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BIOLOGICAL STUDIES IN THE VICINITY OF A SHALLOW-SEA TIDAL MIXING FRONT IV. SEASONAL AND SPATIAL DISTRIBUTION OF UREA AND ITS UPTAKE BY PHYTOPLANKTON

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On six cruises in 1980 the vertical and horizontal distributions of urea concentration and uptake rates were determined in the vicinity of a shallow-sea tidal mixing front in the western Irish Sea. Urea concentrations, while patchy, were similar throughout the year and showed no significant patterns of distribution and no relation to stratification of the water column. Urea uptake rates, on the other hand, showed a consistent and strong relationship to stratification, both vertically and horizontally, fastest rates being found in the less dense water on the stratified side of the front and above the pycnocline. Large differences between waters above and below the pycnocline were found during months of strong stratification. Similar differences occurred between the stratified and mixed surface waters on each side of the front. From relatively low urea uptake rates in March, when stratification was weak, extremely high rates were observed in June and thereafter decreased attaining another minimum at the end of September when stratification was weakening. Urea uptake indices (uptake per unit of chlorophyll *a*) were also highest in the surface stratified waters and followed a similar vertical, horizontal and seasonal distribution pattern as that of urea uptake rates. The seemingly unchanging urea concentrations throughout the year and its extremely fast uptake by micro-organisms indicate a rapid flux of this nitrogenous compound in the surface of the stratified waters. The possible routes of urea regeneration are discussed.

Budget calculation indicate that urea was an important source of nitrogen for phytoplankton in the surface stratified waters when oxidized forms of nitrogen such as nitrate were depleted and that the rapid flux of reduced nitrogen in the form of urea may be a major factor in sustaining high productivity associated with the frontal system.

CONTENTS

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1. Introduction

It is becoming increasingly evident that reduced forms of nitrogen, among them urea, play an important role in sustaining phytoplankton populations in sea water (Carpenter *et al.* 1972; Remsen *et al.* 1974; Webb & Haas 1976; McCarthy 1980; Fogg 1982; Kristiansen 1983). Particularly active urea uptake has been associated with a front in the German Bight (Turley 1980) and in Liverpool Bay (Floodgate *et al.* 1981). Occasional studies have indicated elevated rates of urea uptake in waters above the thermocline, where phytoplankton have to rely more on regenerated forms of nitrogen for growth, in both the stratified waters of the tropical Atlantic (Herbland 1976) and the temperate North Sea (Turley 1980).

Annually recurring shallow sea fronts, which develop during spring and summer and break down during late autumn and winter, are often noted for their productivity (Fogg *et al.* 1985*a*) and are the interface between mixed and stratified waters. In the stratified water column the thermocline acts as a further divide for the waters above and below. The resultant three water masses have very contrasting physical, biological and nutritional characteristics (Fogg *et al.* 1985*a*). It was, therefore, of interest to investigate in detail the seasonal development of the importance of urea in the different water types associated with the shallow sea front in the western Irish Sea.

This study was part of a multidisciplinary investigation into aspects of the phytoplankton and nutrients (Fogg *et al.* 1985*a*), the heterotrophic microbial activity (Lochte 1985), the bacterial numbers and biomass (Egan & Floodgate 1985) and the species abundance of zooplankton (Scrope-Howe & Jones 1985) associated with this front. All these different disciplines are related statistically by Kassab *et al.* (1985) and inter-relationships discussed by Fogg *et al.* (1985*b*).

2. Methods

Measurements of urea uptake and concentration were made on six cruises during 1980 on the R.V. *Prince Madog* in the waters on either side of a front located in the western Irish Sea. Details of the station positions, cruise dates, hydrography, chlorophyll *a*, adenosine triphosphate (ATP) and nutrient measurements are given by Fogg *et al.* (1985*a*). At each

station, a 40 l sample was collected from four different depths by using a pump with 6 cm internal diameter tubing and flow rate of 250 l min^{-1} (Fogg *et al.* 1985*a*). Subsamples for all microbiological and chemical analysis were taken from these volumes.

(*a*) *Determination of urea concentration*

Samples for urea analysis were filtered through a GFC filter and poured into clean, 150 ml screw-capped polyethylene bottles (previously rinsed three times with the sample) and stored at −20 °C for later analysis in the laboratory. When not in use these bottle were stored full of filtered 'aged' sea water. (In the hope of facilitating rapid freezing of the sample, 25 ml disposable plastic scintillation vials were used on one occasion and resulted in gross contamination of the samples, probably from the plastic itself.)

The method used to determine urea concentration was based on the automated adaptation of Demanche *et al.* (1973) of the diacetyl monoxime method described by Newell *et al.* (1967).

I used a Hati A40 II sampler and a Tecam TE-7 Tempette sealed bath filled with liquid paraffin to keep the large heating coil at a constant 94 °C. A metal conductive cooler was used to cool the solution before it entered a 10 cm flow cell in a Technicon colorimeter, connected to a Technicon range expander and a Gould constant voltage transformer. A Servoscribe 1S recorder had a sufficiently high voltage amplification to record the electrical output. A Bemas 15 channel pump delivered the solutions at the following rates: sample (1.20 ml min^{-1}), air (0.16 ml min^{-1}) to segment the sample, NaCl solution (0.42 ml min^{-1}), acid phosphate solution (0.32 ml min^{-1}), and colour solution (0.16 ml min^{-1}). A sampling time of 1 min and a wash time of 2 min were used. Because of peculiarities in the sampler a debubbling system was introduced between the sampler and the pump.

Filtered 'aged' sea water, collected the previous year from the area under investigation, was used for making up standards and as a wash between samples. Standards of 1.0, 2.5, and 5.0 μmol urea-N per litre were made daily. A 34 g l^{-1} NaCl (AR grade) solution made up in ultraviolet-irradiated, distilled, deionized water (a.s.w.) was used as the blank. A standard of 0.5 μmol urea-N per litre was made up in the a.s.w. to enable the determination of the urea concentration in the 'aged' sea water. A series of standards in replicate and a.s.w. blanks were run at the beginning, middle and end of each day's analysis and one standard every sixth sample as a continuous check on reproducibility. Apart from this the procedure was according to Demanche *et al.* (1973).

Analysis of standards showed that Beer's Law was obeyed for concentrations in the range of 0–10 μmol urea-N per litre. The standard deviation of 12 replicate samples containing 1.0 and 2.5 μmol urea-N per litre was 0.06 and 0.10 μmol urea-N per litre, respectively.

(*b*) *Determination of urea uptake rate and index*

Both urease and ATP urea amidolyase (UALase) catalyse the degradation of urea to ammonium and carbon dioxide in micro-organisms (Leftley & Syrett 1973). Therefore, if the carbon in urea is labelled with ^{14}C, then enzymatic hydrolysis will release $^{14}CO_2$ which can be collected and measured. The following method of determining urea degradation by using tracer additions of [^{14}C]urea to natural sea water, takes into account both the $^{14}CO_2$ liberated and the ^{14}C retained within the cells.

Three subsamples were collected in sterile 100 ml glass bottles and 500 μl of labelled [^{14}C]urea (61 mCi $mmol^{-1}$) (Amersham) added to each bottle. This gave a final concentration

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in each bottle of 5 μCi l^{-1} and 0.164 μmol N l^{-1}. The addition of tracer quantities of labelled [^{14}C]urea was an attempt not to appreciably affect the natural substrate concentration and, therefore, the natural uptake rates. It should be noted that the natural substrate concentration was also measured and taken into account in calculating urea uptake rates and indices (see below). One bottle was immediately fixed with 0.5 ml neutral buffered formalin and acted as a control. All samples were incubated in a shipboard incubator at ambient surface sea water temperature and light intensity, one of the remaining bottles was incubated in the dark, while the third experienced natural light conditions. After 4.5 h the incubation was terminated by the addition of 0.5 ml neutral buffered formalin to the samples and stored at ambient temperature until further processing in the laboratory.

In the laboratory, the fixed samples were decanted into 500 ml wide-necked screw-capped glass bottles and a scintillation vial containing an accordion-folded piece (2 cm × 8 cm) of chromatography paper (Whatman no. 1) moistened with 0.25 ml of 2-phenolethylamine was suspended in the air space above each sample to act as a carbon dioxide trap. Each sample was acidified by the addition of 1 ml of 2 M sulphuric acid and the flasks made air tight immediately. The scintillation vials were removed after 24 h and Aquasol (New England Nuclear) added as the scintillation fluid. The efficiency of this method of carbon dioxide capture was determined over a wide range of carbon dioxide levels by using ^{14}C-sodium bicarbonate and found to be 53.3 % (standard deviation, 2.82). After the carbon dioxide trapping procedure the ^{14}C incorporated within the cells was determined by filtering the samples through 0.2 μm pore size membrane filters under low vacuum (below 60 mm mercury), rinsing with filtered sea water, placing in scintillation vials and adding Aquasol.

The absolute activity was determined for each vial by the liquid scintillation counting technique and the quench corrections for each vial determined by the channels ratio method (Herberg 1965).

Urea uptake rates (U_V) and urea uptake indices (U_I) were calculated for samples incubated in both the light and the dark as follows:

$$U_V = U_d(S+A)/A_d t, \quad U_I = U_d(S+A)/A_d tP,$$

where U_d is the activity in $^{14}CO_2$ evolved and ^{14}C in the cells, A_d is the activity added, t is the incubation duration, S is the *in situ* concentration of urea, A is the concentration of added urea and P is the concentration of chlorophyll *a* (taken from Fogg *et al.* (1985*a*).

(*c*) *Statistical treatment*

The analysis of the data was carried out on the Bangor (U.C.N.W.) DEC-10 computer using the Statistical Package for the Social Sciences (S.P.S.S.).

Different water masses could be distinguished by their densities as stratification progressed through the water column during the summer months. By using appropriate density ranges for each cruise (table 1) it was possible to separate the lighter surface layers of the stratified water mass to the west of the front from the heavier bottom waters (those below the pycnocline) and heavier mixed waters to the east of the front (see figure 3 in Fogg *et al.* (1985*a*)). Stepwise discriminant analysis (Kassab *et al.* 1985) showed that the above criteria successfully distinguish between the water masses. Standard two-tailed *t*-tests were carried out on the biological variables grouped according to water mass as described above. All data were included in these analyses, that is, data from the lines of stations as well as drogue stations (see Fogg *et al.* 1985*a*).

