PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Biological Studies in the Vicinity of a Shallow-Sea Tidal Mixing Front I. Physical and Chemical Background

G. E. Fogg, B. Egan, S. Hoy, K. Lochte, S. Scrope-Howe and C. M. Turley

Phil. Trans. R. Soc. Lond. B 1985 **310**, 407-433
doi: 10.1098/rstb.1985.0125

Phil. Trans. R. Soc. Lond. B **310**, 407–433 (1985)　[407]
Printed in Great Britain

BIOLOGICAL STUDIES IN THE VICINITY OF A SHALLOW-SEA TIDAL MIXING FRONT
I. PHYSICAL AND CHEMICAL BACKGROUND

By G. E. FOGG, F.R.S., B. EGAN, S. HOY, K. LOCHTE†, S. SCROPE-HOWE and C. M. TURLEY‡

Department of Marine Biology (University College of North Wales), Marine Science Laboratories, Menai Bridge, Anglesey LL59 5EH U.K.

(*Received* 26 *April* 1984)

[Plate 1]

CONTENTS

A study has been made of the distribution and activities of bacteria and zooplankton as they varied seasonally in 1980 and 1981 in the vicinity of a shallow-sea tidal mixing front in the western Irish Sea (approximate position 53° 20′ N, 5° 45′ W to 53° 50′ N, 5° 0′ W). This paper presents the physical and chemical background to these studies as shown by the variations in temperature and salinity and concentrations of chlorophyll *a*, phaeopigments, cellular adenosine triphosphate (ATP), nitrate, nitrite and ammonium nitrogen, in sections normal to the front. Observations at drogue stations were made to establish the extent of diurnal variations in these properties but these appeared to be small relative to other variations. As the front developed, higher chlorophyll *a* concentrations appeared in the surface stratified water, in contrast to the bottom stratified water and mixed water, with highest concentrations at the surface at the stratified side of the front and in subsurface patches in the vicinity of the pycnocline. As the phytoplankton populations increased nitrate became depleted in the surface stratified water but nitrite and ammonium nitrogen concentrations remained at about the same levels. Cellular ATP concentration did not appear to be a useful measure of total biomass but indicated high biological activity in the surface stratified water.

† Present address: Institute für Meereskunde an der Universität Kiel, Abt Mikrobiologie, Düsternbrooker Weg 20, D-2300 Kiel, F.R.G.
‡ Present address: Institute for Marine Environmental Research, Prospect Place, Plymouth PL1 3DH, U.K.

1. Introduction

Fronts between tidally mixed and thermally stratified waters in shallow seas are marked by distinct variations, which as yet are neither fully described nor explained, in the spatial distribution of organisms (Holligan 1981). The best-known feature is the peak in the standing stock of phytoplankton which is usually found on the stratified side of the front where the pycnocline approaches the surface (see, for example, Pingree *et al.* 1975; Savidge 1976; Bowman & Iverson 1978; Beardall *et al.* 1978; Pingree *et al.* 1978; Simpson *et al.* 1979). This accumulation of phytoplankton may be explained as the result of recently stabilized nutrient-rich mixed water at the front providing particularly favourable conditions for growth (Pingree *et al.* 1975), of passive advection of phytoplankton cells into the frontal region (Okubo 1978), or of nutrient complementation between the abutting water masses (Beardall *et al.* 1978; Beardall *et al.* 1982). These mechanisms are not mutually exclusive and, however the local concentration of phytoplankton arises, it would be expected to be accompanied by increased biomass or activity at other trophic levels. Studies on zooplankton (Dufour & Stretta 1973; Floodgate *et al.* 1981) bear this out. Activity may be further enhanced as fish and sea-birds attracted by the accumulation of food (Brown 1980; E. I. S. Rees, personal communication) move into the frontal region and excrete substances available as phytoplankton nutrients, so that an effect perhaps initiated by physical conditions may undergo biological amplification (Fogg 1981). In a study in Liverpool Bay (Floodgate *et al.* 1981) evidence was obtained suggesting that bacterial and zooplankton distributions and activities were markedly affected by the existence of a front. The importance of bacteria, as producers of biomass as well as in the recycling of minerals, is being increasingly recognized (Williams 1981; Joint & Morris 1982) and much remains to be learnt of the activities of zooplankton at fronts. Since the Liverpool Bay front is a plume front, complicated by river inflow, in further studies of frontal ecosystems it was decided to carry out detailed investigations on a tidal mixing front, more marine in character, in the western Irish Sea.

This front appears in spring approximately along a line from 53° 20′ N, 5° 45′ W to 53° 50′ N, 5° 0′ W, with mixed water to the SE and stratified water to the NW (figures 1 and 2). It had the advantages for this study of being readily accessible from Menai Bridge and of having been the subject of previous studies. It was first described by Simpson (1971), hydrographic sections across it were given by Bruce & Aiken (1975) and its physical oceanography has been discussed by Simpson & Hunter (1974); Allen *et al.* (1980); and Simpson & Bowers (1981). Beardall *et al.* (1982) and Richardson *et al.* (1985) reported on the distribution of phytoplankton and Savidge *et al.* (1984) on primary productivity.

The aim of the research was to obtain quantitative information about the distribution and activities of bacteria and zooplankton as they varied seasonally in the vicinity of the front. Such information considered in relation to the physical and chemical environment and the abundance of phytoplankton should throw light on the mechanisms that give rise to the biological features of fronts and on the interrelations between the various trophic levels.

This paper describes the general methods of working and discusses the hydrographical and chemical background to the biological observations. Subsequent papers will deal with the distribution of bacteria (Egan & Floodgate 1985), microbial activity as determined by glucose uptake (Lochte 1985) and urea metabolism (Turley 1985), distribution of zooplankton

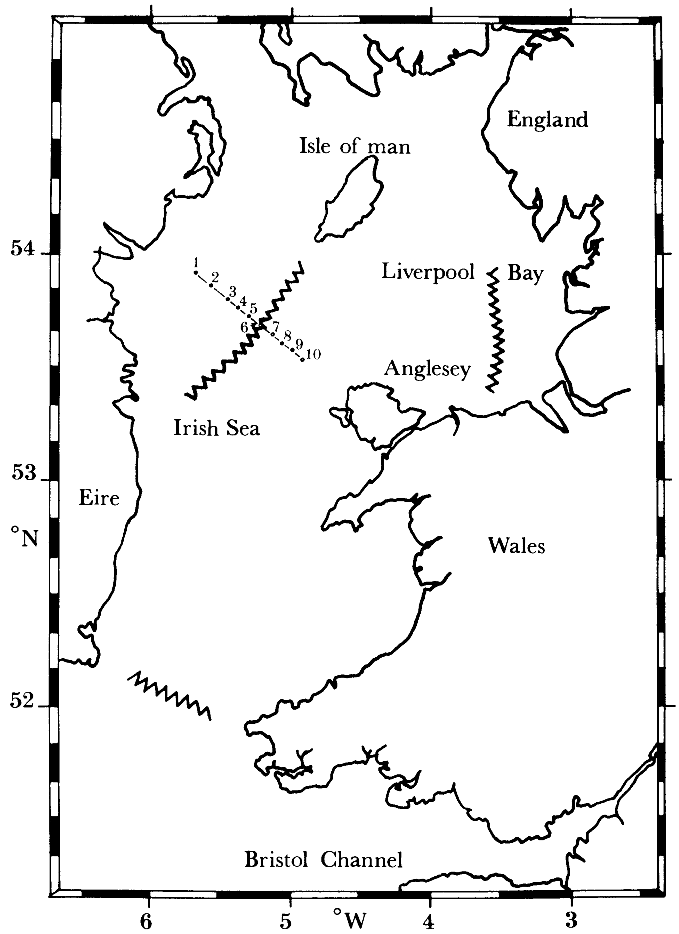

FIGURE 1. The Irish Sea showing the position of fronts (zig-zags) and of the transect across the western Irish Sea front.

(Scrope-Howe & Jones 1985*a*), statistical methods (Kassab *et al.* 1985) and general conclusions (Fogg *et al.* 1985).

2. Methods

Observations were made from R.V. *Prince Madog* at approximately monthly intervals during the existence of the front in the years 1980 (cruises ISEA 1–6, table 1) and 1981 (cruises ISEA 7–10, table 1). On each cruise, stations were occupied along a fixed transect, chosen so as to cross the front at approximately 90° to its general orientation as shown by satellite imagery and to ensure that adequate representation of the mixed and stratified waters was obtained (table 2). An advantage of this survey design was that, tidal flow being nearly parallel to the front and samples from a given transect being taken within 20 h, there is little chance of samples from adjacent stations being confounded.

Surface temperature, conductivity and chlorophyll fluorescence were recorded continuously along the transect. At the stations, vertical profiles of temperature and conductivity were obtained by using a Plessey 9400 conductivity–temperature–depth (c.t.d.) system calibrated against determinations with samples from 1.5 l N.I.O. bottles. However, when the c.t.d. system

Table 1. ISEA cruise dates

cruise		date
ISEA	1	10 March 1980 to 14 March 1980
	2	28 April 1980 to 2 May 1980
	3	2 June 1980 to 6 June 1980
	4	14 July 1980 to 17 July 1980
	5	22 September 1980 to 24 September 1980
	6	8 October 1980 to 10 October 1980
ISEA	7	27 April 1981 to 1 May 1981
	8	22 June 1981 to 26 June 1981
	9	3 August 1981 to 7 August 1981
	10	5 October 1981 to 6 October 1981

Table 2. Positions of ISEA stations

station	latitude	longitude	approximate distance between stations/km
1	53° 54.5′	5° 35.6′	6.0
2	53° 51.8′	5° 32.0′	6.0
3	53° 49.3′	5° 26.6′	4.4
4	53° 47.5′	5° 24.0′	5.2
5	53° 45.3′	5° 20.2′	4.4
6	53° 43.7′	5° 16.6′	5.2
7	53° 41.5′	5° 13.0′	5.2
8	53° 39.0′	5° 9.0′	4.4
9	53° 37.2′	5° 6.0′	4.6
10	53° 35.2′	5° 2.5′	

was not available the physical structure was obtained from six depth casts of N.I.O. (National Institute of Oceanography) bottles, the thermocline being located with a bathythermograph.

Samples for chemical and biological analysis were obtained, after the c.t.d. and N.I.O. bottle casts, by pump. This had a 6 cm internal diameter hose which was lowered vertically to precise depths determined by pressure transducer (Shape S300). In 1980 samples were taken from four predetermined depths, in 1981 six depths were sampled. Water was discharged by a modified submersible centrifugal pump (Flygt B2051) at a flow rate of 250 l min^{-1} into a 40 l rinsed container from which subsamples were taken for biological and chemical analysis. On ISEA 5, because of pump failure, all samples were taken from N.I.O. bottles. Zooplankton net hauls (Scrope-Howe & Jones 1985*a*) were taken after the pump samples.

In addition to the transect stations, drogue stations were occasionally occupied for up to 15 h in both mixed and stratified areas and samples taken with the object of determining diurnal changes in discrete water masses. These were marked by a fixed geometry (cruciform) drogue (Booth 1978) consisting of two intersecting rectangles, each 1 m wide and 2 m high, of plastic canvas suspended just below the surface from a buoy carrying a flag and flashing light for location.

Salinity and density (σ_t) were derived from the c.t.d. data by using tables supplied by the manufacturers. The stratification factor $\overline{V}$, denoting the amount of energy required per unit depth to bring about complete vertical mixing of the water column, was calculated according to Simpson *et al.* (1977). The position of the front may be defined as the line separating mixed water with $\overline{V} > -9$ from stratified water with $\overline{V} < -9$. For purposes of biological interpretation the waters in a section were grouped in two or three masses, the surface stratified water (SSW)

