

## Subsurface patch of a dinoflagellate (*Ceratium tripos*) off Southern California: patch length, growth rate, associated vertically migrating species

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### Abstract

*Ceratium tripos* dominated a multi-species dinoflagellate patch in the sub-surface chlorophyll maximum in August 1978 on the Southern California shelf. The specific growth rate ( $\mu$ ) of *C. tripos* averaged 0.25 d<sup>-1</sup>. Patch length was about 45 km along the shelf. Several members of the sub-surface dinoflagellate assemblage were also present in surface samples, but only during the daytime. These apparent vertical migrators included *Prorocentrum micans*, *C. furca*, *Gonyaulax polyedra* and other less common forms. The growth of *C. tripos* in the California patch is compared with that in a *C. tripos* patch off New York in 1976.

### Introduction

Phytoplankton are not randomly distributed: rather, the species assemblages display a pattern. In shallow coastal waters, the horizontal length scales of the pattern are much greater than the vertical scales and the patterns are elongate in the alongshore direction (Reid *et al.*, 1978; Cullen *et al.*, 1982a). We assume they are determined largely by physical processes. Along the Southern California coast, as in other coastal regions, the spatial patterns of the phytoplankton are not strictly repeatable "... since the species-assemblage encountered at any given time and place need never precisely recur. Nevertheless, it is reasonable to hope that strong environmentally-determined patterns may be sufficiently robust to transcend the particular species-assemblages which serve to define them on any given occasion, ..." (Relevante *et al.*, 1982).

The patchy distribution of phytoplankton has been studied in the past by two fundamentally different methods: (1) Platt (1972) first examined the spatial scales of

fluctuation in chlorophyll fluorescence using spectral analysis of continuous, underway records of *in vivo* chlorophyll fluorescence (Lorenzen, 1966); the culmination of this approach is represented by several studies reported in the book edited by Steele (1978); satellite-measured chlorophyll distributions provide synoptic information and reveal two-dimensional patterns in this region (Smith and Baker, 1982). (2) For many years, phytoplankton species distribution has been examined over time and/or space from analysis of discrete samples of seawater (Estrada and Blasco, 1979).

These two approaches, i.e., spatial variation in chlorophyll fluorescence, a measure of the total phytoplankton biomass, versus spatial pattern of species assemblages, give different and complementary information on phytoplankton patches. Both are useful adjuncts in the study of aspects of water circulation such as frontal features (Holligan, 1978; Seliger *et al.*, 1981) and upwelling patterns (Traganza *et al.*, 1981). Species information can show long-term subsurface flows, as revealed, for example, by the temporal distribution of the dinoflagellate *Prorocentrum mariae-lebouriae* in Chesapeake Bay (Tyler and Seliger, 1978). In the present study we primarily used field observations to examine the role of physical processes in biology; however, to a lesser extent, we also used biological observations as aids in the study of ocean physics. The present work describes the phytoplankton species assemblages collected adjacent to a current meter mooring (described by Winant and Bratkovich, 1981) such that the dynamics of the phytoplankton could be compared with the current meter records to extract length scales and insights on physical correlates of species changes over time.

### Materials and methods

This study was carried out from 10–14 August 1978. A current meter mooring (Winant and Bratkovich, 1981) at 30 m depth included instruments at 3, 12, 19 and 27 m

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below the surface. The R.V. "Ellen B. Scripps" was anchored about 100 m south of the mooring off Del Mar, California (Fig. 1), where the water depth was 30 m. Sea-water was pumped up from 6 and 11 m and analyzed continuously for nitrate plus nitrite (by autoanalyzer; Strickland and Parsons, 1972) and chlorophyll fluorescence (Turner Designs Model 10-005 fluorometer). Temperature was recorded at the 11 m intake. In addition, a hose was lowered through the euphotic zone every 3 h over the 4 d sampling period. Water pumped from this hose provided a vertical profile of chlorophyll fluorescence and samples for phytoplankton enumeration from 1 m depth and the chlorophyll fluorescence maximum. A thermistor affixed to the hose provided temperature data over the depth profile. Analysis of the nitrate, fluorescence and temperature data relative to water motion was described by Cullen *et al.* (1982b); further details on methodology are also described in that report. The present study concerns primarily the phytoplankton species information relative to patchiness.

Phytoplankton samples were preserved with 2% formaldehyde buffered with sodium borate. Fifty-milliliter aliquots were settled 48 h for microscopic analysis by the Utermöhl method. Phytoplankton numbers and cell volumes were used to estimate biomass as carbon (Strathmann, 1967). A list of species and the relative abundance of each was used to compare the phytoplankton assemblage at one sampling with that at all other samplings, using

Whittaker's (1952) percent similarity index (PSI). This index is sensitive primarily to changes in the relative abundance of major taxa. Presence or absence of rare species has little effect on the PSI.