Table 1. Density or temperature characteristics, for each period of investigation, used to define the water masses associated with the western Irish Sea front

(As depicted in figure 3 in Fogg *et al.* (1985*a*)).

	water masses separated by density (σ_t)	
date	surface stratified (SSW)	bottom stratified and mixed (BSW + MW)
12–13 March	26.717–26.812	26.812–26.966
29 April–1 May	26.436–26.701	26.702–26.932
3–6 June	25.860–26.369	26.370–26.695
15–17 July	25.729–26.001	26.001–26.501

	water masses separated by temperature (°C)		
	surface stratified (SSW)	bottom stratified (BSW)	mixed (MW)
23–24 September	13.54–13.78	12.12–12.82	13.81–14.56

Non-parametric (Spearman rank) correlation coefficients have been calculated by using all observations of some physical, chemical and biological variables. Further statistical analyses are given in Kassab *et al.* (1985). One-way analysis of variance (Kassab *et al.* 1985) supports the findings of the *t*-tests.

3. Results

(*a*) *Urea concentration*

There was little variation in the mean value for urea concentration in the different water masses throughout the year (table 2). The distribution of urea concentration along the survey line during the different periods of investigation are given in contour form in figure 1*a–g*. They, however, show great patchiness, both spatially and temporally, no distribution pattern being obvious. For example, low concentrations of urea were associated with frontal waters on 30 April (figure 1*c*) while on 1 May (figure 1*d*) high values were found in these waters.

Urea is most notable for its lack of any consistent relationship to any of the other measured variables (table 5). For example, in June, urea was significantly correlated positively with both chlorophyll *a* and ammonium, while in July, there was a negative significant correlation between urea and both variables.

Nitrate concentration (table 2) showed a marked decrease (sevenfold) in the surface stratified water (SSW) as stratification developed such that it was no longer the dominant nitrogen compound in this water mass. Urea and ammonium had similar concentrations well above that of nitrate, in June and July they together made up over 70% of the total urea-N plus ammonium-N plus nitrate-N. In the bottom of the stratified (BSW) and mixed (MW) water masses, however, nitrate was the dominant nitrogen source (always making up over 50% of the total urea-N plus ammonium-N plus nitrate-N), concentrations remaining similar throughout the year. Nitrite distribution is given in detail in Fogg *et al.* (1985*a*) but represents only a small amount of the total nitrogen. Results of *t*-tests (table 3) indicate that from April onwards there were highly significant differences between nitrate concentrations in the SSW and surrounding water (BSW + MW). With the exception of September, when significant differences occurred in the case of ammonium, similar tests on urea and ammonium indicate that there are no significant differences with regard to these water masses during the period of investigation.

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TABLE 2. SUMMARY OF NUTRIENT CONCENTRATIONS FOR EACH PERIOD OF INVESTIGATION DURING 1980

(Data were pooled according to water masses, as defined in table 1, where SSW is the surface stratified water, BSW is the bottom stratified water mass, MW is the vertically mixed water mass. *n*, Number of observations; $\bar{x}$, mean; s.d., standard deviation; min., is the minimum; max., is the maximum; n.d., not detectable.)

		concentration of urea-N/(μmol N l^{-1})					concentration of ammonium-N/(μmol N l^{-1})					concentration of nitrate-N/(μmol N l^{-1})				
date	water mass	*n*	$\bar{x}$	s.d.	min.	max.	*n*	$\bar{x}$	s.d.	min.	max.	*n*	$\bar{x}$	s.d.	min.	max.
12–13 March	SSW	15	1.88	0.65	0.94	3.77	15	1.29	0.85	0.17	3.56	15	5.82	1.60	3.14	7.66
	BSW	13	1.74	0.49	1.04	2.62	13	1.18	0.84	0.25	3.34	13	5.32	1.84	3.01	8.22
	MW	23	1.54	0.67	0.99	3.40	23	1.49	0.54	0.45	2.56	23	4.53	1.53	2.00	7.66
29 April to 1 May	SSW	37	1.36	0.60	0.32	3.20	37	1.84	1.15	0.20	4.28	37	2.62	1.95	0.09	7.55
	BSW	14	1.45	0.52	0.75	2.84	18	1.78	0.96	0.31	4.02	14	3.81	1.28	1.88	6.67
	MW	23	1.32	0.54	n.d.	2.15	23	1.97	0.88	0.54	3.67	23	4.19	1.63	1.41	7.07
3–6 June	SSW	33	1.25	0.73	0.09	4.24	33	1.36	0.63	0.40	2.50	33	1.03	1.61	n.d.	5.35
	BSW	19	1.38	0.78	0.60	3.47	19	1.66	0.69	0.76	3.07	19	4.32	1.22	0.23	6.38
	MW	32	1.07	0.45	0.43	2.65	32	0.88	0.49	0.41	2.35	32	4.25	1.64	0.35	7.79
15–17 July	SSW	33	1.23	0.46	0.60	3.08	33	1.72	0.85	0.39	3.39	33	0.84	1.32	n.d.	5.84
	BSW	15	1.30	0.50	0.32	1.68	15	1.59	0.93	0.54	3.23	15	4.88	2.44	0.22	8.43
	MW	19	1.27	0.45	0.69	2.38	19	1.87	1.16	0.70	5.59	19	3.80	0.93	1.75	4.83
23–24 September	SSW	13	1.54	1.07	0.55	4.28	13	2.60	0.87	1.50	4.01	13	2.80	1.00	1.34	4.64
	BSW	4	1.10	0.21	0.93	1.33	4	1.91	0.47	1.22	2.23	4	6.01	1.26	4.35	7.06
	MW	23	1.36	0.36	0.80	2.44	23	1.30	0.67	0.30	2.52	23	3.88	0.69	2.26	4.64

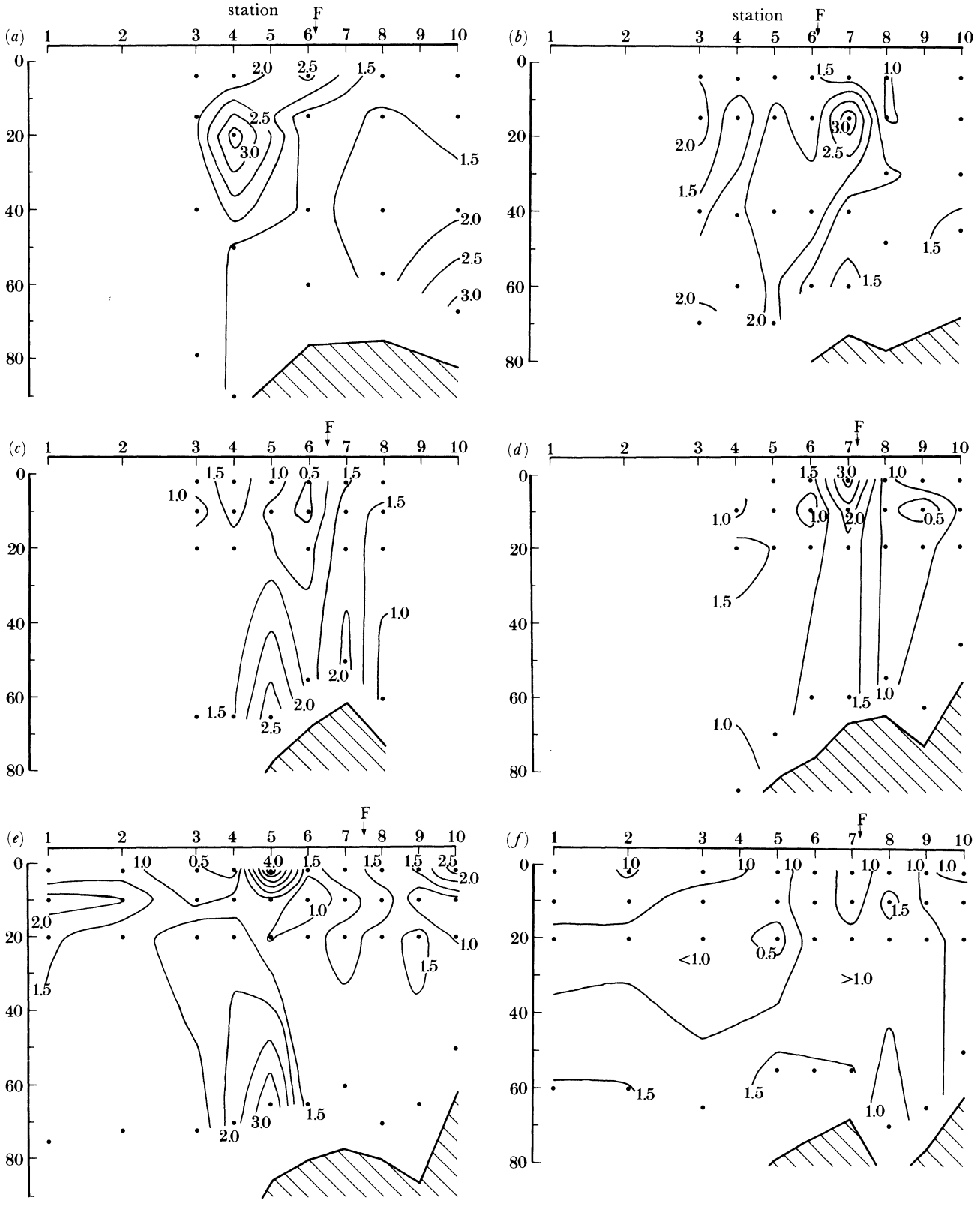

FIGURE 1 (*a*)–(*f*). For description see p. 479.

