The pelagic ecosystem in frontal zones and other environments off the West coast of Brittany

Plankton
Tidal fronts
Continental shelf
Shelf-break
Atlantic Ocean East

Plancton
Fronts de marée
Plateau continental
Talus continental
Océan Atlantique Est

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ABSTRACT

A comparison is attempted between a semi enclosed bay (Rade de Brest), the vicinity of the Ushant tidal thermal front and the Celtic Sea shelf-break, with respect to phytoplankton and zooplankton overall abundance, using dissolved oxygen as a measure of *in situ* photosynthetic activity. A simple conceptual model, of a type termed agricultural, appears to be applicable to both the Rade de Brest and the shelf-break ecosystems, while the case of the Ushant front seems more complex. Different time constants in basic physical processes are tentatively put forward to account for the differences in ecosystem functional structures.

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RÉSUMÉ

L'écosystème pélagique des zones frontales et autres milieux au large de la côte Ouest de Bretagne

Une comparaison est tentée entre une baie semi-fermée (rade de Brest), les environs du front thermique de marée d'Ouessant et le talus continental de Mer Celtique, eu égard à l'abondance globale du phytoplancton et du zooplancton, en utilisant l'oxygène dissous comme témoin de la photosynthèse *in situ*. Un modèle conceptuel simple, d'un type baptisé agricole, paraît applicable à la fois à l'écosystème de la rade de Brest et à celui du talus continental, tandis que le cas du front d'Ouessant semble plus complexe. Une explication des différences dans la structure fonctionnelle des écosystèmes est proposée, en faisant appel aux caractéristiques temporelles des processus physiques fondamentaux.

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INTRODUCTION

Within a relatively short distance of the coasts of Brittany, very different types of marine environments are found, ranging from semi enclosed bays to the open ocean. Contrasting hydrological conditions in these various areas produce differences in biological processes which are not only quantitative but, in some cases, can be relevant to the functional structure of

the ecosystems, especially pelagic ones. Hydrographic differences are maximal in summer, as shown by Figure 1, which also indicates the study areas considered here. The infrared image (*a*) was recorded by the satellite HCMM (NASA) on August 25th, 1978 ; the darker tones correspond to the areas of lower surface temperature. The most conspicuous feature is the Ushant front (A), a sharp boundary between a permanently well mixed area, where temperature usually lies between
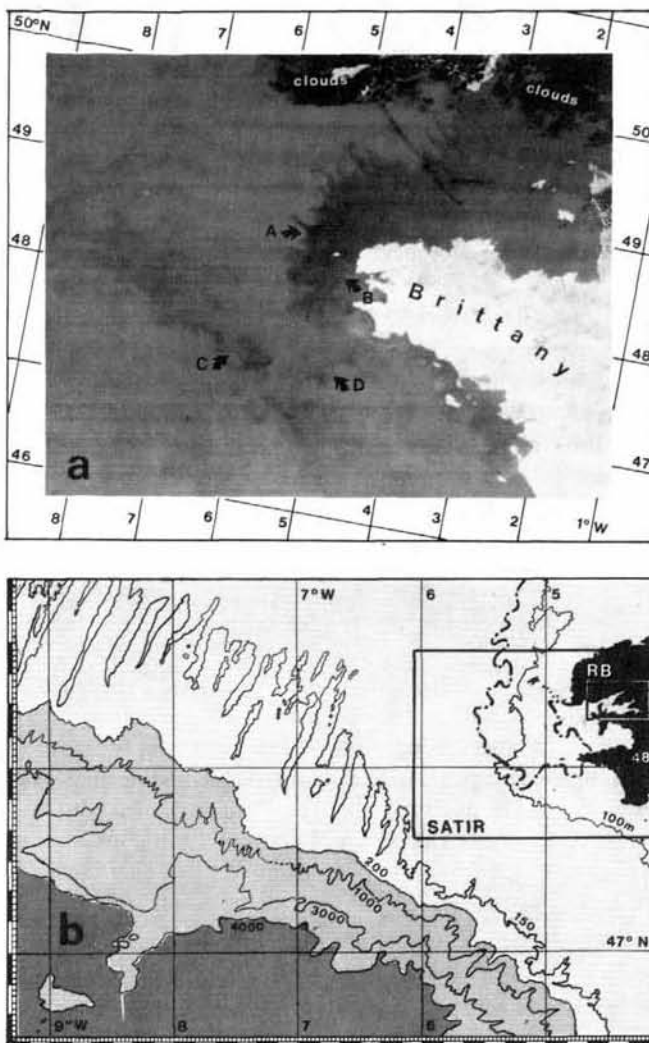
Figure 1