After the anchor station study of 10–14 August, the ship returned to San Diego, sampling at stations off La Jolla and Ocean Beach (Fig. 1) en route. Later, on 16/17 August, a grid pattern of 30 stations was occupied north of the anchor station (Fig. 1: Lines 1 through 6, with five stations on each line designated by letters A–E). Results of that study have been reported by Cullen *et al.* (1982a).

## Results

### Currents

During the 4 d period, the current meter in the surface layer indicated first southerly flow, with large tidal ellipses, followed by increasing northerly flow (Fig. 2). Mean flow over the 4 d was only  $0.49 \text{ km d}^{-1}$  alongshore, northward and  $0.67 \text{ km d}^{-1}$  offshore. The meter at the approximate level of the chlorophyll maximum (12 m) recorded more consistent northerly flow, mean  $5.95 \text{ km d}^{-1}$ , and a small net onshore flow of  $0.52 \text{ km d}^{-1}$  (Fig. 3). Instead of large ellipses, there were cusps in the progressive vector diagram corresponding to maximum onshore excursions of the water.

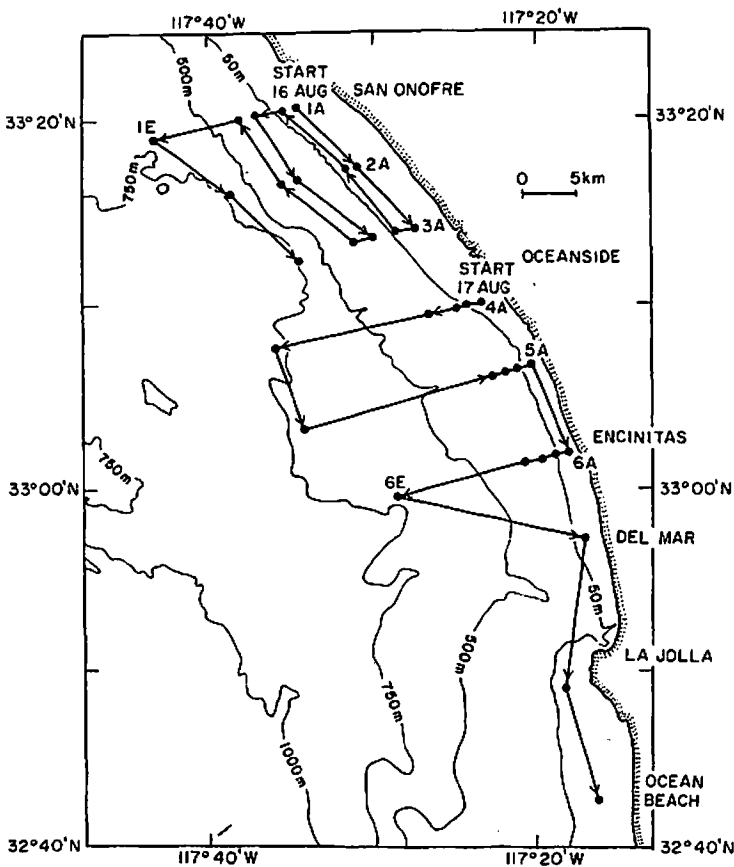


Fig. 1. Location of sampling stations off Southern California in August 1978. The anchor station was off Del Mar at 30 m depth

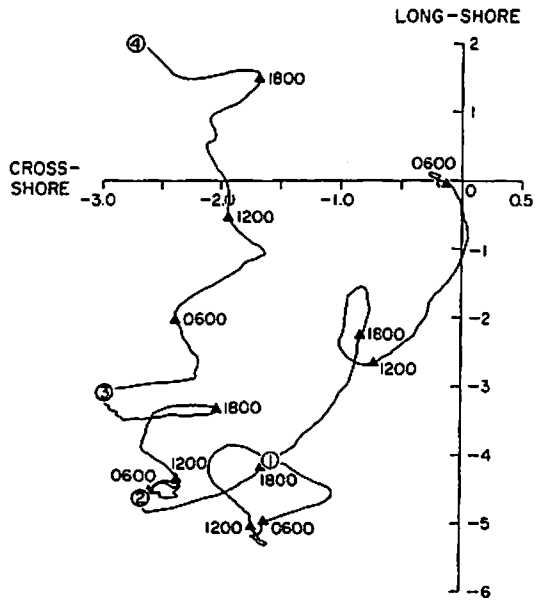


Fig. 2. Progressive vector diagram of near-surface currents off Del Mar, California, 11-14 August 1978. Axes' units are kilometers, positive upcoast and onshore. Time (hrs) is indicated by filled triangles every 6 h. Integers 1 through 4 indicate values at 24.00 hrs on Days 1-4