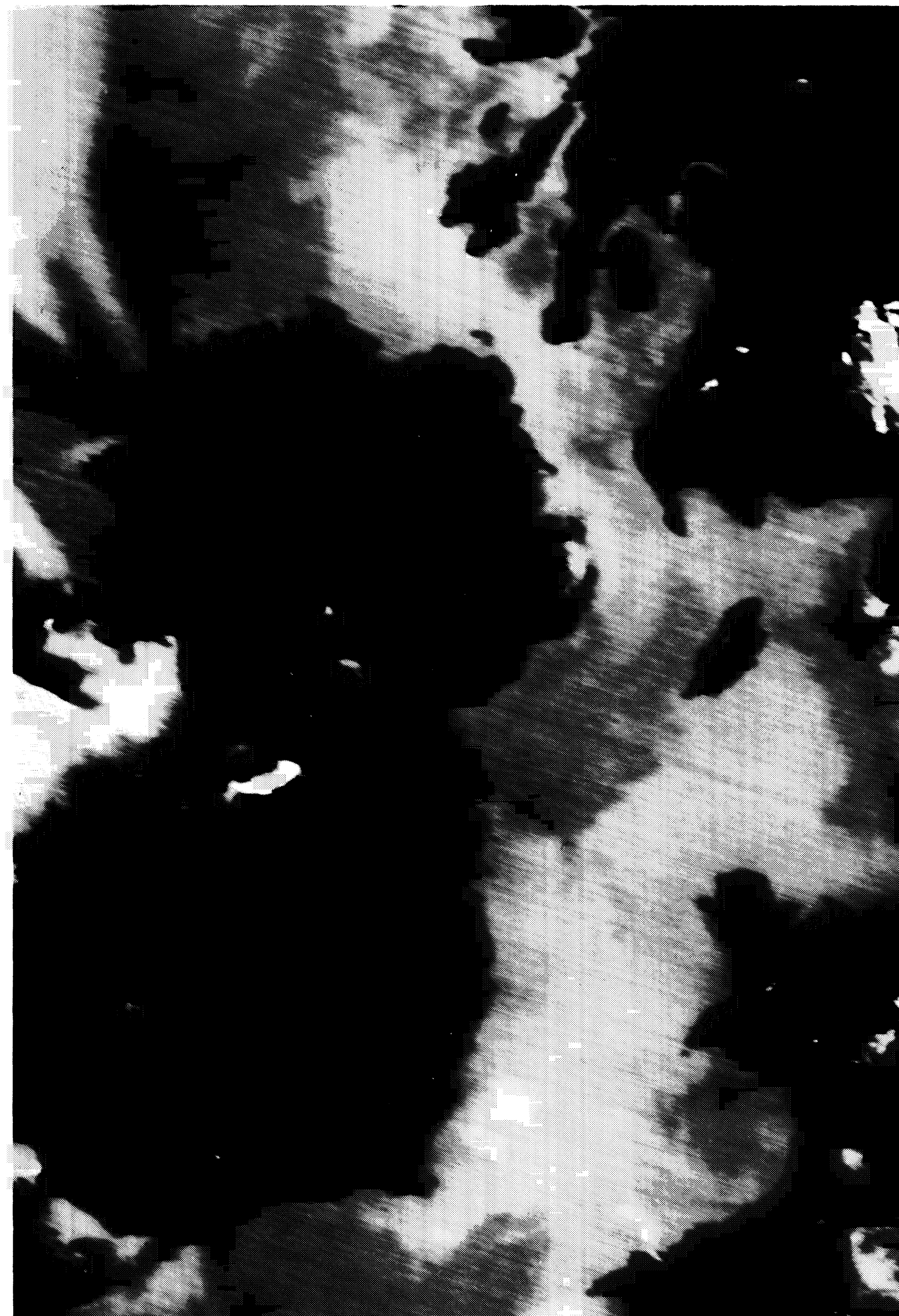

FIGURE 2. Satellite infrared image of the Irish Sea (NOAA5, 21 May 1978, 09h30 G.M.T.) showing the fronts as in figure 1.

(*Facing p.* 410)

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

bounded by the thermocline and the front, and the bottom stratified water (BSW) together with or separately from the mixed water (MW) (figure 3). These masses were initially separated on an *ad hoc* basis by taking $\bar{V}$ as a guide to the position of the front and by using density or temperature, as was most convenient, as criteria for separation (table 3). Later a more refined treatment was used (see Kassab *et al.* 1985) but this did not alter the conclusions drawn in any essential way.

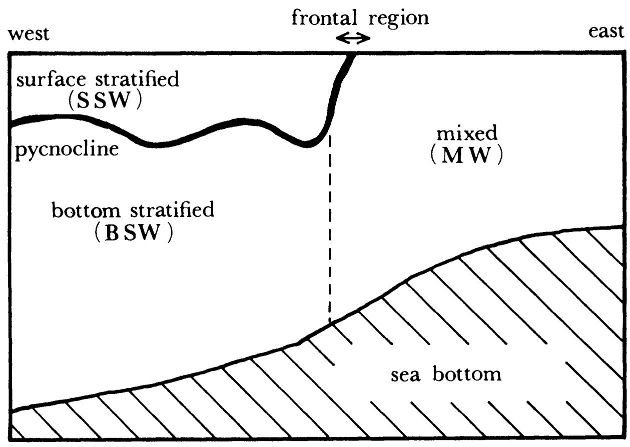

Figure 3. Diagram showing a section normal to a front and the differentiation of the three water masses.

Table 3. Density or temperature characteristics used to define the water masses associated with the western Irish Sea front

(See figure 3.)

cruise	surface stratified (SSW)	bottom stratified (BSW)	mixed (MW)
	water masses separated by density (σ_t)		
ISEA 1	26.72–26.81	26.82–26.93	26.81–26.97
2	26.44–26.70	26.71–26.93	26.74–26.84
3	25.87–26.37	25.37–26.69	26.41–26.49
4	25.70–26.00	26.01–26.50	26.01–26.11
7	26.38–26.60	26.60–26.65	26.50–26.60
8	25.50–26.10	26.10–26.45	26.10–26.20
	water masses separated by temperature (°C)		
5	13.5–13.8	12.1–12.8	13.8–14.6
9	13.0–14.5	9.8–13.0	12.5–13.0

Chlorophyll *a* was determined by fluorometry calibrated against discrete samples. In 1980 continuous records were obtained by using a submersible Variosens fluorometer. In 1981 water was passed through a Turner Designs fluorometer (model 10-000R) from 5 m depth intervals by using the submersible pump. Samples for chlorophyll *a* determination by absorption were filtered on to GF/C filters and extracted with 90% Analar acetone. Chlorophyll *a* and phaeopigment determinations were made by the method of Lorenzen (Strickland & Parsons 1972), measuring extinction on a Cecil Instruments spectrophotometer CD 303.

Cellular adenosine triphosphate (ATP) was determined according to Holm-Hansen & Booth (1966) by using internal standards to assess recovery efficiency (Afghan *et al.* 1977; Jones & Simon 1977) and a DuPont 760 Luminescence Biometer for the measurements.

Nitrate- and nitrite-N were determined in discrete samples by the automated methods described by Strickland & Parsons (1972). Ammonium-N, also determined in discrete samples by an automated procedure, was first estimated by the method of Head (1971) and later by that of Liddicoat *et al.* (1975); these two methods are comparable chemically, only differing in the methods by which the same intermediates and end products are obtained.

All data storage, manipulation and analysis was carried out on the University College of North Wales DEC system-10 computer. It should be noted that some of the statistical tests reported in this paper are of a preliminary nature; the conclusions drawn are, however, confirmed and reinforced by the more refined treatment described by Kassab *et al.* (1985).

3. Results

(*a*) *Hydrography*

Temperature, salinity and density data for 1980 are summarized in table 4. The seasonal pattern of hydrographic changes is best seen in the vertical sections showing variations in σ_t (figure 4*a–g*) and the plots of variations in $\overline{V}$ (figure 5*a–g*). By March 12 the front was already evident in the vicinity of station 7, where $\overline{V}$ had the critical value of -9, with mixed water to the SE ($\overline{V} > -9$) and the beginnings of stratification to the NW ($\overline{V} < -9$). A second line of stations occupied the following day yielded a generally similar picture (figure 4*a* and *b*; figure 5*a* and *b*). There was a temperature inversion in the water column NW of station 6, associated with lower surface salinity (table 4). Difference in temperature and salinity between SSW and BSW plus MW for the pooled results from the two consecutive sections were distinct. (table 5). Although salinity differences were initially the cause of stratification, SSW continued to show somewhat lower salinities throughout the season and there was no evident discontinuity between the situation in March and that later in the year when temperature differences were dominant. The frontal system developed slowly in a somewhat cold, unsettled spring. By 30 April, thermal stratification was evident and, again, the front was in the vicinity of station 7

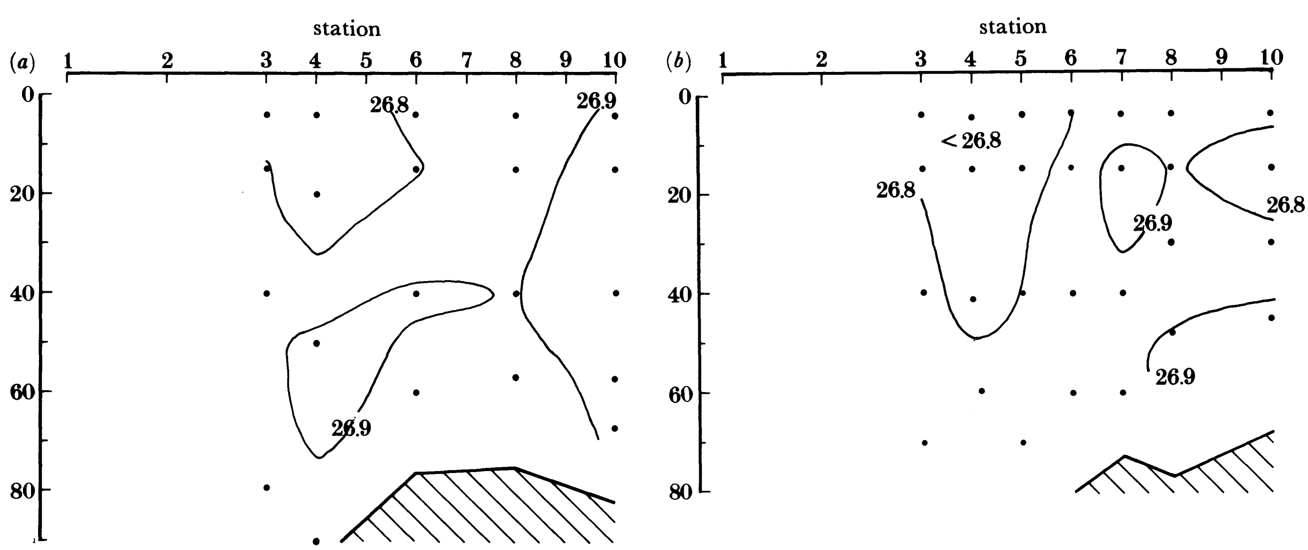

Figure 4 (*a*), (*b*). For legend see facing page.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

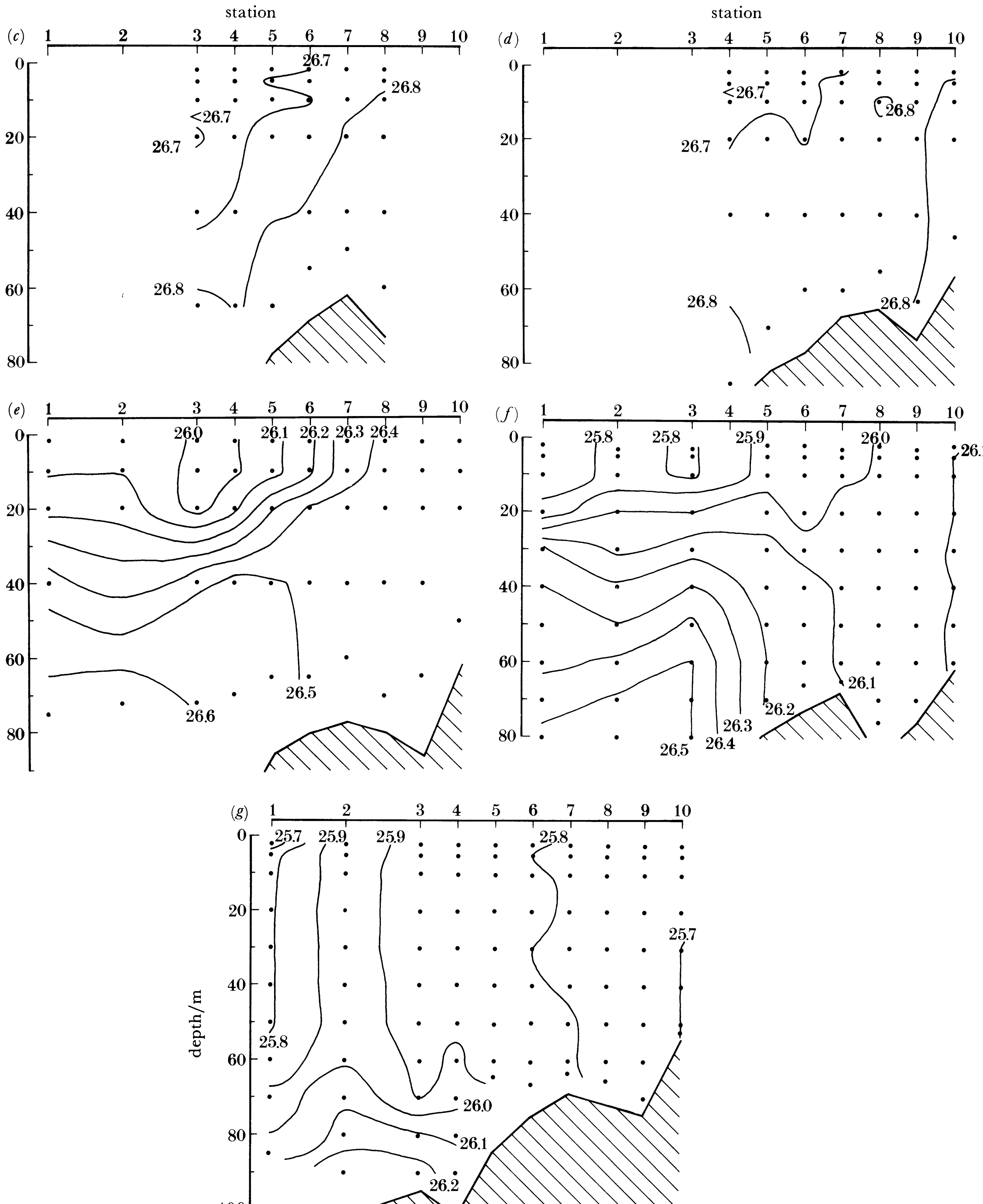

FIGURE 4. Sections in the Irish Sea from 53° 54.5′ N, 5° 35.6′ W to 53° 35.2′ N, 5° 2.5′ W, showing the variation of density (σ_t) during the 1980 season: (*a*) ISEA 1, leg 1, 12 March; (*b*) ISEA 1, leg 2, 13 March; (*c*) ISEA 2, leg 1, 30 April; (*d*) ISEA 2, leg 2, 1 May; (*e*) ISEA 3, 3 June; (*f*) ISEA 4, 15 July; (*g*) ISEA 5, 23 September.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 4. Summary of temperature, salinity and density (σ_t) data for the 1980 season along a section in the Irish Sea from 53° 54.5′ N, 5° 35.6′ W to 53° 35.2′ N, 5° 2.5′ W