Study areas and hydrographic background : a) satellite infrared image showing the typical summer hydrological pattern off Brittany ; b) study areas and bottom topography. The tones of increasing darkness correspond to the continental shelf, the shelf-break and the abyssal plain. Outline of fronts (dot dashed line) recalled from another, randomly chosen, satellite image. For further details, see text.

13.0 and 14.5 °C in the whole water column, and an offshore zone where thermal stratification prevails (about 11-12 °C on the bottom, > 16 °C at the surface). Differences in water depth and strength of tidal currents account for this summer pattern over the continental shelf, as shown by many authors (*e.g.* Simpson, Hunter, 1974 ; Pingree, Griffiths, 1978). Closer to the shore, the Rade de Brest and Bay of Douarnenez make up a coastal environment of their own, the hydrographic limit of which is clearly seen on the picture (B). Along the shelf break outline, a band of relatively cool water outcrops at the surface (C), the significance of which will be considered later ; this seems to be linked with the Ushant frontal system through an area of as yet ill-defined hydrographic structure and poorly known biological significance (D).

The map (*b*) shows the areas in which we have carried out in recent years studies on three contrasting ecosystems. The sampling grid for the shelf break system

extended over most of the charted area west of 5 °W. For the Ushant front, it was restricted to the Iroise sea, enclosed in the box labelled SATIR from the place name and the use of satellite imagery. The smaller box corresponds to the Rade de Brest (RB), a semi enclosed bay. A comparison is made here between the three ecosystems, with respect to a few parameters of critical significance, in an attempt to show how different time constants in basic physical processes could account for the ecosystems' corresponding to different models.

MATERIAL AND METHODS

Chlorophyll *a* and zooplankton biomass are chosen as the biological parameters relevant here. These, however, simply describe the state of the ecosystem at the time of sampling and give no direct indication on its dynamics. Dissolved oxygen, a by-product of photosynthesis, is used to fill the gap in part. The values are expressed as percentage saturation ; supersaturation is considered indicative of *in situ* oxygen production, and therefore phytoplankton growth, which helps in interpreting chlorophyll data. Dissolved oxygen was measured, using the Winkler method, on discrete samples taken with Niskin bottles fitted with reversing thermometers. Water samples from the same bottles were filtered on GF/C filters for the assessment of phytoplankton pigments by the fluorometric method of Yentsch and Menzel (1963), using the equations of Lorenzen (1966). The results are expressed in $mg \times m^{-3}$ for seeking relationships with dissolved oxygen, and in $mg \times m^{-2}$, integrated down to the bottom in shallow areas or down to about 100 m elsewhere, for comparison with zooplankton data. Zooplankton was collected by vertical hauls of the WP2 net (UNESCO, 1968), with a mesh width of 200 µm, from near-bottom to the surface on the continental shelf, from 200 to 0 m elsewhere ; the results are expressed as total content ($mg \times m^{-2}$, dryweight) of the relevant water column. The Bravais-Pearson correlation coefficient *r* is used as an index of relationships between parameters. For chlorophyll and zooplankton, calculations were made on both raw values (arith) and logarithms (log) of data. Only the highest absolute value of *r* is given in each case, together with the indication of the corresponding type of data.

