Topic 1: Production at boundary systems
PHYSICAL CONTROLS ON PHYTOPLANKTON PRODUCTION AT TIDAL FRONTS

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(Fig. 1)

The dependence of phytoplankton photosynthesis on available light is the fundamental biological process relevant to the ecology of tidal fronts. The leading physical process is vertical mixing, through its control on the supply of nutrients essential for growth and on the irradiance experienced by phytoplankton cells. These two processes comprise a simple explanation for enhanced primary production in the vicinity of fronts. Increased understanding can be obtained, for example, from further consideration of the possible mechanisms of nutrient supply. Estimates are made here of the cross-frontal nutrient transfer at the Ushant and Georges Bank fronts, the hypothesis of nutrient complementarity is discussed, and suggestions are made for future research.

INTRODUCTION

In modern biological oceanography, considerable weight is given to the evaluation of the various physical processes that influence the environment in which the organisms live. Progress in understanding the primary productivity at tidal fronts is one of the best examples of the value of combining physical oceanographic and biological oceanographic insights in the study of a problem in marine ecology. Nowhere can be seen with more clarity the degree and variety of physical control on the biological dynamics in the pelagic zone.

In this paper we review first the dependence of photosynthesis on available light and discuss the significance of vertical mixing for the phytoplankton, leading to the conventional explanation for the enhancement of primary productivity at tidal fronts. We then discuss various nutrient supply mechanisms proposed to support such an enhanced production, and estimate their relative importance for the Ushant and Georges Bank fronts in summer. Next we discuss some complications in the phytoplankton physiology and in the physical setting, that lead one to suppose that the conventional model might be an oversimplification. Finally, we point out the difficulties that arise in the application of such an oversimplified picture to a real example and offer some suggestions for further work.
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Review

Relationship between photosynthesis and light

The fundamental biological process that is relevant to productivity in the vicinity of ocean fronts is the dependence of phytoplankton photosynthesis on available light. Once a particular equation has been chosen to describe this relationship (Jassby & Platt, 1976), its parameters can be used to characterise the phytoplankton assemblages in and on either side of the front (Harrison & Platt, 1980; Côté & Platt, 1983) and can usually be interpreted to yield information about the physiology of the phytoplankton (Gallegos & Platt, 1982; Fasham & Platt, 1983; Smith, Platt & Harrison, 1983).

The most important feature of the photosynthesis-light relationship (the light saturation curve) is its nonlinearity. Although it is quasi-linear at relatively low light levels, photosynthesis is depressed through the phenomenon of photo-inhibition at higher intensities. The particular choice of an equation to represent this relationship is of relatively minor importance to the understanding of biological dynamics at fronts (see, e.g. Platt, Denman & Jassby, 1977). The main features of the biology could be revealed, for didactic purposes, through any equation provided that its parameters have a definite physiological interpretation, and it is as well to select one whose mathematics is simple to manipulate.

The light-saturation parameters vary between species and according to environmental conditions (Côté & Platt, 1983), of which the most significant for this discussion is the recent light regime to which the cells have been exposed (Gallegos et al. 1983). The word ‘recent’ is being used to refer to shorter time-scales as our understanding of photoadaptation progresses (Falkowski, 1983; Lewis, Cullen & Platt, 1984).

The fact that available light is an exponentially decreasing function of depth below the sea surface is of crucial importance for understanding what happens to phytoplankton populations at fronts. It means, for example, that the irradiance scale in the light-saturation curve can, in principle, be transformed into a depth scale. The transformation will not be a simple logarithmic one, however, unless the phytoplankton are uniformly distributed with depth and the photosynthesis parameters do not vary with depth. These conditions are not always met (e.g. Cullen, 1982). Because phytoplankton pigments are the dominant component of variability in optical attenuation in the sea (Jerlov, 1976), the vertical distribution of phytoplankton is of profound significance for the shape of the underwater light field.