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TABLE 3. TWO-TAILED STUDENT'S *t*-TEST OF SIGNIFICANCE OF DIFFERENCES BETWEEN SURFACE STRATIFIED WATER MASS (SSW) AND COMBINED BOTTOM STRATIFIED AND MIXED WATER MASSES (BSW + MW) AS DEFINED IN TABLE 1

(Based on the significance of the *F*-test either pooled variance estimates (†) or separate variance estimates (‡) were used. $\bar{x}$, Mean; d.f. degrees of freedom; *p*, probability; n.a., data not available; $p \leqslant 0.05$ is taken as a significant difference. Data for inorganic nitrogen are from Fogg *et al.* (1985*a*).)

		nutrient concentration μmol N l^{-1}				urea uptake rates nmol N l^{-1} h^{-1}		urea uptake indices nmol N l^{-1} h^{-1} μg chl a^{-1}	
		urea-N	ammonium-N	nitrate-N	nitrite-N	in light	in dark	in light	in dark
12–13 March 1980	$\bar{x}$ SSW	1.84	1.33	5.74	0.354	7.2	4.2	n.a.	n.a.
	$\bar{x}$ BSW + MW	1.61	1.38	4.82	0.462	2.8	2.0	n.a.	n.a.
	t-value	−1.20†	0.23†	−1.88†	1.86†	−3.69‡	−3.87‡	n.a.	n.a.
	d.f.	50†	50†	50†	50†	14.5‡	21.4‡	n.a.	n.a.
	p	0.236†	0.817†	0.066†	0.069†	0.002‡	0.001‡	n.a.	n.a.
29 April to 1 May 1980	$\bar{x}$ SSW	1.41	1.89	2.61	0.409	10.9	5.2	9.9	4.9
	$\bar{x}$ BSW + MW	1.37	1.90	4.05	0.440	2.8	1.9	2.3	2.0
	t-value	−0.28†	0.04†	3.60†	1.22†	−5.90‡	−4.36‡	−5.78‡	−3.78‡
	d.f.	72†	73†	73†	74†	42.7‡	43.9‡	37.3‡	50.2‡
	p	0.784†	0.972†	0.001†	0.227†	0.000‡	0.000‡	0.000‡	0.000‡
3–6 June 1980	$\bar{x}$ SSW	1.25	1.36	1.03	0.275	113.4	67.6	102.4	58.0
	$\bar{x}$ BSW + MW	1.19	1.17	4.28	0.400	7.4	4.1	15.7	10.3
	t-value	−0.39†	−1.29†	9.47†	6.21‡	−5.46‡	−4.71‡	−4.62‡	−4.99‡
	d.f.	82†	82†	82†	44.5‡	31.1‡	32.0‡	28.8‡	31.9‡
	p	0.700†	0.201†	0.000†	0.000‡	0.000‡	0.000‡	0.000‡	0.000‡
15–17 July 1980	$\bar{x}$ SSW	1.24	1.68	1.23	0.270	33.6	22.3	87.0	59.8
	$\bar{x}$ BSW + MW	1.29	1.75	4.28	0.387	12.4	6.4	13.4	12.5
	t-value	0.45†	0.31†	7.53†	3.56†	−4.09‡	−5.42‡	−2.77‡	−2.17‡
	d.f.	70†	70†	70†	70†	42.1‡	40.3‡	22.4‡	26.2‡
	p	0.656†	0.760†	0.000†	0.001†	0.000‡	0.000‡	0.011‡	0.039‡
23–24 Sept. 1980	$\bar{x}$ SSW	1.54	2.60	2.80	0.507	12.8	13.6	18.3	18.7
	$\bar{x}$ BSW + MW	1.33	1.39	4.19	0.339	6.5	6.8	20.7	18.7
	t-value	−0.61‡	−4.85†	3.91†	−3.35†	−1.89‡	−1.47‡	0.33‡	0.01‡
	d.f.	9.8‡	38†	38†	38†	10.4‡	10.0‡	20.5‡	20.0‡
	p	0.557‡	0.000†	0.000†	0.002†	0.088‡	0.172‡	0.741‡	0.994‡

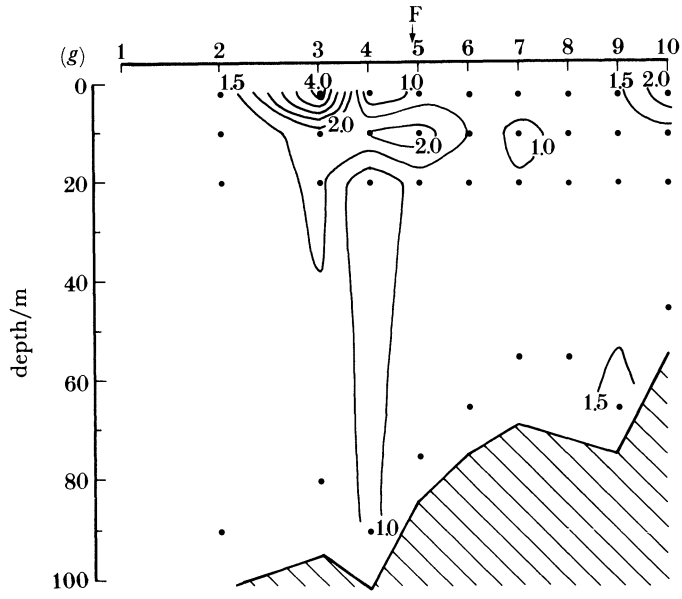

FIGURE 1. Section across the western Irish Sea front along the line of stations shown in figure 1 in Fogg *et al.* (1985*a*). Isopleths show the distribution of urea concentration (in micromoles of urea nitrogen per litre) on (*a*) 12 March 1980, (*b*) 13 March 1980, (*c*) 30 April 1980, (*d*) 1 May 1980, (*e*) 3 June 1980, (*f*) 15 July 1980 and (*g*) 23 September 1980. The sampling depth (●), sea bottom (hatching) and position of front (F) are indicated.

(*b*) *Urea uptake rates*

(i) *Spatial distribution*

The distribution of dark and light uptake rates along the survey line at different times of the year is depicted in contour form in figure 2*a–g* and figure 3*a–g*, respectively, and the summary of all the rates encountered in each water mass is given in table 4. The physical data, measured at the same time as the biological and chemical data which are referred to here are given in Fogg *et al.* (1985*a*). Two survey lines were carried out in the March and April cruises and, since the data were not corrected for tidal phase, differences between the two depth profiles is presumably due to lateral displacement caused by tidal movement of the front. Since light was found to enhance the uptake of urea (table 4) and irradiance changed throughout the day, urea uptake rates and indices determined in the dark are chosen for commenting on the distribution of urea uptake rates and indices. Urea uptake rates and indices determined in the light, although higher than those determined in the dark, do follow the same spatial and seasonal distribution pattern as those determined in the dark.

On 12 and 13 March (figure 2*a*, *b*) urea uptake rates were low but already showed a positive response to the weak stratification west of station 6, rates remaining constantly low throughout the water column in the mixed waters.

Profiles obtained in the following month, 30 April and 1 May (figure 2*c*, *d*) indicate marked association of rates of uptake with stratification and, on average, rates were three times more rapid in the surface of the stratified waters than in bottom stratified or mixed waters (table 4).

One month later on 3 June (figure 2*e*) there were extremely rapid rates of urea uptake which were solely associated with the waters west of the front and above the pycnocline with an average 16-fold difference between the water types. Rates in the waters below the pycnocline and in the mixed water were similar and low.

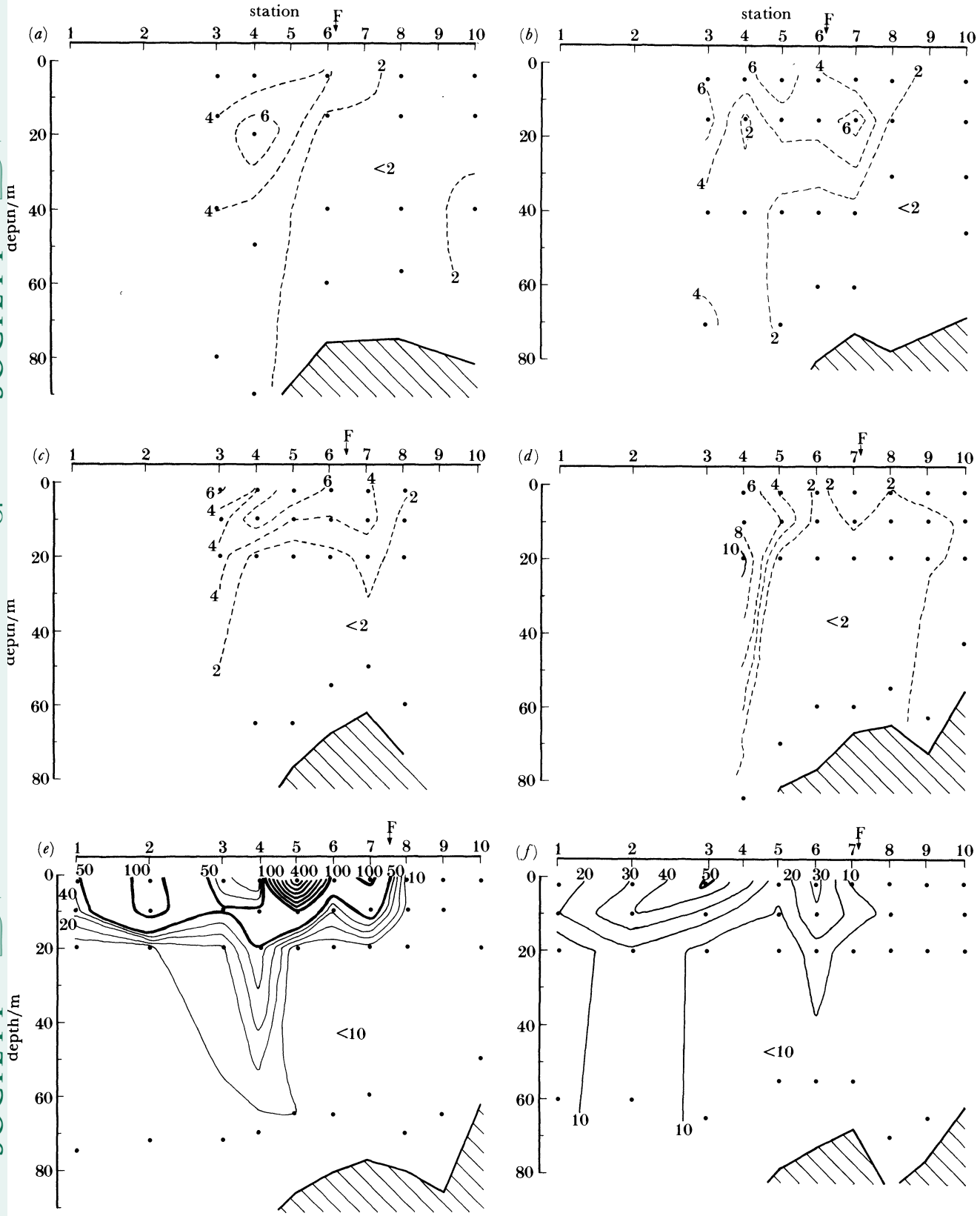

FIGURE 2 (*a*)–(*f*). For description see p. 483.