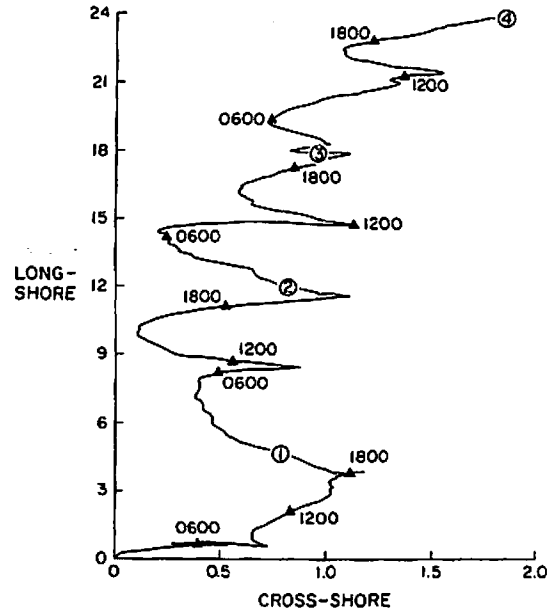


Fig. 3. Progressive vector diagram of currents at 12 m depth. Further details as in legend to Fig. 2

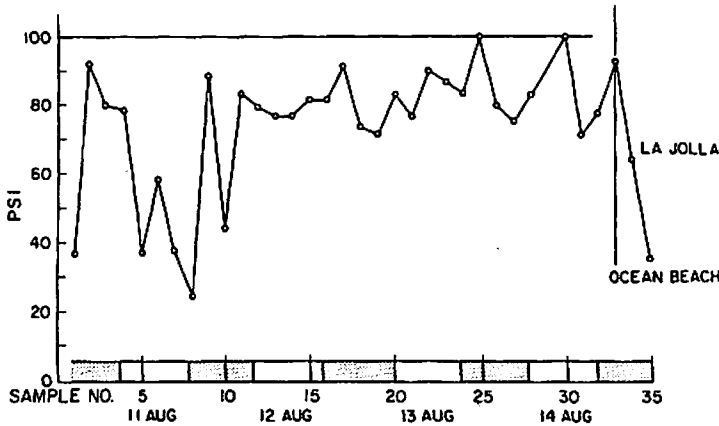


Fig. 4. Temporal change in species assemblage of the sub-surface chlorophyll maximum based upon "percent similarity index (PSI)". Sample No. 25 was taken as 100% and all others are compared with it to define the *Ceratium tripos* assemblage. Samples 1-33 were taken at the anchor station. Samples 34 and 35 were taken later on 17 August 1978 off La Jolla and Ocean Beach, respectively. Stippled bars on abscissa indicate night samples

Length scale of chlorophyll-maximum species assemblages

The percentage similarity at the anchor stations was consistently >70% for the species assemblages of chlorophyll maximum samples after 04.00 hrs on 12 August up to completion of the anchor station on the evening of 14 August (Fig. 4). This assemblage was dominated by the dinoflagellate *Ceratium tripos*. Other motile dinoflagellates had been predominant on the previous day, but had largely dropped out by this time.

The *Ceratium tripos* assemblage first arrived at the anchor station off Del Mar at 04.00 hrs on 12 August and was intercepted again in the grid sampling at 06.00 hrs on 17 August, 5.1 d later and 28 km to the north. The *C. tripos* assemblage was present at Stations 4A, 5A and B, and 6A

and B of Fig. 1 (Cullen *et al.*, 1982a, their Fig. 8). This suggests that the patch moved northward at a velocity of at least 5.5 km d<sup>-1</sup>. The current meter at 12 m depth recorded a mean northward velocity of 5.95 km d<sup>-1</sup>. The agreement between these measurements of flow is noted. We will use a mean flow velocity of 5.7 km d<sup>-1</sup> in calculating the alongshore length scale of the *C. tripos* assemblage.

After completing the station grid on 17 August, the ship returned again (to the south) to port, sampling once more at the anchor station off Del Mar, and stations off La Jolla and off Ocean Beach (Fig. 1). The Del Mar station was still within the *Ceratium tripos* patch, but the La Jolla and Ocean Beach stations were south of it (Fig. 4). The patch length is roughly the distance between Station 4A and the La Jolla station, 39 km, plus the northward flow

between those sampling times ( $5.7 \text{ km d}^{-1} \times 15 \text{ h} = 3.6 \text{ km}$ ) or 43 km.