(Statistics are given for three water masses, surface stratified water (SSW), bottom stratified water (BSW) and mixed water (MW) as defined in table 3. n, Number of observations; $\bar{x}$, the mean; s.d., standard deviation; min., minimum; max., maximum.)

		temperature/°C					salinity (‰)					σ_t				
cruise		n	$\bar{x}$	s.d.	min.	max.	n	$\bar{x}$	s.d.	min.	max.	n	$\bar{x}$	s.d.	min.	max.
ISEA 1	SSW	15	7.85	0.073	7.67	7.97	15	34.30	0.054	34.21	34.38	15	26.77	0.035	26.72	26.81
12–13 March 1980	BSW	13	8.05	0.114	7.90	8.16	13	34.47	0.050	34.37	34.56	13	26.87	0.030	26.82	26.93
	MW	23	8.03	0.079	7.89	8.17	23	34.50	0.059	34.35	34.59	23	26.90	0.041	26.81	26.97
ISEA 2	SSW	37	8.58	0.342	7.68	9.19	36	34.23	0.121	33.99	34.64	36	36.60	0.077	26.44	26.91
29 April to	BSW	15	8.15	0.282	7.83	8.66	15	34.39	0.061	34.25	34.51	15	26.79	0.055	26.71	26.93
1 May 1980	MW	23	8.43	0.082	8.22	8.56	23	34.44	0.033	34.36	34.51	23	26.79	0.019	26.74	26.84
ISEA 3	SSW	33	11.15	0.665	9.41	12.08	33	34.09	0.054	34.02	34.26	33	26.06	0.148	25.87	26.37
3–6 June 1980	BSW	19	9.28	0.414	8.44	9.98	19	34.26	0.054	34.11	34.32	19	26.51	0.078	26.37	26.69
	MW	32	9.99	0.084	9.82	10.25	32	34.33	0.013	34.27	34.35	32	26.45	0.018	26.41	26.49
ISEA 4	SSW	33	12.86	0.375	12.11	13.44	33	34.21	0.039	34.17	34.30	33	25.83	0.094	25.70	26.00
15–17 July 1980	BSW	15	10.69	0.925	9.55	11.98	15	34.26	0.035	34.20	34.30	15	26.27	0.159	26.01	26.50
	MW	19	12.21	0.087	12.04	12.38	19	34.32	0.029	34.28	34.37	19	26.04	0.035	26.01	26.11
ISEA 5	SSW	13	13.66	0.077	13.55	13.77	13	34.44	0.127	34.20	34.67	13	25.84	0.096	25.63	26.00
23–24 September 1980	BSW	4	12.45	0.286	12.11	12.81	4	34.51	0.067	34.47	34.61	4	26.14	0.101	26.04	26.28
	MW	23	14.25	0.215	13.82	14.55	23	34.52	0.020	34.49	34.56	23	25.78	0.040	25.70	25.85
ISEA 6	MW	4	13.47	0.015	13.45	13.48	4	34.21	0.004	34.20	34.21	4	25.70	0.002	25.70	25.70
10 October 1980																

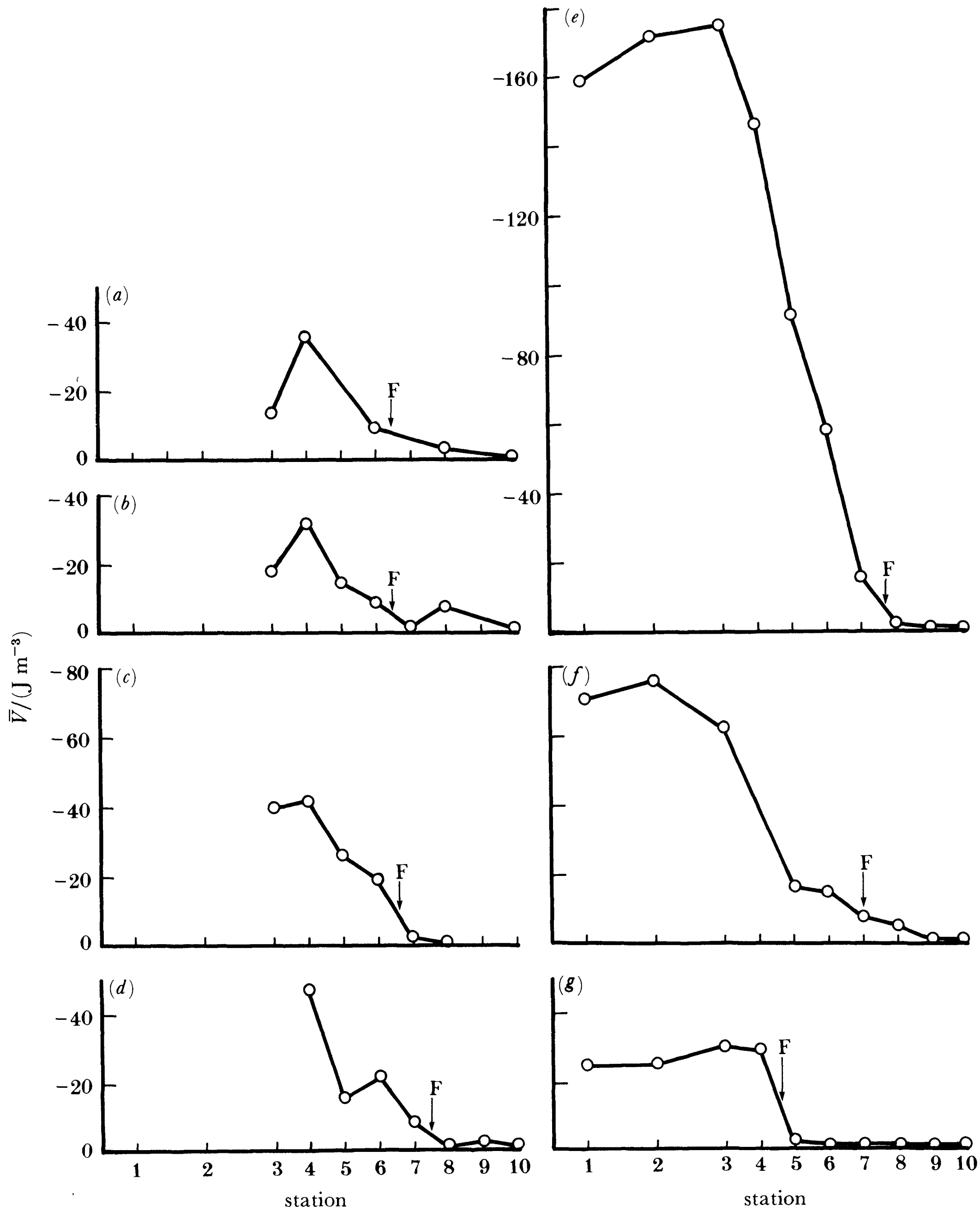

FIGURE 5. Variation of the stratification factor, $\overline{V}$, along a transect from 53° 54.5′ N, 5° 35.6′ W to 53° 35.2′ N, 5° 2.5′ W in the Irish Sea during the 1980 season. Details as in legend to figure 4.

(figure 5*c*). Another line of stations worked the following day (figure 4*d*, 5*d*) showed some minor changes which are presumably attributable to tidal influence: station positions have not been corrected to refer to the same tidal phase. Shifts in the position of the front amounting to 10 km, that is, one or two stations may occur within a few days (Simpson & Bowers 1981). By 3 June, the front was well developed near station 8 (figure 5*e*) and the thermocline was at about 30 m. The situation was similar on 15 July, although the stability of the stratified water mass had declined somewhat (figure 4*f*, 5*f*). By 23 September, after a period of cool, unsettled weather,

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

the thermocline had been lowered to 80 m and the front was less well defined (figure 3*g*, 4*g*). Differences in temperature and salinity between SSW and BSW plus MW were by then small (table 5). Only one station could be occupied on the last cruise of the season (9 October) because of bad weather. By then, increasing mixing processes had, presumably, broken down stratification of the water column and destroyed the biological system associated with the front.

Hydrographic changes in 1981 have been summarized by Richardson *et al.* (1985) from data including that from ISEA cruises and need not be repeated in detail here. (It should be noted that Richardson *et al.* (1985) have numbered the stations in the reverse order to that adopted in this paper.) Stratification was apparent in early April but was broken down by a major storm, becoming established again in early May. The mean position of the front remained more or less stationary in much the same position as in 1980 and disappeared towards the end of September. As in 1980 temperature differences made the main contribution to stratification except that again in early April, salinity differences were dominant at the NW end of the section.

(*b*) *Pigment distribution*

Chlorophyll *a* determinations showed indications of a higher concentration of phytoplankton beginning to develop in the surface stratified water at the end of April (figure 6*a*, *b*; table 6). Somewhat different patterns were found in the two consecutive sections worked on this cruise, however, and there was no statistically significant difference between the concentration of either chlorophyll or phaeo-pigments in SSW and BSW plus MW at this stage (table 5). By 3 June, there was clearly a higher chlorophyll concentration in SSW compared with elsewhere (table 5) with the highest concentration appearing just on the stratified side of the front. Phaeopigments, on the other hand, showed somewhat higher concentrations in BSW (table 6) but no statistically significant difference between those in SSW and in BSW plus MW (table 5). On 15 July, there were high chlorophyll concentrations at the front and in the region of the thermocline with an isolated patch of over 10 μg l^{-1} at 20 m at station 2 (figure 6*d*). The mean concentrations of both chlorophyll and phaeopigments in SSW were, however, not statistically significantly different from those in BSW and MW (table 5). On 23 September, there were again significantly higher concentrations of chlorophyll in SSW than in the rest of the water whereas those of phaeopigments were about equal (table 5). Over the season as a whole there was a slight rise in mean chlorophyll concentrations in SSW from April to July followed by a fall in September (table 6). Phaeopigment concentrations also tended to remain at about the same level except on 23 September when they almost doubled (tables 5 and 6). As would be expected, since chlorophyll is degraded to phaeopigments especially in the deeper water, there is a consistent statistically significant negative Spearman rank correlation between concentrations of these two (ISEA 2: $r_s = -0.430$, $n = 67$, $p = 0.001$; ISEA 3: $r_s = -0.351$, $n = 70$, $p = 0.003$; ISEA 4: $r_s = -0.327$, $n = 45$, $p = 0.028$; ISEA 5: $r_s = -0.474$, $n = 35$, $p = 0.004$).

The more detailed observations of Richardson *et al.* (1984) in the 1981 season confirm this picture. Concentrations of chlorophyll increased generally after the onset of stratification and SSW was found to have significantly greater concentrations than either BSW or MW. The front was distinguished by higher concentrations on its stratified side but its influence was less evident if mean concentrations down to 30 m were considered, because of subsurface chlorophyll patches in the stratified water.

