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Dynamics of the decline of a phytoplankton bloom after an upwelling event

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ABSTRACT: Changes in biochemical composition and ^{14}C-bicarbonate assimilation into photosynthetic products were measured during a phytoplankton bloom in the southern Benguela upwelling region. In the decline phase nitrate levels were < 1 mg at m^{-3} in the upper mixed layer, chlorophyll *a* and protein concentrations decreased and a large proportion of assimilated carbon was detected in the ethanol-soluble fraction at the 50 % light level. As the cells sank out of the mixed layer, chlorophyll *a* and protein concentrations increased in the stable and bottom layers. Although the photosynthetic rate was slower in these layers, increased protein/glucan ratios and the large proportion of carbon incorporated into protein at the 10 and 1 % light levels indicated that the cells in the community were still viable under these conditions.

INTRODUCTION

In the southern Benguela region active upwelling is induced by southerly to south-easterly winds which occur frequently in summer. Large areas of cool water are brought to the surface in plume formations and dense blooms of phytoplankton develop in this water as it moves off-shore and northwards (Andrews and Hutchings, 1980). The growth of these blooms can be rapid; in December 1979 a diatom bloom reached its peak in 3 d (Barlow, 1982c). Chlorophyll *a* concentrations increased by 19.2 mg m^{-3} in the euphotic zone and the highest concentration of protein was measured just prior to peak of the bloom. Carbohydrate concentrations varied briefly, increasing rapidly during the day and decreasing at night. The pattern of carbon assimilation at the 50 % light level was characterized by high activity in the polysaccharide fraction as the bloom developed, but at the peak of the bloom a greater percentage of the label was detected in the ethanol-soluble fraction as the community entered a stationary phase of growth.

The study described above terminated soon after the bloom had reached its peak and only the development phase was investigated. A similar study in December 1980 presented an opportunity for monitoring a declining phase. The phytoplankton community was already in a rapid phase of development at the commencement of the cruise and this was monitored for approximately 36 h until the bloom reached its peak. It was then possible to follow the decline over the next 5 d.

METHODS

A 2 m biplanar tetrahedral drogue, set at a depth of 10 m, was released in a patch of water whose surface temperature was between 11 and 12 °C. The drogue was tracked for 7 d and sampling was conducted at approximately 0800, 1300 and 1900 each day. Initially, the decrease in light intensity down the water column (using a Lambda quantum meter) and temperature were measured. Samples were then drawn from 5 depths in the euphotic zone (1 % light level) and 5 depths below the euphotic zone to 100 m, for analysis of nutrients, species composition, chlorophyll *a*, protein and carbohydrate. Triplicate samples were drawn from depths corresponding to the 50, 10 and 1 % light levels for incubation with ^{14}C-bicarbonate in simulated *in situ* experiments. Procedures for determining nutrients, species and biochemical composition have been outlined by Barlow (1982a, c). Labelling experiments were conducted for 4 h in the morning and 4 h in the afternoon and the differential extraction of filters yielded 3 fractions (Barlow, 1982b, c).

RESULTS

The drogue moved in a northerly direction along the coast (Fig. 1); details of wind regime and hydrography of the parcel of water have been described by Hutchings et al. (in prep.). Fig. 2 shows the spatial distribution of temperature along the course of the drogue. The

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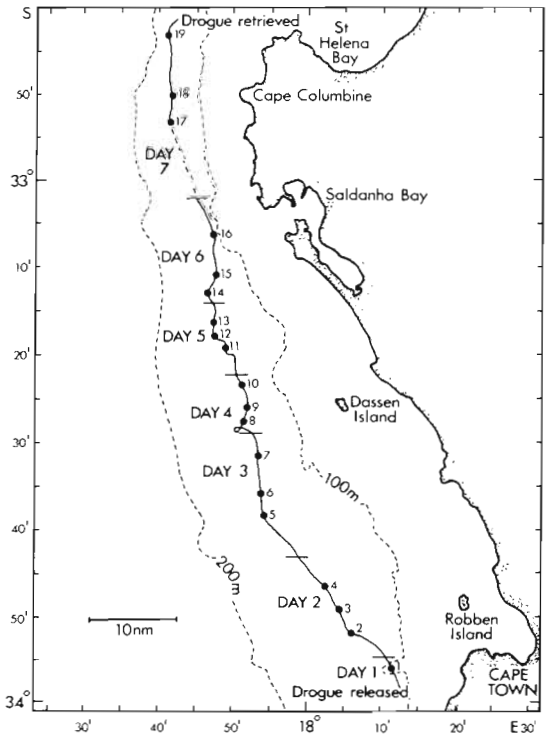

