C fixed l^{-1} at the various photon flux densities according to the method described in Strickland & Parsons (1972) with the exception that no correction was made for isotope discrimination.

Rates of photosynthesis $\cdot m^{-2} \cdot d^{-1}$ were calculated by assuming maximum photon flux density of 1500 μ mole $\cdot m^{-2} \cdot s^{-1}$ to be penetrating the surface at midday and a sinusoidal increase and decrease of light to from this value over a 14 hr day. From the measured light extinction, it was then possible to calculate an average daily light climate at one meter depth intervals through the water column. Using the measured photosynthesis vs. irradience (PvsI) and fluorescence values converted to chlorophyll, daily photosynthetic rates for each 1 m depth interval were calculated. Addition of these values and volume correction yields C fixed $m^{-2} \cdot d^{-1}$.

Along transect 1, phytoplankton samples were collected from 15 m at stations where primary productivity determinations were made and from 3 m at those stations lying between primary productivity stations along the transects. Samples were preserved in Lugols Iodine.

On return to the laboratory, the samples were sedimented in 10 or 50 ml chambers depending upon the cell abundance. Cells were then identified to species and enumerated using an inverted microscope (Utermöhl 1958, Edler 1979). The contribution by each species to the total phytoplankton carbon was then calculated using the stereometric shapes and plasma volume/carbon conversion procedures described by Edler (1979).

The contribution to total phytoplankton carbon made by each species at each station was calculated and a matrix of 54 rows (species) $\times$11 columns (stations) of $\mu g\, C \cdot l^{-1}$ was set up. A matrix of correlations between stations was then generated and an average-linkage cluster analysis performed on this correlation matrix. This analysis was conducted on a DEC Rainbow microcomputer.

Results

Surface chlorophyll distribution showed a marked association with the frontal region separating isothermal and stratified water. Figs 4a and b show surface chlorophyll concentrations and surface to bottom temperature differences (ΔT) during the second coverage of the cruise area (Sept. 22-24). Low chlorophyll values ($<1\ \mu g \cdot l^{-1}$) were associated with surface waters in the stratified region ($\Delta T > 1.5$), while patches of elevated chlorophyll concentration (2-2.5 $\mu g \cdot l^{-1}$) were located in the transitional zone ($\Delta T \cong 1$). A patch of elevated surface chlorophyll was also noted in the isothermal water.

The vertical profiles of chlorophyll *a* determined from the *in vivo* fluorescence intensity data collected during the transect studies (Sept. 17; Sept. 23) are presented as sections in Figs 5a and 6. When these sections are compared to simultaneously collected temperature profiles (Richardson *et al.* 1986), it can be seen that the highest concentrations of pigment are located in the transitional or frontal

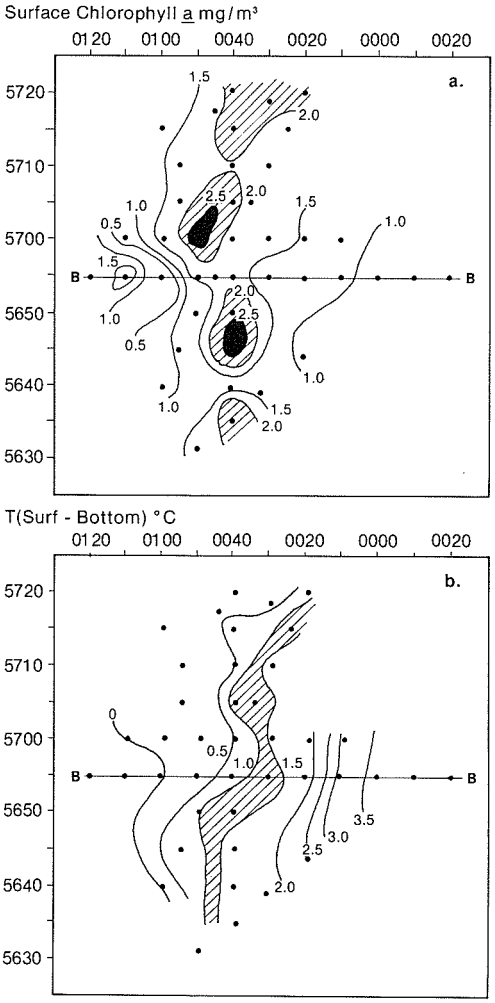

Fig. 4. a, surface chlorophyll concentrations (Sept. 22-24). b, ΔT (surface to bottom temperature difference) (Sept. 22-24).

zone separating isothermal water to the west from stratified waters further offshore. Phytoplankton counts converted to biomass for transect 1 are plotted in Fig. 5b. The peak in concentration of phytoplankton $C \cdot l^{-1}$ occurred in the frontal region.

