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Biological implications of fronts on the northwest European continental shelf

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[Plate 1]

The results of recent biological investigations of three types of frontal system – tidal, coastal, and shelf-break – are summarized. Each is characterized by high standing crops of phytoplankton and is important as a biogeographic boundary between water masses with distinct plankton communities. Evidence for relatively high rates of primary production along tidal fronts is discussed in relation to secondary production.

1. Introduction

It has long been recognized that the annual cycle of plankton production in temperate seas is strongly influenced by the formation and breakdown of the seasonal pycnocline (Sverdrup 1953). With the recent improvement in sampling techniques it has been possible to examine more precisely how physical factors affect the biota. Thus, spatial and temporal variations in the standing crop of phytoplankton on the northwest European continental shelf, a region of relatively strong tides, can now be interpreted in terms of the interaction between mixing by tides and wind and stabilization of the surface layers by solar heating (Pingree 1978). Diatom blooms form under favourable conditions of illumination and inorganic nutrient availability in the spring when the seasonal thermocline becomes established, and again in the autumn as the thermocline starts to be eroded. In the summer high concentrations of phytoplankton are largely confined to the boundary regions between the warm, but nutrient-depleted, surface waters overlying the thermocline and cool, tidally stirred waters in which growth of the plant cells may be restricted by light. This chlorophyll-rich layer forms within the density discontinuity and extends to the surface in frontal zones between stratified and mixed waters.

Although aggregations of plankton along oceanic fronts are well documented in the literature, they have generally been thought to be ephemeral and therefore relatively unimportant in relation to estimates of productivity, especially since such phenomena were often considered to be produced by passive accumulation within convergent flow circulations rather than by active growth of the organisms themselves. Recent observations suggest that fronts in the shelf waters of northwest Europe are regions of relatively high biological productivity and also represent boundaries between dissimilar physical environments with distinct plankton communities. The implications of these findings are discussed in this paper.

It is still difficult to make useful generalizations about the biological properties of frontal systems, even for those within a restricted geographical area, partly because of basic differences in physical structure and dynamics and partly because data on the distribution of organisms are very sparse, both spatially and temporally, and are only interpretable within limits imposed by the resolution of the sampling procedures. For these reasons no attempt has been made to review or to make comparisons with studies on fronts in other shelf seas, even though many of the concepts developed from work in areas such as Chesapeake Bay (Tyler & Seliger 1978; Seliger *et al.* 1981), the Nova Scotian Shelf (Fournier 1977; Fournier *et al.* 1977, 1979; Herman & Denman 1979) and the Bering Sea (Iverson *et al.* 1979*a*, *b*) are applicable to the shelf seas of northwest Europe.

2. PHYSICAL CONSIDERATIONS

Examination of the satellite infrared images taken in summer of the northwest European shelf shows that three types of front, tidal, shelf break and coastal, each of which will be considered in this paper, form boundaries between warm, stratified water and relatively cool, mixed water (figure 1, plate 1). Smaller-scale, transient features that develop in response to tidal flow around islands and headlands and to fresh water run-off from estuaries are relatively unimportant biologically although they may show marked accumulations of positively buoyant organisms and detritus along zones of convergence (Pingree *et al.* 1974).

The tidal fronts have been studied most intensively. Though they were recognized more than 60 years ago and explained in terms of seasonal solar heating at the sea surface and tidal mixing (Matthews 1911, see his plate 3), it is only within the last decade that their positions have been shown to be predictable from numerical models based on just two variables, water depth and tidal stream velocity (Simpson & Hunter 1974; Pingree & Griffiths 1977). However, the structure of each front not only varies in relation to the absolute values of these two parameters, but is also strongly influenced by other factors such as advective flow both parallel (as much as 10–20 cm s^{-1}) and normal to the axis of the boundary, vertical motions of upwelling and downwelling, wind mixing, variations in the contribution of salinity to the density structure, seasonal changes in the stability of the density gradients, internal wave activity on the stratified side of the front, and by eddies and other forms of cross-frontal mixing. These effects are discussed in other papers in this symposium, and here it is sufficient to emphasise that the biological properties of these fronts must be expected to be equally variable over the time-scales (up to five months) for which they persist each year. In general terms, special consideration has to be given to the depth of water: in shallow (less than 50 m) regions the surface thermal structure may become masked by continued warming of the mixed waters so that, by late summer, the isotherms extend to the bottom rather than to the surface. This restricts the mixing of nutrients from beneath the seasonal thermocline.

The physical processes that cause patches and bands of cool water to appear intermittently in summer along coasts where the water is normally stratified under conditions of weak tidal mixing have not been described in any detail, although upwelling induced by offshore winds (Cooper 1961) or by geostrophic effects on alongshore advective currents seems likely to be important. For any given area the spatial extent of these coastal fronts is seen on satellite images to be very variable, and the fronts tend to persist over a time-scale of days rather than weeks.

Shelf-break fronts have been described by Dickson *et al.* (1980) and in greater detail by Pingree & Mardell (this symposium). They appear to be best developed, at least as far as surface structure is concerned, where the topography of the shelf slope is steep and dissected by canyons, and in such regions they are visible on infrared images throughout the summer. The relative importance of tidal mixing and upwelling in determining the structure of the frontal boundary is difficult to determine, and other possible mechanisms for mixing over the continental slope may also be significant (Cooper 1952).