Fig. 1. Course of drogue during 3 to 9 December 1980 and positions of stations (see also Hutchings et al., in prep.)

diatom *Nitzschia seriata* Cleve dominated the bloom and other diatoms (*Rhizosolenia* sp., *Leptocylindrus* sp., *Thalassiosira* sp., *Chaetoceros* sp.) were present in fewer numbers.

The structure of the water along the course of the drogue was determined from temperature, nutrient and chlorophyll *a* concentrations down the water column (Fig. 3a). The upper mixed layer was defined by uniform depth profiles of temperature and nitrate concentration, whilst the stable layer in the region of the thermocline was defined by rapidly decreasing temperatures and increasing nitrate concentrations. The bottom layer had slower decreasing temperatures and high nitrate concentrations. A depth of 40 m was arbitrarily chosen as the lower limit of the upper bottom layer since low chlorophyll *a* concentrations were recorded below this depth (Brown et al., in prep.).

Biochemical composition

A rapid increase in the mean concentration of chlorophyll *a* in the upper mixed layer was observed from 2000 on Day 1 to 0900 on Day 3 (Fig. 4b) (Brown et al., in prep.). During this period there was a concomitant decrease in the mean nitrate concentration to a level < 1 mg at m^{-3} (Fig. 4a). Nitrate concentrations remained below 1 mg at m^{-3} in this layer for Days 3 to 7 and chlorophyll *a* concentrations decreased steadily from 18 mg m^{-3} to levels between 1 and 2 mg m^{-3}. Silicate and phosphate concentrations also decreased as the chlorophyll *a* concentrations increased but did not decrease to < 0.5 mg at m^{-3} for phosphates or < 1 mg at m^{-3} for silicates in the upper mixed layer.

In the stable layer chlorophyll *a* concentrations were similar to those in the upper mixed layer between midday on Day 3 and midday on Day 4, but were greater thereafter. In the upper bottom layer chlorophyll *a* concentrations were lower than in the upper layers during Days 3 to 6, while the highest concentrations of pigment in this layer were measured on Day 7 (Fig. 4b). Nitrate concentrations were always > 2 mg at m^{-3} in the stable and bottom layers (Fig. 4a).

Protein exhibited a similar variation in concentration in all the layers (Fig. 5a), indicating a close correlation between chlorophyll *a* and protein during the development and decline of the bloom. Carbohydrate concentrations (Fig. 5b, c) in the upper mixed layer varied in a