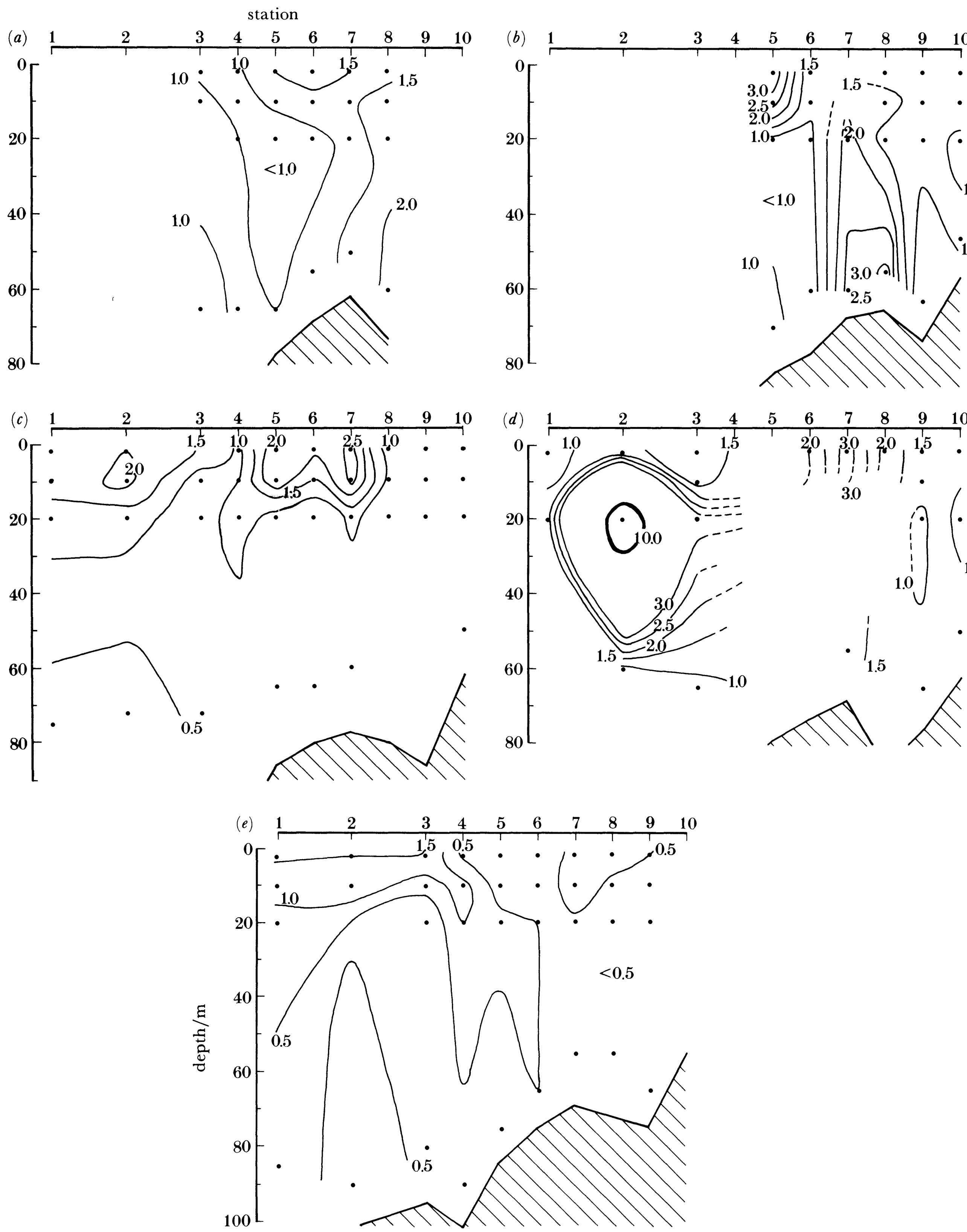

FIGURE 6. Sections in the Irish Sea from 53° 54.5′ N, 5° 35.6′ W to 53° 35.2′ N, 5° 2.5′ W, showing the variation in concentration in micrograms per litre of chlorophyll *a* during the 1980 season: (*a*) ISEA 2, leg 1, 30 April; (*b*) ISEA 2, leg 2, 1 May; (*c*) ISEA 3, 3 June; (*d*) ISEA 4, 15 July; (*e*) ISEA 5, 23 September.

Table 5. 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 3 in the 1980 season

(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. A significant difference is taken as $p \leqslant 0.05$. It should be noted that temperature and salinity, having been used to define the water masses, are not independent variates.)

cruise		temperature °C	salinity (‰)	nitrate µmol l⁻¹	nitrite µmol l⁻¹	ammonium µmol l⁻¹	chlorophyll a µg l⁻¹	phaeopigments µg l⁻¹	ATP ng l⁻¹
ISEA 1	$\bar{x}$ SSW	7.85	34.30	5.74	0.35	1.33			0.31
12–13 March 1980	$\bar{x}$ BSW + MW	8.03	34.49	4.82	0.46	1.38			0.57
	t-value	7.04†	10.98†	−1.88†	1.86†	0.23†	n.a.	n.a.	1.24†
	d.f.	50†	50†	50†	50†	50†			50†
	p	0.000†	0.000†	0.066†	0.069†	0.817†			0.220†
ISEA 2	$\bar{x}$ SSW	8.58	34.23	2.61	0.41	1.89	1.20	0.24	6.58
29 April to	$\bar{x}$ BSW + MW	8.32	34.42	4.05	0.44	1.90	1.26	0.23	2.06
1 May 1980	t-value	−3.88‡	9.17‡	3.60†	1.22†	0.04†	0.43†	−0.07†	−2.33‡
	d.f.	64.8‡	48.7‡	73†	74†	73†	67†	65†	42.9‡
	p	0.000‡	0.000‡	0.001†	0.227†	0.972†	0.671†	0.943†	0.024‡
ISEA 3	$\bar{x}$ SSW	11.15	34.09	1.03	0.28	1.36	1.29	0.19	5.11
3–6 June 1980	$\bar{x}$ BSW + MW	9.73	34.30	4.28	0.40	1.17	0.61	0.20	1.81
	t-value	−18.91‡	10.01†	9.47†	6.21‡	−1.29†	−4.99‡	0.28†	−2.62‡
	d.f.	49.4‡	82†	82†	44.5‡	82†	32.9‡	68†	34.4‡
	p	0.000‡	0.000†	0.000†	0.000‡	0.201†	0.000‡	0.780†	0.013‡
ISEA 4	$\bar{x}$ SSW	12.78	34.22	1.23	0.27	1.68	1.47	0.23	22.61
15–17 July 1980	$\bar{x}$ BSW + MW	11.54	34.29	4.28	0.39	1.75	1.04	0.31	11.13
	t-value	−6.88‡	6.77†	7.53†	3.56†	0.31†	−0.99‡	0.96‡	−2.65‡
	d.f.	42.8‡	70†	70†	70†	70†	28.0‡	28.3‡	57.3‡
	p	0.000‡	0.000†	0.000†	0.001†	0.760†	0.328‡	0.348‡	0.010‡
ISEA 5	$\bar{x}$ SSW	13.66	34.44	2.80	0.51	2.60	0.95	0.46	
23–24 September 1980	$\bar{x}$ BSW + MW	13.98	34.51	4.19	0.34	1.39	0.35	0.42	
	t-value	2.41‡	2.12‡	3.91†	−3.35†	−4.85†	−3.56‡	−0.24†	n.a.
	d.f.	27.4‡	12.6‡	38†	38†	38†	14.2‡	33†	
	p	0.023‡	0.054‡	0.000†	0.002†	0.000†	0.003‡	0.810†	

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 6. Summary of chlorophyll, phaeopigment and adenosine triphosphate data for the 1980 season along a section in the Irish Sea from 53° 54.5′ N, 5° 35.6′ W to 53° 35.2′ N, 5° 2.5′ W

(Statistics are given for the water masses, surface stratified water (SSW), bottom stratified water (BSW) and mixed water (MW) as defined in table 3. n, Number of observations; $\bar{x}$, mean; s.d., standard deviation; min., minimum; max., maximum; n.a., data not available, and n.d. is not detectable.)

		chlorophyll a/(μg l^{-1})					phaeopigments/(μg l^{-1})					ATP (ng l^{-1})				
cruise		n	$\bar{x}$	s.d.	min.	max.	n	$\bar{x}$	s.d.	min.	max.	n	$\bar{x}$	s.d.	min.	max.
ISEA 1	SSW											15	0.33	0.780	n.d.	2.81
12–13 March 1980	BSW			n.a.					n.a.			13	0.66	0.724	n.d.	2.26
	MW											23	0.52	0.646	n.d.	2.43
ISEA 2	SSW	34	1.20	0.670	0.30	3.50	34	0.24	0.242	n.d.	0.80	37	6.58	11.269	n.d.	55.40
29 April to	BSW	13	0.80	0.255	0.30	1.10	13	0.37	0.405	n.d.	1.30	15	2.66	4.037	n.d.	11.45
1 May 1980	MW	22	1.54	0.595	0.50	3.10	20	0.14	0.233	n.d.	0.80	22	1.65	3.097	n.d.	13.19
ISEA 3	SSW	30	1.29	0.726	0.10	2.60	30	0.19	0.200	n.d.	0.80	33	5.11	7.096	n.d.	34.34
3–6 June 1980	BSW	13	0.48	0.262	0.10	1.10	13	0.32	0.248	n.d.	1.00	19	2.26	1.928	0.05	6.47
	MW	27	0.67	0.163	0.40	1.10	27	0.15	0.126	n.d.	0.40	28	1.51	1.36	0.13	5.60
ISEA 4	SSW	23	1.48	2.286	0.10	11.20	23	0.22	0.178	n.d.	0.50	31	25.89	22.071	0.14	86.17
15–17 July 1980	BSW	8	0.80	0.496	0.30	1.60	8	0.24	0.245	n.d.	0.70	13	5.39	6.850	0.07	22.18
	MW	11	1.22	0.334	0.70	1.90	11	0.35	0.336	n.d.	1.20	19	15.06	14.584	0.24	47.35
ISEA 5	SSW	12	0.95	0.549	n.d.	1.60	12	0.46	0.483	n.d.	1.20					
23–24 September 1980	BSW	4	0.35	0.342	n.d.	0.80	4	0.03	0.050	n.d.	0.10			n.a.		
	MW	19	0.35	0.282	n.d.	0.80	19	0.50	0.478	n.d.	1.80					
ISEA 6																
10 October 1980	MW	4	0.38	0.096	0.30	0.50	4	0.63	0.126	0.50	0.80			n.a.		

(*c*) *Cellular adenosine triphosphate concentrations*

ATP concentrations (figure 7, tables 5 and 6) were variable and patchy. There was, however, a clear tendency for concentrations to increase from spring to summer in 1980 by at least an order of magnitude. There was also a consistent tendency for concentrations to be higher in SSW than in BSW or MW. The mean values for these water bodies given in table 5 are significantly different except in March. Spearman rank coefficients (see Kassab *et al.* (1985) for a discussion of their use in this investigation) for ATP (table 7) with σ_t were negative and

TABLE 7. RANK CORRELATION OF ADENOSINE TRIPHOSPHATE (ATP) CONCENTRATION WITH SALINITY, TEMPERATURE, σ_t, CHLOROPHYLL *a* CONCENTRATION, BACTERIAL BIOMASS AND ZOOPLANKTON BIOMASS

(n, Number of valid cases; r_s Spearman correlation coefficient; p, significance.)

cruise		salinity	temperature	σ_t	chlorophyll	bacterial biomass	zooplankton biomass
ISEA 1	n	52	52	52	—	50	12
12–13 March 1980	r_s	0.182	0.283	0.168	—	0.0239	0.524
	p	0.196	0.042	0.235	—	0.869	0.080
ISEA 2	n	73	74	73	68	71	73
30 April to	r_s	−0.135	0.096	−0.325	0.010	−0.205	0.001
1 May 1980	p	0.007	0.414	0.005	0.935	0.086	0.995
ISEA 3	n	80	80	80	67	80	76
3–6 June 1980	r_s	−0.182	0.235	−0.215	0.288	0.250	0.125
	p	0.106	0.036	0.056	0.018	0.025	0.233
ISEA 4	n	68	68	68	41	67	66
15–17 July 1980	r_s	0.053	0.254	−0.232	0.299	0.332	−0.082
	p	0.668	0.036	0.057	0.057	0.006	0.513

statistically significant on 30 April, 3 June and 15 July. On 1 May, 3 June and 15 July, patches of high ATP concentration were evident adjacent to the front on the stratified side. These corresponded approximately with patches of high chlorophyll concentration and overall there was some correlation of ATP with chlorophyll, the Spearman rank coefficients being positive and statistically significant on 3 June and 15 July (table 7). ATP: chlorophyll *a* ratios varied between 0.0016 (BSW and MW, 30 April–1 May) and 0.028 (SSW, 15 July). There are also statistically significant correlations of ATP with bacterial biomass on 3 June and 15 July and a high concentration of ATP near the surface at station 1 on 3 June (figure 7*e*) coincided with a patch of high glucose uptake (Lochte 1985). Otherwise there is no consistent relationship of ATP to either bacterial or zooplankton biomass (table 7). No extensive determinations of ATP were made in the 1981 season.

