

## Biological Studies in the Vicinity of a Shallow-Sea Tidal Mixing Front VII. The Frontal Ecosystems

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# BIOLOGICAL STUDIES IN THE VICINITY OF A SHALLOW-SEA TIDAL MIXING FRONT VII. THE FRONTAL ECOSYSTEMS

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Three, possibly four, ecosystems forming seasonally are associated with the tidal mixing front in the western Irish Sea. They are distinguished not only by the presence or absence of particular species but by their relative intensities of heterotrophic

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activity and degree of organization as shown in the number of statistically significant correlations between the variables pertaining to them. The main body of surface stratified water, at first dominated by an expanding population of phototrophs, attains during the summer a state of dynamic equilibrium in which the standing stock of phytoplankton remains at about the same level, its primary productivity being balanced by high levels of heterotrophic activity and cycling of nitrogen. The bottom stratified water, besides having minimal photosynthetic activity, shows low zooplankton stocks, low heterotrophic activity and the lowest level of organization. Mixed water has lower standing stocks, less heterotrophic activity, lower rates of nitrogen cycling, and is a less highly organized system than the surface stratified water. The stratified water in a band about 10 km wide adjacent to the front does not show conspicuously higher total standing stocks of phytoplankton, bacteria and zooplankton in the water column down to the pycnocline, than the rest of the stratified water. Animals migrating into it do not provide an appreciable extra source of nutrients for the phytoplankton. It does, however, show much higher heterotrophic activity and rates of nitrogen cycling than the rest of the stratified water. This is tentatively attributed to increased photosynthesis, consequent on the redistribution of phytoplankton by frontal eddies, being taken up in increased heterotrophic activity rather than in growth of the phytoplankton itself. A similar situation appears to exist at the plume front in Liverpool Bay but here there is the additional factor of collection at the front of particulate organic matter derived from river inflow.

## 1. INTRODUCTION

The previous papers of this series (Fogg *et al.* 1985; Egan & Floodgate 1985; Lochte 1985; Turley 1985; Scrope-Howe & Jones 1985*a*; Kassab *et al.* 1985) and other publications (Beardall *et al.* 1982; Richardson *et al.* 1985; Scrope-Howe & Jones 1985*b*) have described particular aspects of the tidal mixing front lying in the western Irish Sea between approximately 53° 20' N, 5° 45' W and 53° 50' N, 5° 0' W. In this paper we discuss this frontal system as a whole. As will be seen, it seems justifiable to use the term *ecosystem* to describe its component parts since boundaries can be defined within which the biota are distinctly different, at least in activity, from those that are adjacent.

## 2. A GENERAL COMMENT ON THE STATISTICAL TREATMENT

A feature of this study has been that, observations having been made from frequent stations at several depths along an extensive transect at intervals during the whole period in which the front developed, a sufficiently extensive body of data has been amassed to make possible a more detailed statistical study than has hitherto been attempted in this type of investigation. This more refined study (Kassab *et al.* 1985) has largely confirmed the conclusions based on the elementary statistical analyses that have sometimes been used in considering the particular biological aspects (Fogg *et al.* 1985; Egan & Floodgate 1985; Lochte 1985; Turley 1985; Scrope-Howe & Jones 1985*a*) and also extended our understanding of the system. Many of the variables show non-normal distributions. Logarithmic transformation may produce a distribution closer to normal but non-parametric techniques are most appropriate for many purposes. Nitrite concentrations afford an example of this. The parametric analysis of variance of untransformed data reported by Fogg *et al.* (1985, tables 5 and 8) revealed no important statistically significant differences in concentrations between stratified surface water (SSW), bottom stratified water (BSW) and mixed water (MW). The Kruskal-Wallis non-parametric

analysis of variance of the same data (Kassab *et al.* 1985, table 6), however, shows a clear pattern of differences. Nitrite falls in concentration in SSW compared with BSW and MW as the summer progresses but finally becomes higher in SSW than in the other two water masses in the autumn. This pattern conforms to that reported by Holligan (1981) for the Ushant front on the basis of data that do not, however, appear to have been subjected to statistical analysis.

A second major point is that the division of the water mass into SSW, BSW and MW, initially made on theoretical grounds, has proved entirely justifiable statistically. Most variables examined showed homogeneity of variance for the three water types in most cruises. When a non-parametric analysis of variance was used to test for differences between the three water types, statistically significant differences were found for nine variables out of 14 during stable stratification. A general feature was that when there were differences it was usually the surface stratified water that was different from the other two. The grouping together of data for BSW and MW (Fogg *et al.* 1985) therefore has some justification.

### 3. THE DISTRIBUTION OF BIOMASS

Estimates of biomass in terms of carbon per unit volume for bacteria, phytoplankton and zooplankton as they varied through the 1980 season in the three water masses, SSW, BSW and MW, have been given by Turley (1985). The general levels are similar to the values assembled from the literature by Williams (1984). The general trends, too, are as expected. Phytoplankton tended to remain at much the same level throughout the summer with a decline beginning at the end of September. Bacteria and zooplankton both reached maximum values after the plateau in phytoplankton biomass has been established. SSW usually had the greatest phytoplankton concentration and BSW least. Zooplankton reached its highest values in SSW and concentrations in MW were usually the least. At the beginning of the season bacterioplankton reached higher biomass levels in BSW and MW than in SSW but this position was reversed later in the summer.