Effect of vertical mixing

Any physical process that leads to vertical water motions, either fluctuating or steady, will result in the phytoplankton being moved vertically along the irradiance gradient. A cell that is subjected to variations in its vertical position will be subject to corresponding irradiance variations. The range of time scales of vertical motion in the upper ocean has been described by Denman & Gargett
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(1983). The biological yardstick against which these scales should be compared is the time scale for the division of phytoplankton cells.

In coastal waters, one of the primary sources of turbulence is the friction of the sea floor against tidal currents. Because the strength of this turbulence decreases away from the sea floor, its effect in the euphotic zone is, in general, greatest in shallow water. Of course, for a given water depth, the effect is usually stronger where tidal currents are stronger. One might portion the coastal zone into a region where the depth is shallow enough and/or the tidal currents strong enough for tidally-generated turbulence (and turbulence of other origins) to overcome any tendency for density stratification in the euphotic zone, such as that associated with surface heating, and a region where this is not true. The boundary between such regions is commonly referred to as a tidal front.

The summertime position of such fronts on the northwest European shelf, in the Gulf of Maine and elsewhere has been observed to agree reasonably well with the predictions of a semi-empirical theory that quantifies the influences of depth and tidal current strength (Simpson & Hunter, 1974; Garrett, Keeley & Greenberg, 1978; Pingree, 1978a). On the premise that only a fixed fraction of the dissipated tidal energy is available for mixing buoyant water downwards, this theory predicts that tidal fronts should lie along a particular contour of the parameter $h/u^3$ (where $h$ is the water depth and $u$ is the tidal current amplitude), with its value depending on the surface heating rate and other factors. This criterion provides a parameterization of tidal fronts that is useful in discussions of both the physical oceanography and the primary production of the frontal region.

Although the term ‘tidal front’ and the $h/u^3$ criterion are used in the following discussion of some specific fronts, some uncertainty remains about the exact role of tidally-generated turbulence in the maintenance of these fronts and about the most appropriate criterion for their position. For example, the results of Simpson, Allen & Morris (1978) and Loder & Greenberg (1985) indicate that wind mixing also makes a significant contribution to vertical mixing on the northwest European shelf and in the Gulf of Maine, and Soulsby (1983), Loder & Greenberg (1985) and T. Maxworthy (unpublished) have suggested that other criteria may also account for the observed frontal positions.

**Concept of critical depth**

The significance of vertical turbulence for phytoplankton dynamics was first recognised by Gran & Braarud (1935) in trying to understand their field data on the phytoplankton of the Gulf of Maine and the Bay of Fundy. They realised that net phytoplankton production is the resultant of the opposing processes of photosynthesis and respiration and that if vertical mixing kept the cells away from the illuminated zone for an appreciable fraction of the day, water column respiration could exceed photosynthesis, i.e. net production would be negative.

These ideas were formalised by Sverdrup (1953) in his critical-depth theory
for the onset of the spring phytoplankton bloom. He realised that, in some way, the development of the spring bloom is related to the existence of the incipient thermocline and the associated pycnocline. If the surface mixed layer is deeper than a certain ‘critical depth’, phytoplankton cells spend such a high proportion of their time at light levels below their compensation point (where photosynthesis just balances respiration) that there is no net increase of phytoplankton biomass in the mixed layer. On the other hand, as the thermocline forms, those phytoplankton cells confined to the stable surface layer spend most or all of their day at light levels above their compensation point. In this layer, then, net production is positive and phytoplankton biomass accumulates: a bloom occurs.

More recently, these ideas have been recast by Pingree (1978a) and Pingree, Holligan & Mardell (1978) in a diagram where coastal stations are plotted in a plane for which one dimension is the critical depth (scaled to the optical attenuation length) and the other the parameter $h/\mu^3$. This diagram is useful as the basis for a comparative anatomy of tidal fronts in different parts of the world.