(*d*) *Nitrate, nitrite and ammonium concentrations*

Nitrate concentrations (figure 8, table 8), although not uniform, were high throughout the section on 13 March 1980, but with the formation of the front they fell in SSW compared with BSW and MW (tables 5 and 8). By 3 June nitrate was almost depleted in SSW but remained at around its late winter value in both BSW and MW (figure 8*e*). The situation was similar on 15 July except that by then the concentration in MW had fallen somewhat and there was a locally high concentration at station 5 in SSW. Mixing had reduced the difference in

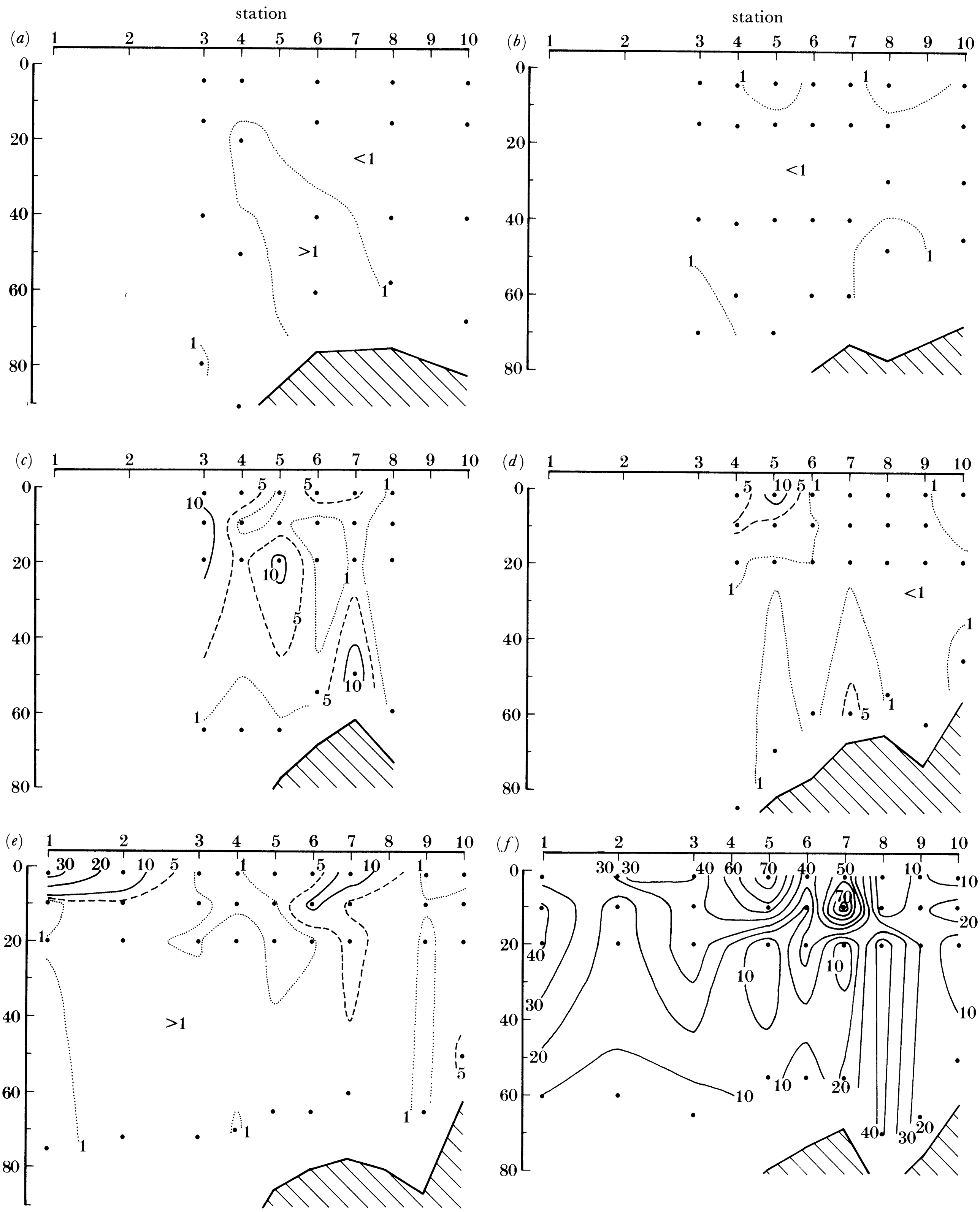

FIGURE 7. Sections in the Irish Sea from 53° 54.5′ N, 5° 35.6′ W to 53° 35.2′ N, 5° 2.5′ W, showing the variation in concentration in nanograms per litre of cellular adenosine triphosphate (ATP) during the 1980 season. (*a*) ISEA 1, leg 1, 12 March; (*b*) ISEA 1, leg 2, 13 March; (*c*) ISEA 2, leg 1, 30 April; (*d*) ISEA 2, leg 2, 1 May; (*e*) ISEA 3, 3 June; (*f*) ISEA 4, 15 July.

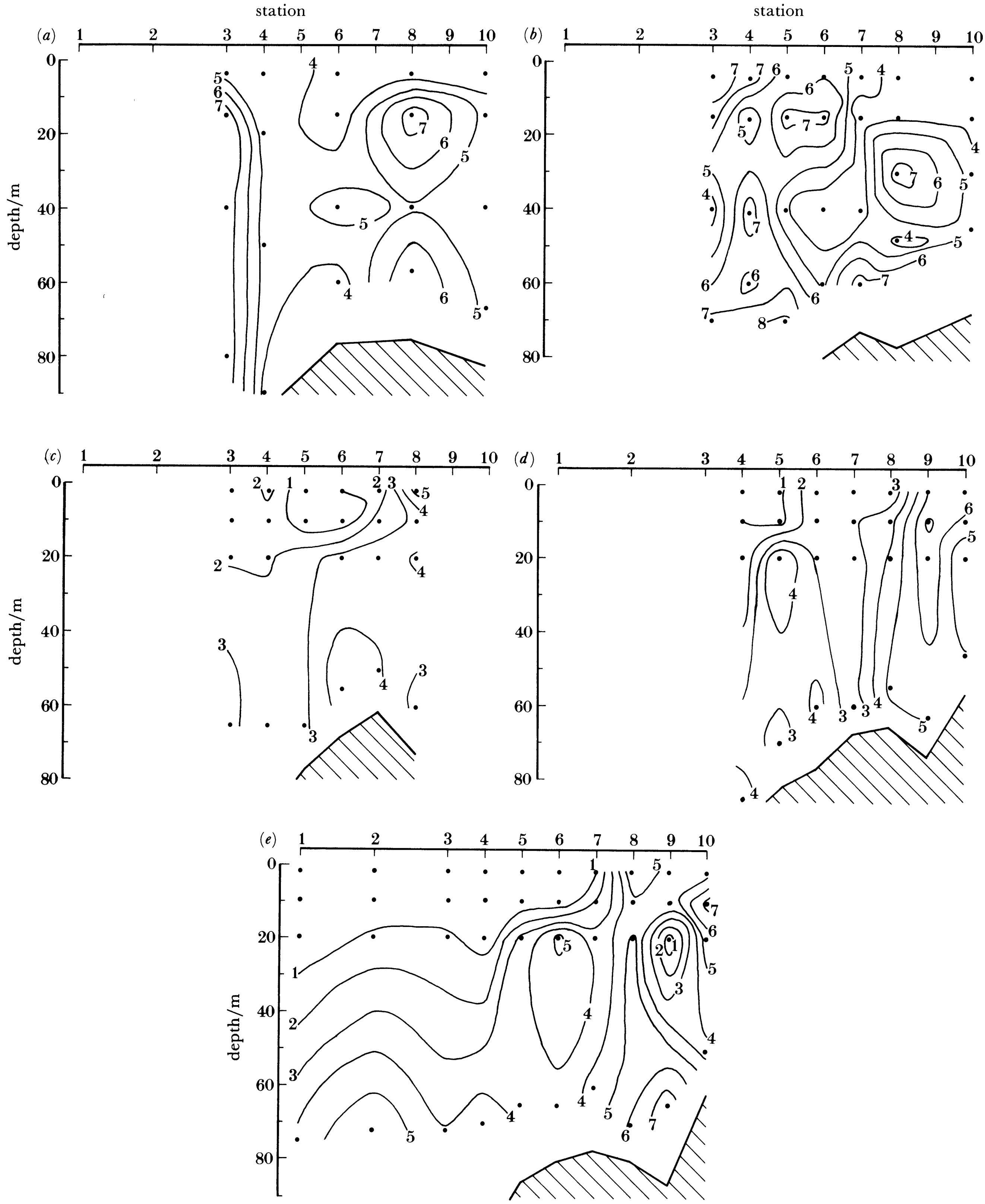

FIGURE 8 (a)–(e). For legend see facing page.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

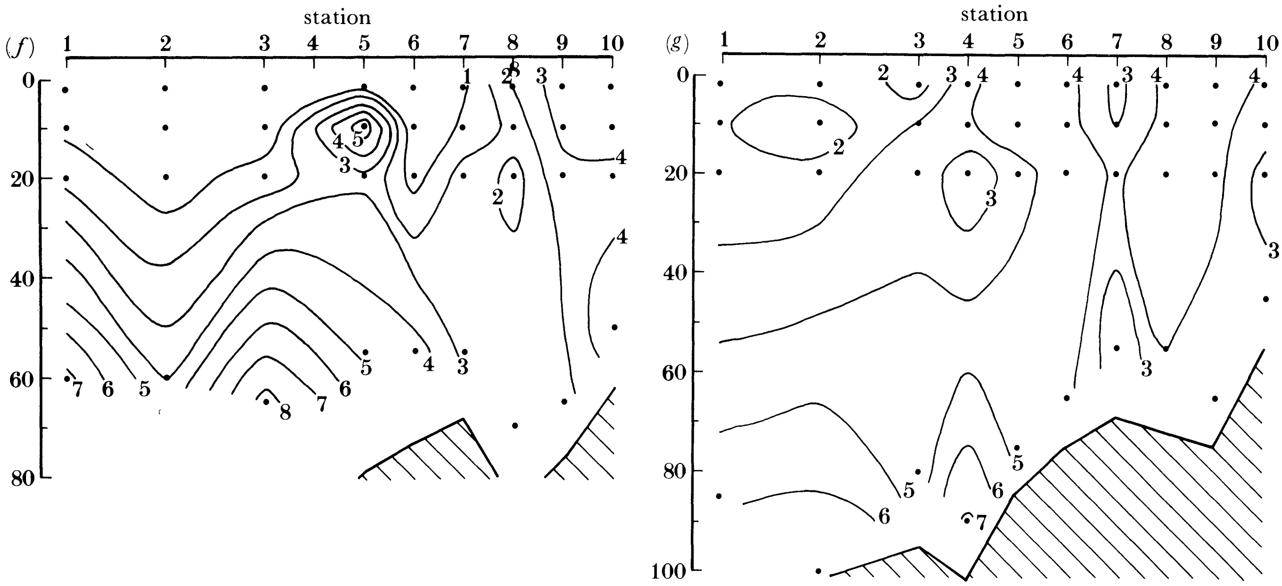

FIGURE 8. Sections in the Irish Sea from 53° 54.5′ N, 5° 35.6′ W to 53° 35.2′ N, 5° 2.5′ W, showing the variation in concentration in micromoles per litre of nitrate during the 1980 season. Details as in legend to figure 4.

concentrations between SSW and MW by 23 September but BSW still maintained a high concentration (table 8).

The relation between nitrate depletion and stabilization is brought out particularly clearly if nitrate concentrations are plotted against σ_t, the results for 1980 being summarized in the statistics given in table 9. The negative correlation on 13 March arose because of the high nitrate concentration in the less dense coastal water at the NW end of the section. By 1 May the influence of stratification was beginning to make itself felt and the correlation had become positive, although not statistically significant. On 3 June and 15 July, the correlation became progressively more positive and on both occasions was highly significant statistically. On 23 September, the correlation coefficient had fallen again and showed a lower level of significance.

A similar sequence of events was observed in 1981 (table 8) but the spring concentrations were higher, the difference between SSW and BSW plus MW in summer was less, and nitrate was not reduced to such low levels in SSW as it was the previous year. On 10 October, following mixing, nitrate concentrations were more or less uniform over the section except at stations 1 and 2, at which concentrations were around 2.20 ± 5.64 compared with 4.11 ± 1.203 over the whole section.

Mean nitrite concentrations on nearly all cruises were around 0.4 μmol l^{-1} and concentrations in SSW and in BSW were usually similar and only in midsummer 1980 was there a statistically significant lower concentration in SSW compared with BSW and MW (tables 5 and 8). Beyond this, nitrite concentrations showed no structure related to the front as Holligan (1981) seems to have found consistently for the Ushant tidal front and the southern Ireland coastal front. Similarly, although concentrations of ammonium nitrogen were variable and patchy (figure 9), these variations did not show any clear relationship to the front or to the distribution of organisms. Mean concentrations remained fairly constant between 1 and 2 μmol l^{-1} over both seasons with no statistically significant differences between SSW and BSW with MW except in September 1980 when the concentration in SSW was higher than in BSW and MW (table 5).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

TABLE 8. SUMMARY OF NITRATE, NITRITE AND AMMONIA DATA FOR THE 1980 AND 1981 SEASONS ALONG A SECTION IN THE IRISH SEA FROM 53° 54.5′ N, 5° 35.6′ W TO 53° 35.2′ N, 5° 2.5′ W

(Statistics are given for three water masses, surface stratified water (SSW), bottom stratified water (BSW) and mixed water (MW) as defined in table 3. n, Number of observations; $\bar{x}$, mean; s.d., standard deviation; min., minimum; max., maximum; n.d., not detectable; n.a., not available.)