The biomass values given in table 1 have been chosen as comparable with those recently given for the Western Approaches by Holligan *et al.* (1984a). The values for the Irish Sea are of the same order of magnitude as those for the Western Approaches and the different plankton fractions were present in about the same relative amounts in the two situations. Frontal waters were somewhat higher in phytoplankton content than either the main SSW or MW but the very high value reported by Holligan *et al.* (1984a) for frontal water was exceptional, being contributed by an essentially monospecific bloom of *Gyrodinium aureolum* collected at the surface presumably as a result of the interaction of vertical migration and the frontal convergence. The value for bacteria in the frontal region in the Western Approaches is higher than in either SSW or MW, in contrast to the values for the Irish Sea (but Holligan *et al.* (1984a) do not give particulars of any statistical analysis). Otherwise, bacterial numbers in the Western Approaches seem distinctly lower than in the Western Irish Sea. This may be related to the more coastal nature of the latter, which also shows, for example, in the abundance of sprat. In neither the Western Approaches nor the Irish Sea were zooplankton biomasses any greater at the front than elsewhere. The zooplankton biomasses are, however, difficult to compare since in 1980 a single copepod species, *Calanus finmarchicus*, accounted for over 90% of the mesozooplankton biomass in the western Irish Sea.

A striking feature in both our results and those of Holligan *et al.* (1984a) is that the biomass

TABLE 1. BIOMASS ESTIMATES OF PLANKTON FRACTIONS AT THE WESTERN IRISH SEA FRONT COMPARED WITH THOSE FROM THE WESTERN APPROACHES FROM HOLLIGAN *ET AL.* (1984*a*, TABLE 4) AVERAGED DOWN TO 24 m

Amounts in micrograms of carbon per litre. SSW, stratified surface water; F, front; MW, mixed water.

	western Irish Sea						Western Approaches		
	(3 June 1980)			(15 July 1980)			(22 July to 2 Aug. 1981)		
	SSW	F	MW	SSW	F	MW	SSW	F	MW
phytoplankton†	39	55	20	44	75	37	17	1104	81
bacteria‡	98	55	63	58	69	17	6	24	9
protozoa	—	—	—	—	—	—	5	41	6
microzooplankton	—	—	—	—	—	—	12	8	4
mesozooplankton§	230	42	8	35	30	6	28	11	16

† Data from Fogg *et al.* (1985), carbon:chlorophyll ratio of 30:1 assumed.

‡ Data from Egan & Floodgate (1985), assuming a carbon content of 0.1 pg  $\mu\text{m}^{-3}$  bacterial volume.

§ Data from Scrope-Howe & Jones (1985*a*).

|| Frontal waters are considered to be at stations 5, 6 and 7 (Fogg *et al.* 1985) down to 20 m.

of heterotrophs (bacteria and zooplankton) is always substantial compared with that of the phytoplankton. We made no quantitative estimates of protozoa and microzooplankton but general observation suggests that they are as important in the western Irish Sea as in the Western Approaches and we assume, with Holligan *et al.* (1984*a, b*), that they play a substantial role in heterotrophic cycling.

#### 4. THE SURFACE STRATIFIED WATER

##### (a) *Phytoplankton*

With the development of the thermocline in April the phytoplankton population in the main part of SSW away from the front built up rapidly and remained at about the same mean level throughout the summer, a level that presumably was largely determined by the amounts of nutrients initially present. Mean chlorophyll concentrations were up to twice those in MW. The distribution of the population was patchy, in fact showing a log-normal distribution (Kassab *et al.* 1985), and, with the exception of the frontal region, concentrated mainly in the region of the pycnocline (Richardson *et al.* 1985). Such concentration at the pycnocline is a commonly observed phenomenon. It presumably arises as the combined effect of sedimentation and nutrient availability and is light-limited and shade-adapted, achieving net photosynthesis only on bright days (Holligan *et al.* 1984*b*).

The nitrogen supply to the phytoplankton in SSW should be discussed further. At the beginning of the season nitrate concentrations were around 5  $\mu\text{mol l}^{-1}$  in 1980 and between 8 and 10.7  $\mu\text{mol l}^{-1}$  in 1981 (Fogg *et al.* 1985). These fell in surface waters in July–August to 0.8  $\mu\text{mol l}^{-1}$  in SSW and 3.8  $\mu\text{mol l}^{-1}$  in MW in 1980 and to 2.1  $\mu\text{mol l}^{-1}$  in SSW and 3.1  $\mu\text{mol l}^{-1}$  in MW in 1981: values about the same as those found in the same area in July 1977 by Beardall *et al.* (1982). Phytoplankton nitrogen at its early summer maximum represented only about a seventh of that initially present as nitrate and presumably the remainder of the nitrogen consumed in production was transformed to organic form by decay, grazing and excretion (Fogg *et al.* 1985). It is not possible, from the data that we have, to estimate the loss by sedimentation from SSW. Since concentrations of phytoplankton decom-



position products such as phaeophytins and ammonium were no higher in BSW than in SSW (Fogg *et al.* 1985) and since only empty diatom frustules were found below the pycnocline (C. M. Turley, unpublished observation) perhaps sedimentation of phytoplankton was not great. Loss from SSW to the sediments of combined nitrogen in faecal pellets may, however, have been considerable (Angel 1984). Since we are considering the main body of SSW, away from the front, input of new nitrogen by lateral advection may be neglected. A rough estimate of upward transport of nitrate nitrogen from BSW may be made by using the empirical formula of Anderson (quoted by McCarthy & Carpenter 1983) to estimate eddy diffusion coefficients,  $K_z$ :