A second calculation of patch length can be made using the time difference between the first appearance of the patch at the anchor station and the sampling time at the La Jolla station (5.7 d) and the distance between these stations (16.3 km). The patch length is then  $5.7 \text{ d} \times 5.7 \text{ km d}^{-1} + 16.3 \text{ km} = 49 \text{ km}$ . The two estimates of patch length, 43 and 49 km are in good agreement for non-synoptic data. The cross-shelf width of the patch was approximately 3 km (Cullen *et al.*, 1982a).

#### Phytoplankton dynamics: growth of the dinoflagellates

Dividing cells were seen only in chlorophyll-maximum samples. Dividing cells of *Prorocentrum micans* were seen only once, at 07.00 hrs on 11 August. Likewise, division stages of *Ceratium furca* were seen only twice, at 04.00 and 07.00 hrs on 12 August. Dividing cells of *C. tripos*, however, were seen on each of the 4 d on station, with a maximum fraction of division stages consistently at 04.00 hrs and a few at 07.00 hrs each day. Cell division rates were calculated from the following equation (Weiler and Chisholm, 1976; McDuff and Chisholm, 1982):

$$\mu = \frac{1}{t} \ln(F_{\max} + 1). \quad (1)$$

Here,  $F_{\max}$  is the ratio of the number of cells in various stages of cell division plus one-half of the recently divided cells to the total number of cells of *C. tripos* at 04.00 hrs. The specific growth rate ( $\mu$ ) averaged  $0.25 \text{ d}^{-1}$  (Table 1).

Cell counts of *Ceratium tripos* exceeded  $10^4 \text{ l}^{-1}$  in the chlorophyll maximum at the anchor station after the patch arrived at 04.00 hrs on 12 August. The counts fluctuated, with a period of about 6 h. *Protooperidinium* sp. "G" cell counts were slightly higher at night than counts of *C. tripos* Form S (Table 3). Because of the large size of *C. tripos* Form S, its biomass greatly exceeded that of all of the other species by roughly an order of magnitude. Thus, the biomass data for the chlorophyll maximum of Fig. 6 refer primarily to *C. tripos* even though the graph is actually the sum of biomasses of all the species recorded. The increasing biomass trend over time (Fig. 6, chlorophyll

Table 1. *Ceratium tripos*. Calculation of cell growth rate ( $\mu$ )

Daytime	No. of cells with:		Total cells	$\mu \text{ d}^{-1}$
	two nuclei	regenerating horns		
11 August, 04.00 hrs	8	3	77	0.12
12 August, 04.00 hrs	38	64	300	0.21
13 August, 04.00 hrs	151	290	555	0.43
14 August, 04.00 hrs	51	36	263	0.23
$\Sigma$	248	393	1 195	0.25 (mean)

maximum) reflects the slowly increasing abundance of *C. tripos*, largely Form S.

Cell concentrations of the three prominent vertical migrators, *Prorocentrum micans*, *Ceratium furca*, *Gonyaulax polyedra*, declined exponentially over time. Fig. 5 shows the counts of these three species in surface samples. Plots of their numbers in the chlorophyll maximum showed the same declining trend (data not shown).

#### Evidence for vertical migrations by dinoflagellates

Three relatively abundant species (*Prorocentrum micans*, *Ceratium furca* and *Gonyaulax polyedra*) were seen in surface samples primarily in the day, with peak concentrations at 13.00 hrs on 11 August and 10.00 hrs on 12 and 13 August (Fig. 5). Concentrations of these organisms in the chlorophyll maximum layer showed an opposite trend. Their abundance at the surface, relative to the total species count in surface and chlorophyll-maximum samples is shown in Table 2 for comparison with *C. tripos*.

Vertical migration of *Ceratium tripos*, if any, was less clear, since this species was nearly always present in the surface samples, although abundance varied from 40 to 6 000 cells  $\text{l}^{-1}$ . Peaks in abundance were at odd times: 19.00 hrs on 11 August, 07.00 hrs on 12 August, 10.00 hrs on 13 August, and 19.00 hrs on 14 August. Concentrations in the chlorophyll maximum were also variable, but high, ranging from 80 000 to 111 000 cells  $\text{l}^{-1}$ . Thus, we conclude that *C. tripos* did not migrate between the chlorophyll maximum and the surface layer. This conclusion is supported by the comparative data of Table 2.