Primary productivity measurements

Estimated rates of carbon fixed $\cdot m^{-2} \cdot d^{-1}$ from alternate stations along the transect lines have been plotted as a function of ΔT in Fig. 7. The average primary production for stations exhibiting $\Delta T \geq 1.5 = 350 \pm 76$ (SE) mg $C \cdot m^{-2} \cdot d^{-1}$, $n = 6$. For mixed and frontal stations ($0 \leq \Delta T < 1.5$), the average estimated rate of carbon fixation was 680 ± 83, $n = 6$.

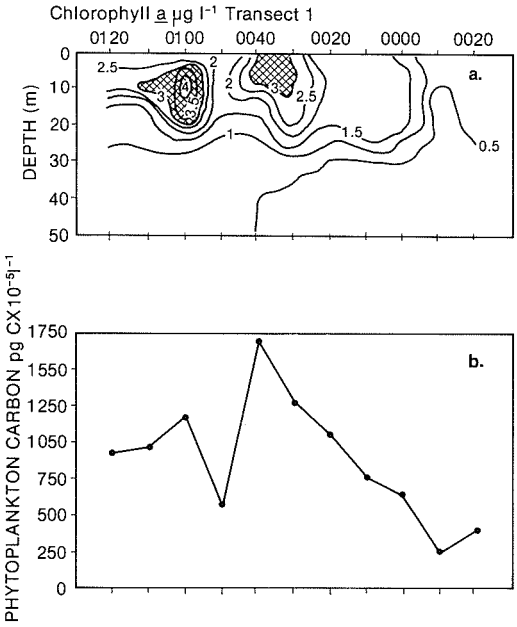

Fig. 5. a, vertical profile of chlorophyll *a* distribution: Transect 1. b, total phytoplankton carbon ($\mu g \cdot l^{-1}$): Transect 1.

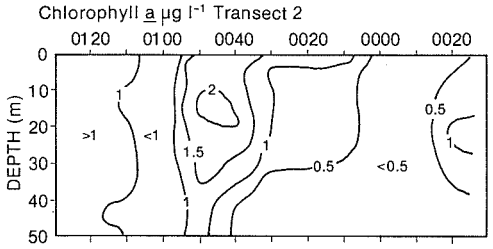

Fig. 6. Vertical profile of chlorophyll *a* distribution: Transect 2.

Thus, the estimated primary production in the surface stratified waters was markedly lower than in frontal or mixed waters. However, on the basis of the data available no difference in primary production could be detected between frontal and isothermal waters. Since chlorophyll biomass was greatest in the frontal zone, the similarity in estimated primary production rates between these two regions implies higher assimilation indices (g C fixed/g chl*a*/h) in mixed water than near the front. There was very little difference in the shape of the photosynthetic response curve between the stations except at station 30, in the thermally stratified water, where light saturation occurred at a lower photon flux density than for the other stations (P_{max} occurred here at 50 $\mu M \cdot m^{-2} \cdot s^{-1}$) and photoinhibition was observed at the highest photon flux densities of the incubation. This may suggest that the surface layer of the water column at station 30 was not well mixed and that phytoplankton at 15 m were adapted to low light intensities.

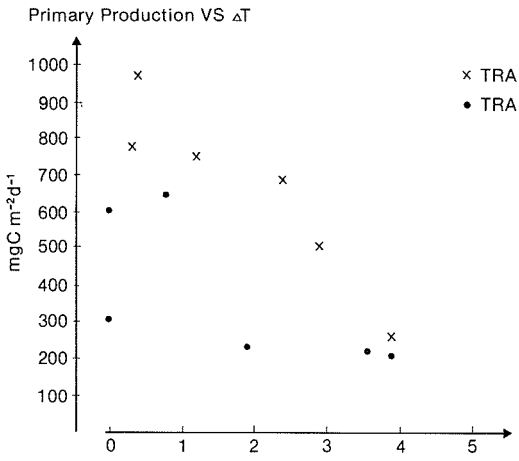

Fig. 7. Estimated rates of photosynthetic carbon fixation (mg $C \cdot m^{-2} \cdot d^{-1}$) for transect stations plotted as a function of ΔT.

Phytoplankton species analysis

The phytoplankton community was composed primarily of dinoflagellates, cryptomonads, and monads (6-10 μm). However, the species occurring on the 2 sides of the front differed. West of the front in coastal mixed water, a greater number of species were observed than in stratified waters. Dominant species (in terms of contribution to total phytoplankton carbon) in this region were: *Gymnodinium* sp., *Ceratium minimum, C. fusus, C. tripos, Prorocentrum micans,* and *Peridinium* sp. Only in the mixed waters was a diatom (*Nitzchia pungens*) found to contribute significantly to phytoplankton carbon. In stratified waters, *Gymnodinium* sp. dominated.

