

Red tide in the upwelling region of Baja California¹

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Abstract

Predominant organisms in a red water dinoflagellate bloom during the seasonal onset of coastal upwelling off Baja California were *Gonyaulax polyedra*, *Ceratium furca*, and *Gymnodinium* sp. The major part of the chlorophyll and the ¹⁴C assimilation in the area was related to the *G. polyedra* population. The maximum concentration of these organisms was associated with low salinity water of the surface California Current. The dinoflagellates remained in the area during the 20-day cruise, although the vertical stability coefficient was low, with no steep temperature gradient. The high concentrations of small copepods suggest them as major grazers of *G. polyedra*.

Red tides have been observed and described in many parts of the ocean. Except for extensive research on the west coast of Florida and on the southern part of the California coast, early studies usually described sporadic observations of a mature red tide without any discussion of the development of the bloom. The onset of red water was thought to be related to an increase in vertical stability, or to freshwater runoff. Several recent studies have described the characteristics of these blooms in semiarid upwelling regions and have stressed the importance of dinoflagellate blooms in pelagic food webs. I here present observations of a red tide made during a 20-day cruise (MESCAL I) to the upwelling region of Baja California, with the RV *Thomas G. Thompson* of the University of Washington. The west coast of Baja California is a typical coastal upwelling system, free from heavy rainfall and river runoff. In these conditions it should be possible to distinguish between the oceanic and terrestrial factors thought to be responsible for generation of red water outbreaks.

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in the MESCAL I expedition, and my fellow oceanographers for kindly providing the hydrographic and biological data.

Methods

The stations occupied between 5 and 23 March 1972 are shown in Fig. 1. Phytoplankton samples were taken at productivity stations from depths corresponding to radiance levels of 100, 50, 25, 10, 7, 3, and 1% of surface light, and at some hydrographic stations at the standard depths of 0, 10, 20, 30, 40, and 50 m. The samples were preserved with a few drops of Lugol's solution (Margalef 1973). Cells were counted and identified with an inverted microscope (Utermöhl 1958; Blasco 1971). I tried to identify all cells to species, but many were flagellates and small dinoflagellates that could not be identified. Chemical and physical observations were made at all depths for all stations. Nutrient analyses were made by AutoAnalyzer with the methods of Murphy and Riley (1962) for reactive phosphorus, Armstrong et al. (1967) for nitrate and silicate, and Slawyk and MacIsaac (1972) for ammonia. Each productivity station included chlorophyll (SCOR-UNESCO 1966), particulate carbon (Menzel and Vaccaro 1964), particulate nitrogen (Pavlou et al. 1974), rate measurements of phytoplankton nitrate uptake by the ¹⁵N method (Dugdale and Goering 1967), estimates of nitrate reductase (Packard et al. 1971), and ¹⁴C uptake measurements (Wolfe and Schelske 1967).

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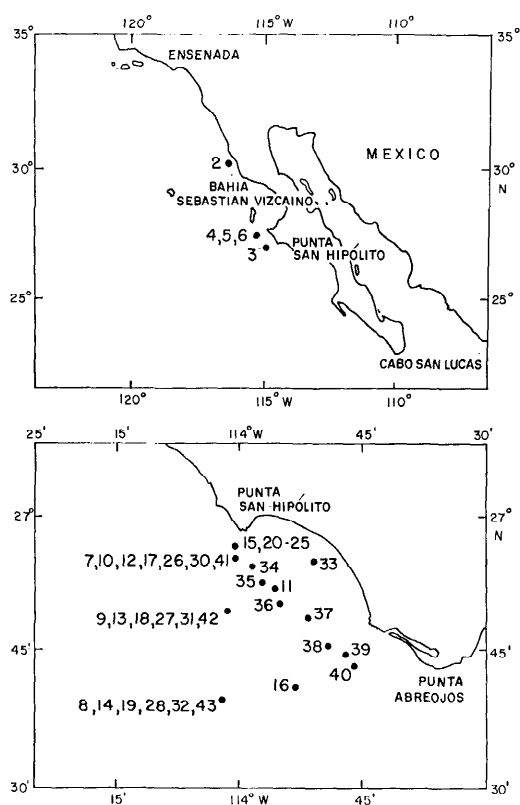


Fig. 1. Location of stations off Punta San Hipólito, Baja California.