Several other thecate dinoflagellates and the naked dinoflagellate *Torodinium* sp. were present at lower concentrations in the samples. Those showing repeated maxima at the surface at the 10 or 13 h sampling times included *Dinophysis caudata*, *Protooperidinium crassipes*, *P. divergens*, *Gonyaulax polygramma* and *Torodinium* sp. Other species, such as *Prorocentrum balticum*, clearly did

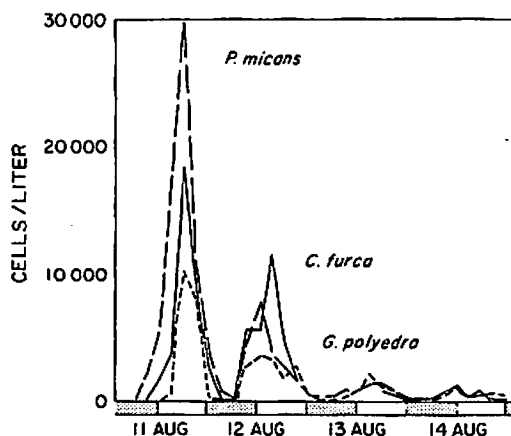


Fig. 5. *Prorocentrum micans* (long-dashed line), *Ceratium furca* (continuous line), and *Gonyaulax polyedra* (short-dashed line). Abundance in surface samples at the anchor station. Stippled bars on abscissa indicate night samples

**Table 2.** *Prorocentrum micans*, *Ceratium furca*, *Gonyaulax polyedra* and *Ceratium tripos*. Fraction of cells found in samples vs time of day, i.e.,

Daytime	cells in surface sample (cells in chlorophyll maximum sample + surface sample)			
	Migrators	Non-migrator		
	<i>Prorocentrum micans</i>	<i>Ceratium furca</i>	<i>Gonyaulax polyedra</i>	<i>Ceratium tripos</i>
11 August, 01.00 hrs	0.29	np	0.33	0.01
13.00 hrs	0.95	0.82	0.93	0
12 August, 01.00 hrs	0.02	0.02	0.04	0.002
13.00 hrs	0.70	0.77	0.69	0.04
13 August, 01.00 hrs	0.59	0.10	0.33	0.002
13.00 hrs	0.82	0.77	0.78	0.009
14 August, 01.00 hrs	0	0	np	0.002
13.00 hrs	0.74	1.00	1.00	0.007

**Table 3.** *Ceratium furca*, *Dinophysis caudata*, *Gonyaulax polyedra*, *Protoperidinium crassipes*, *Prorocentrum gracile* and other thecate dinoflagellates of the chlorophyll maximum samples in the *Ceratium tripos* patch, 22.00 hrs 11 August to 19.00 hrs 14 August. Ranks of 10 most abundant species are given; numerical values are not recorded for ranks > 10. Species are ranked by cell number and by biomass. The most abundant species is assigned Rank 1

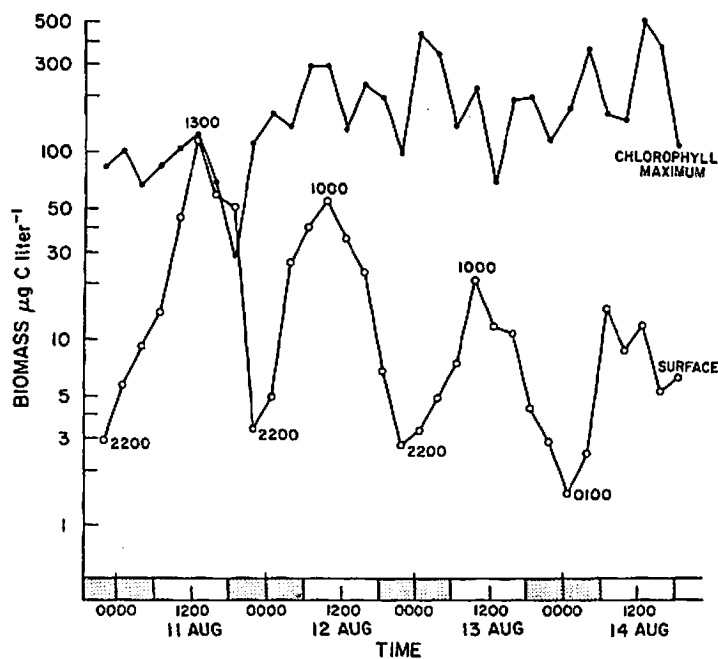
Species present	Rank			
	by cell number:		by biomass carbon:	
	Night	Day	Night	Day
<i>Ceratium furca</i> (30.9) <sup>a</sup>	6	6	8	8
<i>C. fusus</i> (28.9)				
<i>C. lineatum</i> (22.4)				
<i>C. tripos</i> S (48.7)	2	1	1	1
<i>C. tripos</i> A (46.6)	3	3	3	3
<i>C. tripos</i> var. <i>atlanticus</i> (55.4)	5	4	5	5
<i>C. horridum</i> (47.9)				
<i>Dinophysis caudata</i> (42.3)	10		8	10
<i>D. rotundatum</i> (37.3)				
<i>Gonyaulax polyedra</i> (45.9)	8	10	7	9
<i>G. polygramma</i> (53.4)				
<i>G. spinifera</i> (36.6)				
<i>Protoperidinium crassipes</i> (78.9)	9	7	4	4
<i>Protoperidinium</i> sp. "G" (9.0)	1	2	2	2
<i>P. steinii</i> (27.5)				
<i>P. depressum</i> (88.7)			10	6
<i>P. divergens</i> (72.1)				
<i>Prorocentrum gracile</i> (15.8)		9		
<i>P. balticum</i> (14.5)				
<i>P. micans</i> (24.2)	4	5	6	7
<i>Scrippsiella trochoidea</i> (19.4)	7	8		