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TABLE 4. SUMMARY OF UREA UPTAKE RATES AND INDICES FOR EACH PERIOD OF INVESTIGATION DURING 1980

(Data were pooled according to water masses, as defined in table 1, where SSW is the surface stratified water, BSW is the bottom stratified water mass, MW is the vertically mixed water mass. See table 2 for the meaning of the statistical symbols, n.a. is data not available.)

		urea uptake rates nmol N l^{-1} h^{-1}										urea uptake indices nmol N l^{-1} h^{-1} µg chl a^{-1}									
		in light bottles					in dark bottles					in light bottles					in dark bottles				
date	water mass	n	$\bar{x}$	s.d.	min.	max.	n	$\bar{x}$	s.d.	min.	max.	n	$\bar{x}$	s.d.	min.	max.	n	$\bar{x}$	s.d.	min.	max.
12–13 March	SSW	12	7.6	4.1	2.6	18.3	15	4.3	2.1	1.3	8.1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
	BSW	13	4.2	2.8	0.6	8.2	12	2.4	1.4	0.5	4.4	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
	MW	21	1.9	1.0	0.8	5.2	21	1.8	1.3	0.8	7.0	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
29 April to 1 May	SSW	35	11.0	7.9	0.6	37.1	36	5.2	4.4	0.8	24.2	33	9.9	7.2	0.9	28.5	34	4.9	4.0	0.8	18.6
	BSW	14	3.0	3.9	0.5	15.4	13	1.8	1.7	0.2	4.9	12	3.0	2.7	0.4	10.0	11	2.6	2.8	0.2	11.5
	MW	3	2.7	1.5	0.4	4.8	23	2.0	1.2	0.3	5.0	22	2.0	1.7	0.3	8.3	22	1.7	1.6	0.2	7.1
3–6 June	SSW	32	113.4	109.9	3.8	611.7	33	67.6	77.3	2.3	447.6	29	102.4	100.3	3.7	470.1	30	58.0	51.0	2.1	193.2
	BSW	17	4.8	2.7	1.1	9.7	19	4.5	2.4	0.6	10.5	11	18.6	18.8	3.5	56.8	13	17.8	19.7	1.2	60.7
	MW	30	8.8	5.3	1.6	22.3	30	3.9	2.2	1.1	9.0	25	14.4	9.8	3.2	43.5	25	6.4	4.1	1.2	18.0
15–17 July	SSW	28	38.1	27.6	2.9	148.5	32	25.0	17.2	2.0	68.3	20	99.4	132.1	2.2	508.7	23	67.0	114.7	1.6	541.7
	BSW	14	12.6	16.3	1.5	59.3	15	8.1	4.9	0.8	17.3	8	16.4	13.6	3.7	43.8	8	21.3	16.4	1.9	46.5
	MW	18	12.2	4.0	5.7	18.6	17	4.9	2.1	1.0	8.0	10	11.1	6.3	5.5	26.6	9	4.7	2.3	1.7	9.1
23–24 Sept.	SSW	10	12.8	10.1	1.7	32.2	10	13.6	14.2	1.4	46.5	8	18.3	7.8	4.0	25.9	8	18.7	10.4	7.0	31.0
	BSW	3	5.2	1.4	3.6	10.9	3	6.5	2.7	3.4	8.8	3	16.6	13.2	4.5	66.8	3	18.5	14.8	3.8	53.1
	MW	23	6.7	4.7	1.4	23.4	19	6.9	5.3	1.2	21.8	14	21.6	30.2	4.0	119.5	12	18.8	29.1	4.0	108.9
10 Oct.	MW	4	6.1	0.8	5.2	7.2	4	2.2	0.0	2.0	2.3	4	16.8	3.5	11.78	20.0	4	6.1	1.6	4.5	7.7

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Table 5. Spearman rank correlation coefficients

(Urea concentration (urea), dark uptake rates (U_{VD}) and indices (U_{ID}) with density (σ_t), ammonium-N (NH_4), nitrate-N (NO_3), nitrite-N (NO_2), adenosine triphosphate (ATP), chlorophyll *a*, phaeopigments, bacterial numbers and biomass by direct counting, numbers of zooplankton, glucose uptake rates and indices, and light urea uptake rates (U_{VL}) and indices (U_{IL}) measured in this investigation during 1980 by other members of the team (see Introduction for references). The level of significance is indicated by *** being $\leqslant 0.001$, ** being $\leqslant 0.01$ and * being $\leqslant 0.05$, n.a. is data not available.)

	σt	urea	NH_4	NO_3	NO_2	ATP	chlorophyll *a*	phaeo-pigments	bacterial numbers	bacterial biomass	number of zooplankton	glucose uptake rate	glucose index	U_{VL}	U_{IL}
							12–13 March								
urea	−0.16	1.00	−0.03	0.47***	−0.39**	−0.15	n.a.	n.a.	0.23	0.23	0.04	0.01	−0.24	0.52***	n.a.
U_{VD}	−0.47***	0.57***	−0.03	0.41**	−0.39**	−0.13	n.a.	n.a.	0.26	0.26	0.57	0.60***	0.09	0.91***	n.a.
							29 April to 1 May								
urea	−0.11	1.00	0.10	0.17	0.16	0.04	−0.16	−0.01	−0.20	−0.16	0.02	0.20	0.27*	0.27*	0.31*
U_{VD}	−0.53***	0.26**	−0.16	−0.32**	0.00	0.29*	−0.02	0.02	−0.26*	−0.27*	0.47***	0.35**	0.44**	0.78***	0.70***
U_{ID}	−0.49***	0.32**	−0.21	−0.01	0.17	0.17	−0.48***	0.21	−0.42***	−0.41***	0.33**	0.26*	0.50***	0.56***	0.76***
							3–6 June								
urea	0.04	1.00	0.22*	−0.02	−0.08	0.04	0.27*	−0.03	−0.05	−0.06	0.02	0.26*	0.17	0.24*	0.12
U_{VD}	−0.70***	0.31**	0.33**	−0.55***	−0.42***	0.29**	0.45***	−0.12	−0.11	−0.12	0.52***	0.63***	0.43***	0.84***	0.81***
U_{ID}	−0.60***	0.17	0.43***	−0.48***	−0.37**	0.24	0.09	−0.02	0.01	−0.02	0.41***	0.52***	0.28*	0.71***	0.88***
							15–17 July								
urea	−0.04	1.00	−0.26*	0.06	−0.09	−0.30*	−0.39**	0.09	−0.13	−0.13	0.09	−0.12	0.01	0.10	0.32*
U_{VD}	−0.64***	0.17	−0.11	−0.60***	−0.64***	0.12	−0.48***	−0.01	0.40***	0.39***	0.40***	0.56***	0.27*	0.65***	0.75***
U_{ID}	−0.55***	0.33*	−0.17	−0.47***	−0.57***	−0.15	−0.81***	0.17	0.18	0.16	0.38*	0.31*	0.27	0.56***	0.85***
							23–24 September								
urea	−0.15	1.00	−0.13	0.04	−0.07	n.a.	−0.04	0.15	0.25	0.29	n.a.	−0.12	−0.31	0.31	0.35
U_{VD}	0.05	0.31	0.27	−0.10	0.32	n.a.	0.41*	−0.24	0.44*	0.40*	n.a.	0.36*	−0.09	0.86***	0.45*
U_{ID}	0.15	0.37	0.17	0.22	0.20	n.a.	−0.40	0.25	0.10	0.06	n.a.	0.26	0.09	0.47*	0.85***

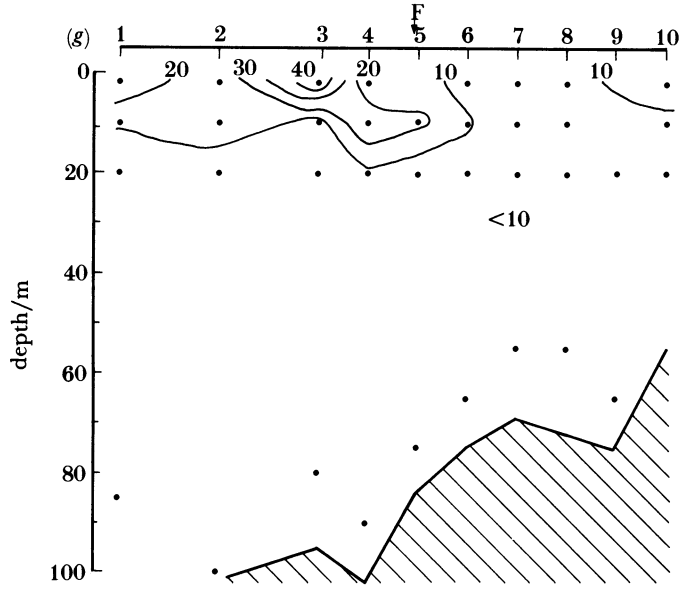

FIGURE 2. Section across the western Irish Sea front along the line of stations shown in figure 1 in Fogg *et al.* (1985*a*). Isopleths show the distribution of urea uptake in the dark (in nanomoles of urea nitrogen per litre per hour) on (*a*) 12 March 1980, (*b*) 13 March 1980, (*c*) 30 April 1980, (*d*) 1 May 1980, (*e*) 3 June 1980, (*f*) 15 July 1980 and (*g*) 23 September 1980. The sampling depth (●), sea bottom (hatching) and position of front (F) are indicated.

By 15 July (figure 2*f*), rates of uptake decreased in the surface stratified waters but still showed a notable association with stratification, being approximately fourfold greater than in either of the other water masses.

Similarly on 23 September (figure 2*g*), when autumn storms had begun to reduce stratification, a decrease in the rates of urea uptake was evident with, on average, only a twofold difference (table 4) between measurements taken in the surface stratified and surrounding waters.

On 10 October severe gales prevented a comprehensive survey being made. However, one station in the mixed water (station 10) was completed. The urea uptake rates for this station (table 4) were lower than those measured in the mixed water during the summer and similar to those measured during March and April–May.

The depth profiles for each month indicate that high urea uptake rates are associated with the warmer, less dense waters above the thermocline. Indeed the correlation coefficients in table 5 indicate that there is a highly significant negative relationship between these rates and density from March to at least mid-July. Results of *t*-tests (table 3) indicate that the apparent differences seen in the profiles between urea uptake rates in the water masses (as defined in table 1 and depicted in figure 3 in Fogg *et al.* 1985*a*) are highly significant from March to mid-July but were not significant at the end of September when autumn gales decreased the degree of stratification.

Urea uptake rates under shipboard, sea surface light conditions (urea uptake rates in the light) for the different months (figure 3*a–g*) have a similar spatial distribution pattern to that described above for uptake in the dark and similar highly significant differences between the surface stratified water mass and surrounding bottom stratified and mixed water masses (table 3).

