Observations on the Diel Migration of Marine Dinoflagellates off the Baja California Coast*

D. Blasco

Bigelow Laboratory for Ocean Sciences; West Boothbay Harbor, Maine, USA

Abstract

The vertical distribution of *Gonyaulax polyedra*, *Ceratium furca*, *Gymnodinium* sp., *Ceratium dens*, *Gonyaulax digitale*, *Prorocentrum micans*, *Polykrikos kofoidii*, and *Peridinium depressum* was followed during two 36 h time-series stations, off the Baja California coast. Water samples were taken at 6 h intervals, at 7 light penetration depths, for phytoplankton identification and for chemical and biological analysis. The results indicate that the dinoflagellates were able to perform vertical migration against the physical water movements, such as upwelling internal waves and wind mixing, that existed in the area during this study. Attempts to correlate the vertical distribution of the dinoflagellates with the seawater density and nitrate distribution lead to the conclusion that even a weak density gradient acted as a barrier to the downward migration, and that nitrate assimilation in darkness was not required for their growth. Differences in the vertical distribution at 12.00 hrs of each species supports the hypothesis that migration is of a phototactic nature. A comparison of this study with previous ones on vertical migration in other areas suggests that a species should not be defined in general as a positive or negative phototactic organism, but that the direction of the migration is related to the light intensity at the sea surface.

Introduction

One of the most typical characteristics of the marine dinoflagellates is their ability to migrate. Descriptions of this vertical migration exist from the beginning of this century (Lohman, 1919; Peters, 1929; both *in* Hasle, 1950), and several papers since have supported these observations and described the factors and characteristics affecting this phenomenon (Halldal, 1958; Hand *et al.*, 1965; Eppley *et al.*, 1968). This literature has been primarily based on laboratory studies; very few papers are of direct observations of nature. Hasle (1950, 1954) described extensively the diurnal vertical distribution of several species of dinoflagellates in the Oslo fjord (Norway), and suggested phototactic migration to explain their diurnal distribution. Seliger *et al.* (1970, 1971) have reported that the combination of

different phototactic responses and different swimming rates in conjunction with a two-layer circulation can produce the monospecific blooms observed in some bays. Holmes *et al.* (1967) and Eppley and Harrison (1975), based on results collected in La Jolla Bay, California (USA), suggest that the combination of vertical migration and the dark assimilation of nitrate are the survival factors for the dinoflagellate blooms.

The idea that independent movement may be of value to dinoflagellates in competition under certain hydrographic conditions is so appealing, that although most of the existing field observations are from rather protected locations, hypotheses have been advanced implicating similar mechanisms for open waters.

Kamykowski (1974) has shown by mathematical analysis that semi-diurnal internal tides will strongly concentrate vertically migrating organisms. Wyatt and Horwood (1973), in an attempt to model red tides, considered the ratio between swimming rates and the vertical water motion as the decisive factor for the red tide outbreaks.

This paper presents data upon the vertical dinoflagellate distribution during two 36 h time-series stations off the Baja California coast during the upwelling season. The relation between these distributions and some of the physical and chemical parameters is discussed.

The following observations were made as a part of an interdisciplinary program to study the dynamics of the Baja California upwelling ecosystem. The investigation was conducted aboard the R.V. "T. G. Thompson" during the Mescal-I cruise in March, 1972.

A background of information on the hydrographical and biological characteristics of the region during the time of the observations is available in Walsh *et al.* (1974) and Blasco (1977).

Materials and Methods

The first 36 h station was an anchor station (Station 20-25) on March 15-16, at Punta San Hipolito, 650 km south of San Diego, California (USA), and the second (Station 34-39), following a drogue drifting along the coast from Punta San Hipolito to the south, on March 20-21. Water samples for phytoplankton identification were taken at 6 h intervals at 100, 50, 25, 10, 7, 3, and 1% light penetration depths, and were fixed with Lugol (Blasco, 1971). The counts were made with an inverted microscope according to Utermöhl (1958). All identified organisms in a 50 cm^3 water volume were enumerated. Chemical and physical observations were made at each station and depth.