Results

Composition and distribution of the phytoplankton—The maximum cell concentration recorded during this study was 70×10^4 cells liter⁻¹. Small flagellates (7- μ m diameter) were the most abundant organisms in all samples. Dinoflagellates occurred less frequently, but were numerically more important than diatoms and coccolithophorides. *Gonyaulax polyedra*, *Ceratium furca*, *Prorocentrum micans*, *Ceratium dens*, *Gonyaulax digitale*, and *Gymnodinium* sp. dominated the dinoflagellate assemblage. *Gonyaulax polyedra* was three times as abundant as all the other dinoflagellates combined. All of these organisms are typical components of red tides along the California coast (e.g. Allen 1946; Holmes et al. 1967; Reid et al.

1970). *Coscinodiscus* and *Pseudoeunotia* were present but contributed little to the total plant biomass; diatoms usually represented <10% of the total assemblage. Longhurst et al. (1967) and Smayda (1974) found *Coscinodiscus* to be the dominant phytoplankter in the area in April and June.

Table 1 summarizes the observations at a time series station off Punta San Hipólito. The phytoplankton attained its maximum in the middle of the 2-week period and decreased sharply toward its end. In contrast, the *G. polyedra* concentration was greatest at the beginning of the study, declined to a minimum on the third day (12 March), and then increased slightly through the remainder of the cruise. The same pattern characterized the dinoflagellates (>20 μ m). The ratio of *G. polyedra* to total phytoplankton or large dinoflagellates to total phytoplankton was lowest at the end of the first week (15 March) and then increased during the second week to the original values. The contribution of the large dinoflagellates to the total phytoplankton biomass in the inshore stations was 22% (mean value); of this number *G. polyedra* contributed 72%. *Gonyaulax polyedra* was observed at all the stations, with highest concentrations within 10 km of shore. Samples taken in the northern part of the region (stations 2–6) indicated that *G. polyedra* was present along the Baja California coast from 30°–27°N.

Since the maximum number of *G. polyedra* observed was 17×10^4 cells liter⁻¹, at least one order of magnitude lower than the maximum cell counts reported for the red water patches on the California coast (Sweeney 1975), I use the term "red tide" with caution in this report.

Relationship between the dinoflagellate bloom and hydrography—Because the hydrographic features of this area for March 1972 have been described by Walsh et al. (1974), only those parameters suspected to have a causal relationship with dinoflagellate blooms are presented here. Figure 2 illustrates the distribution of temperature, vertical stability, nitrate, and the ratio, *G.*

Table 1. Mean phytoplankton densities in upper 40 m, and percentage of total population at time series station 5 km off Punta San Hipólito.

	10	11	12	14	15	16	19	23
	March							
	7	10	12	17	20	24	30	41
	Station							
	10^4 cells liter ⁻¹							
Total cells	29.09	27.93	28.94	35.20	48.45	16.86	16.40	11.83
Dinoflagellates*	10.03	6.97	1.59	2.39	2.38	3.53	5.90	4.83
<i>Gonyaulax polyedra</i>	8.91	5.92	1.09	1.84	1.36	2.89	4.25	3.14
Diatoms	0.33	0.25	0.31	0.36	0.56	0.23	0.15	0.51
	%							
Dinoflagellates*/Total cells	34.4	24.9	5.5	6.8	4.9	20.9	35.9	40.8
<i>Gonyaulax polyedra</i> /Total cells	30.6	21.2	3.8	5.2	3.8	17.1	25.9	26.5
Diatoms/Total cells	1.1	0.9	1.1	1.0	1.1	1.4	0.9	4.3

*Dinoflagellates > 20 μ m.

polyedra: total phytoplankton population, at the time series station 5 km off Punta San Hipólito. Surface temperatures varied from 14°–15°C, decreasing slightly toward the end of the 2-week period. No distinctive thermocline was present, although there was a weak temperature gradient at some of the stations between the 20- and 30-m depths. The vertical stability was low, varying from –5 to 10 in the upper 10 m. The minimum value occurred between 12–15 March; by 23 March the stability had increased to 10. The mixed-layer depth on 10 March was from 40–50 m, and, as the upwelling reached a more steady phase (Walsh et al. 1974), a weak density gradient developed that oscillated between the 20- and 30-m level. The depth of the 1% surface light level varied between 19 and 38 m (mean, 28 m) at the time series station. The nitrate profile showed sharper gradients than those of the other parameters. Surface values oscillated between 0 and 5 μ g-atoms NO₃-N liter⁻¹, but most of the time they were lower than 1 μ g-atom NO₃-N liter⁻¹. In contrast the nitrate con-

centrations below 20 m were constantly higher than 4.00 μ g-atoms NO₃-N liter⁻¹. The temporal structure of the distributions in Fig. 2 suggests that the dominance of *G. polyedra* is related to the increase in nitrate in the euphotic zone and that its minimum concentration occurred when the surface temperature rose and the water column was less stable.

The offshore distribution of *G. polyedra* showed a pattern similar to that of the salinity distribution (Fig. 3). The 33.8‰ isopleth defined approximately the upper and lower boundaries of the bloom. Since the California Current in this area is characterized by low salinity water, the parallelism suggests that the organisms were associated with this water mass.

Relationship between the red water organisms and the biological parameters—On the basis of cell numbers, neither *G. polyedra* nor the large dinoflagellates were predominant in the phytoplankton community, but the correlation between chlorophyll and either the number of *G. polyedra* cells (Fig. 4) or the total number of all large

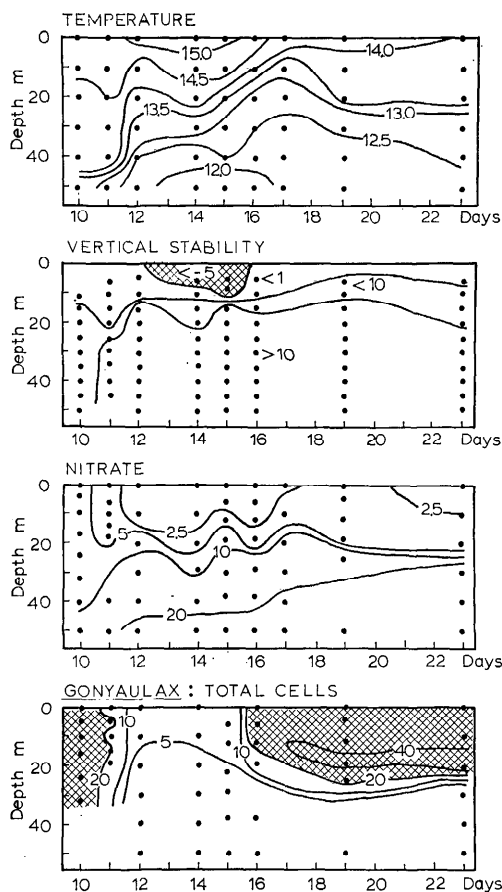


Fig. 2. Time series of temperature ($^{\circ}\text{C}$), vertical stability [$E = 10^{-8} (d\sigma_t/dz)$], nitrate ($\mu\text{g-atom liter}^{-1}$), and *Gonyaulax polyedra*: total phytoplankton cells (%), 5 km off Punta San Hipólito.

dinoflagellates (Table 2) was highly significant.

The importance of dinoflagellates as contributors to the total plant biomass is also reflected in changes of the chemical composition of the water (Table 3). The samples where dinoflagellates represented $>20\%$ of the total cell number have a higher carbon content per cell and a higher C:N ratio, both characteristics of a dinoflagellate population (Strickland et al. 1969), and in the same range of values as those reported by Holmes et al. (1967) for *Gonyaulax* cultures.