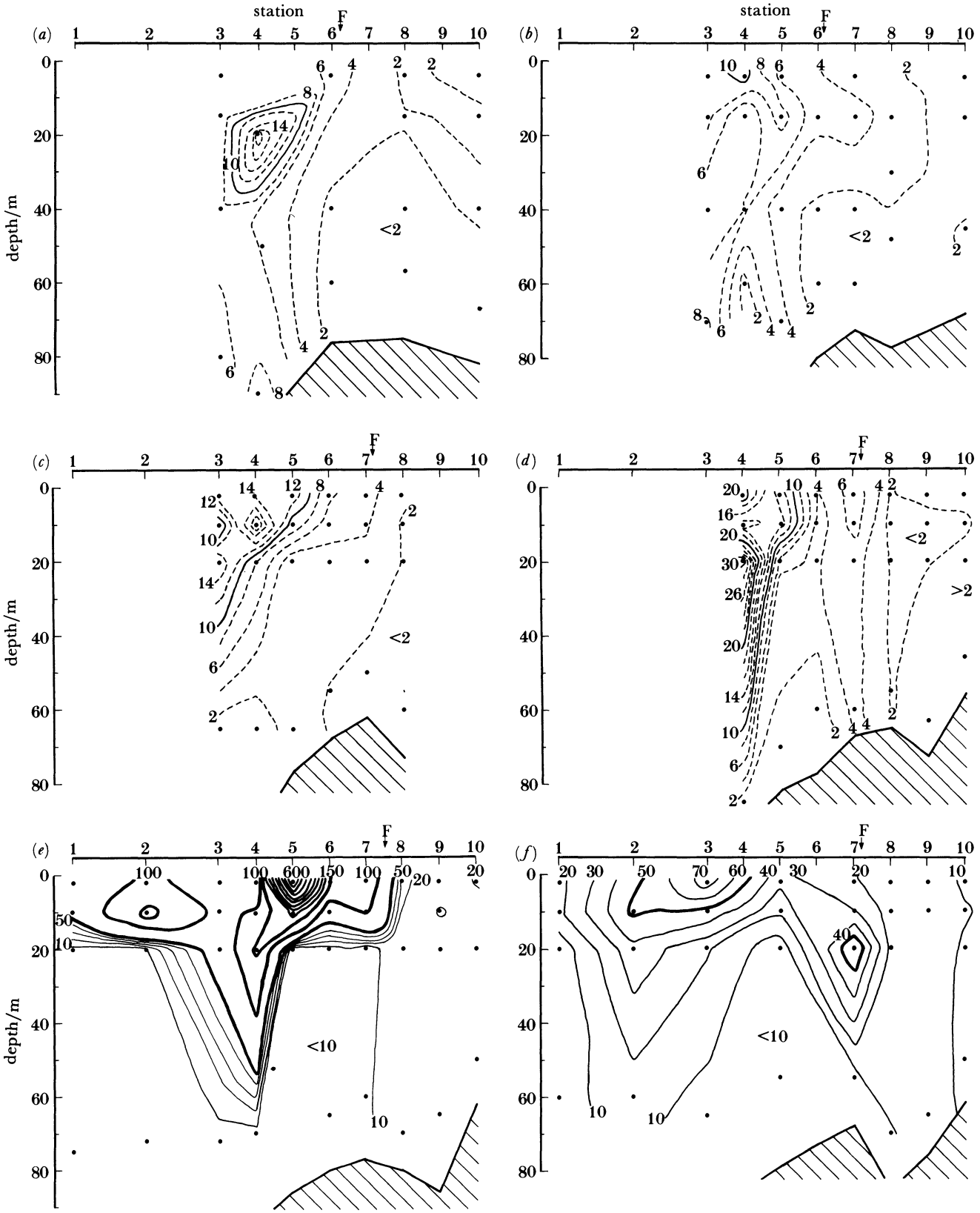

FIGURE 3 (*a*)–(*f*). For description see p. 485.

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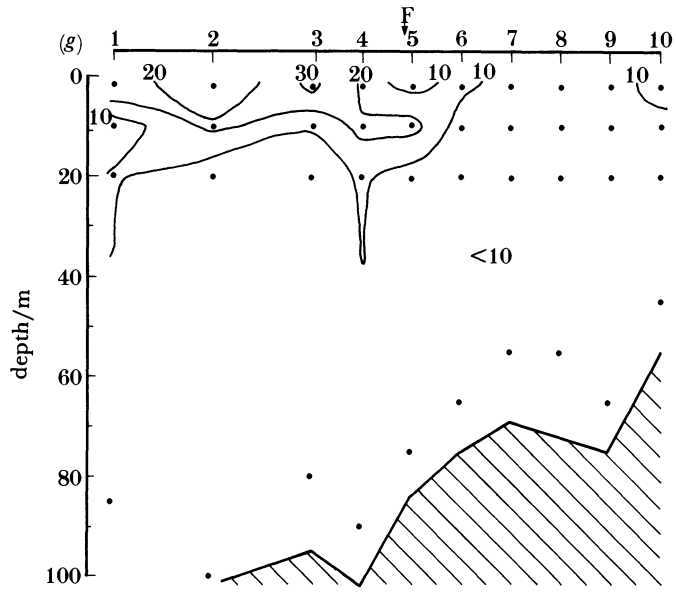

FIGURE 3. Section across the western Irish Sea front along the line of stations shown in figure 1 in Fogg *et al.* (1985*a*). Isopleths show the distribution of urea uptake in the light (in nanomoles of urea nitrogen per litre per hour) on (*a*) 12 March 1980, (*b*) 13 March 1980, (*c*) 30 April 1980, (*d*) 1 May 1980, (*e*) 3 June 1980, (*f*) 15 July 1980 and (*g*) 23 September 1980. The sampling depth (●), sea bottom (hatching) and position of front (F) are indicated.

Light uptake rates are generally higher in the SSW than rates measured in the dark indicating enhanced urea uptake in the light. There is some indication, however that light does not always enhance but may well inhibit uptake in samples taken from deeper water and incubated at sea surface light conditions. This anomaly was investigated in further detail in July 1982 when samples taken above and below the thermocline were incubated in light and dark bottles *in situ* and in the deck incubator (table 6). Lower rates of uptake occurred when the 60 m sample was incubated on deck under sea surface light conditions than in dark bottles. The 4 m samples, on the other hand, showed stimulated light uptake when exposed to the prevailing light conditions when compared with dark conditions. Light uptake rates from samples incubated *in situ* seem to be slightly lower than those incubated in the shipboard incubator. This is probably due to greater light stimulation in the samples in the shipboard incubator as the uptake rates from the two sets of dark bottles were very similar.

TABLE 6. UREA UPTAKE RATES FROM SAMPLES INCUBATED *IN SITU* AND IN A DECK INCUBATOR, IN THE AFTERNOON OF 6 JULY 1982 IN THE STRATIFIED WATER OF THE WESTERN IRISH SEA

(Samples were taken at 4 m (above the thermocline in the SSW) and 60 m (below the thermocline in the BSW) on station 5 (figure 1 in Fogg *et al.* 1985*a*). See table 2 for the meaning of the statistical symbols.)

	deck incubator (at 14.15 °C) urea uptake rates/(nmol N l^{-1} h^{-1})						incubated *in situ* urea uptake rates/(nmol N l^{-1} h^{-1})						
depth	in light bottles			in dark bottles			in light bottles			in dark bottles			*in situ*
m	*n*	$\bar{x}$	s.d.	*n*	$\bar{x}$	s.d.	*n*	$\bar{x}$	s.d.	*n*	$\bar{x}$	s.d.	temperature/°C
4	2	23.97	1.57	4	5.98	0.56	4	16.98	2.63	4	6.35	0.51	13.14
60	3	2.74	0.13	4	6.15	0.65	3	3.95	0.43	3	4.71	0.40	9.45

(ii) *Seasonal distribution*

Urea uptake rates in the mixed waters to the east of the front, despite small variations throughout the year (figure 4), do not change a great deal. In the waters west of the front (SSW) there are more dramatic seasonal changes, from low rates in March and a small increase in April–May they rose to rapid rates by June, a 13-fold increase in mean rates occurring during this period (table 4). After June, where the highest annual uptake rates were measured, there was a gradual decrease, although high rates were still recorded in July. September rates were lower still although, on average, twice as great as those measured in spring.

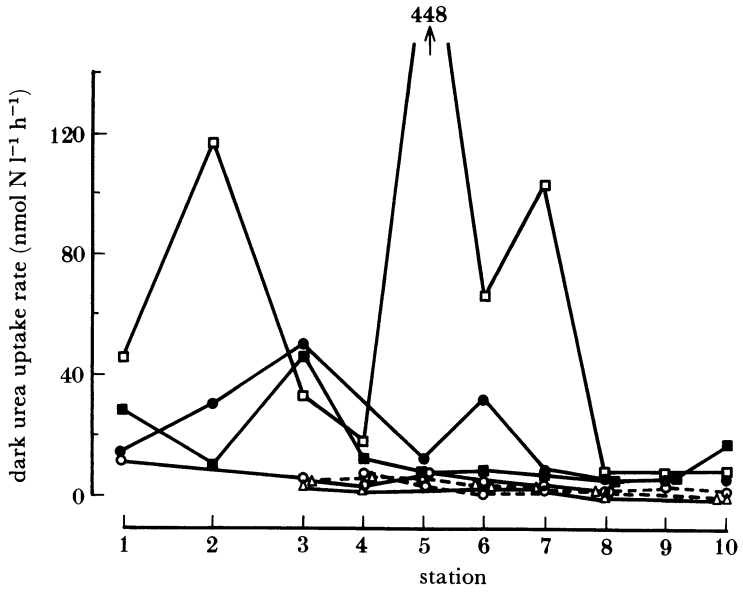

FIGURE 4. Seasonal distribution of surface samples of urea uptake in the dark, along the line of stations shown in figure 1 in Fogg *et al.* (1985*a*), on 12 March 1980 (—△—), 13 March 1980 (– –△– –), 30 April 1980 (—○—), 1 May 1980 (– –○– –), 3 June 1980 (—□—), 15 July 1980 (—●—) and 23 September 1980 (—■—).

(iii) *Distribution on drogue stations*

An attempt was made to study diurnal variation in urea uptake rates by using cruciform drogues (Fogg *et al.* 1985*a*) to try to ensure sampling of the same water over a 15 h period. Physical data indicate, however, that this was not always successful (Fogg *et al.* 1985*a*) and some care should be taken in interpreting drogue observations as diurnal cycles (Lochte 1985). A summary of the uptake rates measured in the different water types during these drogue stations carried out at different times throughout the year, is given in table 7. Above the thermocline, although variable, rates were much higher than those either below the thermocline or in the mixed water. There was less variation with time in the bottom of the stratified water and the mixed water masses. Thus, the differences in urea uptake rates found in the depth profiles along the line of stations cannot be explained by time-dependent anomalies in sampling.