The results from the Rade de Brest were obtained from April 1978 to June 1980 at a single fixed point in the southern basin, downstream River Aulne estuary, at a position (48°18'N, 4°25'W) where marine neritic conditions usually prevail. Field trips were made at fortnightly intervals from April to September, monthly otherwise, on days when tidal amplitude was exactly average and on the neaps to springs increase. On each trip a series of stations were occupied from a moored ship at hourly intervals from low (about 9 h GMT) to high tide (15 h GMT), except on midtide, when the current was too strong. The sampling depths for the hydrological casts were 0, 10 and 15 m (bottom at 18-23 m). Data on the Ushant frontal area were obtained on a number of SATIR cruises performed mainly in summer. Results are as yet available for the 7 first ones (July

1979-August 1981), including SATIR 5 (February 1981) and 6 (May 1981), which were a first attempt to take into account seasonal variations. The data used here come from the stations arranged as a grid which were part of the programme and on which hydrological casts were made with up to 8 sampling depths. Shelf-break data considered were obtained on the first part (September 1981) of cruise ENVAT 81 organised by the French Navy (SHOM : Service Hydrographique et Océanographique de la Marine). The strategy was twofold : one ship worked a grid of stations occupied only once; another made series of measurements of about 24 h duration at 5 points along a single transect across the shelf break. In the latter case the Niskin bottles were replaced by a STD fitted with a rosette and stations including biological sampling were performed 4 to 6 times at each location; results from these have been averaged for examining phytoplankton-zooplankton relationships.

RESULTS AND DISCUSSION

The uncertainty on the model that can be applied to the ecosystem is largest in the case of the Ushant front. This structure is characterized (for a review *see* Holligan, 1981; Le Fèvre *et al.*, 1983) by the existence of high surface chlorophyll values along the front outline, extending at the thermocline level into the stratified area. Fronts have long been known for their unusual biological properties, being the most likely places of occurrence of dinoflagellate blooms. As soon as this was acknowledged, two kinds of models were put forward to account for this characteristic, one resting upon *in situ* phytoplankton growth (*e.g.* Slobodkin, 1953), the other implying passive accumulation mechanisms (for a review, *see* Rounsefell, Nelson, 1966). However, most recent work on frontal ecosystems in north-west European shelf seas rests upon what could be called an agricultural conceptual model, as examplified by the numerical model of Tett (1981) or the synthesis of Holligan (1981). In an agricultural model, production is supposed to take place where high biomass is found and to be dependent on rather simple limiting factors. The thermocline chlorophyll maximum would accordingly be explained by phytoplankton being freed at this level only from both light limitation prevailing in the deeper layer and nutrient (mainly nitrate) limitation in the upper layer. The surface frontal maximum would be explained by an input, through frontal eddies (Pingree, 1978), of nutrients from the homogeneous area, where vertical mixing would result in light limitation. High phytoplankton biomass and production would in turn be expected to support an enhanced zooplankton production, and so on along the food chain.