Conventional explanation for the enhanced summertime phytoplankton biomass at tidal fronts

The critical depth model for the origin of the spring bloom will be a satisfactory description of production only as long as the supply of inorganic nutrients in the surface layer is not exhausted. Once a stable surface layer forms, however, accelerated growth by blooming phytoplankton will lead to a depletion of nutrients in the layer. One therefore expects that, on the stratified side of a tidal front, in very general terms, photosynthesis will be nutrient-limited (i.e. limited by the rate of nutrient regeneration by microheterotrophs), but light-sufficient.

On the other hand, photosynthesis on the mixed side of a tidal front is likely to be light-limited but nutrient-sufficient, although this is dependent on the water depth. For example, at the Ushant tidal front in water of about 100 m depth off the north-west coast of France, observations (e.g. Pingree, Holligan & Head, 1977; Holligan, 1981) indicate that the highest phytoplankton concentrations are in the frontal zone, while over Georges Bank, a shallower region off the eastern North American coast, there are suggestions of high primary production and phytoplankton concentrations in both the frontal zone surrounding the Bank and the vertically well-mixed water over the Bank (Cohen et al. 1982; Flagg et al. 1982; O’Reilly & Busch, 1984). In Pingree et al.’s (1978) classification of tidal fronts according to depth and inorganic nutrient distribution, the Ushant front can be considered to be a deep-water tidal front whilst that around Georges Bank appears to be an intermediate front of the mixing/upwelling type.

The conventional explanation for the enhanced phytoplankton populations found at deep-water tidal fronts is that nutrients are supplied either by horizontal mixing from the mixed side or by vertical mixing through the pycnocline such that phytoplankton growth in the frontal zone is limited by neither light nor nutrients (e.g. Pingree, 1978a; Holligan, 1981). This is a plausible model, and will serve as a convenient picture to guide the following discussion.
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Mechanisms of nutrient supply

Introduction

There are a number of physical mechanisms by which scalar properties such as inorganic nutrients can be supplied to the frontal zone or transferred across tidal fronts (Garrett & Loder, 1981). The mechanisms that are expected to dominate are illustrated schematically in Fig. 1. For the Ushant front, it has been suggested (Pingree et al. 1975; Pingree, 1978b) that the fortnightly variation in the extent of the stratified region due to the spring-neap cycle in tidal mixing and the development of baroclinic eddies on the frontal boundary play significant roles in the summertime supply of nutrients from the light-limited, mixed side to phytoplankton in the frontal zone. In addition, there are observations (Holligan et al. 1984) of substantial primary production associated with the supply of nutrients at the base of the thermocline in the extension of the Ushant front in the western English Channel.

To provide a conceptual framework for evaluating the relative importance of nutrient supply associated with the spring-neap cycle, baroclinic eddies and vertical diffusion through the pycnocline in deep-water tidal fronts, we complement the following discussion with estimates of the rate of supply of nitrate (per unit length of front) to the near-surface region on the Ushant front’s stratified side, using simple physical models and parameterizations.

In a later subsection, we estimate the rate of supply of nitrate from the stratified side of the tidal front surrounding Georges Bank to the Bank’s mixed area, as an illustration of nutrient supply across an intermediate tidal front.
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Spring-neap tidal cycle

If the position of a coastal front is controlled by the strength of tidal currents, it should adjust in response to variations in the currents during the fortnightly and monthly modulation cycles (e.g. Simpson & Bowers, 1981). As the tidal currents weaken, stratification should extend further into the mixed region capturing, in the fortnightly or monthly period $T_M$, the inorganic nutrients contained in the volume described by the pycnocline depth $D$ and the front’s excursion $L_M$. Nutrients are then supplied to the frontal zone at an average rate per unit length of front of

$$Q_M = \frac{(L_M/T_M)}{D} C,$$

where $C$ is the nutrient concentration (e.g. nitrate) on the mixed side. For the Ushant front, the fortnightly cycle should be dominant although the average excursion is not precisely known. But, using Simpson & Bowers’ (1981) typical value for north-west European shelf fronts of $L_M \approx 4 \text{ km}$, and observed values of $D \approx 20 \text{ m}$ and $C \approx 2 \text{ mg at m}^{-3}$ for the Ushant front (Pingree et al. 1977; Pingree, 1979; Holligan, 1981) the average rate of supply of nitrate to the frontal zone is estimated to be $Q_M \approx 0.12 \text{ mg at m}^{-1} \text{ s}^{-1}$.