TABLE 7. UREA UPTAKE RATES MEASURED ON DROGUE STATIONS DURING 1980 IN MIXED AND STRATIFIED WATERS

(Rates determined in the stratified waters are grouped into those above the thermocline (samples from 2 and 10 m) and those below the thermocline (samples 20 and deeper than 60 m) while in the mixed water all samples are pooled in one group. See table 2 for the meaning of the statistical symbols and figure 1 in Fogg *et al.* (1985*a*) for the station positions.)

			urea uptake rates in dark bottles/(nmol N l^{-1} h^{-1})				
date	station	water mass	n	$\bar{x}$	s.d.	min.	max.
29 April	1	SSW	12	7.5	6.2	1.5	24.2
29 April	1	BSW	12	3.2	1.6	1.2	6.2
4 June	4	SSW	12	70.1	32.8	10.9	124.4
4 June	4	BSW	12	5.7	3.9	1.6	15.4
5 June	9	MW	20	3.1	1.3	1.1	6.1
16 July	1	SSW	12	36.3	18.3	11.9	68.3
16 July	1	BSW	12	10.5	4.1	4.9	17.3
17 July	10	MW	12	5.7	2.1	2.2	8.0

(*c*) *Urea uptake indices*

An experiment carried out in July 1982 in the stratified waters of the western Irish Sea involving differential filtration (table 8) indicates that most urea uptake is by organisms above 1.0 μm in size. Since bacteria in the area investigated are smaller than 1.0 μm and are rarely attached to particulate matter (Turley & Lochte 1985*a*) it, therefore, seems that bacterial uptake of urea was only a minor contribution to the overall rate. Thus, chlorophyll *a* was used, as a measure of biomass, to determine the urea uptake indices. This, of course, assumes that heterotrophic organisms greater than 1.0 μm do not assimilate urea. Dark and light indices were calculated from uptake rates measured in the dark and light. Uptake indices for March could not be calculated as chlorophyll *a* concentrations were not available.

TABLE 8. UREA UPTAKE RATES IN DIFFERENTIALLY FILTERED SAMPLES

(Samples were taken from 4 m (above the thermocline) and 60 m (below the thermocline) incubated in light bottles *in situ* in the afternoon of 6 July 1982 in the stratified water mass (station 5, figure 1 in Fogg *et al.* (1985*a*) in the western Irish Sea. The meaning of the statistical symbols is given in table 2.)

	in situ urea uptake rates/(nmol l^{-1} h^{-1})						
	unfiltered sample			fraction of sample below 1.0 μm			
depth/m	n	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	percentage of unfiltered sample
4	4	16.98	2.63	4	0.27	0.08	1.6
60	3	3.95	0.43	4	0.41	0.04	10.4

During April–May there were highly significant differences between the indices in the SSW and BSW + MW waters (table 3). Although this is not altogether evident on the depth profile for 1 May (figure 5*b*), it is notable on the depth profile for 30 April (figure 5*a*), where higher indices are clearly associated with waters above the pycnocline, there being a twofold difference in their mean indices (table 4).

For June, *t*-tests (table 3) indicate highly significant differences between the SSW and surrounding water. This is easily seen in the depth profile in figure 5*c* in which indices are usually five- to tenfold higher in the waters above the thermocline.

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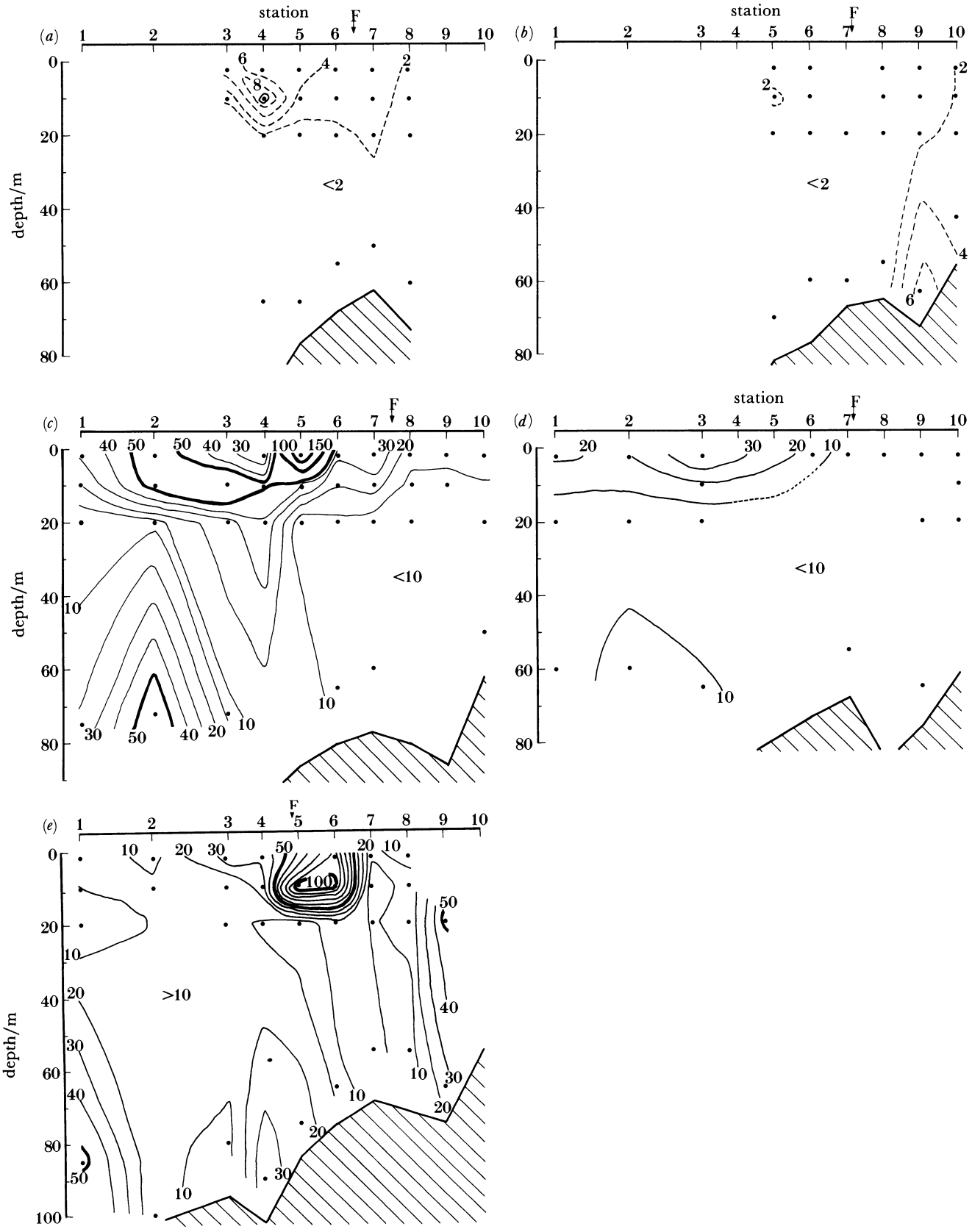

FIGURE 5. Section across the western Irish Sea front along the line of stations shown in figure 1 in Fogg *et al.* (1985*a*). Isopleths show the distribution of urea uptake indices in the dark (in nanomoles of urea nitrogen per litre per hour per microgram of chlorophyll *a* on (*a*) 30 April 1980, (*b*) 1 May 1980, (*c*) 3 June 1980, (*d*) 15 July 1980 and (*e*) 23 September 1980. The sampling depth (●), sea bottom (hatching) and position of front (F) are indicated.

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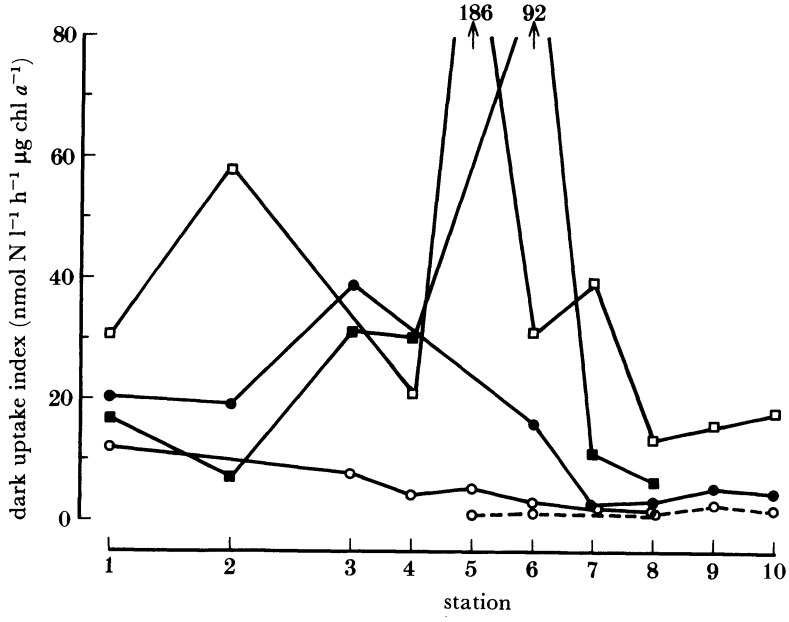

FIGURE 6. Seasonal distribution of surface samples of urea uptake indices in the dark, along the line of stations shown in figure 1 in Fogg *et al.* (1985*a*), on 30 April 1980 (—○—), 1 May 1980 (--○--), 3 June 1980 (—□—), 14 July 1980 (—●—) and 23 September 1980 (—■—).

During July, there were also significant differences in both light and dark indices measured in the SSW and BSW+MW (table 3, figure 5*d*). By September, the *t*-tests reveal that there are no significant differences despite some high indices in the surface waters of stations 5 and 6 in the region of the front (figure 5*e*).

A seasonal pattern is evident in urea uptake indices (figure 6). Generally, to the west of the front, in the SSW, indices were higher throughout the year. Indices decreased from stratified to mixed waters, with high indices sometimes being found in the transitional frontal region. In April, dark indices were low and by the next month indices in waters above the thermocline had risen by about ten times (table 4) and remained high for a further month. Although there is great variability in SSW indices, mean indices in June and July are the same but decrease substantially by September (table 4).

Above the thermocline light indices were on average twice as high throughout the year as the dark indices, and like the dark indices, increased from April to June; high values were maintained through to July but decreased again by September when there was little difference between the two indices (table 4).

(*d*) *Relation with other variables*

The statistical significance of Spearman rank correlations between urea concentrations, uptake rates and indices and some physical, chemical and biological variables are given in table 5 while correlations matrices for all variables are given by Kassab *et al.* (1985).

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4. Discussion

Among the interesting aspects of this investigation are the relatively constant, albeit patchy, urea concentrations throughout the year and the water column, the strong relationship between urea uptake and stratification, and a notable seasonal development in urea degradation, particularly above the thermocline. A similar relationship with hydrography has been noted before (Turley 1980; Floodgate *et al.* 1981). A temperature quotient (Q_{10}) of 2.6 for dark urea uptake rates can be calculated from the 60 m sample (table 6) incubated *in situ* (9.45 °C) and incubated on deck (14.5 °C) and is around the value calculated for metabolic reaction of phytoplankton to temperature (Eppley 1972). If the change of dark urea uptake rate or index in the SSW between April and June is attributed to temperature effects alone a mean Q_{10} of around 50 would be calculated. Such an unrealistically high Q_{10} indicates that temperature is not the main factor that regulates urea uptake. The relation between stratification and urea uptake must therefore be indirect, probably through other biological and chemical components of the ecosystem. Indeed, the multiple intercorrelations and principal components analysis in Kassab *et al.* (1985) indicate that many chemical and biological functions are similarly effected directly or indirectly by stratification. The onset of stratification in early spring triggers increased biological activity in the form of phytoplankton growth in the SSW, this results in the disturbance of a homogeneous winter system, when major perturbations in chemical and biological components do not occur. The phytoplankton, which seems to have developed in spring at the expense of the nitrate (which reaches very low concentrations in the SSW during summer), turn to reduced forms of nitrogen for growth, such as urea (urea uptake in the SSW is very fast) during summer. The partial isolation of the waters above the thermocline owing to stratification caused an imbalance of one of the components of this ecosystem and this rapidly spreads throughout the rest of the biota (Lochte 1985; Scrope-Howe & Jones 1984, 1985).