$$K_z = 118[(t/z) \times 10^3]^{-1.34},$$

where  $t/z$  is the  $\sigma_t$  gradient at the top of the thermocline. For cruise ISEA 3 (3 June 1980) this gives  $K_z = 0.68 \text{ m}^2 \text{ h}^{-1}$  and with a nitrate nitrogen gradient of  $0.4 \text{ mmol m}^{-4}$  over the same depth range gives an influx of  $6.5 \text{ mmol N m}^{-2} \text{ d}^{-1}$  (data from Fogg *et al.* 1985). Similarly, for cruise ISEA 4 (15 July 1980),  $K_z = 1.13 \text{ m}^2 \text{ h}^{-1}$  and the gradient was  $0.15 \text{ mmol N m}^{-4}$ , giving the influx as  $4.05 \text{ mmol N m}^{-2} \text{ d}^{-1}$ . Turley (1985) estimated the nitrogen requirement of the phytoplankton in May 1980 as  $0.4 \text{ mmol m}^{-3} \text{ d}^{-1}$ , that is,  $8 \text{ mmol N d}^{-1}$  in a 20 m water column. The phytoplankton thus appears dependent on regenerated nitrogen for some half to a quarter of its total requirement. Holligan *et al.* (1984b), whose estimates of the upward flux through the thermocline of nitrate in the Western Approaches fall in the same range as ours, similarly concluded that about half the nitrogen requirement of the phytoplankton was met by regenerated nitrogen. Whereas nitrate, and to a lesser extent nitrite, decreased in concentration in SSW as the summer advanced, the reduced nitrogen compounds ammonium and urea fluctuated irregularly in concentration (Turley 1985; Kassab *et al.* 1985). These fluctuations presumably reflect changing balances between production by heterotrophic processes and consumption. Turley (1985) suggested that in May 1980 the turnover of urea was sufficient to supply 48% of the nitrogen requirement of the phytoplankton. Later in the year urea could have provided all the nitrogen required. It does not seem likely that there is appreciable input of new combined nitrogen by biological fixation. The evidence for fixation by marine coccoid cyanobacteria is as yet unsatisfactory and a strain isolated from this sea area was found not to possess the property (El Hag 1984).

#### (b) *Bacteria*

As the summer progressed the mean bacterial count in SSW rose and was finally higher than that in MW by a factor of between two and three (Egan & Floodgate 1985). This is opposite to the situation found in the Western Approaches by Holligan *et al.* (1984) but since they do not indicate the statistical significance of their results it is difficult to know what importance to attach to this. Distribution was patchy (negative binomial, see Egan & Floodgate (1985) and Kassab *et al.* (1985)) but there was no apparent association with seston and no tendency for high concentrations to occur in the region of the pycnocline. There was no consistent correlation of bacteria with phytoplankton (Kassab *et al.* 1985, table 4). Like others (van Es & Meyer Reil 1982; Pomeroy *et al.* 1983; Azam & Ammerman 1984) we have the impression that most bacteria are freely suspended in the sea water rather than attached to particles. Azam & Ammerman (1984) from consideration of microenvironmental factors have proposed that freely suspended bacteria will tend to cluster around sources of dissolved organic matter. This may provide an explanation for the contagious distribution of bacteria observed in this study

although the scale of the distribution is much larger than that evidently envisaged by Azam & Ammerman.

Heterotrophic uptake of glucose, which appears to be largely a bacterial activity, increased in SSW as a whole as the summer progressed (Lochte 1985). However, there was not statistically significant correlation between glucose turnover rate and bacterial numbers in individual samples from the first three cruises although in the two later ones there was a highly significant positive correlation (Kassab *et al.* 1985, table 4). One cannot look to differences in either temperature or substrate concentration to explain the variations in glucose uptake rate (Lochte 1985) which presumably is indicative of varying activity in some fraction of the total bacterial population.

Bacterial metabolism does not necessarily lead to growth either in terms of cell division or increase in protoplasm. In the short-term neither the incorporation of label from [ $^{14}\text{C}$ ]glucose into cell material nor into respired carbon dioxide provides unambiguous evidence of growth: non-proliferating metabolism includes, for example, the production of storage polymers. One of the striking features of bacterial counts in non-estuarine sea water is the relative constancy at about  $10^5$ – $10^6$  cells per millilitre (Pomeroy *et al.* 1983; Holligan *et al.* 1984; Egan & Floodgate 1985) of which between 4% and 38% are in an active state (van Es & Meyer-Reil 1982). It may be that the growth kinetics of marine bacteria are to some extent controlled by a density function. Thus the rate of diffusion of substrate molecules could be a factor setting population densities at the observed level. On this view marine bacteria are K-strategists (Andrews 1984) with enzymic activities that are not necessarily closely coupled with growth.

On the other hand, there is increasing evidence of bacterial production in sea water at a level 10–50% of that of primary production and of a substantial population of predators dependent on bacteria (van Es & Meyer-Reil 1982; Holligan *et al.* 1984; Williams 1984). In experiments carried out *in situ* in dialysis bags in the stratified area near the western Irish Sea front Lochte & Turley (1985) found that in water filtered free of predators, bacterial production near the surface equalled that of phytoplankton. Direct counts and [ $^{14}\text{C}$ ]glucose uptake measurements agreed in showing that bacterial growth rates were considerably higher near the surface than at depth, surface water populations having generation times of about one day. Holligan *et al.* (1984a) also conclude that bacterial production is of the same order as phytoplankton production in stratified waters in the English Channel. Bactivoracious microflagellates have been studied by Fenchel (1984) and populations of these organisms in the waters of the English Channel are such that their consumption is commensurate with bacterial production (Newell & Linley 1984). This points to a rapid cycling of carbon through bacteria with predator–prey kinetics determining an equilibrium level of standing stock (Lochte & Turley 1985).