On this rationalisation of the existence of enhanced photosynthesis at tidal fronts, the width of the zone of higher productivity should be commensurate with the fortnightly or monthly excursion of the front; the rate of production for populations within this zone should vary on a time scale of two weeks or one month as the captured nutrients are depleted; and the potential new primary production that could be ascribed to this mechanism could be estimated from the quantity of nutrients captured each cycle.

Baroclinic eddies

It is apparent from the surface signature of tidal fronts seen in satellite infrared imagery that the fronts are generally not smooth and stationary, but rather have wave-like instabilities with typical wavelengths between 20 and 40 km (e.g. Pingree, 1979). These are believed to be part of the process of baroclinic instability through which the potential energy associated with the differential stratification across the front is released. The instabilities often grow into baroclinic eddies which detach from the front and provide a mechanism of intermittent cross-frontal exchange, such as for mixed water and the inorganic nutrients therein, to the light-sufficient surface waters in the frontal zone.

Two approaches can be taken in estimating the rate of cross-frontal transfer of a scalar property by baroclinic eddies. Pingree (1979) used a semi-empirical formula developed by Green (1970) for poleward heat transport by baroclinic eddies in the atmosphere to estimate the heat transfer across the tidal fronts in the Celtic Sea. For any scalar property (such as nitrate) with a cross-frontal concentration difference $\Delta C$, this formula can be written as

$$Q_E = \frac{\gamma (g \Delta \rho D / \rho)^{1/3}}{D} D \Delta C,$$

(2)
where $g$ is the gravitational acceleration, $\rho$ is a typical density, $\Delta \rho$ is the difference in surface density across the front and $\gamma$ is a dimensionless constant found by Green (1970) to have the value $0.0055$ (although laboratory experiments by Griffiths & Hopfinger (1984) in a two-layer fluid indicate that its value may be as much as an order of magnitude larger). Taking the values of $\Delta \rho/\rho \approx 6.7 \times 10^{-4}$, $\Delta C \approx 2$ mg at $m^{-3}$ and $\gamma = 0.0055$ as typical of the Ushant front (Pingree et al. 1975, 1977; Holligan, 1981), the average rate of supply of nitrate by baroclinic eddies per unit length of front is estimated to be $Q_E \approx 0.08$ mg at $m^{-1} \ s^{-1}$.

The rate of cross-frontal transfer by baroclinic eddies can also be estimated by considering the eddies to be cylinders of water and estimating the volume, scalar concentration and frequency of exchange of the cylinders (Garrett & Loder, 1981). Assuming that the cylinders have (the pycnocline) depth $D$ and radius $4L_R$, where $L_R \approx (g \Delta \rho D/\rho f^2)$ is the internal Rossby radius of deformation and $f$ is the Coriolis parameter, and that two cylinders (one from each side) are exchanged across each $16L_R$ (i.e. 4 cylinder radii) of along-frontal distance during a time interval $T_E$, the rate of cross-frontal transfer by baroclinic eddies per unit length of front can be estimated as

$$Q_E = \pi (L_R/T_E) D \Delta C.$$

Using Pingree's (1979) value of $L_R \approx 3.3$ km and the previous values of the other parameters for the Ushant front, the estimate of $Q_E$ obtained from (2) implies a value of 60 days for $T_E$. This time scale reflects the spatial and temporal intermittency of the eddy formation process. However, the value estimated above is much longer than the expected and observed eddy development time scale of a few days (Pingree, 1979; James, 1984), which may indicate that the value assumed for $\gamma$ is too low for the Ushant front.

The Ushant front: significance of various mechanisms

Using the above estimates, we now proceed to assess the relative importance of nitrate supply to the Ushant front by the spring-neap mixing cycle and baroclinic eddies and by other physical processes. Associated with the horizontal density gradients across the front, there should be a residual frontal circulation. Typically, the residual currents in a tidal front are primarily along the front and hence along isolines of various inorganic nutrients (e.g. James, 1978; Simpson, 1981), but a weak cross-frontal circulation induced by internal friction is also expected (James, 1978) and may play a significant role in cross-frontal exchange (Garrett & Loder, 1981). However, using values of density and friction representative of the Ushant front in Garrett & Loder's (1981) formulae for the cross-frontal flux in the surface Ekman layer and for the cross-frontal flow at the base of this layer, a nitrate flux and a flow speed of less than $0.01$ mg at $m^{-1} \ s^{-1}$ and $0.04$ cm $s^{-1}$ respectively are predicted. This nitrate flux is much smaller than that estimated for the spring-neap cycle and baroclinic eddies, so that the residual circulation induced by internal friction appears to be of minor significance to the Ushant front's nutrient supply.
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The discussion of nutrient supply to the near-surface region on the stratified side of the Ushant front has so far focused on horizontal transfer from the mixed side. But the highest concentrations of nitrate and silicate in the Ushant region are at depth on the stratified side. The rate of supply of such scalars to the near-surface region by vertical mixing can be estimated from

\[ Q_v = K_v (\Delta C/\Delta z) L_w, \]

where \( K_v \) and \( \Delta C/\Delta z \) are the vertical eddy diffusivity and the vertical concentration gradient respectively in the frontal zone’s pycnocline, and \( L_w \) is the width of the zone in which there is significant transfer. This estimate is highly dependent on the rather uncertain value of \( K_v \), but, as a first estimate, we use the value \( K_v \approx 10^{-4} \text{ m}^2 \text{ s}^{-1} \) obtained by Pingree & Pennycuick (1975) in a study of vertical transfer through the thermocline at Station B1 in the English Channel where the water column has a similar hydrographic structure to that in the Ushant frontal zone. Then, taking \( \Delta C/\Delta z \approx 2 \text{ mg at m}^{-3}/10 \text{ m} \) as representative of a 10 km wide zone in the Ushant front, the rate of vertical transfer of nitrate per unit length of front is estimated as \( Q_v \approx 0.2 \text{ mg at m}^{-1} \text{ s}^{-1} \). The implicit assumptions in this choice of \( L_w \) are that towards the mixed side, where there is increased vertical mixing, there is little vertical gradient in nitrate concentration; and towards the stratified side, where there is a higher vertical nitrate gradient, the vertical mixing is substantially reduced.

The above estimates of the rate of physical supply of external nitrate to the near-surface region in the frontal zone, where increased phytoplankton abundance is observed, are crude but they suggest that the spring-neap cycle, baroclinic eddies and vertical mixing may all be contributing significantly to a total supply rate per unit length of front of about \( 0.4 \text{ mg at N m}^{-1} \text{ s}^{-1} \). Assuming that nitrogen and carbon were utilized in photosynthesis in accordance with the Redfield ratio, this external nitrate supply could support carbon fixation at a rate per unit length of front of about \( 2.8 \times 10^3 \text{ g C m}^{-1} \text{ d}^{-1} \), or at an average rate of about \( 0.28 \text{ g C m}^{-2} \text{ d}^{-1} \) in a 10 km wide frontal zone.

It should be added that, although the transfer mechanisms discussed here may play critical roles in the nutrient supply process, they generally cannot account for the total chain of events in the supply of nutrients from their source to the small scales on which utilization occurs. In addition to the important role of small-scale turbulence discussed later in this review, the spring-neap cycle supply mechanism requires that nutrients be resupplied to the front’s expanded mixed side during spring tides, the baroclinic eddy mechanism requires that nutrients be continually available on the mixed side, and the vertical transfer mechanism requires a continual source of nutrients below the pycnocline in the frontal zone.

Cross-frontal transfer of nitrate on Georges Bank

Recent observations (Cohen et al. 1982; O’Reilly & Busch, 1984) indicate that the high rate of primary production of 1–2 g C m\(^{-2}\) d\(^{-1}\) is maintained over Georges Bank throughout the summer. This high productivity is generally
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attributed to enhanced nutrient regeneration in the shallow, vertically well-mixed waters over the central Bank, and the ready supply of new nutrients from the deeper waters surrounding the Bank (Cohen et al. 1982; Riley, 1982; Yentsch, 1984). The external supply of nutrients to Georges Bank can be envisaged to consist of two stages: the transfer across the side of the Bank including that across the summertime tidal front, and the subsequent distribution within the mixed region over the Bank. The latter stage has been examined by Loder et al. (1982) who inferred a horizontal dispersion coefficient of 150–380 m² s⁻¹ from a heat budget for the central Bank in summer, and estimated that roughly 20–40% of the nitrogen demand by the observed primary production within a 45-km radius of the Bank’s centre could be accounted for by this dispersion rate acting on the observed nitrate distribution. To complement Loder et al.’s (1982) study and present an example of how a tidal front may influence the primary production of a neighbouring mixed region, we now estimate the summertime rate of cross-frontal transfer of nitrate on the sides of Georges Bank.

With the crude assumptions that the transfer rate is uniform at all positions around the Bank and that the vertical profile of nitrate in the front is linear, increasing from zero at the sea surface to 4 mg at m⁻³ at the seafloor roughly consistent with Pastuszak, Wright & Patanjio’s (1982) observations, we consider the rate of cross-frontal transfer across the Bank’s 60-m isobath. This external nitrogen supply can then be compared with the total nitrogen demand of the mixed region which, at a primary production rate of 2 g C m⁻² d⁻¹ over the 1.4 × 10⁶ km² area inside the 60 m isobath (Hopkins & Garfield, 1981), is about 3.9 × 10⁶ mg at N s⁻¹.

A variation in the position of the Georges Bank tidal front associated with the fortnightly or monthly modulation cycle has not been reported, but such a variation seems likely considering north-west European shelf observations and Loder & Greenberg’s (1985) predictions. Taking L_M ≈ 5 km as a tentative value for the monthly excursion, which should be larger than the fortnightly excursion around Georges Bank, replacing the pycnocline depth D in (1) by the water depth h = 60 m and using C ≈ 2 mg at m⁻³, the average rate of supply of nitrate to the mixed region associated with its expansion during each monthly cycle is estimated as Q_M ≈ 0.26 mg at m⁻¹ s⁻¹ per unit length of front, yielding a net supply rate of 1.1 × 10⁵ mg at N s⁻¹. Thus, the monthly mixing cycle supply mechanism may account for about 2.7% of the nitrogen demand on Georges Bank, and a second, probably smaller, contribution may be associated with the fortnightly cycle.

The significance of baroclinic eddies to the nitrate supply on Georges Bank is dependent on their uncertain vertical extent. Assuming that the eddies are confined above the pycnocline of depth D ≈ 20 m and that the value γ = 0.01 is more appropriate to Georges Bank (Csanady, 1985), and taking Δρ/ρ ≈ 10⁻³ and ΔC ≈ 0.67 mg at m⁻³ as representative of summer, the rate of supply of nitrate to the mixed region is estimated from (2) as Q_E ≈ 0.06 mg at m⁻¹ s⁻¹ per unit length of front with a net supply rate of 0.2 × 10⁵ mg at N s⁻¹. This estimate is consistent with the observed value of L_E ≈ 4.4 km and an eddy time interval of