<sup>a</sup> Equivalent spherical diameter ( $\mu\text{m}$ ) used in biomass carbon calculations

not show this pattern and we conclude they, like *Ceratium tripos*, did not undergo regular vertical migrations between the chlorophyll maximum and the surface. Migrations of smaller ambit are not ruled out by these data.

### Biomass variations

Species of the chlorophyll-maximum samples are ranked by biomass in Table 3. The total phytoplankton biomass (of cells > 15  $\mu\text{m}$  diam) was higher in the chlorophyll maximum than the surface, save for the afternoon of 11 August when the biomasses were similar. The biomass in the chlorophyll maximum tended to increase while decreasing in the surface samples (Fig. 6). Phytoplankton other than thecate dinoflagellates comprised less than 2  $\mu\text{g}$  carbon  $\text{l}^{-1}$  (mean value =  $0.50 \pm 0.36$  SD). A striking 24 h periodicity in biomass is apparent for surface samples (Fig. 6) due to variations in the abundance of the thecate dinoflagellates. The times of maximum (10.00 to 13.00 hrs) and minimum abundance (22.00 to 01.00 hrs) are consistent with an explanation based on diurnal vertical migration of dinoflagellates. Nevertheless, horizontal motions of the surface water past the sampling station may also have contributed to the periodicity. An unidentified coccolithophorid, present only in the surface samples at this station, was also significantly more abundant in daytime samples than at night ( $p < 0.05$ ). Cross-shore currents in the surface waters were often offshore around noon and onshore at midnight (Fig. 2). A patch of this coccolithophore located generally inshore of the station would have displayed the pattern observed above. Similarly, an onshore center mass

**Fig. 6.** Biomass carbon estimates for phytoplankton in surface and chlorophyll-maximum samples at the anchor station. Times of maxima and minima are indicated for surface samples

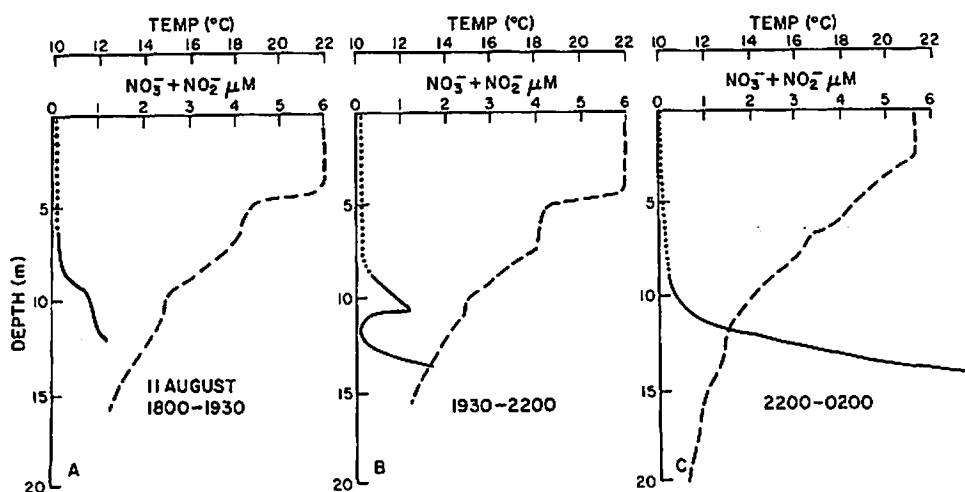


Fig. 7. Nitrate (continuous lines) and temperature (dashed lines) profiles versus depth at the anchor station. Nitrate profiles were reconstructed from nitrate vs temperature relationships over time for the periods: (A) between 18.00 and 19.30 hrs 11 August 1978; (B) 19.30–22.00 hrs 11 August 1978; (C) 22.00 hrs 11 August to 02.00 hrs 12 August 1978. Temperature profiles were measured at 17.50 hrs 11 August (A and B) and 04.30 hrs 12 August (C)

of the dinoflagellates, relative to the station position, could account for part of the variability in dinoflagellate (and total) biomass in the surface samples.