Either of these hypotheses could explain the great variation in heterotrophic activity despite relative constancy of bacterial numbers. Further observations are necessary to decide between them and it is perhaps likely that both mechanisms operate but with different fractions of the bacterial flora.

### (c) *Zooplankton*

The highest standing stocks of zooplankton were found in SSW between April and June and were both higher and about a month earlier in developing than in MW (Scrope-Howe & Jones 1985a). The distributions had a negative binomial form (Kassab *et al.* 1985). Vertical

migrations of some species occurred, but only when chlorophyll levels were low and evenly distributed, and did not go below the thermocline. At higher chlorophyll levels with patchy phytoplankton distributions, zooplankton ceased vertical movement and tended to concentrate in the phytoplankton patches (Scrope-Howe & Jones 1985 *b*). There was no overall correlation, however, of zooplankton in SSW with either phytoplankton or bacteria (Kassab *et al.* 1985). There was a correlation with glucose uptake rate which may be interpreted as a response of bacterial metabolic activity to zooplankton leftovers and excretory products (Lochte 1985; Kassab *et al.* 1985).

Certain species of zooplankton are characteristic of SSW and others are absent from it (Scrope-Howe & Jones 1985 *a*). Scattering layers detected by echo-sounding are produced by zooplankton (and also, of course, by bubbles and fish) and these, too, show distinct differences in stratified and mixed waters. The concentration of the scattering agents at particular depths in SSW contrasts with their diffuse distribution in MW and corresponds with the distribution of zooplankton as determined by sampling. These patchy distribution patterns of zooplankton are evidently reflected in those of fish and sea-birds (see p. 563).

#### (d) *Interrelations and cycling*

Before stratification sets in the pelagic community is one in which photosynthetic growth takes place in a medium containing an excess of mineral nutrients. With the limitation on nutrients imposed by the formation of the thermocline this expanding community transforms into one in which the magnitudes of standing stocks become stabilized and heterotrophic processes intensify so that the energy input from photosynthesis is now channelled into the cycling of nutrients. This transformation can be regarded as one from *r*- to *K*-selection (Andrews 1984). The balanced community found in summer is one in which organisms and processes are closely interrelated and its development is brought out clearly by statistical analysis. Whereas in March only seven statistically significant correlations were found among the variables measured in SSW, the number increased to 31 in April and to 40 in July. With the beginning of breakdown of the thermocline in September the number fell to 12 (Kassab *et al.* 1985, table 4). This is more extreme than the situation in mixed water for which there were 14 statistically significant correlations in March, 21 in April, 29 in July and 13 in September. The lesser impact of nutrient limitation in the mixed water resulted in a less tightly organized balance of organisms and processes. The cycling of carbon and nitrogen we suppose to be generally similar to that discussed in a number of recent papers (for example Fogg 1982; Goldman 1984; Williams 1984).

### 5. THE BOTTOM STRATIFIED WATER

BSW generally had less than half the chlorophyll *a* concentration than had SSW and from determinations of penetration of solar radiation into these waters (Mitchelson 1984) it is not to be expected that much photosynthesis or phototrophic uptake of urea occurs below the pycnocline. As we have seen there is no evidence of extensive sedimentation of algal cells from above. Bacterial numbers, sometimes, and heterotrophic activity, usually, were less in BSW than in SSW (Kassab *et al.* 1985). As would be expected from this only a small part of the total zooplankton population was found below the pycnocline but *Microcalanus pusillus*, a recognized deep-water species, was found near the bottom of the water-column (Scrope-Howe & Jones



1985*b*). The generally low level of ammonium nitrogen in BSW throughout the summer (Fogg *et al.* 1985; Kassab *et al.* 1985, table 6) does not give the impression of active mineralization in the water column. The correlation analysis mentioned in the preceding paragraph indicated that BSW was a less highly organized system with only 24 statistically significant correlations of variables in July compared with 40 for SSW.

It should be noted that it is an oversimplification to regard BSW as a homogenous water mass. The hydrographic sections given by Fogg *et al.* (1985) indicate the presence below the main body of BSW of the core of high salinity and high nutrient water, which Slinn (1974) found associated with the trough to the west of the Isle of Man.

## 6. THE MIXED WATER

The chlorophyll *a* concentration in MW was less throughout the season than in SSW (Fogg *et al.* 1985; Richardson *et al.* 1985). Nitrate concentrations remained high (Fogg *et al.* 1985) and, suspended particulate matter being higher and consequently light penetration less than in the stratified water (Mitchelson 1984), it seems that the phytoplankton population was light-limited. The low rate of urea uptake that was observed (Turley 1985) is to be expected of phytoplankton in this physiological state. One would also expect release of extracellular products of photosynthesis to be low (Fogg 1983) and the relatively low level of bacterial numbers and of heterotrophic activity observed in MW throughout the season fit in with this expectation. Holligan *et al.* (1984*b*), too, found less heterotrophic activity in MW in the Western Approaches as compared with that in SSW. Zooplankton stocks were also much lower than in SSW and the maximum occurred about a month later than on the other side of the front (Scrope-Howe & Jones 1985*a*). This is in accord with the conclusion of Holligan *et al.* (1984*a*) that phytoplankton is the dominant plankton fraction in mixed water whereas zooplankton biomass considerably exceeds that of phytoplankton in stratified water. The ecosystem is thus one in which both the biomass and activity of heterotrophs is less than in SSW and, as already noted, correlation analysis shows it to be less tightly organized.