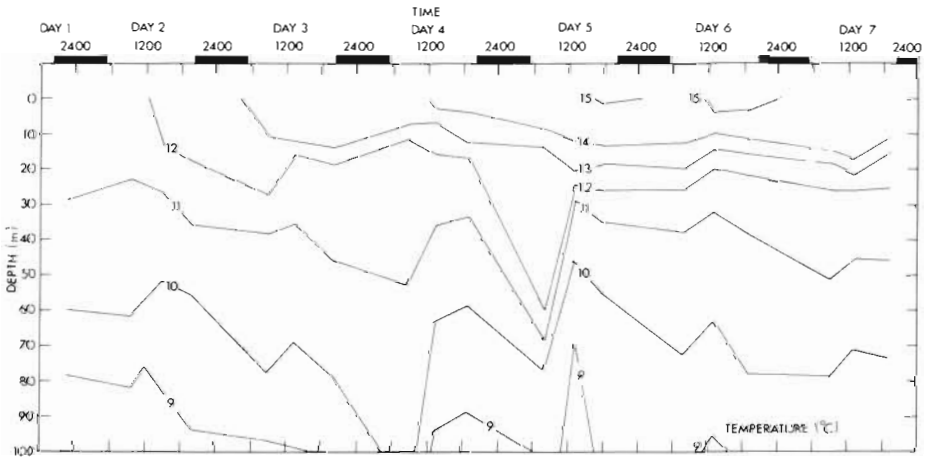

Fig. 2. Spatial distribution of temperature along the course of the drogue. Black bars: dark period (Brown et al., in prep.)

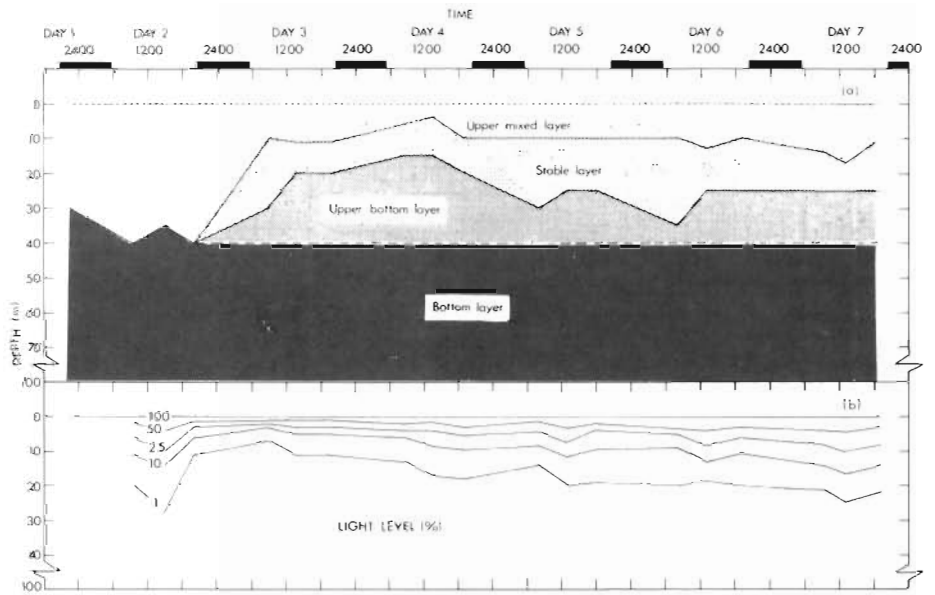

Fig. 3. Structure of the water (a), and light penetration (b), along the course of the drogue (Brown et al., in prep.)

diel pattern, generally increasing during the day and decreasing at night. Acid-soluble carbohydrate (glucan) is the main energy reserve in diatoms (Myklestad, 1978) and the diel changes in this fraction accounted for most of the variation in total carbohydrate concentration. In the stable and bottom layers carbohydrate concentrations did not vary in a distinct diel pattern and concentrations were greater in the upper mixed layer than in the lower layers.

To illustrate the difference in cellular composition of the community between the various layers protein/glucan ratios are presented in Fig. 5d. It may be observed that the ratio is > 1 in the upper mixed layer during Days 2 and 3 and < 1 for Days 4 to 7. Initially, the ratios in the stable and upper bottom layers on Days 2 and 3 were lower than in the upper mixed layer, but from noon on Day 4 to Day 7 they were greater. Ratios in the upper bottom layer were generally greater than in the stable layer for Days 4 to 7.