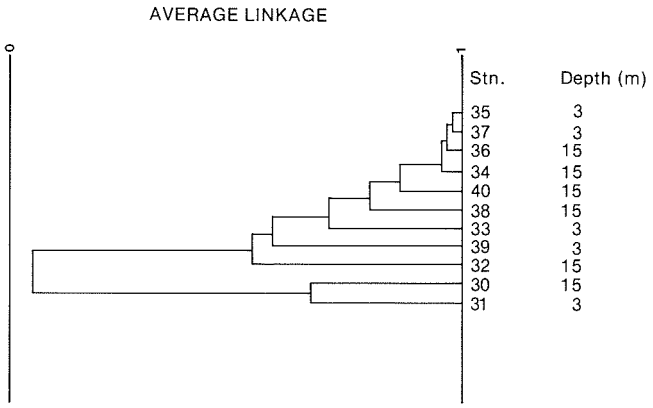

Fig. 8. Cluster diagram for average linkage analysis based on a correlation matrix of $\mu g\ C \cdot l^{-1}$ for each species and station along Transect 1.

Table 2.

Station	30	31	32	33	34	35	36	37	38	39	40
Carbon/Chl*a*	43.5	86.8	43.4	81.3	54.6	95.6	64.6	39.2	40.7	35.5	42.2
Sample depth	15 m	3	15	3	15	3	15	3	15	3	15

The calculated carbon/chlorophyll *a* ratios (Table 2) indicate that, in mixed waters, the ratio is similar for samples collected at 3 and 15 m. In stratified waters, however, considerable differences are noted. This is probably due to increased concentrations of chlorophyll $a \cdot \text{cell}^{-1}$ in low light (15 m) cells and suggests a slower vertical mixing rate in the surface waters of the stratified region than in near coast waters.

Discussion

As noted by Richardson *et al.* 1986 and Munk *et al.* 1986, centres of patches of herring larvae in the Aberdeen Bank area in September 1984 were located along a front separating thermally stratified and mixed waters. We have demonstrated here that this same region exhibited patches of elevated chlorophyll biomass in surface waters.

This observation is reminiscent of results from a study made by Renk *et al.* (1976). These workers surveyed the same area from 16 September-15 October in 1974 and their data on the mean concentration of chlorophyll in the upper 30 m of the water column showed that the greatest concentrations of chlorophyll occurred in patches lying between 00°00′ and 01°00′W – precisely the same region in which we observed patches of high surface chlorophyll. Although these workers did not record water temperature, Richardson *et al.* (1986) have suggested, on the basis of a literature survey, that the front separating mixed and stratified waters in this region is often positioned between 0° and 1°W in September. Thus, it seems reasonable to suggest that the patches of elevated surface chlorophyll observed by Renk *et al.* occurred in this same frontal zone and that such patches may be a common feature of this region in September.

Examination of the hydrography of the region (Richardson *et al.* 1986) indicates that the area of thermally stratified water probably extends over the entire survey area during the summer months, the front being situated well inshore. Under these circumstances, persistent nutrient depletion of the surface mixed layer would be expected and indeed, extremely low concentrations of chlorophyll *a* (<0.5 mg $\cdot$ m^{-3}) were recorded in the surface water throughout the entire region during a cruise by FRV Scotia during July 1984 (Heath, unpublished data).

The increased vertical advection and reduced solar heating during the autumn, leading to destratification of the nearshore waters, recession of the frontal zone, and consequent increased area of isothermal waters would be expected to lead to remineralization of this euphotic zone by nutrient rich waters previously isolated

below the thermocline. Given that light is not limiting at the time of year when these events occur, an autumnal bloom of phytoplankton would be expected in both the mixed and transitional (frontal) zones, accounting for the increased biomass and production rates observed in these waters during these investigations, compared to those observed in the stratified area.

The hypothesis that elevated production rates and phytoplankton biomass in the mixed and transitional zones represent an autumn bloom promoted by increased advection rates and remineralization is supported by the fluorescence data. Several authors have stressed the need for careful control of measuring techniques before chlorophyll fluorescence data can be used to make inferences concerning phytoplankton physiology (i.e. Vincent 1980). However, it seems from reported data that the effects of nutrient limitation upon *in vivo* fluorescence yield are more significant than those generated by light limitation or other factors (Kiefer 1973); depletion of inorganic nutrients causing an increase in fluorescence yield per unit chlorophyll *a*. The close relationship between parameters of the chlorophyll *a* vs fluorescence intensity relationship presented in this paper clearly indicate that the fluorescence yield per chlorophyll *a* is directly related to stratification. This is consistent with the hypothesis of remineralization through increased advection. However, other effects besides nutrient status could be important in determining fluorescence yields, in particular the species composition of the phytoplankton. There is no way of judging whether or not the difference in species distribution observed during these investigations could have accounted for the yield differences.

Acknowledgements

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