## 7. THE FRONTAL REGION

### (a) *Standing stocks at the front*

The water mass extending from the western Irish Sea front to 15 km or so on the stratified side has some different biological characteristics from the rest of the surface stratified water. In the first place, the distribution of chlorophyll differs in that the total amount in the water column above the pycnocline, which is only marginally more than elsewhere in SSW, tends to be uniformly distributed instead of being concentrated on the pycnocline (Richardson *et al.* 1985). The higher surface concentration in this region is a general feature of fronts that has attracted much attention and has been variously explained. Thus Pingree *et al.* (1975) attributed it to the conjunction of a stabilized water column with nutrient enrichment from the adjacent mixed water allowing greater standing stocks. Nutrient complementation between the abutting water masses (Beardall *et al.* 1978, 1982) is another possibility. Fogg (1981) suggested that the physical and chemical conditions at a front might be a trigger rather than the principal factors sustaining production; migration of animals into the frontal region, once organic matter starts accumulating, providing an extra input of nutrients.

This idea of biological amplification can now be looked at more closely. As we have seen the frontal area did not show any persistent influence on zooplankton abundance; only twice during 12 cruises over two years were numbers higher at the front than elsewhere in the surface stratified water and in both these cases were associated with local chlorophyll maxima. These peaks were caused by substantial increases in numbers of nauplii of a single copepod, indicating that they were not brought about by mechanical aggregation (Scrope-Howe & Jones 1985*a*). The level of standing stock of zooplankton at the front, as elsewhere in SSW might, of course, be maintained by an increased rate of input in the face of increased predation.

That increased predation probably occurs in the frontal zone is evident on records from a 24 kHz echo-sounder. Patches of dense, often layered, scattering are regularly found at pycnocline depths within a few kilometres of the stratified side of the front. These features occur where the front lies across tidal streams as its western end and in the Celtic Sea as well as on the line regularly worked in the present studies (E. I. S. Rees, unpublished observations). At the frequency used the echoes are likely to be from fish and macroplankton though a response could come from very high densities of small particles and bubbles. Pronounced layers are regularly seen to form at dawn, descending at about  $0.8 \text{ m min}^{-1}$  to form a day time layer at 60–65 m. In the western Irish Sea basin there is a slight secondary pycnocline at this depth which is the top of a pool of colder water with a slightly lower oxygen content (Slinn 1974; Collins 1981). The speed of descent suggests that fish are the main component of the migrating layer of scattering organisms. The fish caught here in Isaac Kidd trawls have been mainly O-group sprats (*Sprattus sprattus*) though they are always caught with an order of magnitude greater biomass of *Meganyctiphanes norvegica*.

Transect counts of sea birds also imply increased activity by opportunistic mobile predators on the stratified side of the front. Numbers of birds are typically about an order of magnitude greater on the stratified side of the front. An exception to this occurs off the Irish coast south of Dublin where the mixed water is presumed to be downstream of two sources of enrichment, namely the Irish coastal current and the terminal part of the baroclinic jet of the western Irish Sea front. On our transect line (Fogg *et al.* 1985) resting flocks of several hundred Manx shearwater (*Puffinus puffinus*) are regularly found within 5 km of the top of the rise in surface temperature. However, it is not clear whether these are day time aggregations within an area where they feed on organisms coming to the surface at night or are temporary accumulations at a hydrographic boundary of birds in transit to island colonies on the Welsh coast, where they only land at night. If the former activity pattern is true then, like all the other bird species, the shearwaters will be net exporters of biomass and nutrients from the front. If the latter were the case then they could make a localized contribution to nutrient enhancement.

To try to put the role of the birds in nutrient regeneration into context crude estimates have been made by using literature sources of food consumption rates and its nutrient content (table 2). The inputs thus calculated come to  $8 \mu\text{mol N m}^{-2} \text{ d}^{-1}$  and  $0.5 \mu\text{mol P m}^{-2} \text{ d}^{-1}$ . An alternative calculation with the higher consumption rates suggested by Furness (1984) would approximately double the possible nutrient regeneration.

It is less easy to derive even approximate figures for fish biomass but echo sounder records suggest that the volume of shoals, presumed to be clupeids, might be in the range of  $500\text{--}5000 \text{ m}^3 \text{ km}^{-2}$ . Figures for the school density of foraging fish of about  $0.6 \text{ kg m}^{-3}$  are given in the review of clupeid biology by Blaxter & Hunter (1982). This would be equivalent to a fish biomass of  $0.3\text{--}3.0 \text{ g m}^{-2}$ . A production:biomass ratio of 2 seems reasonable for short

TABLE 2. ESTIMATED NUMBER OF BIRDS AND THEIR FOOD CONSUMPTION WITHIN A 10km BAND ON THE STRATIFIED SIDE OF THE WESTERN IRISH SEA FRONT

(E. I. S. Rees, unpublished results.)

		number per square kilometre	mass† per bird g	consumption‡ as percentage of bird mass	predation mg m <sup>-2</sup> d <sup>-1</sup>
small fish (sprat) feeders	guillemot	12	1000	20	2.4
	razorbill	1	850	20	0.2
	Manx shearwater	15	425	25	1.6
	kittiwake	5	400	25	0.5
					4.7
larger fish feeders	gannet	2	3000	20	1.2
scavengers and other foods	large gulls	6	850	20	1.0
	fulmar	4	800	20	0.6
total consumption					7.5 mg m <sup>-2</sup> d <sup>-1</sup>

For purpose of nutrient regeneration it is assumed that the food is fish and all is converted to nutrients in proportion to concentrations in whole fish.