Labelling patterns

There was generally a greater incorporation of ^{14}C into ethanol-soluble compounds and polysaccharides than into protein at the 50 % light level (Fig. 6a). The amount of carbon fixed in protein was 0.8 mg C mg Chl a^{-1} h^{-1} on Day 2, but this declined to 0.35 to 0.6 mg C mg Chl a^{-1} h^{-1} on Days 3 and 4. During Days 5 to 7 the incorporation was between 0.5 and 1.0 mg C mg Chl

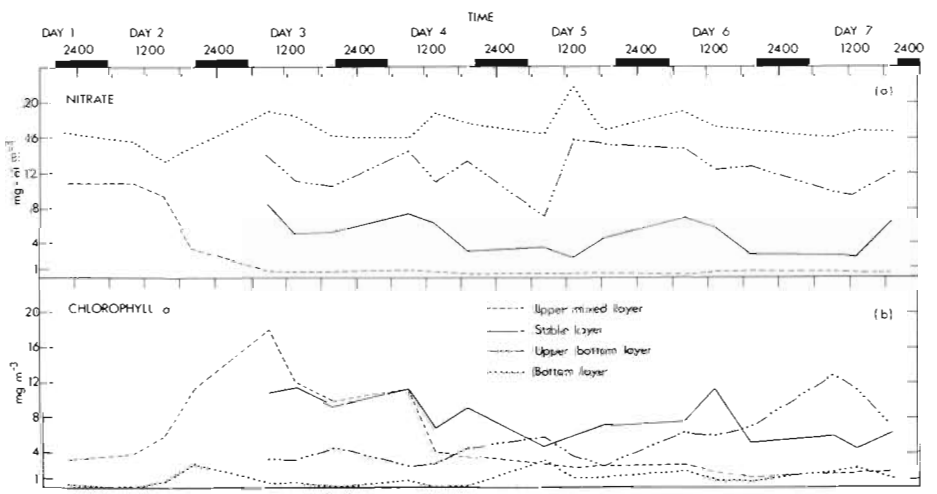

Fig. 4. Mean concentrations of nitrate (a), and chlorophyll *a* (b), integrated over the depth of each layer shown in Fig. 3a (Brown et al., in prep.)

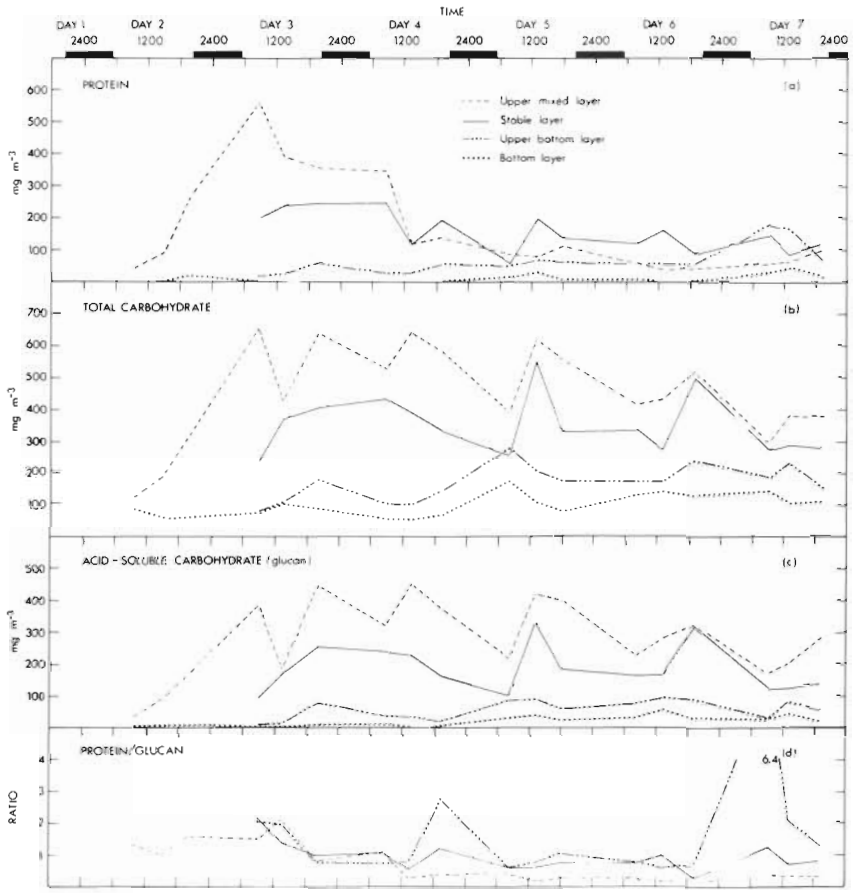

Fig. 5. Mean concentrations of protein (a), total carbohydrate (b), acid-soluble carbohydrate (c), and the protein/glucan ratio (d), integrated over the depth of each layer shown in Fig. 3a