cruise		nitrate (μmol l⁻¹)					nitrite (μmol l⁻¹)					ammonium/(μmol l⁻¹)				
		n	$\bar{x}$	s.d.	min.	max.	n	$\bar{x}$	s.d.	min.	max.	n	$\bar{x}$	s.d.	min.	max.
ISEA 1	SSW	15	5.82	1.603	3.14	7.66	15	0.35	0.203	0.10	0.61	15	1.29	0.854	0.17	3.56
12–13 March 1980	BSW	13	5.32	1.843	3.01	8.22	13	0.42	0.228	0.08	0.72	13	1.18	0.842	0.25	3.34
	MW	23	4.53	1.527	2.00	7.66	23	0.49	0.168	0.10	0.68	23	1.49	0.539	0.45	2.56
ISEA 2	SSW	37	2.62	1.949	0.09	7.55	37	0.41	0.112	0.15	0.56	37	1.84	1.151	0.20	4.28
29 April–	BSW	14	3.81	1.282	1.88	6.67	15	0.46	0.135	0.06	0.62	14	1.78	0.958	0.31	4.02
1 May 1980	MW	23	4.19	1.633	1.41	7.07	23	0.43	0.090	0.32	0.71	23	1.97	0.877	0.54	3.67
ISEA 3	SSW	33	1.03	1.608	n.d.	5.35	33	0.28	0.106	0.06	0.49	33	1.36	0.628	0.40	2.50
3–6 June 1980	BSW	19	4.32	1.220	0.23	6.38	19	0.40	0.074	0.25	0.50	19	1.66	0.691	0.76	3.07
	MW	32	4.25	1.644	0.35	7.79	32	0.40	0.047	0.30	0.49	32	0.88	0.494	0.41	2.35
ISEA 4	SSW	33	0.84	1.315	n.d.	5.84	33	0.24	0.111	0.03	0.49	33	1.72	0.851	0.39	3.39
15–17 July 1980	BSW	15	4.88	2.437	0.22	8.43	15	0.27	0.124	0.07	0.43	15	1.59	0.931	0.54	3.23
	MW	19	3.80	0.928	1.75	4.83	19	0.48	0.086	0.33	0.62	19	1.87	1.163	0.70	5.59
ISEA 5	SSW	13	2.80	0.996	1.34	4.64	13	0.51	0.168	0.31	0.80	13	2.60	0.869	1.50	4.01
23–24 September 1980	BSW	4	6.01	1.255	4.35	7.06	4	0.28	0.093	0.18	0.36	4	1.91	0.467	1.22	2.23
	MW	23	3.88	0.687	2.26	4.64	23	0.35	0.143	0.13	0.50	23	1.30	0.665	0.30	2.52
ISEA 6	MW			n.a.					n.a.					n.a.		
10 October 1980																
ISEA 7	SSW	34	8.04	2.346	0.99	12.12	33	0.50	0.163	0.22	0.88	33	1.60	0.729	0.44	3.96
27 April– 1 May 1981	BSW	15	7.33	2.310	4.88	12.94	15	0.59	0.187	0.28	0.88	15	1.02	0.485	0.45	2.17
	MW	11	10.66	0.755	9.58	12.38	11	0.38	0.095	0.17	0.54	11	1.89	0.641	0.92	3.16
ISEA 8	SSW	26	2.40	1.183	0.59	5.07	26	0.46	0.107	0.20	0.61	26	2.63	1.560	0.51	5.59
22–26 June 1981	BSW	18	3.85	1.488	1.90	8.03	18	0.51	0.093	0.30	0.67	18	2.48	1.686	0.75	6.57
	MW	16	3.05	1.795	1.42	8.64	16	0.50	0.121	0.25	0.78	16	3.05	1.802	0.44	6.40
ISEA 9	SSW	27	2.06	0.843	0.67	4.15	27	0.34	0.183	0.07	0.72	27	1.10	0.672	0.30	3.06
3–7 September 1981	BSW	27	3.19	1.115	1.31	6.24	27	0.40	0.190	0.09	0.78	27	0.83	0.524	0.17	2.57
	MW	6	3.09	0.735	2.13	3.88	6	0.41	0.042	0.35	0.47	6	1.49	0.404	0.99	2.24
ISEA 10	MW	61	4.11	1.203	1.46	5.62	61	0.23	0.143	0.04	0.54	61	0.53	0.407	n.d.	1.53
5–6 October 1981																

Table 9. Relations of nitrate concentrations (in micromoles per litre) to σ_t values in the 1980 season along a section in the Irish Sea from 53° 54.5′ N, 5° 35.6′ W to 53° 35.2′ N, 5° 2.5′ W

(*n*, Number of pairs of values; *r*, Pearson correlation coefficient; *b*, linear regression slope coefficient with standard error; *f*, variance ratio; *p*, probability.)

cruise	*n*	*r*	*b*	*f*	*p*
ISEA 1 12–13 March	52	−0.307	−7.701 ± 3.367	5.233	0.026
ISEA 2 30 April–1 May	75	0.167	2.674 ± 1.847	2.096	0.152
ISEA 3 3–6 June	84	0.688	6.712 ± 0.780	73.997	0.000
ISEA 4 15–17 July	72	0.822	9.593 ± 0.792	146.805	0.000
ISEA 5 23–24 September	40	0.461	4.528 ± 1.411	10.297	0.003

Table 10. Pearson correlation coefficients (*r*) between nitrate, nitrite and ammonium concentrations for the 1980 and 1981 seasons along a section in the Irish Sea from 53° 54.5′ N, 5° 35.6′ W to 53° 35.2′ N, 5° 2.5′ W

(*n*, Number of pairs of values; *p*, probability.)

cruise		nitrate with nitrite		nitrate with ammonium		nitrite with ammonium	
	n	*r*	*p*	*r*	*p*	*r*	*p*
ISEA 1 12–13 March 1980	52	−0.961	0.000	−0.379	0.006	0.447	0.001
ISEA 2 30 April–1 May 1980	75	0.040	0.731	0.192	0.098	−0.129	0.270
ISEA 3 3–6 June 1980	84	0.692	0.000	0.050	0.654	0.084	0.445
ISEA 4 15–17 July 1980	72	0.305	0.009	−0.058	0.631	0.232	0.050
ISEA 5 23–24 September 1980	40	−0.666	0.000	−0.493	0.001	0.788	0.000
ISEA 7 27 April–1 May 1981	60	−0.831	0.000	0.340	0.007	−0.365	0.004
ISEA 8 22–26 June 1981	60	0.240	0.060	0.432	0.000	0.365	0.004
ISEA 9 3–7 September 1981	60	0.085	0.425	−0.072	0.500	0.131	0.245
ISEA 10 5–6 October 1981	61	−0.820	0.000	−0.486	0.000	0.468	0.000

On 26 June, 1981, concentrations were high throughout the section with maximum values at 20 m depth. By 10 October concentrations had declined to a mean for the whole section of 0.53 $\mu mol\ l^{-1}$.

Relations between nitrate, nitrite and ammonium concentrations are complex (table 10). both at the beginning and end of each of the two seasons there were statistically significant negative correlations of ammonium and nitrite with nitrate concentrations whereas in early

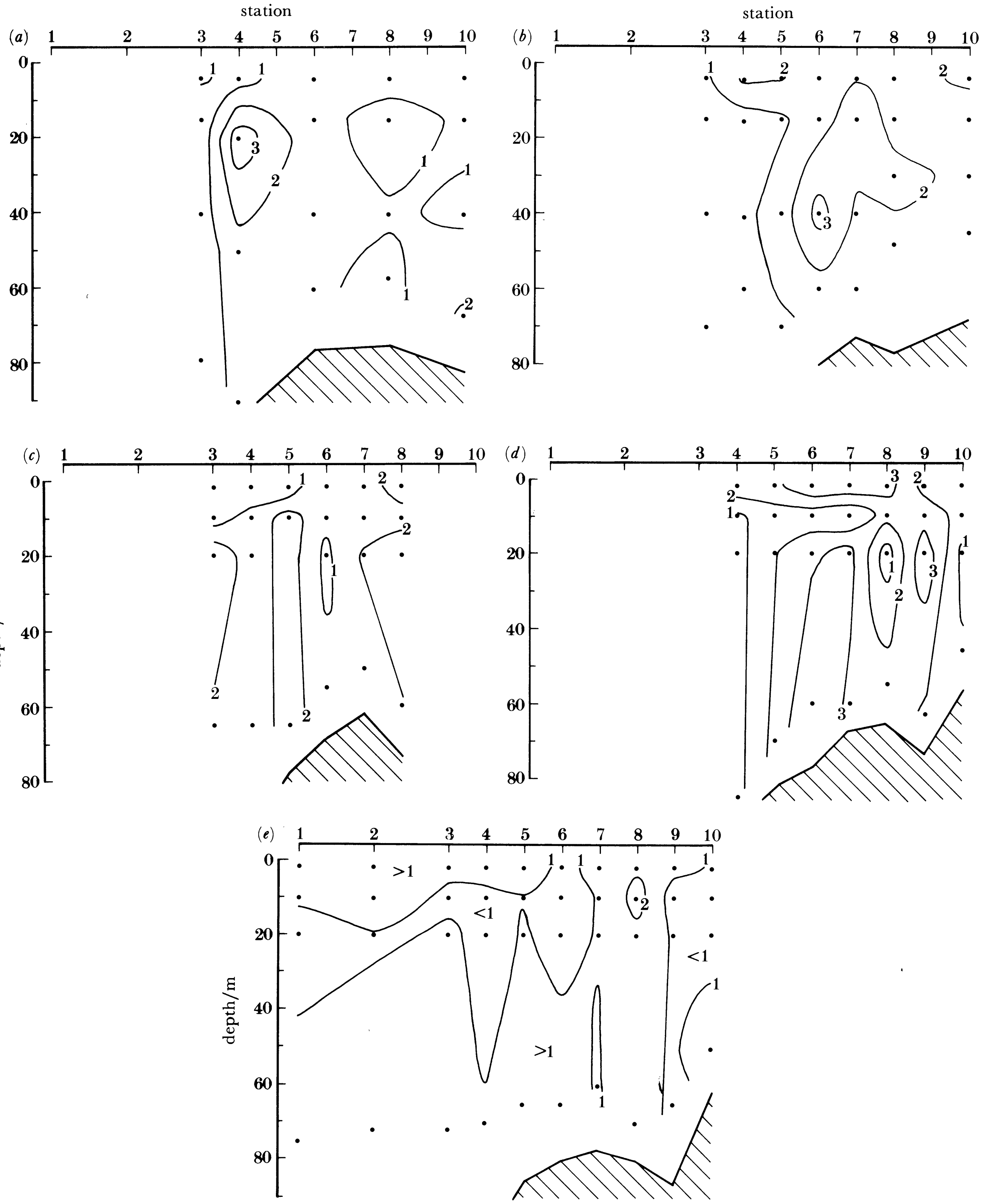

FIGURE 9 (a)–(e). For legend see facing page.

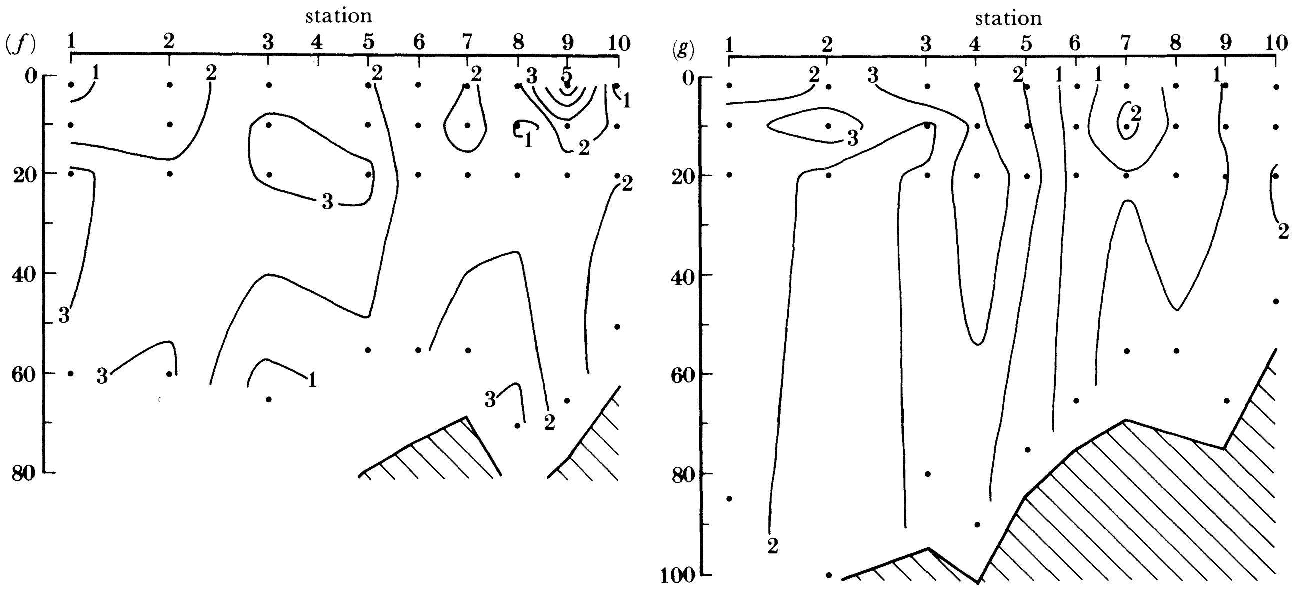

FIGURE 9. Sections in the Irish Sea from 53° 54.5′ N, 5° 35.6′ W to 53° 35.2′ N, 5° 2.5′ W showing the variation in concentration in micromoles per litre of ammonium nitrogen during the 1980 season. Details as in legend to figure 4.

summer these correlations were positive. By contrast, the correlations of nitrite and ammonium were mainly positive, usually with statistical significance. These changing correlations are presumably related to the shifting balance between nitrification and uptake by phytoplankton. From autumn to early spring inverse relationships between ammonium and nitrite concentrations and that of the product of nitrification, nitrate, might be expected. In summer when inorganic nitrogen sources are depleted it seems reasonable to suppose that rapid uptake by algae would result in parallel fluctuations in their concentrations. A statistically significant negative correlation of ammonium with nitrite found for 28 April, 1981 was at a time when both nitrate and nitrite concentrations were at a maximum.