Results

The dinoflagellate species most abundant during these studies were *Gonyaulax polyedra, Ceratium furca, Gymnodinium* sp., *Ceratium dens, Gonyaulax digitale, Prorocentrum micans, Polykrikos kofoidii,* and *Peridinium depressum.* Very few diatoms were present. *Pseudonotia doliolus* and *Coscinodiscus* sp. were the most abundant. Mean cell concentration for each species is given in Table 1. A summary of some chemical and biological parameters are also presented in the same table.

Upwelling occurred during these studies (Walsh *et al.*, 1974), and therefore a strong thermocline was not observed, but a weak density gradient was located between the 20 and 30 m level.

During the first study, nitrate concentration at the surface was lower than 0.5 µg-at N l^{-1}; during the drogue study it was initially 8 µg-at N l^{-1}, and then

Table 1. Mean values of cell concentration (10^3 cells l^{-1}), temperature, nitrate and chlorophyll for two time series stations of Baja California coast. Each time series station was sampled 6 times at all 7 depths. The mean values were calculated from the 100, 50 and 25% light level samples for the upper part of the euphotic zone (Top), and from the 10, 7, 3 and 1% light level samples for the lower part of the euphotic zone (Bottom)

	Stations 20-25		Stations 34-39	
	Top	Bottom	Top	Bottom
Organisms				
Gonyaulax polyedra	49.28	13.85	59.41	36.33
Ceratium furca	4.79	2.98	6.64	5.33
Gymnodinium sp.	4.92	1.23	21.70	9.92
Ceratium dens	0.24	0.10	0.78	0.49
Gonyaulax digitale	0.21	0.09	0.15	0.10
Prorocentrum micans	0.16	0.04	0.25	0.26
Polykrikos kofoidii	0.14	0.02	0.20	0.09
Pseudoeunotia doliolus	1.97	0.43	1.15	0.81
Coscinodiscus sp.	0.15	0.15	0.83	0.56
Environmental parameters				
Temperature (°C)	14.67	12.75	14.17	12.69
Nitrate (µg-at N l^{-1})	0.52	10.79	3.69	5.79
Chlorophyll (µg l^{-1})	4.22	1.56	7.82	5.55
Depth of euphotic zone (m)	38.0		27.0	
Total solar radiation at 12.00 hrs (langleys min^{-1})	1.33		1.45	

decreased gradually to less than 0.5 µg-at N l^{-1}. Approximately at the same depth as the density gradient was an increase in the nitrate concentration up to 10 µg-at N l^{-1}. At both stations the distribution of nutrients and density appeared to exhibit the vertical structure of an internal wave regime (Walsh *et al.*, 1974).

A previous analysis of the chlorophyll and particulate nitrogen vertical pro-

files during the day and night hours (Walsh *et al.*, 1974) suggested diurnal change in the vertical distribution of the phytoplankton population. The vertical distribution of the total dinoflagellates indicates the same phenomenon (Fig. 1).

In Table 2, the vertical distribution of the maximum concentrations of some species at different times of the day is presented. A common characteristic for the dinoflagellates is a tendency to concentrate at a specific depth during the light hours and to disperse in the dark hours. However, two distinct distribution types occur at noon: *Gonyaulax polyedra* maintains maximum numbers at the surface, while the others (*Ceratium furca*, *Gymnodinium* sp., *Ceratium dens*, *Gonyaulax digitale* and

Fig. 1. Vertical distribution of chlorophyll and dinoflagellates during 36 h anchor station off Baja California

Prorocentrum micans) displace their maxima to the 50 and 25% light levels. No distinct pattern is observed in the distribution of the maxima for the diatom species. The two different types of noon behavior appear also in the time-sequence profiles of *Gonyaulax polyedra* and *Ceratium furca* (Figs. 2 and 3). In the same figures, the gradient of seawater density is also shown.