a^{-1} h^{-1}. At 10 % light carbon uptake into ethanol-soluble compounds and polysaccharides was slower than at 50 % light since a significant proportion of the label was incorporated into protein (Fig. 6b). On Day 3, however, a larger proportion of ^{14}C was detected in the ethanol-soluble fraction than in the polysaccharide and protein fractions. Incorporation into protein was the dominant process at the 1 % light level (Fig. 6c).

DISCUSSION

The parcel of water followed by the drogue was confined to the upper mixed layer and sheared over the other layers along the course taken by the drogue (Fig. 3a). Mixing, diffusion and shear of water flow probably changed the characteristics of the original parcel considerably by the end of the study (Boyd, 1982), but since the species composition was similar at all the stations it may be assumed that the same community was being investigated. A study of a declining bloom could therefore be undertaken on a single community over several days.

When nitrate concentrations declined to levels < 1 mg at m^{-3} on Days 3 and 4 a large proportion of assimilated carbon was held in the ethanol-soluble fraction at the 50 % light level and the rate of uptake into protein was reduced (Fig. 6a). This indicated that the bloom had entered a stationary phase of growth and protein and chlorophyll *a* concentrations began to decrease in the upper mixed layer (Fig. 4b and 5a). The continued decrease in chlorophyll *a* and protein concentrations in the mixed layer, with increasing concentrations of these components in the stable and upper bottom layers over the following 4 d, indicated a steady decline of the bloom as the cells sank out of the mixed layer into the stable layer (Days 4 to 6) and upper bottom layer (Day 7) (Fig. 4b and 5a).

The rate of decrease in chlorophyll *a* and protein concentrations in the upper mixed layer during the decline was slower than the rate of increase in these concentrations during the development phase. It appears that the cells had an adequate supply of energy and nitrogen to maintain some growth for a few days following nutrient depletion. High carbohydrate concentrations during this period (Fig. 5b, c) confirm