(*e*) *Drogue stations*

Data obtained at the drogue stations have been incorporated in the general body of results discussed above but their intended primary object was to establish the extent to which diurnal changes might have contributed to the variations observed at the fixed stations, which took about 20 h to occupy per transect. The general hydrographic situations at four drogue stations are shown in figure 10. The minimal changes in salinity and temperature observed at 10 m at all four stations show that the drogue was effectively maintaining its position in the subsurface water. However, both above and below 10 m there were some marked changes indicating lateral advection into the water column. Thus, at station 1 on 29–30 April, there were considerable fluctuations in both salinity and temperature at 2 m, presumably caused by wind drift bringing in less saline inshore water. Fluctuations in the salinity of the bottom water at the same station may be attributed to differences in direction and strength of currents at different depths in the water column, as may also a fluctuation in salinity at 20 m at station 4 on 4–5 June. The drogue station in mixed water (station 9, 5–6 June) showed much less fluctuation in all measured characteristics at all depths than that at the other stations, in stratified waters.

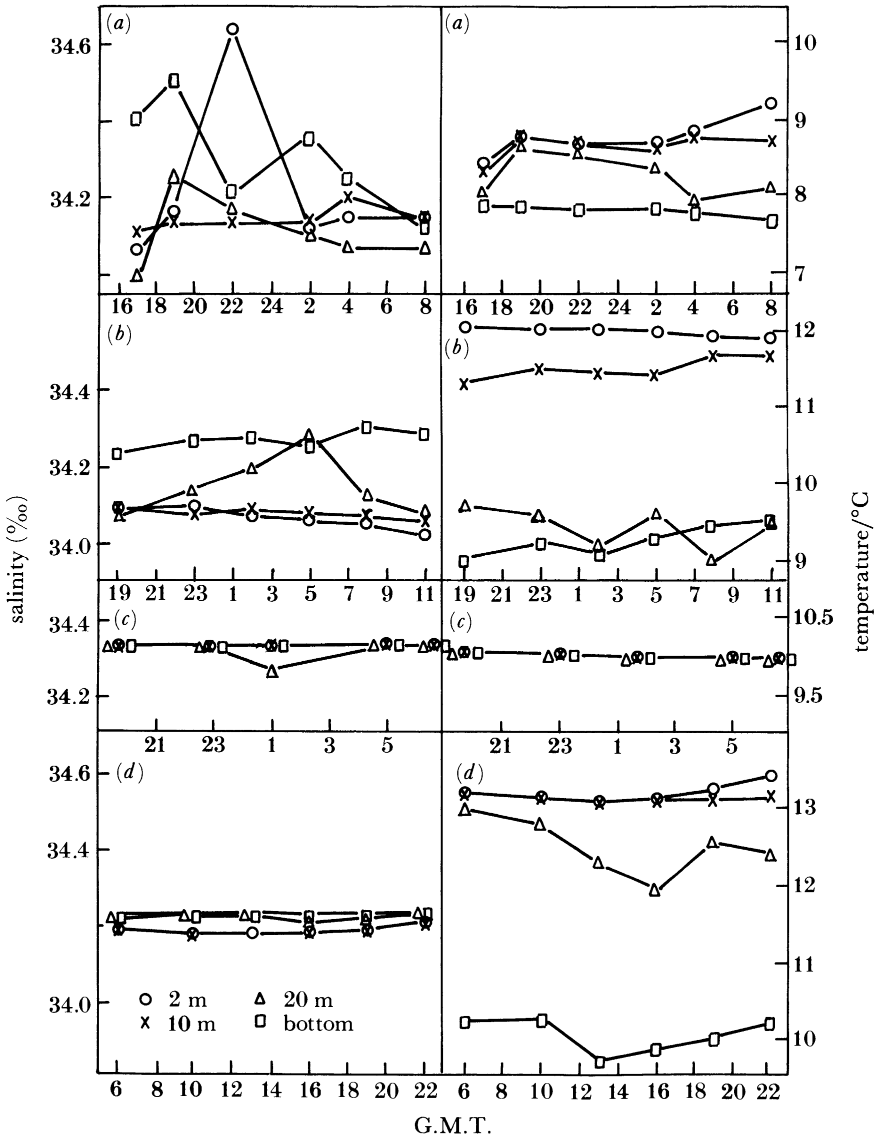

FIGURE 10. Variation with time in salinity and temperature at drogue stations in the western Irish Sea: ○, 2 m; ×, 10 m; △, 20 m; □, bottom. (*a*) ISEA 2, station 1 (53° 54.5′ N, 5° 35.6′ W), 29–30 April 1980; (*b*) ISEA 3, station 4 (53° 47.5′ N, 5° 24.0′ W), 4–5 June 1980; (*c*) ISEA 3, station 9 (53° 37.2′ N, 5° 6.0′ W) 5–6 June 1980; (*d*) ISEA 4, station 1 (53° 54.5′ N, 5° 35.6′ W) 16 July 1980.

Variations with time in nutrient concentrations, chlorophyll concentrations, etc., at different depths at the drift stations present a confused picture in which no regular pattern is apparent. For example, there was no indication of an increase in nitrite concentration during the daylight hours similar to that reported by French *et al.* (1983). In trying to assess the extent of diurnal variations it seems best to concentrate on data from 10 m, at which depth, as just discussed, disturbance by lateral advection seems to have been minimal. Even here, fluctuations appear random and inconsistent, giving the impression of being related to small scale patchiness rather than diurnal variation in biological activity. This impression is supported by the statistics given in table 11 from which it will be seen that fluctuations in mixed water (ISEA 3 station 9) were

TABLE 11. SALINITY, TEMPERATURE AND CONCENTRATIONS OF NITRATE, AMMONIUM, ATP AND CHLOROPHYLL *a* AT DROGUE STATIONS

(Means, standard deviation, minima and maxima at 10 m over the period of the observations. Times G.M.T.)

		$\bar{x}$	s.d.	s.d. as a percentage of $\bar{x}$	max.	min.
ISEA 2	salinity (‰)	34.140	0.0292	0.08	34.199	34.106
station 1	temperature/°C	8.62	0.149	1.7	8.75	8.31
16h00 on 29 April 1980	nitrate/(μmol l^{-1})	3.23	1.28	40	5.79	1.81
to 08h00 on 30 April 1980	ammonium/(μmol l^{-1})	1.74	1.02	59	2.99	0.27
six sets of observations	ATP/(ng l^{-1})	5.66	6.87	121	32.88	0.00
	chlorophyll/(μg l^{-1})	1.05	0.35	33	1.70	0.70
ISEA 3	salinity (‰)	34.074	0.0123	0.036	34.090	34.056
station 4	temperature/°C	11.50	0.14	1.2	11.71	11.31
19h09 on 4 June 1980	nitrate/(μmol l^{-1})	1.72	2.29	133	5.09	0.00
to 11h09 on 5 June 1980	ammonium/(μmol l^{-1})	1.89	0.54	29	2.36	0.76
six sets of observations	ATP/(ng l^{-1})	7.97	5.53	69	19.80	2.68
	chlorophyll/(μg l^{-1})	0.98	0.38	38	1.10	0.50
ISEA 3	salinity (‰)	34.337	0.0055	0.016	34.347	34.332
station 9	temperature/°C	10.00	0.01	0.12	10.05	9.99
19h10 on 5 June 1980	nitrate/(μmol l^{-1})	3.87	1.39	36	5.46	2.06
to 07h10 on 6 June 1980	ammonium/(μmol l^{-1})	0.59	0.17	28	0.89	0.41
five sets of observations	ATP/(ng l^{-1})	1.55	0.64	42	2.55	0.13
	chlorophyll/(μg l^{-1})	0.70	0.00	0.00	0.70	0.70
ISEA 4	salinity (‰)	34.183	0.009	0.03	34.201	34.173
station 1	temperature/°C	13.16	0.04	0.03	13.22	13.10
06h00 to 22h00 on	nitrate/(μmol l^{-1})	0.35	0.29	85	0.85	0.09
16 July 1980	ammonium/(nmol l^{-1})	1.62	0.85	53	3.39	0.91
six sets of observations	ATP/(μg l^{-1})	13.82	15.52	112	42.69	0.14
	chlorophyll/(μg l^{-1})	0.52	0.32	62	1.10	0.10

consistently less than those in stratified water. Drogue stations have provided useful information about the vertical migration of zooplankton (Scrope-Howe & Jones 1985*b*) and have therefore been discussed in detail here in spite of largely negative results. However, the main conclusion to be drawn for the purposes of this present paper is that individual measurements of nutrient or biological quantities should be considered circumspectly and more reliance put on mean values derived from large numbers of observations.

4. DISCUSSION

The information presented above shows that the front with which we are dealing conforms to the general pattern of a shallow-sea tidal mixing front which has emerged from previous studies. Although varying slightly from cruise to cruise, its position is about the same as recorded by Bruce & Aiken (1975) for 1971, by Simpson & Hunter (1974) for 1973, by Simpson & Bowers (1981) for 1978, and by infrared satellite images for 1980 reproduced by Simpson (1981). The hydrographic sections obtained by us show much the same sequence of events in 1980 and 1981. A phytoplankton maximum of about the same relative concentration develops at the front on the stratified side as reported on the Ushant front (Pingree *et al.* 1975) and the general sequence of phytoplankton distribution over the season is generally similar to that for this other front (Holligan 1981). We did not study the floristic composition of the phytoplankton but Beardall *et al.* (1982), who also found this phytoplankton maximum at the western Irish Sea front, found the species composition to be different on either side of the front, with flagellates forming a greater proportion of the total in SSW and diatoms becoming more numerous on the mixed side, in a similar manner to that described by Holligan (1981) for the Ushant front. The distribution of minute coccoid cyanobacteria, which seem to contribute a substantial proportion of the chlorophyll *a* in these waters, shows some relation to the front but there is no marked difference in the cell concentrations in the water masses that it separates (El Hag 1984).

An anomalous feature shown by the hydrographical sections is that a halocline exists in the late winter at station 1, at the NW end of the transect. An inshore water mass in this position has been described by Foster *et al.* (1976). There is some biological evidence also that a different water mass is sometimes present at this station (see, for examples, figure 7*e*; Lochte (1985); and Scrope-Howe & Jones (1985*a*)). However, for most purposes results from this station have been included with the others on the stratified side of the front.

The possibility must be considered that some of the variation encountered in a transect arose from diurnal changes in the plankton and its activities rather than from truly spatial variations. Nevertheless, as already discussed, the changes with time in biological properties seem to have been small compared with other variations and it appears that the sections give a reasonable representation of spatial variations. The patchiness in distribution observed particularly for chlorophyll *a*, ATP, nitrate and ammonium is evidently a real phenomenon and its scale, extending over two or three stations, that is, about 10 km, is similar to that found elsewhere (Therriault & Platt 1978). Patchiness will be discussed with particular relation to bacteria in a later paper (Egan & Floodgate 1985).

The results reported in this paper do not throw any light on the processes that lead to the phytoplankton maximum at the front. The finding of Richardson *et al.* (1985), with which we agree, that this maximum is associated with the surface layer and that, because of subsurface patches elsewhere in the stratified water, the influence of the front is much less evident if chlorophyll is averaged to 30 m, seems an important one. However, from the scheme for frontal structure put forward by Simpson (1981) it does not appear that the frontal chlorophyll maximum could have originated by movement of a subsurface maximum along the pycnocline up to the surface.

Following the establishment of thermal stratification the progressive exhaustion by phytoplankton growth of the nitrate in the surface layer was very evident. Assuming a chlorophyll *a*:nitrogen ratio of 0.15, the nitrate disappearing would have provided for a phytoplankton biomass in surface stratified water some seven (1980) or ten (1981) times greater than those actually observed. This represents the difference between production and stock and, presumably, much of the nitrogen unaccounted for was transformed to dissolved organic form by decay, grazing and excretion (Butler *et al.* 1979). The concentrations of nitrite and ammonium varied little, suggesting a dynamic equilibrium in their production and consumption. Except in the autumn, the mean concentration of nitrite only fell below 0.4 μmol l^{-1} when nitrate was reduced below 1 μmol l^{-1}, in agreement with the findings of Harrison & Davis (1977). The mean ammonium concentration during the spring and summer was always above the critical value of 1 μmol l^{-1} at which it begins to inhibit uptake of nitrite and nitrate nitrogen (McCarthy 1980). No correlation of ammonium and phaeopigment concentrations, as observed by Therriault & Platt (1978) and attributed by them to the activity of grazing zooplankton, was observed. Presumably any such effect was masked by rapid turnover of ammonium nitrogen.

The uptake of nitrogen by phytoplankton in the frontal system is discussed further in a later paper in this series (Turley 1985). The generally positive correlations between nitrite and ammonium concentrations are perhaps to be expected since both are substrates for nitrification. Negative correlations occurred only in spring when nitrate concentrations and phytoplankton standing stock were high, conditions which are conducive to nitrate reduction and nitrite excretion by phytoplankton (Vaccaro & Ryther 1960; Carlucci *et al.* 1970). In agreement with this the concentration of nitrite was at its highest (table 8) and correlated negatively with that of nitrate (table 10) at these times.