These assumptions imply some predictable characteristics in the ecosystem, the existence of which can be checked from field data. One of them is that high phytoplankton biomass would correspond to high levels of photosynthetic activity; a high oxygen content should therefore be found at chlorophyll maxima. Figure 2 shows examples of vertical profiles of chloro-
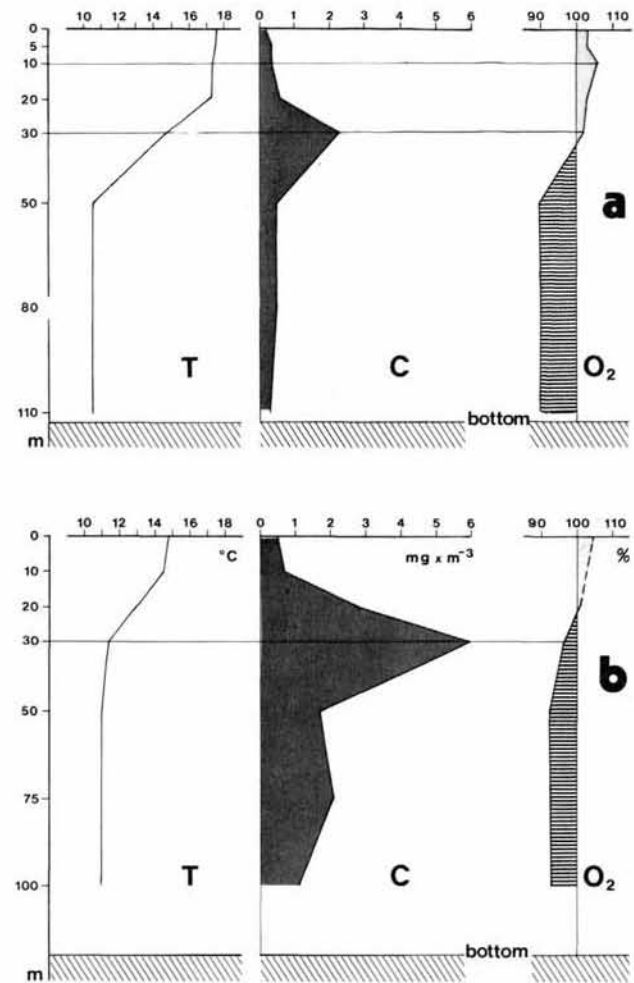
Figure 2

Vertical profiles of temperature (T), chlorophyll a (C) and dissolved oxygen (as percentage saturation) in the vicinity of the Ushant front. Numbers in ordinate are actual sampling depths. For further details, see text.

phyll *a* and oxygen from SATIR cruises matched with corresponding temperature profiles. The thermocline chlorophyll maximum is indeed observed, but not a corresponding increase in oxygen. In one case (*a* : 48°08′N, 5°40′W, 27 August 1980), the chlorophyll maximum corresponds only to a slight supersaturation, while the chlorophyll value is low at the level of maximal oxygen saturation, and therefore photosynthetic activity. In the other case (*b* : 48°08′N, 5°20′W, 12 June 1980), the chlorophyll maximum is even higher with a slight undersaturation; the level of maximal photosynthesis cannot be determined, the oxygen value being missing at 10 m. Phaeopigments values were, however, almost nil on these two instances and a number of similar ones, which would indicate a " healthy " phytoplankton population. Even if the phytoplankton is not actually very productive at the level of the chlorophyll maximum, the cells could therefore have a potential for production and resumed growth might be triggered by slight changes in environmental conditions. This could, for instance explain why some ^{14}C experiments do yield high carbon intake rates in samples from this level (Pingree *et al.*, 1976). Furthermore, when

all available data from cruises SATIR 1-7 are considered together ($n = 686$ pairs of values), a highly significant correlation between chlorophyll and oxygen is obtained ($r = 0.36$, $P < 0.01$, log). When large numbers of data are available, however, r is not a mere indication of the existence of a correlation; its value shows the extent to which the variables are correlated. This value is here fairly low, indicating that in a number of cases high phytoplankton biomass values can exist in the Ushant frontal area without a correspondingly high primary production. Mechanisms other than *in situ* growth and simple limitations (*e.g.* passive accumulation) should therefore be involved in the working of the ecosystem. Further evidence against the agricultural model is the absence of a significant overall phytoplankton-zooplankton correlation for the same set of cruises ($r = 0.18$, log, $n = 111$). Processes taken into account in the agricultural model do, however, play some part, as shown by the statistical significance of the correlation between chlorophyll and oxygen. This was higher on some individual cruises, two of which also yield a phytoplankton-zooplankton correlation.