If fish dry mass is 15% of wet, and N is 9.5% of dry mass, then a total consumption of fish of 7.5 mg m<sup>-2</sup> d<sup>-1</sup> results in 0.11 mg m<sup>-2</sup> d<sup>-1</sup> or 8 µmol N m<sup>-2</sup> d<sup>-1</sup> being consumed. Similarly, if P is 1.4% of dry mass then 0.016 mg P m<sup>-2</sup> d<sup>-1</sup> or 0.5 µmol P m<sup>-2</sup> d<sup>-1</sup> is consumed.

† Mass mainly from Cramp (1977–83).

‡ Based on Furness (1978).

lifespan fish such as sprats, which would give an annual figure in the range 0.6–6.0 g m<sup>-2</sup>. These figures span the value for pelagic fish production of 2 g m<sup>-2</sup> used in the North Sea ecosystem model of Steele (1974). Brander & Dickson (1984), however, show that fish yields in the Irish Sea on a kilogram per hectare basis are only a third of those from the North Sea. They suggest that this may be a reflection of the late, single, peak in the production cycle seen in many parts of the Irish Sea, but this does not apply to the stratified area. Bird aggregation at the front occurs particularly in the later half of the summer. If this is taken to be about 75 days then the expected fish consumption by the birds would be equivalent to about 0.35 g m<sup>-2</sup> of small fish and 0.09 g m<sup>-2</sup> of larger species, giving a total of 0.44 g m<sup>-2</sup>. The consumption of small fish would be equivalent to about 11% of the median value of the production estimate range. Thus it is in the same order of magnitude as the annual bird predation rate for other areas where sea birds are abundant, for example, 29% for Shetland waters (Furness 1978), 22% for waters off Oregon (Wiens & Scott 1975), 14% for an area off British Columbia where sea birds feed on herring outside the breeding season (Robertson 1972), and 20% off South Africa (Furness & Cooper 1983).

The contribution of fish to nutrient regeneration in the suprapycnocline water may also be derived from these estimates. Assuming that the small fish mainly consume copepods at a rate of 10% of body mass per day, that these have a nitrogen content of 2% of wet mass and that the fish excrete two-thirds of the nitrogen they ingest, then they might regenerate in the range of 5–56 µmol N m<sup>-2</sup> d<sup>-1</sup>. However, if allowance is made for diurnal vertical migration the amount returned to photic depths might come down to 2–20 µmol N m<sup>-2</sup> d<sup>-1</sup>. If the echo sounder records are an indication of the degree of patchiness of the fish then, although overall nutrient regeneration by the fish cannot account for much of the amounts needed to sustain phytoplankton production (compare the estimated requirement of 8 mmol N m<sup>-2</sup> d<sup>-1</sup>), they

could have important local effects. Elevated ammonia concentrations have been found behind menhaden schools (Oviatt *et al.* 1972) and behind anchovy schools ambient values have been calculated to be nearly doubled (Smith & Eppley 1982). Reviewing the impact of clupeid schools on the environment Blaxter & Hunter (1982) conclude that they can have a major influence on ecosystems through selective predation, which reduces the mean size of the zooplankton. By aggregating at localized parts of the front clupeid fish could amplify the rates of cycling and amplify the tendency towards non-normal distributions of many attributes. They might even be possible 'key' species in keeping the frontal ecosystem in a state of rapid turnover.

Overall, it seems that the contributions from birds and fish are negligible and there is no appreciable general biological amplification such as that suggested by Fogg (1981).

(b) *Primary productivity and heterotrophic processes*

If the total algal biomass in the euphotic part of the water column is actually little different from that in the surface stratified water away from the front (Richardson *et al.* 1985) explanations such as discussed in the previous paragraph need not be called upon anyway. Bacterial (Egan & Floodgate 1985) and zooplankton populations (Scrope-Howe & Jones 1985*a*; Kassab *et al.* 1985) are not significantly different near the front than elsewhere in the surface stratified water. It may be, however, that photosynthetic efficiency (carbon fixation per unit amount of chlorophyll *a*) is greater in the frontal region than elsewhere. Savidge *et al.* (1985) have reported results of primary productivity determinations in the Irish Sea by a continuous recording technique. They did not find higher rates in the frontal region but then this technique would have missed any contribution from picoplankton, which might amount to as much as 50% of the total (El Hag 1984), and extracellular products of photosynthesis were not determined (as will be discussed below, these may be of particular importance). Jacobson *et al.* (1983) found photosynthetic efficiencies at a nearshore front off the Georgia coast, U.S.A., to be about 1.5 times greater than those in mixed or in the main stratified water. Holligan *et al.* (1984*b*) found photosynthetic efficiencies to be actually less in frontal water in the Western Approaches than it was in either mixed or the main body of stratified water. There thus does not seem to be any great increase in photosynthetic efficiency at fronts. For production of phytoplankton biomass in the frontal zone the model of Tett (1981), based on general theory of phytoplankton growth and with vertical turbulent mixing as the dominant factor, appears to give an adequate account. However, there are increased rates of heterotrophic activity in the stratified water adjacent to the front, as shown in higher cellular ATP concentrations (Fogg *et al.* 1985) and glucose (Lochte 1985) and urea (Turley 1985) uptake rates, which may be up to eight times those observed in stratified water away from the front. It is these, rather than increases in standing stocks, that need to be explained. Similar indications of increased heterotrophic activity in the vicinity of fronts have been reported by Floodgate *et al.* (1981, see below) and by Jacobson *et al.* (1983). These latter authors found higher heterotrophic potentials, as determined by glucose uptake, immediately adjacent to the front on the stratified side of the nearshore front they studied. Pomeroy *et al.* (1983), working on the same area, found localized patches of high adenylate energy charge indicative of high heterotrophic activity in the frontal region. Holligan *et al.* (1984*b*) found microheterotroph respiration to be highest in frontal water in the Western Approaches. The explanation for these features may perhaps be found in the effects of eddies.

Eddies in shallow-sea fronts are evident in satellite images (see, for example, Fogg *et al.* 1985,



figure 2; James 1981, figure 2) but have not yet been studied in great detail. Garrett & Loder (1981) considered that their horizontal scale might be of the order of 10 km. Simpson (1981) put their scale in the 20–40 km range and surmised that the time required for their development might be about three days, that is, of the same order as the generation time of phytoplankton cells. Besides the eddies generated by the baroclinic jet, as discussed by these authors, there may be standing eddies caused by flow over the irregular sea bottom that is found in the vicinity of this front. The interleaving of water masses that occurs in an eddy may, of course, be an important mechanism for nutrient enrichment of stratified water (Holligan 1981). However, perhaps more importantly, the rotational movement of water in the isopycnal surface layer will result in vertical circulation (Angel & Fasham 1983) and this might be expected to pick up phytoplankton accumulated on the pycnocline and redistribute it through the water column. To give substance to this idea velocities of water movements within the eddy need to be known. Estimates of upward velocities in large cyclonic eddies are of the same order as sinking rates of some phytoplankton (Owen 1981). There seems to be no information for smaller eddies, but assuming the eddy extends down no further than the pycnocline and that it persists for several days it does not seem unreasonable to suppose that a phytoplankton population might be moved through 40 m to the surface by such convection. It is significant that the higher concentrations of chlorophyll at the surface adjacent to the front are somewhat episodic rather than continuous with time (Richardson *et al.* 1985) in keeping with the idea that they are contained in eddies passing along the front.

If this happens, then a low-light-adapted phytoplankton population is redistributed, more light energy becomes available to the population as a whole, and part of it may be exposed to inhibitory intensities near the surface. If the nutrient supply within the eddy is limited, the increase in photosynthesis that results from the greater availability of light can result in minimal growth only and it is likely that excess photosynthetic products will be released in extracellular form. The transfer of a low-light-adapted population with ample carbon dioxide supply to high light and limiting carbon dioxide was found by Watt & Fogg (1966) to be especially conducive to release of glycollate by *Chlorella* and the eddy would seem to provide just such a change in conditions. The kinetics of extracellular release appear to be similar for marine phytoplankton and glycollate is perhaps the major extracellular product (Fogg 1983). Uptake of extracellular products of phytoplankton is largely a function of bacteria (Fogg 1983) and Wright & Shah (1975) obtained evidence that for most marine bacterial strains glycollate acts as a 'co-metabolite', providing energy for the assimilation of other organic substances rather than providing carbon for cell synthesis directly. It thus appears plausible that entrainment in an eddy leads to an injection of potential chemical energy which cannot all be used for synthesis of biomass and which promotes an increased rate of cycling in the microheterotrophic population. The long doubling time of larger zooplankton makes it unlikely that they would be affected much by enclosure in an eddy and their vertical migration will promote movement in and out (Angel & Fasham 1983).

We suppose then that eddies have an effect on the frontal ecosystem superimposed on that envisaged by Pingree *et al.* (1975) and formulated mathematically in the model of Tett (1981). Transects will show rather different structures according to whether they pass through eddies radially or tangentially. The differences in distribution of ATP (Fogg *et al.* 1985, figure 7*c, d*) or urea uptake (Turley 1985, figure 3*c, d*) observed in sections made on consecutive days might be explained in this way as well as the striking concentrations of activity (see, for example,



Turley 1985, figure 3*e*) that are sometimes but not always observed. However, since our data are not tidally corrected we cannot be sure of this. Pomeroy *et al.* (1983) have noted separation between areas dominated by autotrophs and by heterotrophs at a front off the coast of Georgia, U.S.A.

#### 8. COMPARISON WITH THE PLUME FRONT IN LIVERPOOL BAY

Finally, it is of interest to compare the western Irish Sea front with another that we have studied in detail (Floodgate *et al.* 1981; Foster *et al.* 1982*a, b*). The main points of difference between the two are set out in table 3.