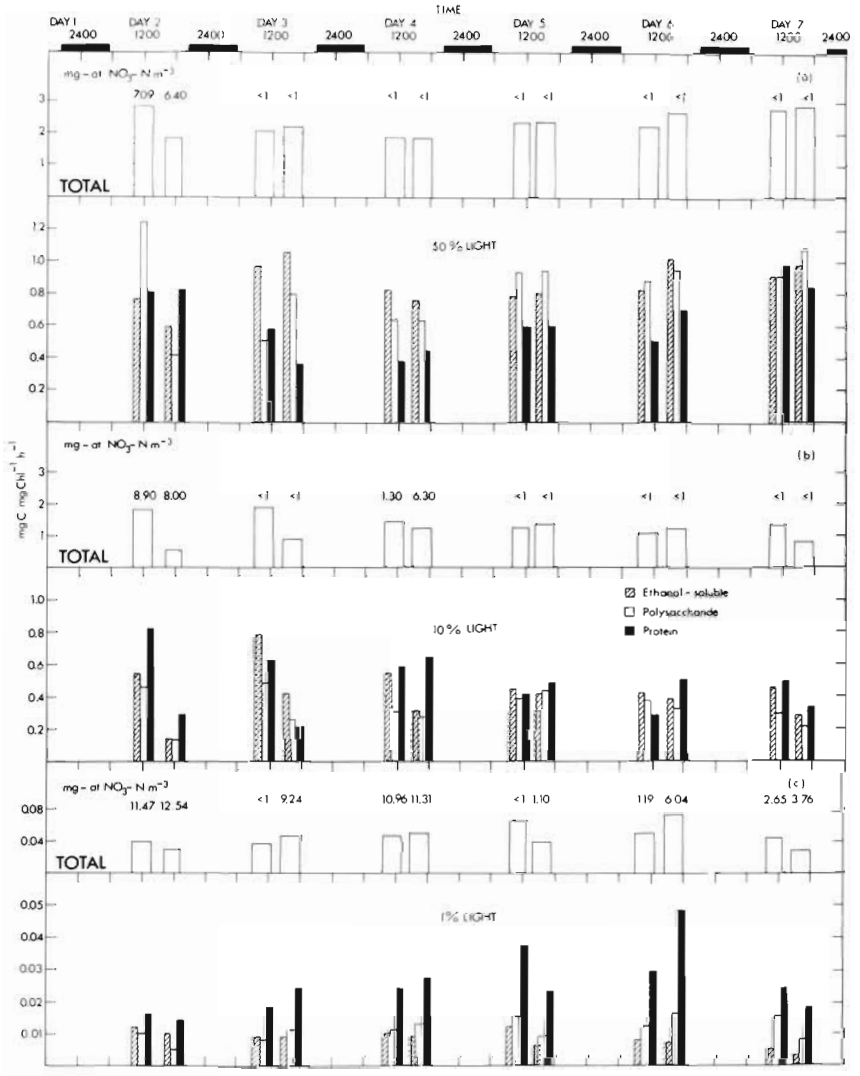

Fig. 6. Rates of photosynthesis over 4 h and assimilation of carbon into ethanol-soluble, polysaccharide and protein fractions at 50 % (a), 10 % (b), and 1 % (c) light levels. Relevant nitrate concentrations included for comparison

that adequate reserves of energy were available, with polysaccharide being synthesized during the day and utilized at night. This diel variation in carbohydrate production has also been observed by Morris and Skea (1978), Hitchcock (1980), Morris et al. (1981) and Barlow (1982c).

No measurements of nitrogen reserves were made during this study but the recent finding of Collos (1982) and Dortch (1982) show that some diatoms have the ability to buffer the effect of a changing and growth-limiting nitrogen supply. *Skeletonema costatum* (Grev.) Cleve, for instance, can quickly store unassimilated nitrogen in large pools of amino-acids and nitrate when growing on a large supply of nitrate (Dortch, 1982). When the external nitrate supply is low (< 1 µM), growth is maintained by utilizing the stored internal nitrogen reserves.

The ability of diatoms to utilize such reserves may explain why increased uptake of carbon into protein was observed for the community at the 50 % light level during Days 5 to 7 when the external nitrate supply was low (Fig. 6a). At this light intensity active photosynthesis continued, despite the decline in the bloom, with excess CO_2 and energy being stored in polysaccharides and ethanol-soluble compounds (Fig. 6a). By Day 7 the rate of assimilation of carbon into protein per unit of chlorophyll *a* was faster than on any other day during the study. The lower uptake into protein during Days 3 and 4, compared to Days 5 to 7, suggests that there was a lag in the rate of utilization of the internal nitrogen pool when the bloom entered a stationary phase of growth.

The decline in the bloom in the upper mixed layer when nitrates were depleted complements the findings

of Eppley et al. (1979) that nitrate is a major factor regulating phytoplankton production in the upwelling area off southern California. At the end of the bloom protein/glucan ratios in the lower layers were greater than in the upper mixed layer (Fig. 5d) and a large proportion of carbon was incorporated into protein at the 10 and 1 % light intensities (Fig. 6b, c). This indicated that the cells in these layers were still viable, with an adequate supply of nitrate being available (Fig. 4a). The photosynthetic rate was slower at these low light levels (Fig. 6b, c) and it appears that the community conserved the synthesis of protein at the expense of carbohydrate under these conditions. This may be a mechanism whereby a community can be maintained until mixing transports cells to higher light levels in the upper euphotic zone.

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