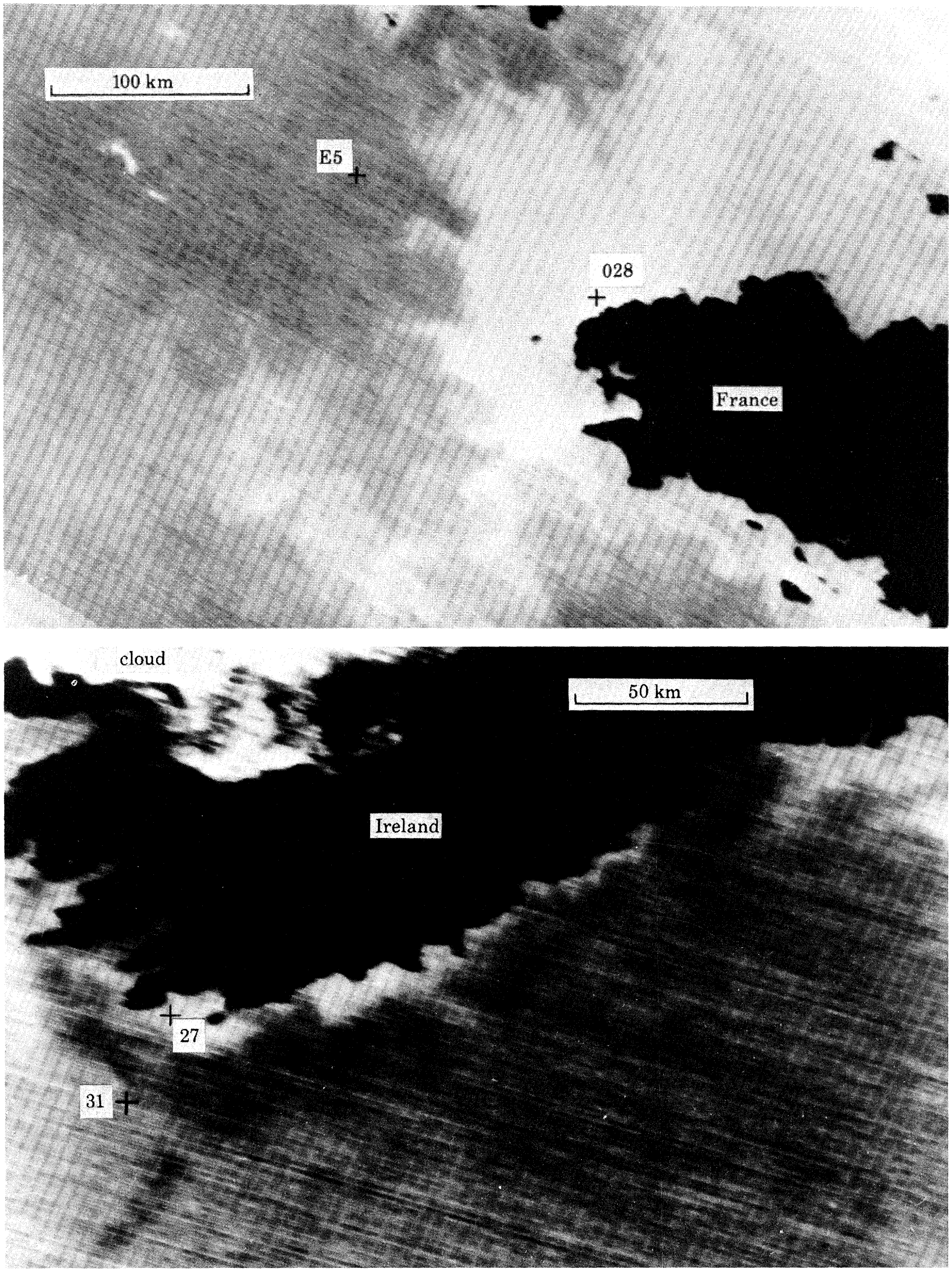

Figure 1. Infrared images from the NOAA-5 satellite showing (*a*) tidal and shelf-break fronts in the southern Celtic Sea on 20 August 1976, and the positions of stations E5 and 028, and (*b*) coastal front along the coast of southern Ireland on 11 June 1978, and the positions of stations 31 and 27. The light areas on the satellite images indicate cooler water.

3. Summary of biological observations

Attempts to describe in detail the biological properties of fronts are severely hampered by the difficulties of sampling in complex and dynamic physical environments. For example, the distributions of planktonic organisms have to be considered in horizontal as well as vertical dimensions, account being taken of continuity between the frontal boundary and the subsurface thermocline as well as diel patterns in vertical migration. Another problem is that the relative importance of biological processes (growth and grazing rates) as opposed to physical processes (aggregation and dispersion) in determining the distribution and abundance of individual species can never be clearly defined. More generally, it is not easy to specify the scales over which different components of the ecosystem may be displaced relative to one another by residual flows – it is possible that energy at the level of phytoplankton and primary herbivores is largely exported away from frontal regions before its consumption at higher trophic levels. The available field data must be considered with these concepts in mind.

The main features of the biology of fronts on the northwest European shelf are illustrated with data from the Celtic Sea (see figure 1). The fronts in this region have been studied for several years, continuous sampling methods being used for both surface and subsurface waters, and are considered to be representative of others around the British Isles at least within the constraints imposed by the bottom topography (including water depth) and advection.

Tidal fronts

The first observations to relate the distributions of planktonic organisms to tidally induced differences in the temperature structure of the water column were made by Le Fèvre & Grall (1970) and Grall *et al.* (1971) in the region around Ushant. Subsequently, with the use of fluorometers and autoanalysers for continuous measurements of chlorophyll *a* fluorescence and of dissolved inorganic nutrients, it was shown that in summer both surface (frontal) and subsurface (thermocline) temperature discontinuities are characterized by closely coupled changes in chlorophyll concentrations and nutrient levels. Such observations have been made, in varying detail, for the Ushant frontal system which extends around the coast of Brittany into the western English Channel (Pingree *et al.* 1975, 1977, 1979; Grall *et al.* 1980), the Celtic Sea front between Ireland and Wales (Savidge 1976; Savidge & Foster 1978), fronts in the Irish Sea (Savidge 1976; Foster *et al.* 1976; Beardall *et al.* 1978), the Islay front between northern Ireland and Scotland (Pingree *et al.* 1978; Simpson *et al.* 1979) and the fronts around the Orkney and Shetland Isles (Pingree *et al.* 1978; Dooley 1978, this symposium) and southern North Sea (Harding *et al.* 1978; Pingree *et al.* 1978).

In mid to late summer, when the density structure is best developed, considerable variations have been found in the form of the chlorophyll signal; in shallow water systems the phytoplankton may be most abundant in the mixed waters, whereas in fronts in deep waters (more than 50 m) the surface discontinuity and the thermocline generally exhibit well defined and often intense chlorophyll maxima. On some occasions spectacular blooms of the dinoflagellate *Gyrodinium aureolum* have been associated with the frontal boundary, extending into the warm surface water above the thermocline.

For any one frontal region, the spatial distribution of chlorophyll also varies with time. Thus, in the western English Channel, where the water depth is about 100 m and advective flows are relatively weak (Pingree *et al.* 1978), the Ushant front defines in late April and early May the limit of the spring diatom outburst and associated depletion of inorganic nutrients (figure 2), even though the gradients in temperature (density) are relatively weak so early in the year. As the season progresses the diatoms that are not removed by grazing tend to sink and are replaced by flagellates (mainly dinoflagellates) which are more or less confined to the boundary zone between the warm, wind-mixed layer and the cool, tidally mixed water (figure 3, also see figure 8).