Cellular ATP concentrations provide a good index of biomass where a more-or-less homogenous population of micro-organisms exists in a relatively stable environment (Karl 1978) or when a preliminary size fractionation is carried out to reduce the heterogeneity of the sample (Burney *et al.* 1979). Therriault & Platt (1978) found a correlation between ATP and chlorophyll over a year in St Margaret's Bay, Nova Scotia. In this investigation cellular ATP concentrations were highly variable and, although they showed a general relation to biological productivity, had no consistent correlation with chlorophyll, bacterial biomass or zooplankton biomass individually. Since phytoplankton may contribute from 60 to 70% of the total ATP in the open sea (Burney *et al.* 1979) and the ATP content of algal cells varies as much as tenfold between light and dark (Urbach & Kaiser 1972) as well as with other factors, such inconsistency is to be expected. It seems that cellular ATP concentrations are more valuable as an index of physiological state than of biomass (Sakshaug 1980). The distribution of values found in this investigation supports the hypothesis that the stratified surface water, especially that adjacent to the front, is a zone of intense biological activity. The few determinations of primary productivity that we did gave no convincing evidence of this and Savidge *et al.* (1984), by using continuous recording of primary productivity by a radiocarbon technique, found no major activity associated with chlorophyll maxima in the vicinity of the front in July 1977. However, the filter they used did not retain particles of less than 10 μm and, as noted above, there is evidence that a substantial proportion of the phytoplankton consists of cyanobacteria which would pass such a filter. In further papers of this series (Turley 1985; Lochte 1985) other kinds of evidence will be presented which support the hypothesis of intensified biological activity in the stratified water adjacent to the front.

The work described in this paper was supported in part by a grant (no. GR3/3938) from the Natural Environment Research Council. We are also grateful to our colleagues in the Department of Physical Oceanography of the University College of North Wales for much advice and practical help, to Dr K. Richardson for chlorophyll determinations, and to the officers and crew of R.V. *Prince Madog* for their unfailing cooperation.

References

Afghan, B. K., Tobin, R. A. & Ryan, J. F. 1977 An improved method for quantitative measurements of ATP and its application to measure microbial activity in natural waters, activated sludges and sediments. In *2nd Bi-Annual ATP Methodology Symposium*, March 22–24, 1977 (ed. G. A. Borun), pp. 349–389. San Diego, Calif.: SAI Technology Comp.

Allen, C. M., Simpson, J. H. & Carson, R. M. 1980 The structure and variability of shelf sea fronts as observed by an undulating CTD system. *Oceanologica Acta* **3**, 59–68.

Beardall, J., Fogg, G. E., Foster, P., Miller, I., Spencer, C. P. & Voltolina, D. 1978 Phytoplankton distributions in the western Irish Sea and Liverpool Bay and their relation to hydrological factors: a progress report. *Biol. Contemp.* **5**, 163–175.

Beardall, J., Foster, P., Voltolina, D. & Savidge, G. 1982 Observations on the surface water characteristics in the western Irish Sea: July 1977. *Estuar. coast. shelf Sci.* **14**, 589–598.
Booth, D. A. 1978 The evaluation of a Lagrangian current meter system and its application to water movement in the Irish Sea. Ph.D. thesis, University of Wales.
Bowman, M. J. & Iverson, R. L. 1978 Estuarine and plume fronts. In *Oceanic fronts in coastal processes* (ed. M. J. Bowman & W. E. Esaias), pp. 87–104. New York: Springer-Verlag.
Brown, R. G. B. 1980 Seabirds as marine animals. In *Behaviour of marine animals.* Vol. 4. *Marine birds* (ed. J. Burger, B. L. Olla & H. E. Winn), pp. 1–39. New York: Plenum Press.
Bruce, R. H. & Aiken, J. 1975 The undulating oceanographic recorder – a new instrument system for sampling plankton and recording physical variables in the euphotic zone from a ship underway. *Mar. Biol.* **32**, 85–97.
Burney, C. M., Johnson, K. M., Lavoie, D. M. & Sieburth, J. Mc. N. 1979 Dissolved carbohydrate and microbial ATP in the North Atlantic: Concentrations and interactions. *Deep Sea Res.* **26**, 1268–1291.
Butler, E. J., Knox, S. & Liddicoat, M. J. 1979 The relationship between inorganic and organic nutrients in sea water. *J. mar. biol. Ass. U.K.* **59**, 239–250.
Carlucci, A. F., Hartwig, E. O. & Bowes, P. M. 1970 Biological production of nitrite in sea water. *Mar. Biol.* **7**, 161–166.
Dufour, P. & Stretta, J. M. 1973 Fronts thermiques et thermohalins dans la région du Cap Lopez (Golfe de Guinée) Juin–Juillet 1972: Phytoplancton, zooplancton, micronecton et pêche thomière. *Doc. Scient. Centre Rech. Océanogr. Abidjan* **4**, 99–142.
Egan, B. & Floodgate, G. D. 1985 Biological studies in the vicinity of a shallow-sea tidal mixing front. II. The distribution of bacteria. *Phil. Trans. R. Soc. Lond.* B **310**, 435–444.
El Hag, A. G. D. 1984 *Studies on coccoid blue-green algae in sea water.* Ph.D. thesis, University of Wales.
Floodgate, G. D., Fogg, G. E., Jones, D. A., Lochte, K. & Turley, C. M. 1981 Microbiological and zooplankton activity at a front in Liverpool Bay. *Nature, Lond.* **290**, 133–136.
Fogg, G. E. 1981 Modelling phytoplankton production at shelf-sea fronts: contribution to discussion. *Phil. Trans. R. Soc. Lond.* A **302**, 614–615.
Fogg, G. E., Egan, B., Floodgate, G. D., Jones, D. A., Kassab, J. Y., Lochte, K., Rees, E. I. S., Scrope-Howe, S. & Turley, C. M. 1985 Biological studies in the vicinity of a shallow-sea tidal mixing front. VII. The frontal ecosystems. *Phil. Trans. R. Soc. Lond.* B **310**, 555–571.
Foster, P., Savidge, G., Foster, G. M., Hunt, D. T. E. & Pugh, K. B. 1976 Multivariate analysis of surface water characteristics in the summer regime of the western Irish Sea. *J. exp. mar. Biol. Ecol.* **25**, 171–185.
French, D. P., Furnas, M. J. & Smayda, T. J. 1983 Diel changes in nitrite concentration in the chlorophyll maximum in the Gulf of Mexico. *Deep Sea Res.* **30**, 707–722.
Harrison, P. J. & Davis, C. O. 1977 Use of the perturbation technique to measure nutrient uptake rates for natural phytoplankton populations. *Deep Sea Res.* **24**, 247–255.
Head, P. C. 1971 An automated phenolhypochlorite method for the determination of ammonia in sea water. *Deep Sea Res.* **18**, 531–532.
Holligan, P. M. 1981 Biological implications of fronts on the northwest European continental shelf. *Phil. Trans. R. Soc. Lond.* A **302**, 547–562.
Holm-Hansen, O. & Booth, C. R. 1966 The measurement of adenosine triphosphate in the ocean and its ecological significance. *Limnol. Oceanogr.* **11**, 510–519.
Joint, I. R. & Morris, R. J. 1982 The role of bacteria in the turnover of organic matter in the sea. *Oceanogr. Mar. Biol. Ann. Rev.* **20**, 65–118.
Jones, J. G. & Simon, B. M. 1977 An investigation of errors in direct counts of aquatic bacteria by epifluorescence microscopy, with reference to a new method for dyeing membrane filters. *J. appl. Bact.* **39**, 317–329.
Karl, D. M. 1978 Distribution, abundance and metabolic states of micro-organisms in the water column and sediments of the Black Sea. *Limnol. Oceanogr.* **23**, 936–949.
Kassab, J. Y., Whitaker, C. J. & Floodgate, G. D. 1985 Biological studies in the vicinity of a shallow-sea tidal mixing front. VI. A general statistical study. *Phil. Trans. R. Soc. Lond.* B **310**, 521–554.
Liddicoat, M. I., Tibbitts, S. & Butler, E. I. 1975 The determination of ammonia in sea water. *Limnol. Oceanogr.* **20**, 131–132.
Lochte, K. 1985 Biological studies in the vicinity of a shallow-sea tidal mixing front. III. Seasonal and spatial distribution of heterotrophic uptake of glucose. *Phil. Trans. R. Soc. Lond.* B **310**, 445–469.
McCarthy, J. J. 1980 Nitrogen. In *The physiological ecology of phytoplankton* (ed. I. Morris), pp. 191–233. Oxford: Blackwell Scientific Publications.
Okubo, A. 1978 Advection–diffusion in the presence of surface convergence. In *Oceanic fronts in coastal processes* (ed. M. J. Bowman & W. E. Esaias), pp. 23–28. New York: Springer-Verlag.
Pingree, R. D., Pugh, P. R., Holligan, P. M. & Forster, G. R. 1975 Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. *Nature, Lond.* **258**, 672–677.
Pingree, R. D., Holligan, P. M. & Mardell, G. T. 1978 The effects of vertical stability on phytoplankton distributions in the summer on the northwest European Shelf. *Deep Sea Res.* **25**, 1011–1028.
Richardson, K., Lavin-Peregrina, M. F., Mitchelson, E. G. & Simpson, J. H. 1985 Seasonal distribution of chlorophyll *a* in relation to physical structure in the western Irish Sea. *Oceanol. Acta.* **8**, 77–86.)

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Sakshaug, E. 1980 Problems in the methodology of studying phytoplankton. In *The physiological ecology of phytoplankton* (ed. I. Morris), pp. 57–91. Oxford: Blackwell Scientific Publications.

Savidge, G. 1976 A preliminary study of the distribution of chlorophyll *a* in the vicinity of fronts in the Celtic and western Irish Seas. *Estuar. coast. mar. Sci.* **4**, 617–625.

Savidge, G., Foster, P. & Voltolina, D. 1984 Intense localised productivity in the Irish Sea. *Estuar. coast. Shelf Sci.* **18**, 157–164.

Scrope-Howe, S. & Jones, D. A. 1985*a* Biological studies in the vicinity of a shallow-sea tidal mixing front. V. Composition, abundance and distribution of zooplankton in the western Irish Sea, April 1980 to November 1981. *Phil. Trans. R. Soc. Lond.* B **310**, 501–519.

Scrope-Howe, S. & Jones, D. A. 1985*b* The vertical distribution of zooplankton in the western Irish Sea. *Estuar. coast. Shelf. Sci.* (In the press.)

Simpson, J. H. 1971 Density stratification and microstructure in the western Irish Sea. *Deep Sea Res.* **18**, 309–319.

Simpson, J. H. 1981 The shelf-sea fronts: implications of their existence and behaviour. *Phil. Trans. R. Soc. Lond.* A **302**, 531–546.

Simpson, J. H. & Bowers, D. 1981 Models of stratification and frontal movement in shelf seas. *Deep Sea Res.* **28**A, 727–738.

Simpson, J. H., Edelsten, D. J. Edwards, A., Morris, N. C. G. & Tett, P. B. 1979 The Islay front: physical structure and phytoplankton distribution. *Estuar. coast. mar. Sci.* **9**, 713–726.

Simpson, J. H., Hughes, D. G. & Morris, N. C. G. 1977 The relation of seasonal stratification to tidal mixing on the continental shelf. In *A voyage of discovery.* (ed. M. Angel), pp. 327–340. Suppl. to *Deep Sea Res.*

Simpson, J. H. & Hunter, J. R. 1974 Fronts in the Irish Sea. *Nature, Lond.* **250**, 404–406.

Strickland, J. D. H. & Parsons, T. R. 1972 *A practical handbook of seawater analysis*, 2nd edn. *Bull. Fish. Res. Bd Can.* **167**, 1–310.

Therriault, J.-C. & Platt, T. 1978 Spatial heterogeneity of phytoplankton biomass and related factors in the near-surface waters of an exposed coastal embayment. *Limnol. Oceanogr.* **23**, 888–899.

Turley, C. M. 1985 Biological studies in the vicinity of a shallow-sea tidal mixing front. IV. Seasonal and spatial distribution of urea and its uptake by phytoplankton. *Phil. Trans. R. Soc. Lond.* B **310**, 471–498.

Urbach, W. & Kaiser, W. 1972 Changes of ATP levels in green algae and intact chloroplasts by different photosynthetic reactions. In *Proc. 2nd Int. Cong. Photosynthesis*, vol. 2 (ed. G. Forti, M. Avron & A. Melandri), pp. 1401–1411. The Hague: Junk.

Vaccaro, R. F. & Ryther, J. H. 1960 Marine phytoplankton and the distribution of nitrite in the sea. *J. Cons. perm. int. Explor. Mer.* **25**, 260–271.

Williams, P. J. le B. 1981 Incorporation of microheterotrophic processes into the classical paradigm of the planktonic food web. *Kieler Meeresforsch.* **5**, 1–28.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

FIGURE 2. Satellite infrared image of the Irish Sea (NOAA5, 21 May 1978, 09h30 G.M.T.) showing the fronts as in figure 1.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES