FRONTS, UPWELLING AND COASTAL CIRCULATION: SPATIAL HETEROGENEITY OF *CERATIUM* IN THE GULF OF MAINE

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ABSTRACT

The accumulation of dinoflagellates at tidal fronts has been a popular explanation for the distribution of blooms in coastal waters throughout the world. We sought to test this hypothesis with frequent sampling from March to September, 1987, along a 30km transect from Portsmouth, New Hampshire into the southwestern Gulf of Maine, a region subject to recurrent outbreaks of PSP. No evidence of a tidal front was found in the CTD profiles; however, a dense bloom of *Ceratium longipes* was found offshore in June, closely linked to a wind-driven coastal upwelling. Distributions of *Alexandrium tamarense* (=*Protogonyaulax tamarensis*) suggest that it may respond to the same physical forcings as *C. longipes* even though it remained a small fraction of the total phytoplankton biomass.

INTRODUCTION

The formation of toxic dinoflagellate blooms at tidal fronts has been described for coastal areas the world over [1]. The location of these fronts may be predicted based on the strength of the tidal current, u, and the water depth, h, using the Simpson and Hunter hu^{-3} criterion [2]. The characteristics of such a front are a well-mixed region inshore of the front, and a stratified region offshore. The front itself should be indicated by isopycnals intersecting the surface or the bottom. The dinoflagellate bloom is predicted to follow the pycnocline, with maximal cell densities at the front.

We examined this hypothesis by sampling a transect in the southwestern Gulf of Maine which spanned the depths at which tidal fronts were predicted to occur [3]. With approximately bi-weekly sampling throughout the bloom season we hoped to characterize the temporal changes of the bloom, as aliased by the cruise dates. Measurements were made of conductivity, temperature, *in situ* fluorescence, chlorophyll, dissolved nitrate+nitrite, and cell densities of *Ceratium longipes* and *Alexandrium tamarense (=Protogonyaulax tamarensis).*

METHODS

The study transect was located in the southwestern Gulf of Maine, extending from Portsmouth, New Hampshire into Jeffreys Basin (Figure 1). The transect was approximately 30km long, with five stations at ~7km intervals. Station 1 was located

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outside the harbour mouth in waters of 10 - 15m depth, while the water column at Station 5 extended to 170m. The two cruises described below took place on May 26 and June 5, 1987. Seven additional cruises were made, but will not be described here.

The ship used was the 45ft vessel, R/V Jere A. Chase, owned by the University of New Hampshire. From the A-frame of this vessel, 40m of 2cm internal-diameter hose was lowered into the water, with a Sea Bird "SeaCat" CTD attached at the hose inlet. A small submersible pump brought water onto deck, where it passed into a bubble trap, through a Turner Designs flow-through fluorometer, and into buckets on deck. The fluorometer was connected to a portable computer which displayed fluorescence in real time as well as storing the data to disk. The hose was raised at two metres per minute, with a flow of two litres per minute. Five litres were collected in each bucket, and subsampled as follows: one litre was filtered through 20µm mesh and the filter backwashed and fixed in 10% formaldehyde for cell counts, while 500ml was filtered through GF/A filters for chlorophyll analysis, and the filtrate frozen for nutrient analyses.

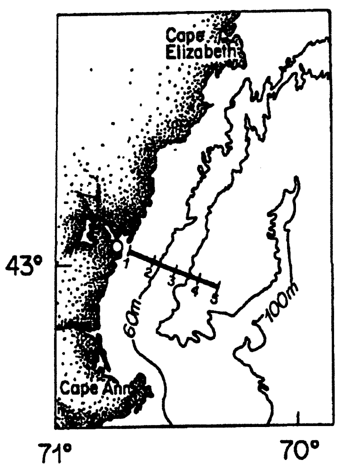

Figure 1. The study transect and the five stations are indicated in this figure. Cape Ann is just north of Boston. The transect begins at Portsmouth, NH on the New Hampshire-Maine border. The transect was approximately 30km long with stations ~7km apart.

RESULTS

One of the objects of this study was to look for a link between dinoflagellate blooms and tidally-generated fronts. No characteristics of a tidal front were seen in any of the CTD transects, although the surface temperature distributions on June 18 and July 2 would resemble a tidal front in satellite imagery. However, analysis of the temperature and salinity distributions indicates that there was an upwelling system present within the transect, centred between Stations 2 and 3. The density profiles of May 26 and June 5 (Figure 2) show this upwelling well. In May, the upwelling occured over a broad horizontal area between Stations 2 and 3, as shown by the upward curve of the isopycnals. By June, the solar heating restricted the upwelling to Station 2, while wind-mixing caused the isopycnals to surface at Station 3. Other more extensive cruises have shown that this upwelling extends 150km northward along the coast up to the Monhegan Island area. The upwelling is likely forced by longshore winds, although buoyancy effects such as freshwater input and solar heating may also play a role. Further data analysis combined with modelling studies are beginning to elucidate the relative contributions of the various forcings.

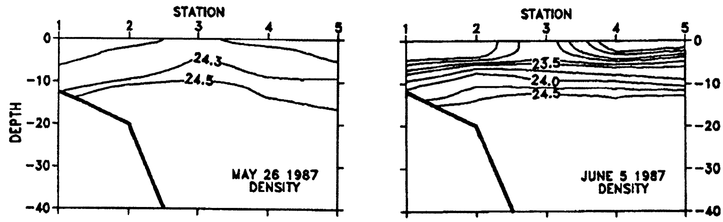

Figure 2. Density (σ_t) contours from May 26 (left panel) and June 5 (right panel). Upwelling is thought to cause the upward curvature at Station 3 in May, and Station 2 in June. The surfacing of the isopycnals in June at Station 3 is caused by surface mixing.

Closely associated with this upwelling was a concentrated band of *Ceratium longipes*, located at Station 3 at 10m depth. This bloom of *C. longipes*, seen in both the fluorescence and cell-density profiles, was developing offshore during May, becoming a band 5m thick and about 15km wide by June 5 (Figure 3). Peak cell denisities reached 5,000 cells l^{-1} in late June, and the bloom had dissipated by early July.

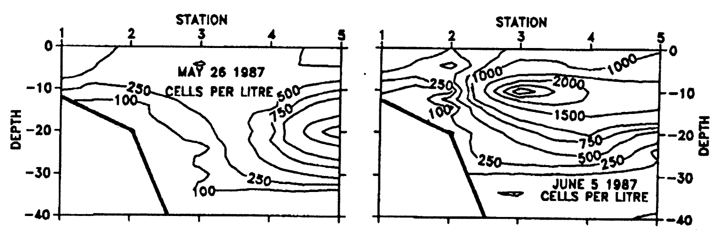

Figure 3. The left panel shows the cell concentrations of *Ceratium longipes* during the May 26 cruise, while the right panel shows the June 5 cruise. Note the high cell concentrations at Station 3 in June, at 10m depth.

Modelling studies combined with data analysis indicate that the strongest upwelling would be at Station 2 (vertical velocities ~0.001 cm s^{-1}), thus the bloom lies offshore of the peak upwelling. The peak horizontal velocities are of the order of 1 cm s^{-1}. Heaney and Eppley [4] have shown *Ceratium furca* to swim vertically at speeds of ~0.03 cm s^{-1}, thus it is probable that the *C. longipes* species which formed this bloom could maintain its depth during upwelling.

DISCUSSION

The close association of the *Ceratium longipes* bloom with the hydrographic features is indicative of the role the water motions play in generating and maintaining a dinoflagellate bloom. Upwelling along the coast can supply nutrients to the cells to maintain *in situ* growth, and can also promote localized accumulation of the cells if the required behavioural response is displayed. In this case, slower swimming in the cooler sub-pycnocline waters [4] would lead to the distribution seen. This scenario remains hypothetical, as vertical migration patterns were not studied during the 1987 field season.

Although the bloom which occurred was a *Ceratium* bloom, cell counts of *Alexandrium tamarense* were also made. Although *Alexandrium* usually blooms in the study region during spring, no such bloom was seen. It is conceivable, though, that such a bloom could occur under the conditions described above. If this were the case, then large subsurface concentrations of toxic cells could build up offshore, to be delivered to shellfish beds when the winds shifted. This mechanism could account for the rapid rise in toxicity seen during PSP outbreaks along the western Gulf of Maine coast. The temporal duration of the bloom, combined with the presence of southward-flowing longshore currents, suggests that the *Ceratium longipes* bloom extended northward in a band about 15km from shore. This spatial pattern is similar to that depicted by Yentsch *et al.* [1] for the area north of our transect. However, the generating mechanism proposed in that study was not upwelling, but tidally-generated fronts. We have shown that wind-driven coastal upwelling will generate biological patterns similar to those proposed for tidal fronts, emphasizing the need for relatively dense, accurate hydrographic measurements coincident with the biological measurements.

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