(*a*) *Urea uptake and its importance as a nitrogen source*

Active urea uptake can occur in darkness, as seen in this investigation, and has been particularly related to nitrogen-deprived cells (Rees & Syrett 1979). Uptake was often found to be markedly stimulated by light, probably because the active uptake mechanism may be driven by light-dependent phosphorylation (Rees & Syrett 1979). Similar light-dependent uptake of urea has been found by Webb & Haas (1976) and Mitamura & Saijo (1975, 1980*a*). The inhibited uptake of urea in deeper water samples exposed to sea surface light conditions may indicate an adaptation of the phytoplankton to grow at low light intensities as proposed by Samuelsson & Richardson (1982).

Increased phytoplankton growth resulting from increased stability of the water column, as seen in this investigation in the western Irish Sea, following stratification in early spring is a well-known phenomenon (see, for example, Pingree *et al.* 1976, 1978; Ignatiades 1979). Phytoplankton use nitrate as a nitrogen source for their growth (McCarthy 1980). Since nitrate originates mainly from the sediments rather than the water column (Billen 1978), it is not surprising to find that it decreased in the SSW where wind-mixing and diffusion were not sufficient to replace it, as has been frequently observed in stratified surface waters (Simpson & Hunter 1974; Beardall *et al.* 1978; Turley 1980; Holligan 1981). Nitrate, initially the most abundant of the combined nitrogen sources in the SSW, decreased in importance until midsummer when it became a minor part of the available nitrogen (Fogg *et al.* 1985*a*).

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Although, there may have been some diffusion of nitrate from below the thermocline this will not be sufficient to meet the nitrogen demand of the phytoplankton population in the waters above (Broecker 1974; King & Devol 1979), cells situated in the thermocline removing the nitrate at the lower part of the thermocline boundary (Pingree *et al.* 1977).

Urea, unlike nitrate, did not decrease with the onset of stratification despite increase in the rate of its uptake. Urea uptake rates were enhanced when nitrate decreased in the surface stratified waters (there being a highly significant negative correlation between them, table 5) and may, therefore, be a major alternative source of nitrogen for the phytoplankton in this ecosystem. This negative relationship with nitrate concentration is in accordance with the findings of Rees & Syrett (1979) that the urea uptake mechanism develops rapidly in cells deprived of nitrogen. The cell's ability to take up nitrate can also be lost as a response to nitrogen deficiency (Dortch *et al.* 1982).

It is easy to envisage that after the initial nitrate-dependent bloom those species develop that are capable of adjusting their nutrient uptake capabilities to exploit other nitrogen sources likely to be produced *in situ* in the SSW. Indeed, clonal differences in such uptake capabilities have been found (McCarthy & Goldman 1979). Butler *et al.* (1979), who found an annual succession from winter dissolved inorganic nitrogen dominating to summer dissolved organic nitrogen dominating in the English Channel, proposed that there may be a change from inorganic nitrogen phytoplankton users in early spring to species able to use organic nitrogen in summer.

A mean net primary productivity of 2.69 μg C l^{-1} h^{-1} was calculated from 19 measurements carried out in the SSW during the April–May cruise at different times during the daytime (K. Richardson, personal communication). Assuming a 12 h daylight period, this gives a daily C fixation rate of 32.4 μg C l^{-1} d^{-1} and assuming a C:Chlorophyll *a* ratio of 30:1 (Strickland 1965) the mean standing stock of phytoplankton is 36 μg C l^{-1} (table 9) this gives a doubling rate of 0.90 per day. By using a C:chlorophyll *a* ratio of 16.4:1, which was obtained in this water mass (see legend to table 9), a doubling rate of 2.0 per day can be estimated.

During the April–May cruise a daily primary production of 32 μg C l^{-1} d^{-1} would require a nitrogen demand of 400 nmol N l^{-1} d^{-1}, assuming a Redfield (1958) atomic C:N ratio of 6.625:1. Dark and light urea uptake rates were measured during the same period under the same incubation conditions as the primary productivities. Mean dark urea uptake rates in the SSW were 5.22 nmol N l^{-1} h^{-1} and over a 12 h night period this gives a potential uptake rate of 62.6 nmol N l^{-1} $12h^{-1}$ darkness. Mean urea uptake rate during daylight hours was 11.02 nmol N l^{-1} h^{-1} and over a 12 h daylight period this gives a potential uptake of 132.2 nmol N l^{-1} $12h^{-1}$. Taking both night-time and day-time uptake into account, we therefore have a rate for the SSW in April–May of 194.8 nmol N l^{-1} d^{-1}. Urea, therefore, appears to have contributed 48% of the above phytoplankton nitrogen demand in the SSW at this time of the year and this is in good agreement with the work of McCarthy (1972) and Webb & Haas (1976).

If we assume that primary productivity remained at the above daily rates during the 32 day period to 3 June, the decrease in nitrate concentration, from 2.62 to 1.03 μmol N l^{-1}, during the same period indicates that this form of nitrogen had only contributed 12% of the nitrogen demand, assuming no further input of nitrate into the SSW. Organic nitrogen compounds, other than urea, may also have contributed to the nitrogen demand to some extent (North 1975; Butler *et al.* 1979). Ammonium is likely to be an important source of nitrogen (McCarthy

et al. 1977; Eppley *et al.* 1979; Glibert 1982; Glibert *et al.* 1982; Kristiansen 1983) and since its concentration did not change in the SSW to any great extent throughout the year (Fogg *et al.* 1985*a*) it may have been in a state of rapid flux similar to that described here for urea.

In the SSW in June, one month later, mean urea uptake rates in the light and dark were 113.4 and 67.6 nmol N l^{-1} h^{-1}, respectively, and by using a 12 h night-time and day-time period as above there is a potential daily urea uptake rate of 2172 nmol N l^{-1} d^{-1}. Assuming the above C:N ratio this would mean a primary productivity of 173 μg C l^{-1} d^{-1}. With a mean standing stock of 38.7 μg C l^{-1} (estimated by using a C:chlorophyll *a* ratio of 30:1, see table 9)

TABLE 9. MEAN STANDING STOCK OF PLANKTON DURING THE DIFFERENT PERIODS OF OBSERVATION DURING 1980

(Phytoplankton standing stock was calculated from chlorophyll *a* (taken from Fogg *et al.* 1985*a*) using (*a*) C:chlorophyll *a* ratio of 30:1 (Strickland 1965) and (*b*) C:chlorophyll *a* ratio of 16.4:1 determined from samples taken in the western Irish Sea in 1983. Phytoplankton cell carbon was determined from numbers and volume by the direct count procedure described in Lochte & Turley (1985) and chlorophyll *a* by the method of Lorenzen (Strickland & Parsons 1972). Standing stock of bacterioplankton was calculated according to the procedure outlined in Floodgate *et al.* (1981) using the direct counts from Egan & Floodgate (1985). Zooplankton standing stock was taken from Scrope-Howe & Jones (1985) who calculated it from the size and number of each species for each sample. Each water mass is as defined in table 1, n.a., data not available.)

		bacterioplankton	phytoplankton μgC l^{-1}		zooplankton
date	water mass	μgC l^{1}	(*a*)	(*b*)	μgC l^{-1}
12–13 March	SSW	6.5	n.a.	n.a.	2.0
	BSW	9.2	n.a.	n.a.	1.6
	MW	6.1	n.a.	n.a.	0.6
29 April to 1 May	SSW	20.6	36.0	19.7	35.8
	BSW	27.0	24.0	13.1	47.3
	MW	69.1	46.2	25.3	42.7
3–6 June	SSW	31.7	38.7	21.2	193.8
	BSW	52.6	14.4	7.9	65.0
	MW	43.5	20.1	11.0	16.5
15–17 July	SSW	14.8	44.4	24.3	69.1
	BSW	14.4	24.0	13.1	27.7
	MW	7.5	36.6	20.0	20.0
23–24 September	SSW	11.5	28.5	15.6	n.a.
	BSW	2.3	10.5	5.7	n.a.
	MW	6.1	10.5	5.7	n.a.
10 October	MW	n.a.	11.4	6.2	n.a.

or 21.2 μg C l^{-1} (estimated by using a C:chlorophyll *a* ratio of 16.4:1, see table 9) a doubling rate of 4.5 per day or 8.2 per day, respectively, is required to achieve this productivity. These estimates of doubling rates are very high and would require a specific growth rate (μ) of 3.1 and 5.7 respectively which must be close to the maximum possible, regardless of the C:Chl *a* ratio used. Although μ_{max} for marine plankton is typically around 0.5 per day (table 2 in Goldman *et al.* 1979) high values have been found in oligotrophic waters where nutrient turnover was fast and concentrations low or undetectable (Koblentz–Mishke & Vedernikov 1976). Lochte (1985) shows that there is rapid bacterial recycling of dissolved organic matter in the SSW. It is possible that a rapid flux is maintaining these high phytoplankton growth

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rates and that steady-state conditions are found in the SSW in part due to rapid recycling of nutrients by bacteria and in part due to continuous grazing by zooplankton, phytoplankton production being balanced by disappearance. The mean standing stock of chlorophyll *a* in the SSW (table 9) did, in fact, remain constant from the April–May cruise to the July cruise.

Another interpretation of the high daily phytoplankton urea uptake rates found in June may be that uptake rates and growth rates are uncoupled as found with ammonium and urea uptake under saturating concentrations in two laboratory grown marine diatoms (Horrigan & McCarthy 1981, 1982). They suggest that such a capability in a natural phytoplankton community might well be an advantage in waters where nutrient concentrations are low and where the phytoplankton have to rely on regenerated nitrogen. The SSW of this investigation, where there is the most rapid uptake of urea, fits this description. Urea uptake is an active mechanism with high affinity for urea at the concentrations measured here and it is possible to create a higher concentration of free, unchanged urea inside laboratory-grown marine phytoplankton cells (Rees & Syrett 1979). Conover (1975*a*), however, found no accumulation of urea in the internal cell pool of *Thalassiosira fluviatilis* and since the majority (over 90%) of the ^{14}C-labelled urea was recovered in the form of CO_2 during this investigation, accumulation in intact form seems unlikely. If phytoplankton growth and urea uptake in these waters are uncoupled then nitrogen from urea must be stored in another form, presumably ammonium, and not be immediately channelled into protein production.

Regardless of how they are interpreted, the urea uptake rates indicate that nitrogen, even ignoring the large contribution ammonium is also likely to make, is not limiting phytoplankton growth in the SSW. As temperature, light and rapid nutrient turnover are known to affect the magnitude of μ_{max} positively (Eppley 1972; Goldman & Carpenter 1974) the SSW may provide near-ideal growth conditions for non-siliceous phytoplankters. Accurate determination of *in situ* growth rates would be required to verify this hypothesis. Similar indications have been found in the inner Oslo fjord where nitrogen limitation is only rarely approached despite large standing stock of phytoplankton, rapid turnover of nitrogen and low concentrations of urea, ammonium and nitrate (Kristiansen 1983).

The calculation of urea uptake indices is an attempt to relate urea degradation to biomass, measured in this case by chlorophyll *a*. Therefore, a direct comparison between urea degradation abilities of the phytoplankton at different times of the year and in different water masses is possible. These indices show that the massive urea uptake found in June is due to a larger phytoplankton population, taking urea up at the same rate per chlorophyll *a* as to be found the following month (table 4). The indices also indicate that the vertical and horizontal differences in the distribution of urea uptake rates are not due to differences in population size but are actual differences in uptake rates.

(*b*) *Urea production*

Although urea concentrations are patchy they remain in a similar range throughout the year, this in combination with high rates of removal by the phytoplankton indicates that there is an equally rapid production of urea within the SSW. The concentration of urea would depend on the rate of degradation on one hand and its rate of regeneration on the other, and this flux may be so rapid that no pattern or uniformity of distribution emerges. The lack of any pattern, small patch size and inconsistent relationship with other variables as seen for urea in this investigation has been observed by other workers (McCarthy 1970; Remsen 1971; McCarthy

& Kamykowski 1972; Turley 1980). The crucial question is: which biological component, or components, is or are, responsible for maintaining this rapid flux of urea?

Fish (Sedletskaja 1975) and sea birds (Bourne & Harris 1979) have been reported to concentrate in the productive regions around fronts and both have been observed to so congregate in the western Irish Sea by I. Rees (personal communication) and, therefore, contribute to urea production either directly in the case of some fish, (McCarthy & Whitledge 1972) particularly the elasmobranchs (Baldwin 1964), or indirectly in the case of sea birds via uric acid decomposition (Antia & Landymore 1974; Steinmann 1976).

Zooplankton may well contribute significant amounts of urea, ranging from under 10% (Corner & Newell 1967; Mitamura & Saijo 1980*b*) to 50% (Eppley *et al.* 1973) of the total nitrogen excreted. This variation in the percentage of nitrogen excreted as urea may be related to the feeding state of the zooplankton before the experiment (McCarthy 1971). There is evidence that the zooplankton in the stratified waters do not migrate below the thermocline (Scrope-Howe & Jones 1984, 1985). Thus, any nitrogen removed by grazing by zooplankton would remain within the ecosystem of the SSW. On the other hand, there may be some removal of nitrogen by migrating organisms such as euphausids and fish that ascend to feed in the SSW at night, returning to the BSW at dawn (Turley & Lochte 1985*b*).

The contribution of nitrogen excretion by zooplankton to the nitrogen phytoplankton requirement is often argued to be small (Jawed 1973; Williams & Muir 1981), particularly the contribution of the larger copepods (Dagg *et al.* 1980, 1982) and, at times high (Davis & Sleep 1981) with seasonal and regional differences (Vargo 1979). There is no consistent correlative evidence from this investigation to suggest that either zooplankton or phytoplankton are important urea producers; for instance, during June there is a positive correlation between urea and both nitrate and chlorophyll *a* but a month later the correlation with both variables is negative. No significant positive relation between urea concentration and zooplankton numbers was found at any time. However, this lack of correlation between these potential urea producers and its concentration is not surprising considering the rapid flux of this nutrient. Indeed, the highly significant positive correlations between urea uptake rates and zooplankton numbers from April–May to July (table 5) may well support the hypothesis that either zooplankton grazing or excretion, or both, are important contributing factors in the flux of urea.

Degradation of purines and pyrimidines, which occur in large quantities on land, by terrestrial bacteria and fungi often result in the production of urea (Vogels & Van der Drift 1976). If the micro-organisms contain urea-degrading enzymes, urease or UALase, then ammonium can be produced. However, not all bacteria have such an enzyme system and rather produce urea as the end product of degradation of these compounds (Vogels & Van der Drift 1976). In the marine environment bacteria do not make a significant contribution to urea degradation (table 8) (Remsen *et al.* 1972; Mitamura & Saijo 1975; Webb & Haas 1976) and those that are urease-positive may not be members of the marine flora (Steinmann 1976). It, therefore, seems that in the marine environment urea may well be the end product of degradative pathways by bacteria that would otherwise produce ammonium via urease.

Data concerning the concentration and degradation of purines and pyrimidines are limited in the marine environment but since both groups of compounds are such basic components of living organisms it seems likely that they are of similar importance in the marine environment. Hypoxanthine and guanine excretion may be common in marine ciliates (Soldo *et al.* 1978) and

ciliates are becoming increasingly recognized as important contributors to the bioenergetics of the planktonic community (Heinbokel 1978; Heinbokel & Beers 1979; Stout 1980; Pace 1982). Both ciliates and flagellates were found in large numbers in the SSW during a cruise in July 1982 in the western Irish Sea (Lochte & Turley 1985). Flagellates have also been observed to be dominant above the thermocline in other stratified areas (Holligan & Harbour 1977; Davis & Sleep 1981). The phytoflagellate *Ochromonas malhamensis* excretes urea as the end product of arginine and urate degradation (Lui & Roels 1970). However, under starvation conditions, this versatile micro-organism produces a higher level of urease so that the excreted urea may be re-used for protein synthesis. This mechanism, if common to other phytoflagellates such as those present in large numbers in the SSW, would be an excellent survival strategy.

Maita *et al.* (1973) obtained urea from bacterial decomposition of arginine added to sea water and argued that this is the major source of urea in sea water. Webb & Johannes (1979) also found urea produced by microbial breakdown of this amino acid which can be excreted by crustaceans (Smith & Young 1955). Ornithine as well as urea may be produced by the breakdown of arginine (Remsen *et al.* 1974) and the high concentration of ornithine and low concentration of arginine found in the Baltic (Mopper & Lindroth 1982) may indicate that the production of urea in this manner is plausible. Phytoplankton can also excrete significant amounts of combined nitrogen as polypeptides (Fogg 1966) or as free amino acids during bloom periods (Hammer & Eberlein 1981) and some may synthesize urea directly (Conover 1975*b*). Indeed, Lee & Cronin (1982) found that total amino acids accounted for 40–60% of the particulate organic nitrogen flux and that 80% of the amino acids produced in the surface waters during primary productivity was decomposed above 14 m. Satoh (1980) and Satoh *et al.* (1980) also conclude that increase in urea concentration in waters containing decomposing phytoplankton is due to its production by bacterial decomposition of organic matter including phytoplankton. Similarly, decomposition of zooplankton by bacteria has been reported to produce significant quantities of urea (Mitamura & Saijo 1980*b*).

The most striking relationship between rate of urea uptake and another measurement of activity, rather than a standing stock, is that of bacterial activity measured by the uptake of [^{14}C]glucose in tracer amounts. Not only are they significantly correlated throughout the year but the pattern of activity throughout the water column as seen in the form of profiles are remarkably similar (Lochte 1985). It can, therefore, be stated that high rates of urea uptake by phytoplankton occur when there is rapid turnover of dissolved organic compounds by bacteria. As pointed out above, heterotrophic breakdown of organic matter often leads to the production of urea. It, therefore, seems likely that bacterial action may well be playing an important role in the production of urea in the waters above the thermocline. Glibert (1982) found a similar balance between ammonium uptake and regeneration and that the size fraction below 10 μm and often that below 1 μm was responsible for its remineralization. *In situ* bacterial productivity measurements would be required to test this hypothesis and to give a reliable estimate of the amount of nitrogen made available by bacterial action on dissolved organic compounds. This aspect is currently under investigation and will be reported elsewhere.

There are, therefore, many candidates for the producers of urea but the major contributor, or contributors, within this ecosystem remains an open question and an area of research begging further attention.

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(c) *Competition for urea*

It has often been found that urea uptake, particularly in coastal waters, is carried out nearly exclusively by phytoplankton (see, for example, McCarthy 1972; Remsen *et al.* 1972; Mitamura & Saijo 1975; Webb & Haas 1976; Herbland 1976) as found during this investigation. This has led to the conclusion that phytoplankton are more effective competitors for urea than bacteria. However, since there would be no energetic advantage for bacteria in using urea as a nitrogen source, and they can achieve such an advantage by using other organic nitrogen compounds, it is tempting to suggest that bacteria do not actually compete with phytoplankton for urea but rather ignore the molecule. For instance, Torrella & Morita (1982) observed a positive chemotactic response of a starving marine *Vibrio* towards a wide range of amino acids but not towards urea. Furthermore, bacterial use of combined nitrogen, which may well be largely provided by extracellular products released from phytoplankton, may directly result in the supply of urea for phytoplankton use. The close relationship between urea uptake by phytoplankton and glucose uptake by bacteria would support the hypothesis that phytoplankton and microheterotrophs are interactively coupled by feedback mechanisms to ensure homoeostasis (Smith & Higgins 1978). The balance between the uptake and production of urea further indicates that these mechanisms may be very complex.

Indeed, one can take this hypothesis even further and include the grazers as the rapid primary production is not expressed in high standing stock. It, therefore, seems likely that grazing by zooplankton is an important factor regulating the abundance and species composition of the phytoplankton (Ryther & Sanders 1980) and in ensuring homoeostasis, particularly as they remain an integral part of the ecology of the SSW (table 9) not migrating below the thermocline during the day (Scrope-Howe & Jones 1984, 1985).

It is, therefore, proposed that all three trophic levels, the bacteria, phytoplankton and zooplankton are in a very close interdependent association and this accounts for the sustained productivity of these waters. It seems that it is physical mixing of the water body that destroys this finely balanced homoeostasis in late autumn just as it was the stabilizing of the water column that enabled its development in spring.

A most pertinent question remains open and that is at what rate does this dynamic system function? Although we cannot establish accurate rates of production from direct measurements of growth, urea and glucose uptake rates indicate that the speed is very fast indeed. We do know, however, that the SSW is more dynamic and functions at a far faster rate than either the waters below the thermocline or the mixed waters to the east of the front.

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