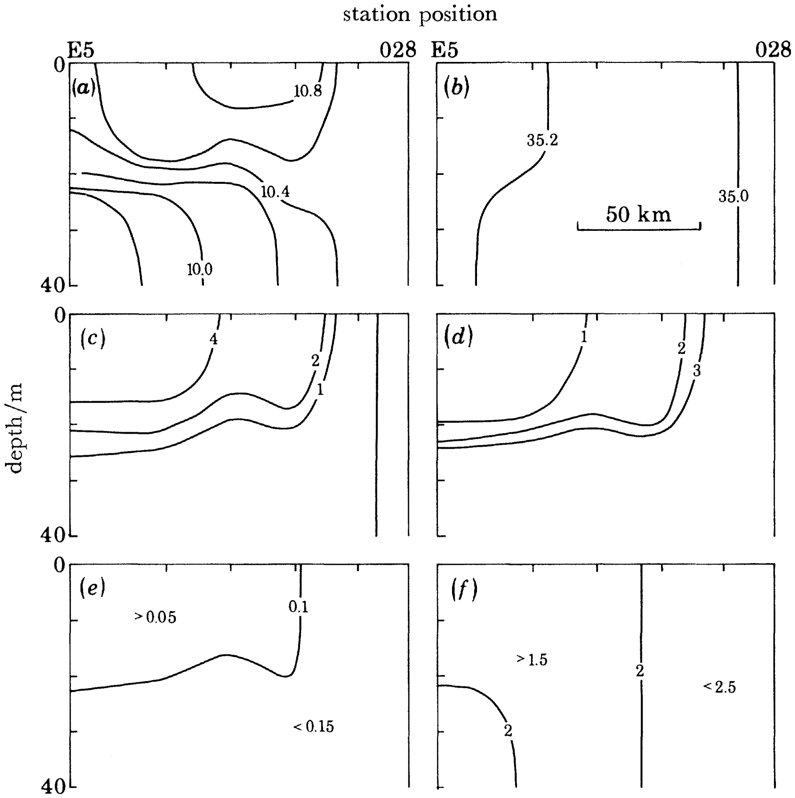

FIGURE 2. Sections across the Ushant tidal front between stations E5 and 028 (see figure 1) on 30 April 1980 for (*a*) temperature/°C; (*b*) salinity (‰); (*c*) chlorophyll *a*/(mg m^{-3}); (*d*) nitrate/μM; (*e*) nitrite/μM; and (*f*) silicate/μM. Marks on the top axis indicate the location and number of stations on which the sections are based. Each parameter was measured continuously at the surface (2 m) between stations and on vertical profiles at each station.

Sampling at higher resolution, with an *in situ* undulating Batfish system, shows considerable fine-scale structure close to the frontal boundary but still with strong coherence between temperature and chlorophyll distributions (figures 4*a*, *b*). The vertical displacements of the contours are probably caused by internal waves and eddies (Pingree *et al.* 1979). Such mixing processes also give rise to equally complex patterns in the surface distribution of chlorophyll along the front which are seen in satellite images (Viollier *et al.* 1981).

To illustrate more precisely changes in the chemical properties of the water, surface measurements of dissolved oxygen, nitrate and nitrite across the Ushant front are reproduced in figure 4*c*. Vertical profiles through the base of the thermocline are very similar, with increases in inorganic nutrients confined to the lower part of the temperature gradient below the chlorophyll peak (Pingree *et al.* 1977). The distribution of inorganic phosphate is similar to that of nitrate.

Profiles for ammonium across the front and the thermocline generally show no structure, with concentrations about 0.5 µm ammonia in midsummer, but occasionally higher values are observed within or below the thermocline.

The depth of the mixed water off Ushant is 60–100 m. Here the growth of plant cells appears to be limited by light, even in midsummer, so that inorganic nutrients are never fully depleted (figure 3). In this type of situation both lateral and vertical mixing processes will tend to make nutrients available to the phytoplankton within the frontal boundary, and in this sense the Ushant front represents a nutrient-rich system. By contrast, shallow water fronts, in which the mixed water tends to become nutrient-depleted and the subsurface thermal structure effectively isolates the nutrient-rich water below the thermocline, are nutrient-poor systems characterized by relatively low concentrations of chlorophyll *a*. Examples of such fronts are found in the shallow parts of the Irish Sea (Beardall *et al.* 1978) and the North Sea (Pingree *et al.* 1978).

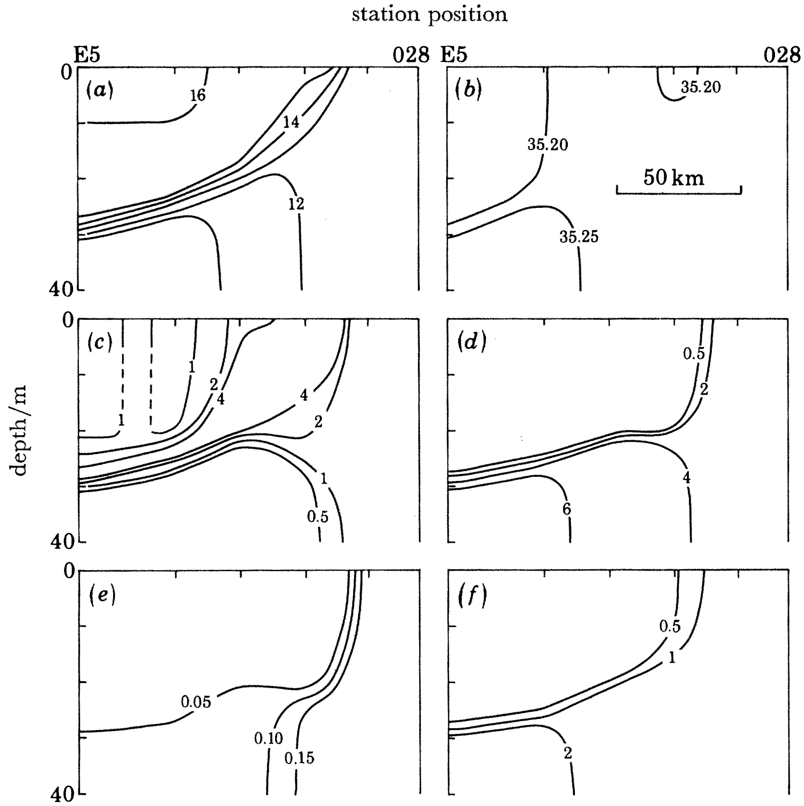

Figure 3. Sections across the Ushant tidal front between stations E5 and 028 (see figure 1) on 1 August 1980 for (*a*) temperature/°C; (*b*) salinity (‰); (*c*) chlorophyll *a*/(mg m^{-3}); (*d*) nitrate/µm; (*e*) nitrite/µm; and (*f*) silicate/µm. Also see notes to figure 2.

Since the work of Grall *et al.* (1971) who described different zooplankton communities for the coastal, mixed offshore and stratified offshore waters around Ushant, very little information about the distribution of zooplankton across tidal fronts has become available. Some data on ciliates in the Islay front are presented by Simpson *et al.* (1979), and evidence for a relatively high biomass of zooplankton in the Ushant system was found by Grall *et al.* (1980). Zooplankton samples collected along a section across the Ushant front each year since 1976 show that the distribution and abundance of the major species is extremely variable (R. P. Harris & P. M.

Holligan, unpublished observations; see table 1), but without further analysis of these data no general account can be given of their distribution relative to that of the phytoplankton.

Coastal fronts

In stratified waters the surface concentrations of chlorophyll *a* tend to increase close to the shore, probably owing to higher fluxes of inorganic nutrients resulting from enhanced vertical mixing and drainage from the land. The associated gradients in temperature and salinity are generally weak, but on occasions the underlying pycnocline is disturbed sufficiently to create sharp density boundaries at the surface similar to tidal fronts.

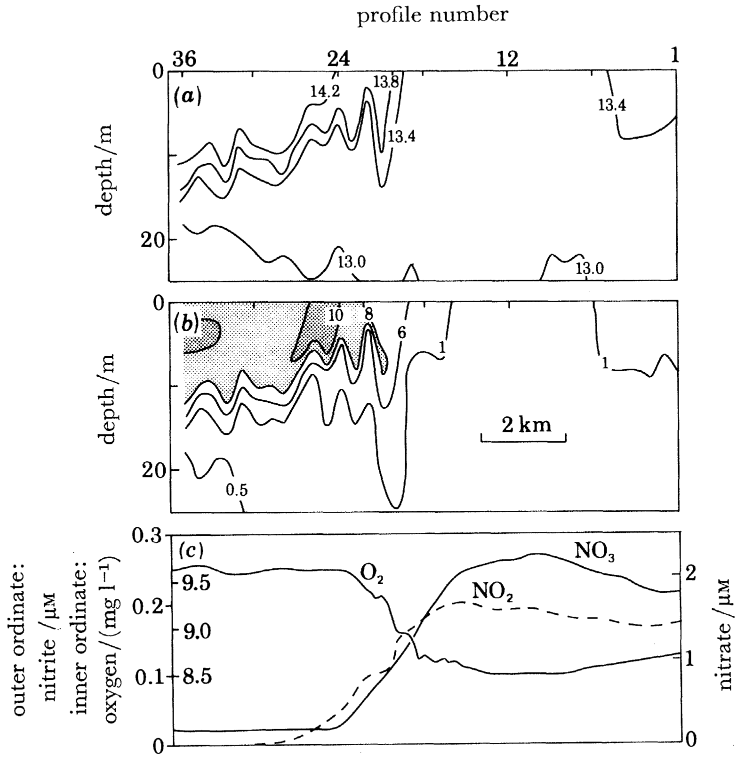

FIGURE 4. Sections for (*a*) temperature/°C and (*b*) chlorophyll *a*/(mg m^{-3}) through the boundary of the Ushant tidal front on 6 August 1980. The data were obtained with an undulating CTD–fluorometer system towed at 8 knots (*ca.* 4 m s^{-1}); (*c*) surface (2 m) measurements of oxygen/(mg l^{-1}), nitrate/μM and nitrite/μM made along the same track.

A section through a feature of this type, off the coast of south west Ireland (figure 1), is illustrated in figure 5. In the frontal region diatoms were dominant, and there were high levels of inorganic nutrients at the surface. The distributions of chlorophyll and species (see figure 6) suggest that the phytoplankton population did not originate from the subsurface thermocline where the chlorophyll maximum was very weakly developed. This is further supported by the salinity structure which indicates upwelling of bottom water, a condition likely to have favoured the growth of diatoms rather than dinoflagellates, at least as long as levels of inorganic nutrients in the surface water remained high. On the other hand, summer blooms of the dinoflagellate *Gyrodinium aureolum*, have been reported from this area (Ottway *et al.* 1979; Pybus 1980) and may have been initiated from offshore, subsurface populations.

Apart from accounts of comparable hydrographic conditions along the south coast of Norway in the autumn (Braarud & Heimdal 1970; Tangen 1977), which also preceded blooms of *Gyrodinium aureolum*, there are no other detailed descriptions of the biology of coastal fronts in areas of weak tidal mixing. Satellite images show, however, that such features are not uncommon.

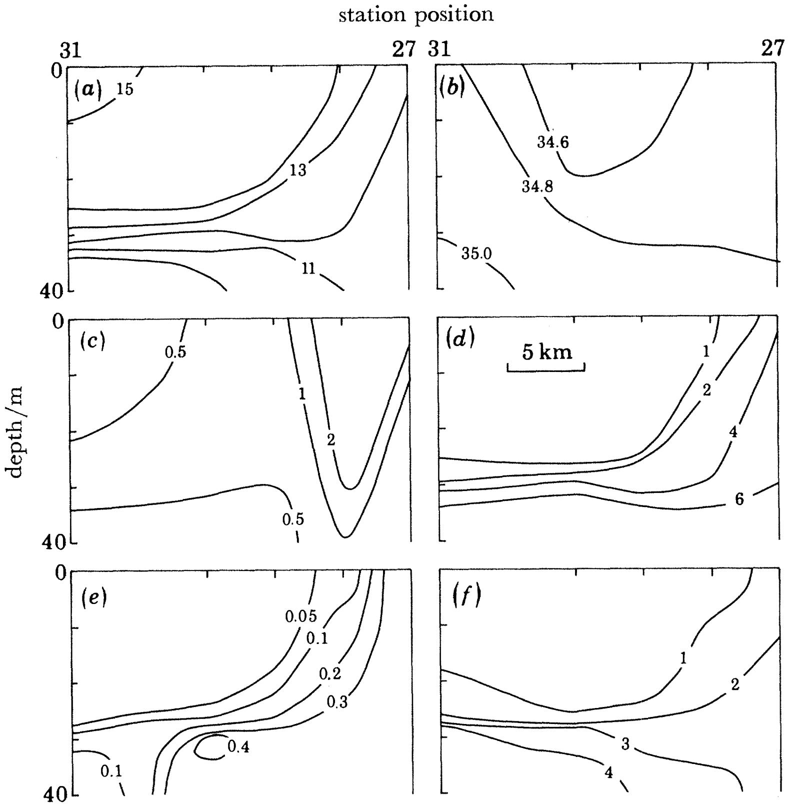

FIGURE 5. Sections across the coastal front along the coast of southern Ireland between stations 31 and 27 (see figure 1) on 12 August 1980 for (*a*) temperature/°C; (*b*) salinity (‰); (*c*) chlorophyll *a*/(mg m^{-3}); (*d*) nitrate/μM; (*e*) nitrite/μM and (*f*) silicate/μM. Also see notes to figure 2.

Shelf-break fronts

Continuous surface records for chlorophyll fluorescence and other hydrographic parameters often show abrupt changes at the edge of the continental shelf. In spring and early summer the diatom outburst appears to develop later and persist longer than in adjacent shelf and oceanic waters, probably owing to greater vertical mixing at the shelf break, and the very patchy distributions of inorganic nutrients and chlorophyll described by Steele *et al.* (1971) for the Rockall Bank may be typical of conditions along the margin of the shelf at this time of year. During the summer relatively high levels of chlorophyll persist in surface and subsurface layers along a broad band between stratified oceanic and shelf waters along the southern margin of the Celtic Sea (Pingree & Mardell, this symposium), but it is not yet certain whether this feature is also found to the west and north of Ireland and Scotland where the continental slope is less steep.

Table 1. Differences in the abundance (number/m^{-3}) of the major zooplankton taxa across the Ushant tidal front†

	28 July–4 August 1976					17–18 August 1977			
	stratified	frontal			mixed	stratified	frontal		mixed
station number...	E5	6	5	4	1	E5	025	026	027
Calanus spp.	64	352	75	122	24	38	139	93	85
Centropages spp.	68	61	60	73	26	35	242	93	35
Amphipoda	+	8	60	180	81	< 1	< 1	15	27
Euphausiacea	14	123	7	39	6	11	83	75	8
Spiratella retroversa	108	47	48	167	6	629	105	1042	80
Sagitta spp.	3	133	120	174	49	19	11	25	12
chlorophyll a/(mg m^{-2})	120	490	—	100	38	21	19	33	21
time of sampling (G.M.T.)	14h00	20h00	01h30	22h30	15h30	18h10	22h10	02h47	06h08
surface-to-bottom temperature difference/°C	8.1	7.3	5.7	5.5	1.3	7.5	7.2	4.9	< 0.1

† Samples were collected in 1976 by oblique tows to a depth of about 80 m of a 30 cm Lowestoft sampler fitted with a 270 μm mesh net, and in 1977 with a 70 cm net (200 μm mesh) hauled vertically from the bottom to the surface. Volumes of filtered water were measured with flow-meters fitted at the mouth of the nets. The positions of the 1976 station are shown in figure 2*a* of Pingree *et al.* (1977).