The approach used and its significance are further illustrated by the results from the other two ecosystems. Those from the Rade de Brest are given in Figure 3 where any single point on the curve for a given parameter corresponds to the general mean for the relevant field trip. The overall impression is that of a good agreement in the variations of all three parameters, and therefore of a possible validity of the agricultural model. This is confirmed by the correlations obtained (on individual values) both between chlorophyll and oxygen ($r = 0.67$, $P < 0.01$, $n = 374$, log) and chlorophyll and zooplankton biomass ($r = 0.40$, $P < 0.01$, $n = 185$, log). An important point is that zooplankton is better correlated ($r = 0.50$, $P < 0.01$, $n = 176$, log) with oxygen saturation (average of the 3 sampling levels) than it is with chlorophyll, being indeed more dependent on phytoplankton production than biomass. At the beginning of July 1979, for instance, a situation is found where a rather low phytoplankton stock is nevertheless quite productive (high oxygen supersaturation) and supports a relatively high zooplankton stock. The results from cruise ENVAT 81 are given in Figure 4, which shows that phytoplankton and zooplankton biomasses exhibit a rather similar pattern, with a strong offshore-inshore gradient and a relative maximum along the shelf-break. The offshore-inshore gradient being irrelevant to the shelf-break ecosystem, correlations have been calculated only for those stations where the depth was at least 150 m. The chlorophyll-oxygen relationship is very strong ($r = 0.76$, $P < 0.01$, $n = 301$, arith). Phytoplankton and zooplankton also exhibit a highly significant correlation ($r = 0.63$, $P < 0.01$, $n = 23$, arith) but according to the small number of data available the correlation can only be detected, not really evaluated. The oxygen-zooplankton correlation has not been calculated; as for SATIR, a significant way of expressing oxygen saturation from a complex profile by a single figure has yet to be found.

Time constants in fertilization processes can tentatively be put forward to account for the differences observed
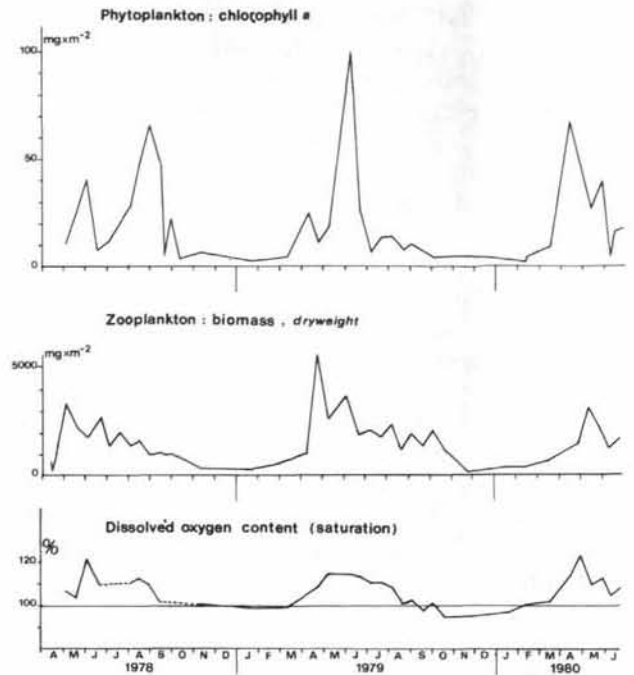