Another source of information on the vertical distribution of the different dinoflagellates are the phytoplankton data of the productivity stations taken during the cruise (Table 3). Since the time at which these stations were taken varied between 8.00 and 11.00 hrs, more variability in their distribution can be expected. On the basis of Table 3, it is possible to classify the species versus light preferences. *Gonyaulax polyedra* has a clearly positive response towards high intensity; *Ceratium furca*, *Gymnodinium* sp., *Ceratium dens* and *Gonyaulax digitale* have a wider depth distribution; *Prorocentrum micans* and *Polykrikos kofoidii* show an inclination to avoid the surface and a tendency for maxima in subsurface layers. Finally, *Peridinium depressum* appears to have a negative phototactic response.
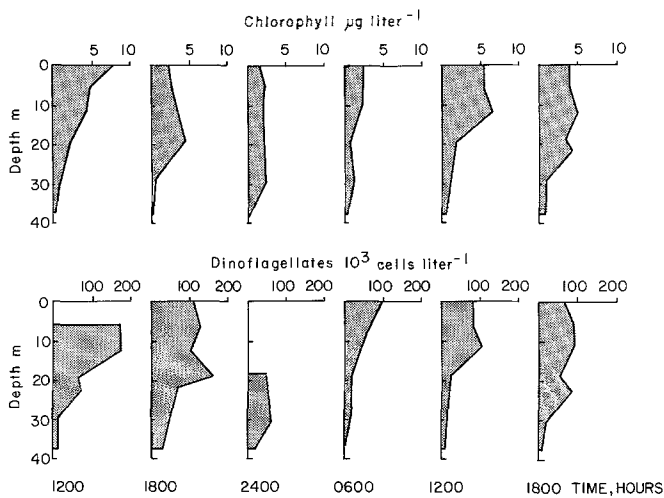
Discussion and Conclusions

The changes in the vertical distribution of the dinoflagellates within a 24 h period suggest that vertical migration might occur. The results presented here did not show a vertical migration as clearly as has been reported on other occasions or for other areas (Hasle, 1950; Eppley *et al.*, 1968), probably be-

Table 2. Number of observed maxima of some dinoflagellates and diatoms at various light penetration depths at different times of day. Summary of all observations during two 36 h studies

Species	Light depths (%) at:																											
	24.00 hrs							06.00 hrs							12.00 hrs							18.00 hrs						
	100	50	25	10	7	3	1	100	50	25	10	7	3	1	100	50	25	10	7	3	1	100	50	25	10	7	3	1
Dinoflagellates																												
Gonyaulax polyedra			1	1				2	1						3								2	1				
Ceratium furca	1						1	2	1							1	1	1								1	2	
Gymnodinium sp.			2					2		1				1		1	1					2	1					
Ceratium dens			2					2	1				1		1	2						2					1	
Gonyaulax digitale	1	2		1				2	1						1	2						2					1	
Prorocentrum micans	1					1		2						1	2	1						1		2				
Diatoms																												
Pseudoeunotia doliolus	1		1					1				1	1		1			2				2		1				
Coscinodiscus argus	1					1		2			1					1	1						2	1				
Thalassiosira excentrica	1	1							2	1					2	1						1				1	1	