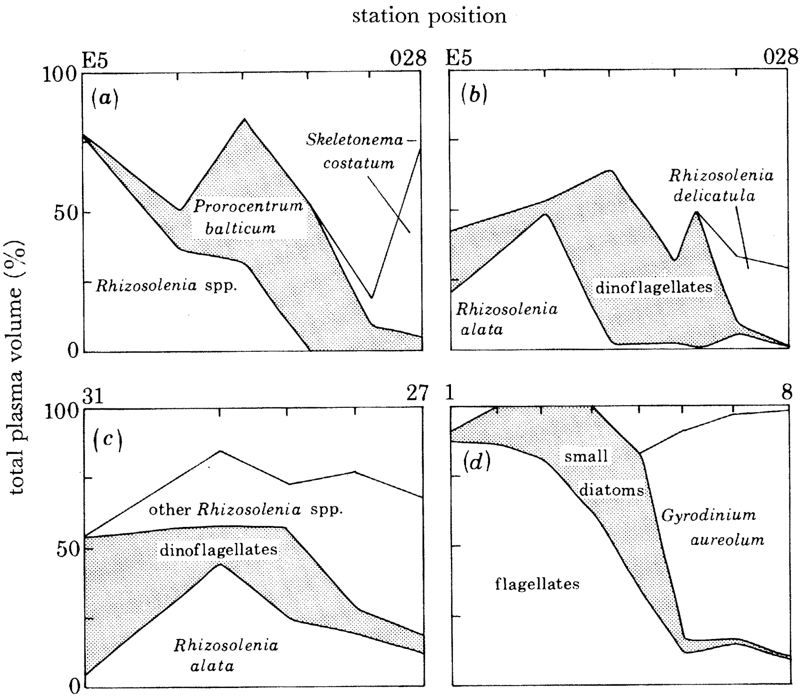

Figure 6. Changes in the composition of phytoplankton populations across frontal regions. Plasma volumes have been calculated from cell counts to allow direct comparison between species or groups of species.

(*a*) The Ushant tidal front on 30 April 1980 (see figure 2). The small flagellates were excluded from the total plasma volume as a high proportion were non-photosynthetic.

(*b*) The Ushant tidal front on 1 August 1980 (see figure 3). The dinoflagellate *Gyrodinium aureolum* was dominant at all stations but, for illustration, has been omitted from the total plasma volume.

(*c*) The coastal front along the coast of southern Ireland on 12 August 1980 (see figure 5).

(*d*) The shelf break front in the southern Celtic Sea on 23 July 1976 (see figure 4 in Pingree & Mardell, this symposium).

The data for (*a*) and (*b*) are derived from integral samples for the surface layer and thermocline, whereas (*c*) and (*d*) are based on discrete samples collected at the depth of the fluorescence maximum.

4. Fronts as biogeographic boundaries

Phytoplankton

Accounts of the species composition of phytoplankton populations in frontal regions have been given by Grall *et al.* (1971), Pingree *et al.* (1978, 1979), Beardall *et al.* (1978), Simpson *et al.* (1979) and Holligan *et al.* (1980). Considerable differences between mixed and stratified waters have always been observed, although the form of these appears to vary both with geographical location and with time of year. Generally, by midsummer, diatoms (including benthic species) tend to be most abundant in the more mixed waters and dinoflagellates in the front and thermocline, whereas in the surface layer above the thermocline small flagellates, large *Ceratium* spp. and *Rhizosolenia alata* are usually the dominant groups.

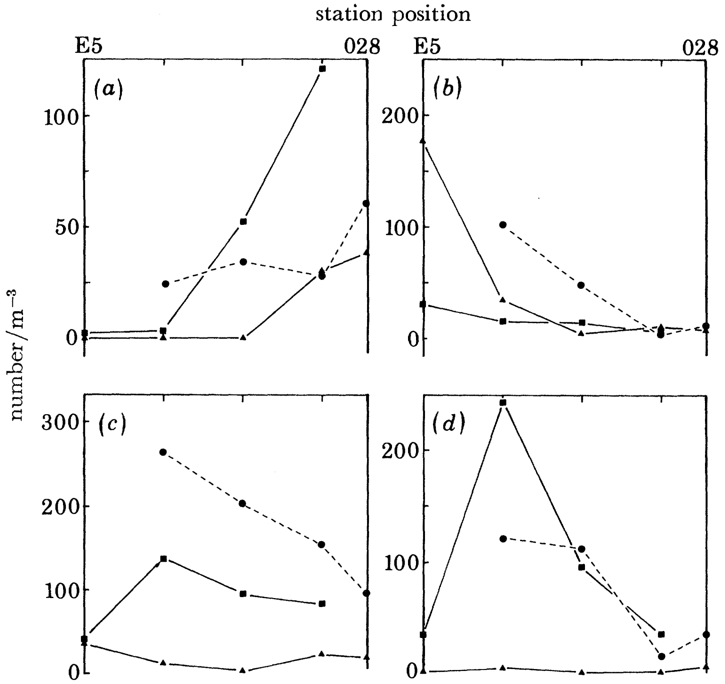

FIGURE 7. Changes in the abundance (number m^{-3}) of copepods across the Ushant tidal front on 17–18 August 1977 (■—■), 23 April 1978 (▲—▲), and 16 June 1978 (●– – –●). The samples were collected with a vertical net in August, and with a Lowestoft sampler in April and June (see notes to table 1). (*a*) *Acartia clausi*; (*b*) *Metridia lucens*; (*c*) *Calanus* spp.; (*d*) *Centropages* spp.

Examples of such distributions are given in figure 6 for the frontal systems bordering the Celtic Sea. In each case species or groups of species have well defined distributions in relation to the frontal boundary, and these almost certainly reflect physiological adaptations with respect to light, nutrients and other environmental factors. Also each entity is distinct morphologically (i.e. cell size, chain formation, etc.) which in turn affects grazing processes. These diagrams do not show variations in standing crop of the phytoplankton, which are indicated in the corresponding sections for chlorophyll *a*.

Zooplankton

Marked changes in the zooplankton populations occur across both the tidal and shelf-break fronts. The distributions of some copepod species in the Ushant front are illustrated in figure 7.

Thus *Acartia clausi* is consistently most abundant in the cool, tidally mixed water, as was also observed by Grall *et al.* (1971), and other organisms with similar distributions include *Temora longicornis* and cladocerans. By contrast *Metridia lucens*, and also the gastropod *Spiratella retroversa*, tend to be confined to the stratified side of the boundary. A third group, which includes *Calanus* and *Centropages* species, shows no obvious relation with the hydrographic structure.

Data from the continuous plankton recorder surveys not only support such observations for tidal fronts on the shelf, but also provide many examples of species whose distributions are limited by the shelf-break boundary (Bary 1963). Three groups of organisms were listed by Colebrook *et al.* (1961) – neritic, intermediate and oceanic – and the distributions of these in the Celtic Sea (Edinburgh Oceanographic Laboratory 1973) correlate, in varying degrees at the species level, with the mixed, stratified and oceanic régimes defined by the tidal and shelf-break fronts. These distributional patterns do show temporal anomalies, especially in regions with strong advective flows such as to the north of Scotland (for example, Aiken *et al.* 1977), but it is equally remarkable how consistent they are in many areas even from summer to winter. The relative importance of abiotic (for example, restricted mixing across discontinuities) and biotic factors (responses of the organisms themselves to changes in the environment) in maintaining these patterns is uncertain (Bary 1964).

Long-term changes

Southward (1980), in a review of long-term changes in the plankton of the western English Channel, concluded that some combination of climate-related effects, including water circulation and temperature, is responsible for instabilities in the ecosystem. Since variations in the hydrography of this area are likely to be closely interrelated with the dynamic properties of the Ushant frontal system, at least during the summer, it is possible that the stability and even location of the temperature gradients are modified at the same time as changes in the structure of the plankton community occur. Some support for this suggestion is found in the existing field data. The plankton associations found in the stratified and mixed waters either side of the Ushant front resemble, at least in some respects, those characterized by the indicator species, *Sagitta elegans* and *Sagitta setosa* (Russell 1933, 1935). The distributional limits of these two chaetognaths (Southward 1962) tend to lie close to the predicted positions of tidal fronts. Some of the areas for which long-term changes in the plankton have been well documented, such as station E1 off Plymouth (Russell *et al.* 1971) and the southern North Sea (Colebrook *et al.* 1978), are known from infrared satellite images to be strongly influenced by frontal boundaries.

Both advection normal to the stratification contours and wind-mixing can have significant effects on frontal structure (Simpson this symposium), but there is no evidence that changes of this type have actually occurred in the western English Channel. Also it is not at all certain whether variations in the stability of tidal fronts and the seasonal thermocline will affect directly the structure of the planktonic ecosystem, or whether both are determined independently by advective flow or some other external influence. In either case series of compatible biological observations in frontal regions over appropriate temporal and spatial scales are likely to provide valuable new information about this problem.

5. Plankton production in tidal fronts

Phytoplankton

Most determinations of phytoplankton biomass in tidal fronts have been based on samples collected at discrete depths, mainly from the surface layer, and expressed as chlorophyll *a* concentration. For some frontal systems sections of chlorophyll *a* have been constructed (Pingree *et al.* 1975, 1976, 1978; Dooley 1978; Simpson *et al.* 1979) but these give no indication of changes with time, either during a single year or for different years. Holligan (1979) presented data for the Ushant front that showed very large differences in the standing stock of chlorophyll, integrated for the upper 30 m of the water column, in 1976 and 1977.

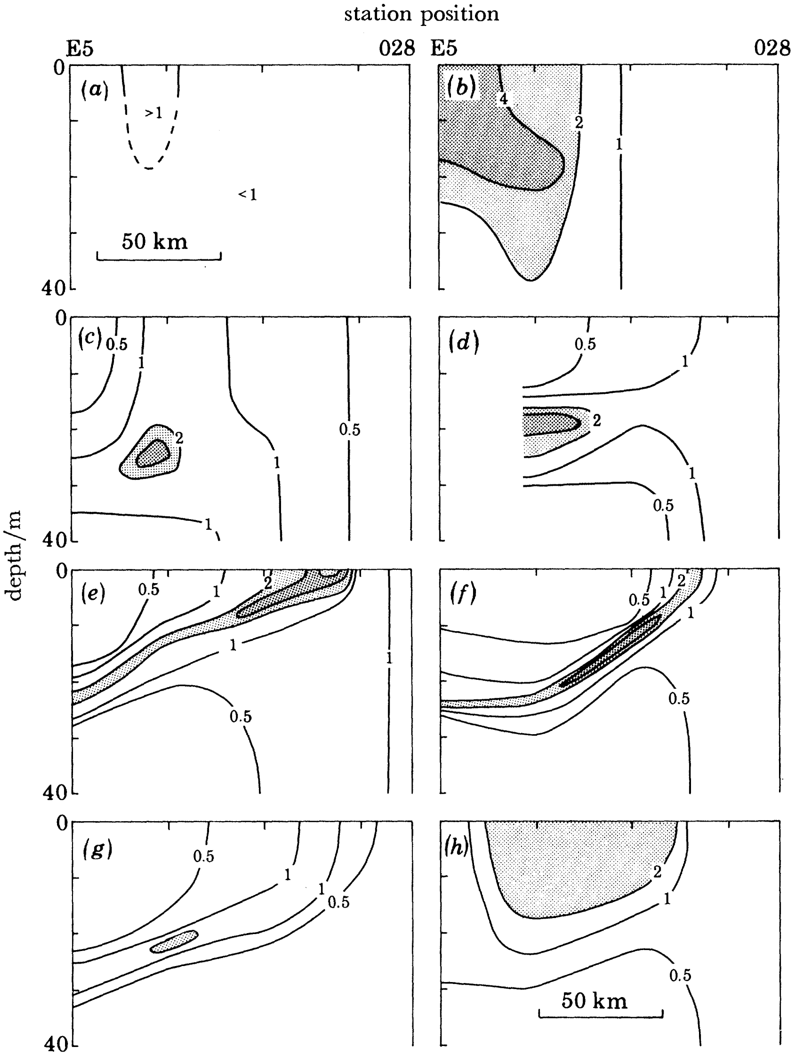

Figure 8. Sections for chlorophyll $a/(\mathrm{mg\ m^{-3}})$ across the Ushant tidal front on (*a*) 23 April 1978; (*b*) 6 May 1977; (*c*) 29 May 1977; (*d*) 16 June 1978; (*e*) 12 July 1978; (*f*) 17–18 August 1977; (*g*) 1 September 1977; and (*h*) 25 September 1978. The same contouring intervals are used in each diagram. Also see notes to figure 2.

Observations on the distribution of chlorophyll *a* across the Ushant front between April and September are summarized in figures 8 and 9. After the spring diatom outburst the combined effects of sinking and grazing lead to considerable patchiness in the distribution of chlorophyll, but as the flagellate populations become established in July a more continuous chlorophyll-rich layer develops in the thermocline and extends to the surface at the frontal boundary. Finally, by late September, the phytoplankton are again most abundant in the surface water adjacent to the front. The highest standing crops of phytoplankton are found close to or on the stratified side of the front during July and August. Furthermore, although the integral values for chlorophyll *a* are very variable, the maximum concentrations in the water column may exceed those in the spring for as long as six weeks at this time of year, even at the most stratified stations. These summer populations have generally been dominated by dinoflagellates, in particular *Gyrodinium aureolum*, but at station E5 in August 1976 a bloom of an unidentified coccolithophorid gave chlorophyll values greater than 50 mg m^{-3} in the thermocline.

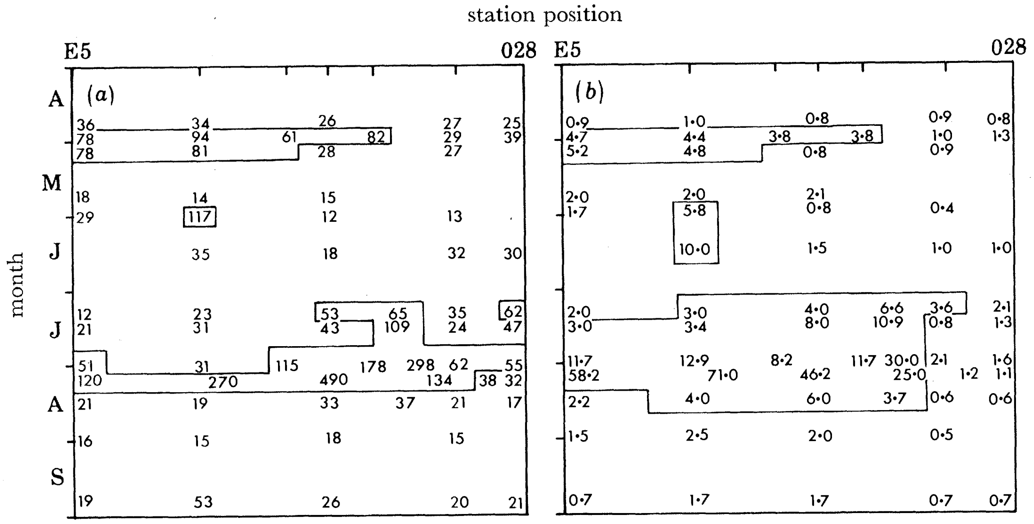

FIGURE 9. Values for (*a*) the standing crop/(mg m^{-2}) and (*b*) the maximum concentration/(mg m^{-3}) of chlorophyll *a* across the Ushant tidal front for April–September 1976–80. Boxes enclose levels (*a*) more than 50 mg m^{-2} and (*b*) more than 3.0 mg m^{-3}. The standing-crop measurements represent the surface and the thermocline layer in stratified water, and the upper 30 m in mixed water (stations 028 and the adjacent 027). From May to August the maximum concentration of chlorophyll in stratified waters was consistently found in the thermocline except when surface blooms of the dinoflagellate *Gyrodinium aureolum* occurred.

Interpretation of chlorophyll distribution in terms of primary production is still not possible owing to a lack of comparable information on *in situ* rates of photosynthesis. Assimilation indices vary by a factor of four or more in July and August (Pingree *et al.* 1975; Savidge & Foster 1987; Holligan, unpublished results), with the highest values between 4 and 7 mg C/mg Chl *a* per hour for thermocline and surface samples in which the ambient concentration of nitrate exceeded 1.0 μM. By comparison, values less than 1 mg C/mg Chl *a* per hour have been obtained for blooms of *Gyrodinium aureolum* when levels of nitrate have been as low as 0.2 μM. With measured phytoplankton carbon : chlorophyll ratios generally between 50 and 100 and a day-length of about 14 h, these give maximum potential cell division rates in the range 1.0–0.15 day^{-1}.

Direct evidence for nitrate-limitation of phytoplankton growth in fronts has been found by Savidge (1976) and Beardall *et al.* (1978) from enrichment experiments. Although regenerated forms of dissolved nitrogen, such as ammonium and urea, are utilized by the plant cells, it is the flux of nitrate that determines overall net production (Eppley & Peterson 1980). Since the chlorophyll maxima in thermoclines and fronts generally lie in the lower part of the temperature gradient and displace the nitrate gradient accordingly (Pingree *et al.* 1977; Pingree 1978, fig. 24), it is necessary to consider mixing across the nitrate gradient rather than across the temperature gradient (Eppley *et al.* 1977). On some profiles in the Ushant front the maximum concentration of chlorophyll has been observed at a temperature only 0.2 °C above that of the bottom mixed water, and under such conditions the cells must be able to obtain nitrate (and other nutrients) more rapidly than at higher positions in the thermocline. Another important factor is the ability of dinoflagellates to migrate vertically in the water column. Although there have been no direct observations of this phenomenon in tidal fronts, average values for particulate nitrogen above the thermocline during blooms of *Gyrodinium aureolum* may exceed those of the total available combined nitrogen (about 10 μM, including organic forms) by a factor of two or more. It must be assumed, therefore, that the nitrogen content of the cells is maintained by uptake of nitrate within the thermocline followed by migration towards the surface.

In conclusion, it seems that estimates of primary production in tidal fronts will depend on a rigorous seasonal analysis of the relative distributions of chlorophyll and nitrate, together with appropriate measurements of rates of photosynthesis under varying light intensities and rates of nitrate supply to the surface waters. Regeneration is clearly important in determining the concentration of nitrate below the thermocline (in this context note the distributions of nitrite shown in figures 2, 3 and 5), in supplementing the supply of nitrogen to phytoplankton within frontal boundaries and the thermocline, and in providing the main source of utilizable nitrogen for autotrophs in surface waters above the thermocline, but overall it may be considered dependent upon and proportional to the input of nitrate by cross-frontal and vertical mixing (Eppley *et al.* 1977). Preliminary microbiological studies on fronts in the Irish Sea have provided evidence for the importance of bacteria in regeneration processes (Floodgate *et al.* 1981).

Zooplankton

Apart from the few observations of Grall *et al.* (1980) and Floodgate *et al.* (1981) there are no published reports describing a higher standing stock of zooplankton in frontal regions than in the mixed and stratified waters to either side. Data on the distribution of the major groups of zooplankton across the Ushant front in 1976 and 1977 (table 1) confirm that the highest concentrations do occur close to the front, but there is great variability between stations and no obvious relation with annual differences in phytoplankton biomass. Although no conclusions can yet be made about zooplankton production in fronts, particularly without information about growth or mortality rates, it is clear that attempts to investigate this problem will have to take into account much spatial and temporal patchiness in the distribution of individual species.

6. DISCUSSION

In this paper, the term front has been used to include persistent or recurrent discontinuities in surface temperature, which on the northwest European shelf develop in response to tidal mixing and other forms of vertical instability, and the adjacent regions with a shallow thermocline. For tidal fronts, this may be considered equivalent to the transitional region between the 1.5 and 2.0 stratification contours as defined by Pingree & Griffiths (1978), and represents about 12 % by area of the whole shelf region. No comparable estimate can yet be given for the shelf-break and coastal fronts. A second point to emphasise is that fronts appear to be relatively productive, at least in terms of the standing stock of chlorophyll, for much of the growth season between April and September

Although the physical properties of frontal systems are becoming more clearly understood, the precise ways in which the distributions and growth of planktonic organisms are affected by turbulence at different scales are still not at all clear. There is no convincing evidence that advection along frontal boundaries does lead to uncoupling of the planktonic food chain at the level of either nutrient–phytoplankton or phytoplankton–herbivore interactions. The former would be relatively easy to detect through anomalous distributions of nitrate, or other nutrients considered to limit growth of the plant cells, in stratified water. The observed concentrations of nitrate above the thermocline (generally 0.2–0.5 μM nitrate) show very great spatial uniformity at any one time, and, although their values are high compared with those for nutrient-depleted oceanic waters, they are not a measure of inorganic nitrogen levels within the cells and may just be indicative of a relatively rapid turnover of nitrogen that is being maintained by vertically migrating herbivores feeding in the subsurface chlorophyll maximum and excreting nearer the surface.

The observed variations in chlorophyll concentrations are more difficult to interpret since these are dependent on the balance between two biological processes, growth of the algal cells and grazing by the herbivores, that are both difficult to measure. However, the persistence of a high biomass of phytoplankton in frontal regions over time-scales of weeks to months, together with data to suggest that zooplankton is similarly distributed, gives support to the view that some overall balance between primary and secondary production is being attained. The wide extent and persistence of blooms of *Gyrodinium* suggests lack of grazing control, but they are not confined to the frontal boundary and instead may reflect unfavourable conditions for herbivores within the bloom rather than any direct physical effect. There is also little direct evidence that high chlorophyll concentrations in frontal regions are produced by accumulation within convergent or divergent flows – the dominant phytoplankton species have not been shown to exhibit appropriate rates of sinking or upward swimming, or to have spatial distributions that conform to such physical processes. It is possible, however, that zooplankton migrating diurnally across the thermocline could be held within frontal regions by opposing flows in the bottom and surface water.

So the general hypothesis that the combined effects of vertical mixing and surface stabilization maintain favourable nutrient and light conditions for the growth of phytoplankton in frontal regions (Pingree *et al.* 1975) still seems the most tenable. To the stratified side of the front, the mean concentration of chlorophyll in the thermocline and surface layer decreases with distance from the frontal boundary as the water column becomes more stable. This supports the concept that, under adequate illumination, the standing crop of plant cells becomes proportional to the flux of nutrients (Goldman *et al.* 1979). However, for both the surface front and subsurface thermocline, it is still not certain which physical and biological processes are most important in determining this flux.

The other main difficulty in assessing the productivity of fronts is the evaluation of information on the standing stock of organisms at each trophic level, especially when species composition is variable. For the phytoplankton, with relatively short generation times, much can be inferred from data on rates of carbon fixation and ambient levels of inorganic nutrients and light, provided phytoplankton carbon can be reliably estimated. However, cell size and morphology have profound effects on grazing processes (Steele & Frost 1978), and the proportions of diatoms, dinoflagellates and small flagellates in natural populations are very variable. Little can yet be said about secondary production without more precise knowledge of seasonal changes in zooplankton abundance in mixed, stratified and frontal waters and about the effects, direct or indirect, of hydrographic conditions on the population dynamics of individual species. Clearly, in a physically dynamic environment, rates of feeding and reproduction are critical, and so it may be most practical to investigate secondary production in fronts in terms of particular species or groups of species.

An alternative approach is to consider directly the top predators in the ecosystem (Iverson *et al.* 1979*b*). Surveys of larval fish (Harding *et al.* 1977) and fish eggs (Lockwood 1978) as well as casual observations on fishing activity along frontal boundaries indicate that these regions are important in various ways for fish. Also, the distributions of feeding seabirds have been related to the positions of tidal fronts (Bourne & Harris 1979), and sightings of cetaceans are most frequent along the shelf break (Evans 1980). However, these problems, like that of long term changes in zooplankton indicator species, require further study before the biological implications of shelf frontal systems can be fully assessed.

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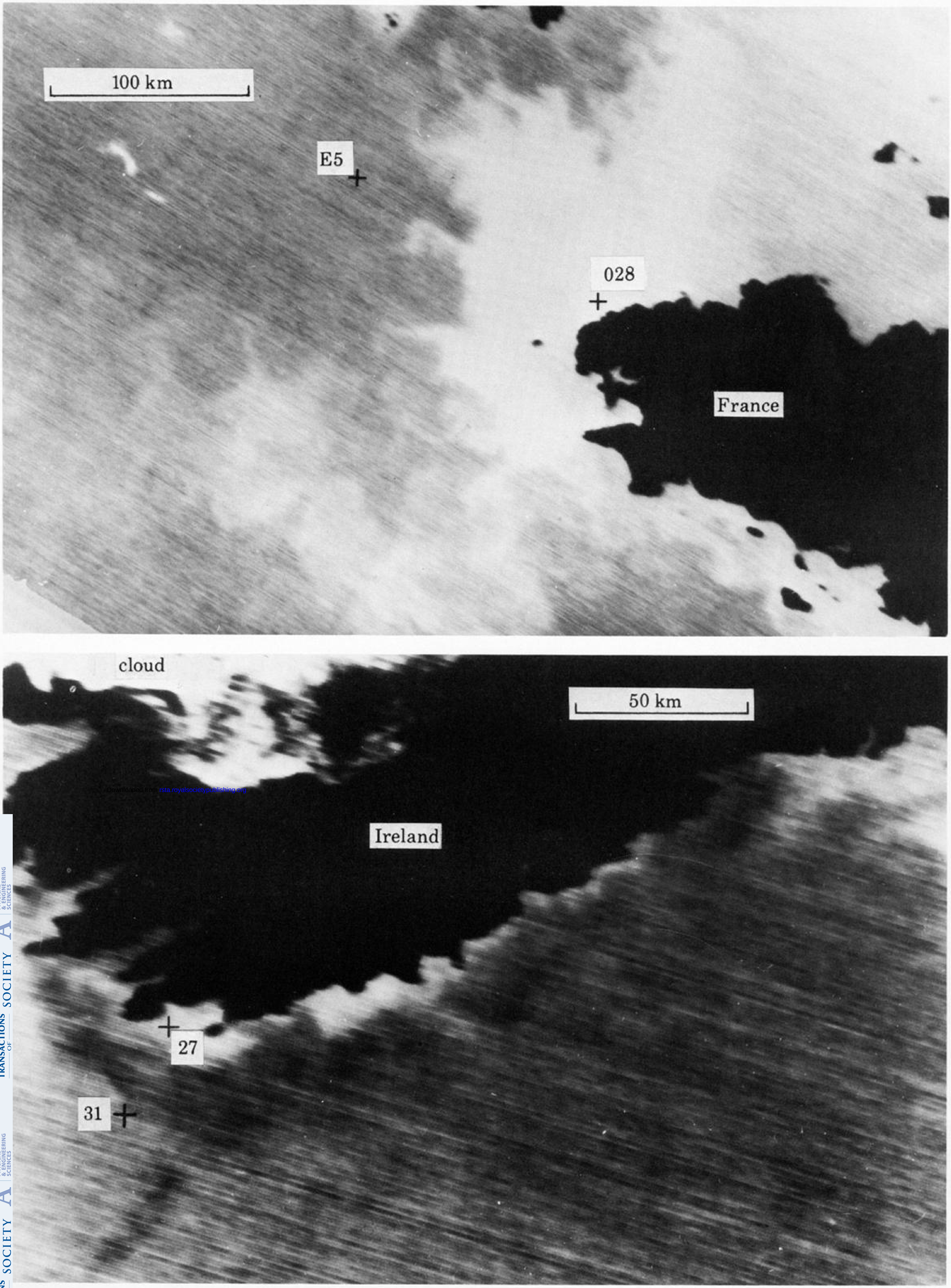

IGURE 1. Infrared images from the NOAA-5 satellite showing (*a*) tidal and shelf-break fronts in the southern Celtic Sea on 20 August 1976, and the positions of stations E5 and 028, and (*b*) coastal front along the coast of southern Ireland on 11 June 1978, and the positions of stations 31 and 27. The light areas on the satellite images indicate cooler water.