#### Change in nitrate-temperature relationships associated with the advent of the patch of *Ceratium tripos*

A hiatus appeared in the nitrate vs temperature relationship between 19.30 and 22.00 hrs on 11 August at the anchor station. Instead of the smooth, inverse relationship seen before and afterward, the relationship during the hiatus showed a secondary nitrate maximum at 14 °C. The temperature-depth profiles and nitrate-temperature relations were used to reconstruct nitrate vs depth profiles (Fig. 7). The hiatus appears to be an intrusion (Fig. 7B), as indicated by the nitrate maximum at 10 m depth. This feature and the hump in nitrate at 10 m in Fig. 7A were transient. Fig. 7C shows the relation observed on arrival of the *Ceratium tripos* patch, and this relation persisted throughout the observations.

## Discussion

### Taxonomic problems

There are some problems associated with the taxonomy of *Ceratium tripos* arising from the variation in cell size and shape at different stages in the life cycle (Hasle and Nordli, 1951; Von Stosch, 1964). In the present study, three forms were recognized: a large rugged cell (S), a smaller cell (A) often with incomplete antapical horns, and a cell with long antapical horns (*C. tripos* var. *atlanticum*). It seems likely that the first is a pre-division stage. The last is a cell with completely regenerated horns and it is interesting to note that it was particularly abundant on 12 August, before *C. tripos* became the dominant organism in the assemblage. It is possible that subsequent division proceeded so rapidly that the horns did not reach maximum length. There is also some evidence from our data

that the proportion of S:A forms was greater just before division time. For the purposes of this paper the three forms were grouped together. It is also noteworthy that *C. lineatum* became more important in the assemblage at the La Jolla and Ocean Beach stations, which were south of the *C. tripos* patch. These small cells may have been sexual stages of *C. tripos*, as discussed and illustrated by Von Stosch (1964).

### Patch dimensions and persistence

The two measurements of the length of the patch of *Ceratium tripos* in the longshore direction (43 and 49 km) average 46 km, and the approximately 3 km width of the patch reported earlier (Cullen *et al.*, 1982a) provide a geometric mean patch diameter of 12 km and a ratio of major:minor axes of 15. Interestingly, the mean current speeds were 5.95 km d<sup>-1</sup> longshore and 0.45 km d<sup>-1</sup> cross-shore, with a longshore/cross-shore velocity ratio of 13. It is tempting, given this correspondence, to regard the patch shape as being determined by the low-frequency currents.

The minimum radius of a stable phytoplankton patch can be calculated, since diffusion tends to disperse a patch while phytoplankton growth within the patch tends to enhance the patch (Kierstad and Slobodkin, 1953; Okubo, 1978). The information needed to make the calculation is the patch size ( $R$ ), the eddy diffusivity corresponding to the size ( $K_{x,y}$ ), and the specific growth rate of the phytoplankton ( $\mu$ ). From the 46 km and 3 km patch dimensions we derive a geometric mean  $K$  of 10<sup>5</sup> cm<sup>2</sup> s<sup>-1</sup> (Okubo, 1971). The *Ceratium tripos* growth rate averaged 0.3 d<sup>-1</sup> or 0.35 × 10<sup>-3</sup> s<sup>-1</sup>. The critical patch radius ( $R_{cr}$ ) required to prevent diffusive loss from exceeding replacement of cells by growth is, then,

$$R_{cr} = 2.4 (K/\mu)^{1/2} = 4 \text{ km.} \quad (2)$$

In fact, the geometric mean patch radius observed was 6 km. The size of the patch of *C. tripos* and associated species exceeded the minimum size required for stability.