TABLE 3. A SUMMARY OF THE CHARACTERISTICS OF THE WESTERN IRISH SEA AND LIVERPOOL BAY FRONTS

	SSW, surface stratified water; MW, mixed water.	
	western Irish Sea	Liverpool Bay
physical determinants	solar heating; depth and tidal currents <sup>1</sup>	freshwater input from rivers; solar heating <sup>2</sup>
duration	March–April to Sept.–Oct. <sup>1</sup>	intermittent throughout year <sup>2</sup>
nutrients	nitrate rapidly depleted in SSW, regenerated N (NH <sub>4</sub> <sup>+</sup> and urea) then important in summer <sup>3</sup> silica limiting <sup>4</sup> no urea peak on front <sup>6</sup>	nitrate remains high in SSW, continuous supply from rivers silica not limiting <sup>5</sup> urea peak at front <sup>7</sup>
dominant phytoplankton	diatoms in MW flagellates in SSW <sup>4</sup>	diatoms in MW and SSW <sup>8</sup>
bacterial numbers	high in SSW no peak at front <sup>9</sup>	high in SSW peak at front in spring <sup>7</sup>
zooplankton numbers	high in SSW no peak at front <sup>10</sup>	peak at front <sup>7</sup>
cellular ATP concentration	high in SSW, peak at front <sup>3</sup>	high in SSW peak at front <sup>7</sup>

<sup>1</sup> Simpson & Hunter (1974).

<sup>2</sup> Czitrom (1982).

<sup>3</sup> Fogg *et al.* (1985).

<sup>4</sup> Beardall *et al.* (1982).

<sup>5</sup> Foster *et al.* (1982*a*).

<sup>6</sup> Turley (1985).

<sup>7</sup> Floodgate *et al.* (1981).

<sup>8</sup> Foster *et al.* (1982*b*).

<sup>9</sup> Egan & Floodgate (1985).

<sup>10</sup> Scrope-Howe & Jones (1985).

At the plume front in Liverpool Bay stratification is established in the shallower water, inshore of the front, and is stabilized by salinity differences arising from river inflow except in the summer, when it is maintained also by surface heating. Stratification, however, seems only to exist in relatively calm weather (Czitrom 1982) and the situation is complex, with five different water masses involved (Foster *et al.*, 1982*b*). The stratified water is enriched at the beginning of the season by combined nitrogen and phosphate derived mainly from terrestrial discharges and it develops higher phytoplankton populations, consisting mainly of diatoms, in the spring than does the offshore mixed water. A high chlorophyll concentration becomes associated with the front in late spring but Foster *et al.* (1982*b*) are of the opinion that this represents a residue of the dense phytoplankton population which a few weeks earlier

characterized the whole of the stratified area, rather than a population that has developed in response to the particular conditions at the front. This again may be an effect of frontal eddies similar to that just discussed. Whereas SSW in the western Irish Sea is a nearly closed system, the equivalent water mass in Liverpool Bay is open in that it receives a steady input of nutrients from river water during the summer.

In the late winter the Liverpool Bay front is characterized by a peak in bacterial numbers, just inshore of the discontinuity, apparently related to particulate and dissolved organic matter brought in by land run-off (Floodgate *et al.* 1981). This is a point of difference from the western Irish Sea front. By late spring and early summer, however, this peak has disappeared and the two fronts resemble each other in that the distribution of bacteria does not seem to be greatly affected by the discontinuity. Nevertheless, immediately on the stratified side of both fronts there is a region of high microbial activity, as evidenced by high cellular ATP:carbon ratios and high urea uptake rates and in the western Irish Sea there is further evidence of this in high heterotrophic indices (Lochte 1985). An important difference between the two fronts at this time, May–July, is that the Liverpool Bay front is a region of high numbers of copepods (Floodgate *et al.* 1981) whereas the western Irish Sea front shows zooplankton peaks only occasionally (Scrope-Howe & Jones 1985*a*). The explanation for this may lie in the accumulation of food in the form of organic detritus at the Liverpool Bay front. It is to be noted that urea concentrations are some four times higher at the front than they are elsewhere in Liverpool Bay (Floodgate *et al.* 1981), whereas in the western Irish Sea they tend to be patchy without any clear relation to the front (Turley 1985). Possibly this difference is related to that in zooplankton distribution although we do not regard the net zooplankton as a major source of urea (Turley 1985).

## 9. CONCLUSIONS

This interdisciplinary study has produced a sufficient body of different kinds of data to enable it to be shown statistically that the three water masses, surface and bottom stratified water and mixed water, associated with a tidal mixing front are distinct, although seasonal, ecosystems. The main body of surface stratified water quickly passes from its initial phase of unrestricted phototrophic growth to one in which biomass is fixed by nutrient limitation and populations of phytoplankton, bacteria and zooplankton show a considerable degree of homeostasis. These populations show close interdependent association, with a high level of heterotrophic activity and associated high rate of nutrient turnover. This balanced community is destroyed when the water column becomes destabilized in autumn. In contrast, the water below it, which, of course, sustains minimum photosynthesis, shows low levels of heterotrophic activity and a lower level of organization. In the mixed water the phytoplankton becomes light- rather than nutrient-limited, heterotrophic activity and interdependence of the trophic levels being intermediate between those in the other two water bodies. Slightly higher phytoplankton concentrations in the surface stratified water immediately adjacent to the front seem explicable in terms of nutrient supply and stability of the water column, being more favourable than on either side as suggested by Pingree *et al.* (1975). However, this water shows particularly high heterotrophic activity and intensified cycling, which we suggest may be an indirect effect of frontal eddies. Angel & Fasham (1983) have drawn attention to the biological interest of the larger scale oceanic eddies and it seems possible that eddy formation may provide an

explanation for phytoplankton distribution over wide areas of the Southern Ocean (Hayes *et al.* 1984). The smaller scale eddies on shallow sea fronts seem to be of similar biological interest as transient ecosystems and, although the logistics of investigating them in detail presents difficulties it seems well worth attempting.

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