CELL CONCENTRATION

TIME(hrs) 1230   1800   0030   0620   1200   1800
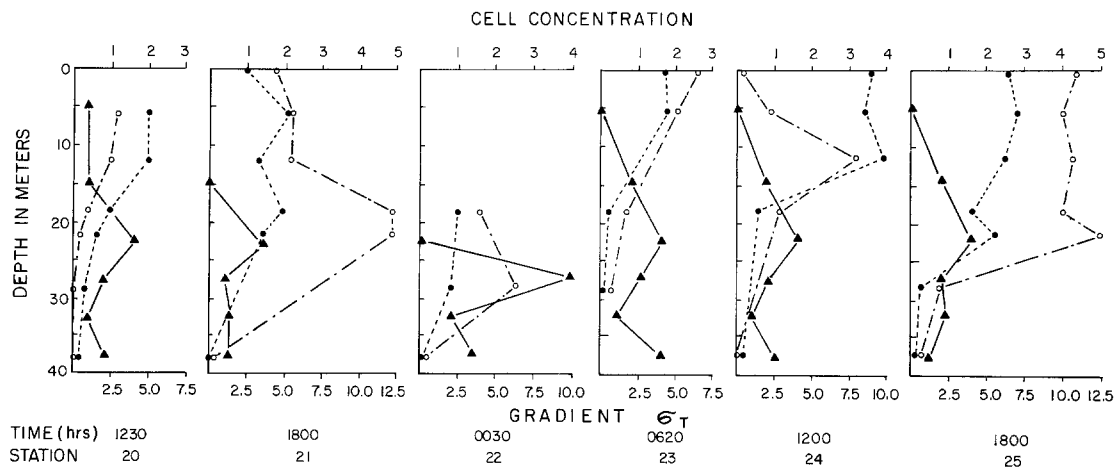STATION   20   21   22   23   24   25

Fig. 2. Vertical distribution of *Gonyaulax polyedra*, *Ceratium furca*, and seawater density gradient (σ_T) during 36 h anchor station off Baja California. *G. polyedra* (filled circles) is in 10^3 cells 1^{-1}, *C. furca* (open circles) in 10^2 cells 1^{-1}, and σ_T gradient (triangles) in 10^{-2} m^{-1}

CELL CONCENTRATION

TIME(hrs) 2400   0700   1200   1845   0100   0700
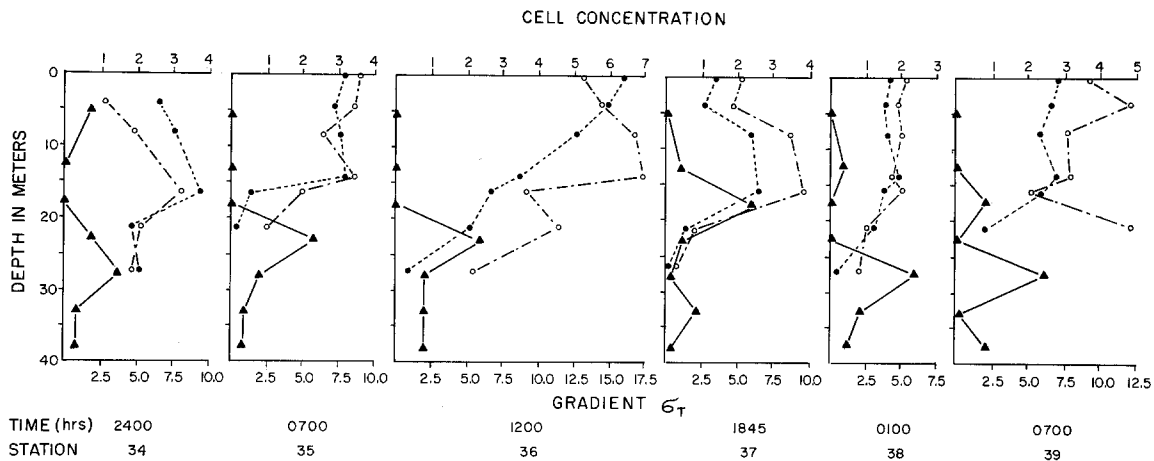STATION   34   35   36   37   38   39

Fig. 3. Vertical distribution of *Gonyaulax polyedra*, *Ceratium furca*, and seawater density gradient (σ_T) during 36 h drogue study. Symbols and parameters as in Fig. 2

Table 3. Distribution of maximum numbers of organisms with respect to light penetration depth. Summary of 10 productivity stations taken between 08.00 and 11.00 hrs during Mescal-I cruise off Baja California coast

Species	Light depth						
	100%	50%	25%	10%	7%	3%	1%
Gonyaulax polyedra	5	1	1	0	1	2	0
Ceratium furca	3	3	1	1	0	1	0
Gymnodinium sp.	2	3	2	1	0	0	0
Ceratium dens	2	2	3	1	0	0	0
Gonyaulax digitale	3	2	4	1	0	0	0
Polykrikos kofoidii	1	4	4	1	0	2	0
Prorocentrum micans	1	3	1	3	1	1	0
Peridinium depressum	1	0	4	2	2	0	1

cause the distribution of the organisms during this study was determined by a combination of migrational pattern and physical water movements such as vertical upwelling, internal waves, wind mixing, etc. The upwelling effect should be positive during the upward migration and negative during the downward migration. It can be therefore concluded from the night and afternoon distribution of the dinoflagellates (Figs. 1, 2, and 3) that the swimming speed of the organisms was higher than 1 to 2 x 10^{-2} cm sec^{-1}, the estimated vertical upwelling velocity (Walsh et al., 1974). This swimming speed agrees with those reported in the order of 2 to 5 x 10^{-2} cm sec^{-1} (Hasle, 1950, 1954; Hand et al., 1965). The effect of the internal waves and of the wind mixing upon the migrational pattern of the dinoflagellates is more complex, and with the data obtained here is not possible to determine. Nevertheless, the consistent differences of the distribution
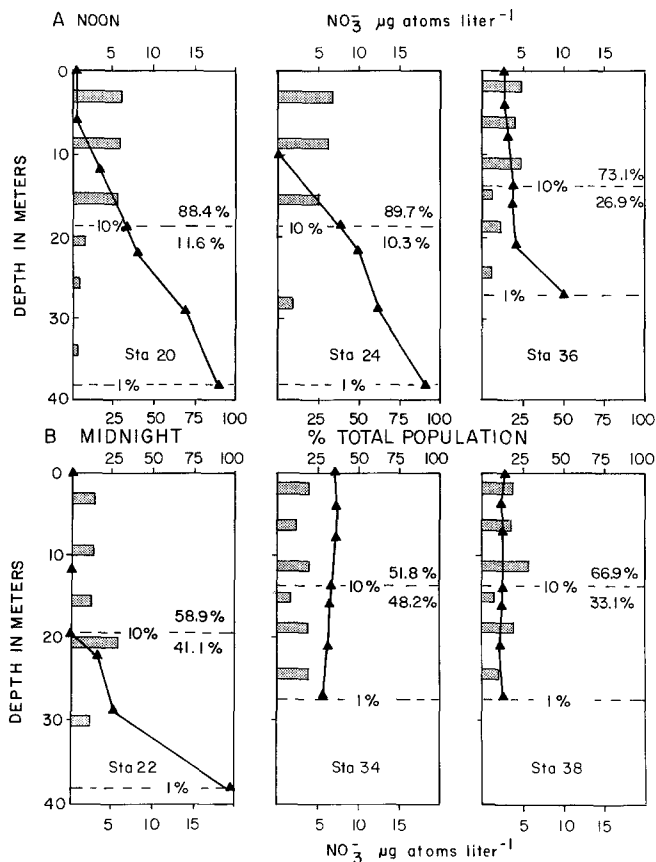
Fig. 4. Vertical distribution of dinoflagellate population and nitrate concentration at noon (A) and midnight (B). Dinoflagellates (bars) are expressed as percentage of total integrated dinoflagellate population over euphotic zone; nitrate (triangles) is expressed as µg-at N^{-1}; and the 10 and 1% surface light penetration depths as dashed lines

within the different species suggest that the organisms studied overcame these effects to a certain degree.

The vertical migration of dinoflagellates has been well documented, but the question remains as to what extent their migrational ability is related to environmental parameters. It has been observed in laboratory experiments that, although some dinoflagellates display similar swimming velocities over wide temperature and salinity ranges, they respond quite drastically to a rapid temperature or salinity change. In both cases, a sharp decline in motility results (Hand et al., 1965). Although this type of response could be useful in interpreting the concentration of dinoflagellates at specific depths in the ocean (Eppley et al., 1968; Kiefer and Lasker, 1975), direct observations are scarce and contradictory, and most have been obtained where the salinity gradients were strong due to the presence of freshwater at the surface (Hasle, 1954; Seliger et al., 1970, 1975; Braarud, 1976). In Figs. 2 and 3, out of 6 observations made during the evening and night, on 4 occasions the maximum of the density gradient coincides with a peak in density for both species (Gonyaulax polyedra and Ceratium furca). This coincidence occurs at a different depth each time, and is more obvious when the maximum of the density gradient is shallower. A possible explanation is that the density of dinoflagellates at a certain depth reflects the maximum distance that the organisms can swim, but the coincidence at the shallower depths suggests that the density gradient, although it was very weak, acted as a barrier to vertical migration by slowing the migration velocity of the dinoflagellates. The same phenomenon has been observed in laboratory experiments on the dinoflagellate Cachonina nieii by Kamykowski and Zentara (1977).

The results of this study also enable a re-examination of the interaction between dinoflagellate migration and light and nitrate distributions. The results have been integrated between light depths and expressed as fractions of the total integrated dinoflagellate population over the euphotic zone, in order to know which fraction of the dinoflagellate population is exposed to a certain light intensity and nitrate concentration. These results (Fig. 4) show that, although the majority of the dinoflagellates tend to be in the upper part of the euphotic zone at noon, they are almost evenly distributed between the surface and the 10% light depth and then display a sharp decline in numbers below this light level. Of the three noon observations shown in Fig. 4A, two had very low nitrate concentrations (<0.5 µg-at N l^{-1}) between the surface and the 25% light level; however, nitrate concentrations between the 25 and 10% light levels, where more than one-fourth of the population was localized, were around 5 µg-at N l^{-1}. Based on this, and on the fact that the half-saturation light value for nitrate uptake during these observations was at the 10% light depth (MacIsaac, in press), it can be assumed that most of the nitrate assimilation took place below the 25% light depth. One-third of the population divided daily during this study (Walsh et al., 1974); therefore, if it is assumed that some ammonia assimilation took place, growth of the population during this study could have occurred without dark nitrate assimilation, as proposed by Dong-Ping Wang and Walsh (1976).

Table 4. *Ceratium furca*. Direction of migration with respect to sea surface at different light surface intensities

Area	Time (hrs)	Light intensity (langleys min^{-1})	Direction of migration	Source
Baja California	7.00	0.4	Positive	Blasco (present study)
Baja California	12.00	1.3	Negative	Blasco (present study)
Oslo fjord	11.15	0.6	Positive	Hasle (1954)
Bahía Fosforescente, Puerto Rico	12.00	97,000 lux	Negative	Seliger (1971)

Fig. 4. also shows that at midnight the population density below the 10% light level increased by one to four times the density at noon, indicating that a small fraction of the population had migrated downwards in the water column. This was also observed by Eppley *et al.* (1968).

Finally, we observed that *Gonyaulax polyedra*, *Ceratium furca*, *Gymnodinium* sp., *Ceratium dens*, *Gonyaulax digitale*, and *Prorocentrum micans* migrated towards the light early in the morning; however, with the exception of *Gonyaulax polyedra*, they reacted negatively to the higher light intensity of the surface at noon (Table 2). This observation supports the hypothesis that migration is of phototactic nature and that each species responds to a different light threshold (Hasle, 1954), although it does not exclude the theory that the organism itself follows a circadian rhythm or that migration depends on the physiological state of the organism (Eppley *et al.*, 1968). The disagreement concerning the direction of the migration of one species, *Ceratium furca*, at different times of the day or in different areas (Table 4), suggests that each species has a characteristic light sensitivity. The differences in light sensitivity between various species needs further investigation, but it is a factor meriting consideration as a possible explanation of the patchiness and monospecifity of dinoflagellate blooms.

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Dr. D. Blasco
Bigelow Laboratory for Ocean Sciences
West Boothbay Harbor, Maine 04575
USA