Figure 3

Variation of dissolved oxygen and plankton overall abundance at a fixed point in the Rade de Brest.
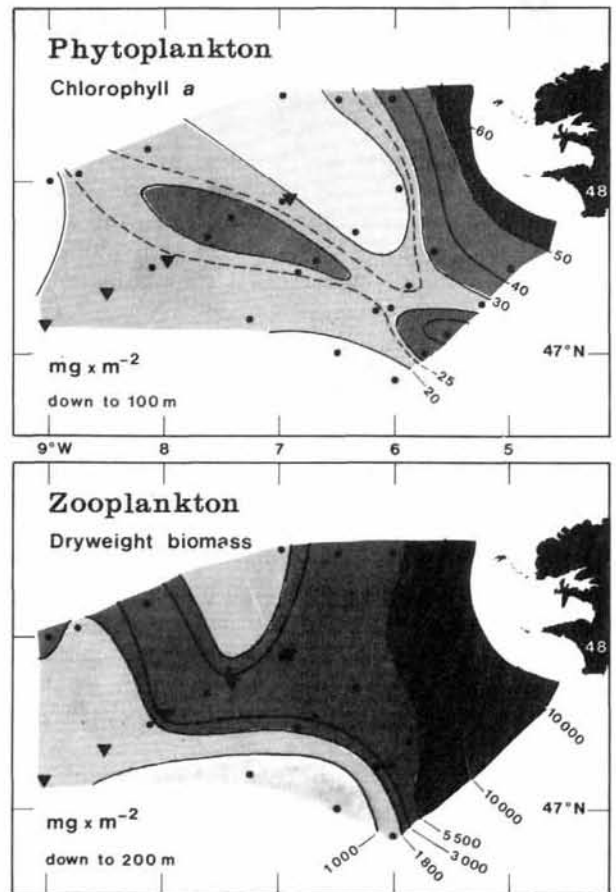

Figure 4

Geographical pattern of plankton abundance on the first part of cruise ENVAT 81 (8-15 September 1981).
Dots correspond to positions where single stations were worked (Hydrographic Vessel L'Espérance). At positions indicated by triangles, 4 to 6 stations were occupied within a 24 h time-span, the results of which are averaged (Oceanographic Vessel D'Entrecasteaux). For bathymetry, see Figure 1b.

in the ecosystems. Pingree and Mardell (1981) have reviewed and discussed the various mechanisms which can be involved in shelf-break hydrography. Recent work partly based upon cruise ENVAT 81 (Mazé, 1983 ; Le Tareau et al., 1983) has confirmed that generation of internal waves over the slope is the major phenomenon, resulting in an internal tide with a period of about 12 h and a range up to 50 m. Wind-induced vertical mixing down to considerable depths is favoured by conditions prevailing at high internal tide, hence the surface cooling. This appears to be the main fertilizing process and everything happens as if its effects were time integrated by the ecosystem. Although the basic physical mechanisms are quite different, the biological characteristics in the area turn out to be similar to those of an upwelling, a classical example of an ecosystem to which the agricultural model applies. The Rade de Brest, where fertilization mainly occurs through land runoff, also behaves as if a kind of permanent regime prevailed, with no other time constants than the annual cycle and longer term fluctuations. This, however, could be in part an effect of a sampling strategy eliminating neaps-springs variations. In the Ushant front area, the working of the ecosystem appears more complex and somewhat more puzzling. Neaps-springs adjustment has been shown to be the main factor in variation of such structures, although its extent is limited, once the front is well-established, by a feed-back mechanism (Simpson, 1981 ; Simpson, Bowers, 1981). Increase in tidal range erodes the stratification, thereby releasing nutrients from the cold bottom water mass, which could *then* be involved in cross-frontal exchanges as suggested by Pingree (1978). Further work is in progress (Le Corre et al., in prep.) on this fortnightly fertilization process, while reviewing available data (Le Fèvre et al., 1983) does show that highest chlorophyll values occur on spring tides or slightly after them. Short-lived fornightly phytoplankton blooms are therefore a distinct possibility. Passive mechanisms such as surface frontal convergence and surviving cells from the previous bloom settling on the pycnocline could account for some other observed characteristics such as the profiles on Figure 2. The apparent lack of correlation between phytoplankton and zooplankton could then be due to the usual time lag in the response of zooplankton to changes in the phytoplankton stock. Alternatively, this time lag could result in the zooplankton's being unable to benefit from a phytoplankton bloom lasting for a few days every second week. This question remains to be solved, together with the relative part that active and passive processes play in building up large phytoplankton stocks.

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