We can also speculate on the time required to develop the concentration of *Ceratium tripos* in the patch. If one assumes that (1) the minimum detectable concentration of *C. tripos* in our observations was 1 cell in 100 ml of seawater examined, or  $10 \text{ cells l}^{-1}$ ; (2) the maximum observed *C. tripos* concentration was  $100\,000 \text{ cells l}^{-1}$ , an increase of  $10^4$ , and (3) the  $0.3 \text{ d}^{-1}$  exponential growth rate of *C. tripos* were uniform over time, then about 31 d would have been required to achieve this concentration change. It is unlikely that the patch of *C. tripos* resulted from physical aggregation as opposed to growth, as implied in the calculation above, as we are unaware of a mechanism of physically concentrating motile, but not vertically migrating, dinoflagellates in subsurface layers as observed here and in the Chesapeake Bay. There, Tyler and Seliger (1978) have observed subsurface patches of *Prorocentrum mariae-lebouriae* that persisted for periods of weeks to months. A persistent, subsurface patch of *C. tripos* was also recorded earlier in the New York Bight (Malone, 1978).

#### Diurnal vertical migration

*Ceratium tripos* migrated about 1.8 m in the vertical in Ford Pond Bay, New York (Staker and Bruno, 1980). Such a small ambit would have been undetectable in our work. Staker and Bruno discovered diurnal vertical migrations in several other species, including two which occur also off southern California: *Prorocentrum micans*, ambit 3.9 m; *C. fusus*, ambit 2.0 m.

The biology of *Ceratium tripos* was reviewed by Malone *et al.* (1979). They note that Nordli (1957) had not observed phototaxis in the laboratory, but that Hasle (1950) had also found light-dependent vertical migrations in the field. *C. tripos* is usually most abundant near the bottom of the euphotic zone and large populations have been observed below the euphotic zone (Malone *et al.*, 1979).

In the present study, we found evidence for vertical migration in known-migrating species, such as *Prorocentrum micans*, *Ceratium furca* and *Gonyaulax polyedra*. There are 5 species showing similar behavior and which are presumed migrators: *Dinophysis caudata*, *Protoperidinium crassipes*, *P. divergens*, *Gonyaulax polygramma* and *Torodinium sp.*

#### Are there advantages in vertical migration?

Previously it was postulated that the vertical migration of *Gonyaulax polyedra* would enhance survival, since daylight hours could be spent in the nutrient-depleted surface layer with ample light for photosynthesis while the dark hours could be spent in the nitracline with ample nutrients (Holmes *et al.*, 1967; Eppley and Harrison, 1975). Yet, in the present study, *G. polyedra* gradually disappeared from the *Ceratium tripos* patch rather than outcompeting *C. tripos*. Since the vertical migrators, such as *G. polyedra*, spent their days in the surface circulation (Fig. 2), and nights

in the subsurface flow (Fig. 3), the separation of *G. polyedra* from the *C. tripos* patch probably does not represent the result of competitive interaction, but entrainment in divergent flows or selective grazing. On the other hand, several other species of the *C. tripos* patch persisted over the observation period even though their occurrence in daytime surface samples suggested that they might have been migrating. These species included *Dinophysis caudata*, *Protoperidinium crassipes*, *P. divergens* and *Torodinium sp.*

#### Growth of *Ceratium tripos*

The mean specific growth rate ( $\mu$ ) observed in the field samples was  $0.25 \text{ d}^{-1}$  (Table 1). The maximum rate observed in cultures is similar, 0.3 to  $0.4 \text{ d}^{-1}$  at light saturation (Nordli, 1957). In the large, persistent bloom of *Ceratium tripos* in 1976 off New York, the cells were aggregated in a discrete subsurface layer as in the present study, but deeper in the euphotic zone. For the New York bloom, growth rates, as estimated from photosynthesis per biomass and from increases in cell density over time, were  $0.04$  to  $0.06 \text{ d}^{-1}$ . Earlier, Elbrächter (1973) found rates from  $0.03$  to  $0.3 \text{ d}^{-1}$  in Kiel Bay. Growth rate varied with temperature and was highest,  $0.3 \text{ d}^{-1}$ , at  $16^\circ\text{C}$ . This high rate is similar to that observed here and approaches the light-saturated rate of Nordli (1957). The implication for our data is that the irradiance at the depth of the chlorophyll maximum may have been saturating for *C. tripos* photosynthesis. That was not the case for the New York studies, where samples incubated aboard ship in photosynthesis vs irradiance studies indicated that the *in situ* growth rate of 0.04 would be increased to  $0.3$ – $0.4 \text{ d}^{-1}$  at light saturation (Malone, 1978). Falkowski *et al.* (1980) proposed 15% of surface irradiance as a saturating value for *C. tripos* growth rate and photosynthesis. Off California, the chlorophyll maximum moved with the semidiurnal internal tide between 6 and 17 m, mean irradiance was about 10% of surface irradiance, and mean temperature was about  $14^\circ\text{C}$  (Cullen *et al.*, 1982 b), consistent with the published requirements for near-maximum growth rate.

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