It has been well documented (Margalef

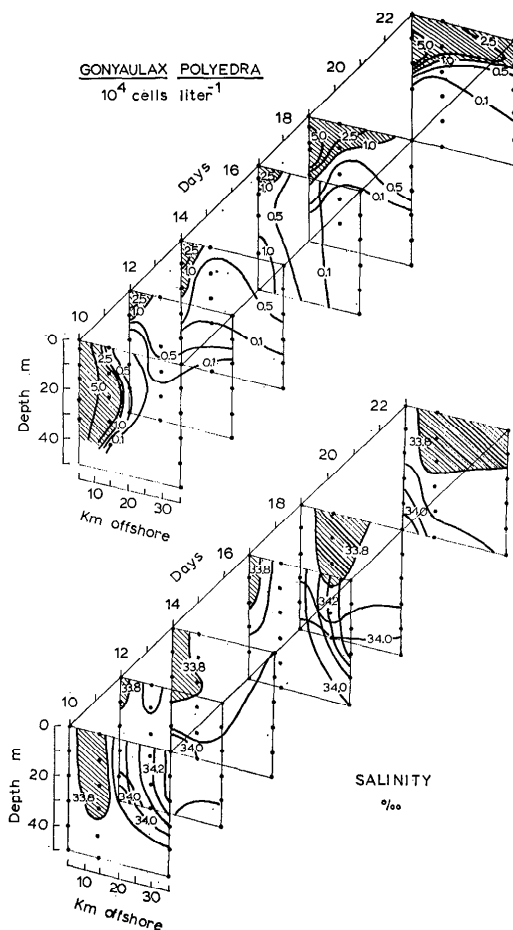


Fig. 3. Time series of repeated onshore transects of *Gonyaulax polyedra* and salinity.

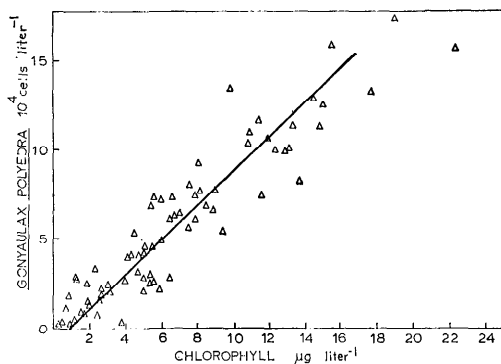


Fig. 4. Relationship between *Gonyaulax polyedra* and chlorophyll a at all stations.

Table 2. Regression equations: $y = A + B$ cell concentration (10^4 cells) where y is μg Chl a or μg ^{14}C , 95% confidence limits for the slope and correlation coefficient, r .

	Chlorophyll μg				Carbon assimilation $\mu\text{g}^{14}\text{C day}^{-1}$			
	A	B	r	N	A	B	r	N
Total cells	3.25	0.087	0.45	82	521.3	0.895	0.07	30
		+0.038				+4.45		
Total cells-Dinoflagellates*	4.07	0.083	0.33	82	545.7	1.136	0.07	30
		+0.053				+6.79		
Total Dinoflagellates	0.96	0.790	0.93	80	114.0	34.70	0.61	30
		+0.062				+17.40		
<i>Gonyaulax polyedra</i>	0.97	1.030	0.93	80	125.4	62.40	0.77	30
		+0.092				+19.50		

* Dinoflagellates > 20 μm .

1968; Malone 1970) that standing crop and phytoplankton productivity are not always directly related, and it has been suggested that physical concentration is one of the major factors in red water blooms. The regression lines of carbon production versus the different fractions of the phytoplankton populations shown in Table 2 indicate that even if the presence of the dinoflagellates could be explained by a physical mechanism, the population was actively growing and was responsible for a high percentage of the total primary productivity. Furthermore, the estimated

growth rate for the dinoflagellate population, $0.82\text{--}0.79\text{ d}^{-1}$, agrees with the field values for the whole phytoplankton population (Walsh et al. 1974).

An independent estimate of the contribution of the dinoflagellates to the production of the area can be made by using the chlorophyll content and assimilation index of both fractions—dinoflagellates and nanoplankton. Based on a ratio of *Gonyaulax* to nanoplankton of 24:1 in chlorophyll content and 1:2 in assimilation index (Holmes et al. 1967; Malone 1970) for all the stations where the ratio *Gonyaulax*:

Table 3. Mean values of chemical composition of organisms from field measurements, in picograms per cell. Total number of samples in parentheses. Mean standard deviation below.

	Mescal I		Holmes et al. 1967	
	Dinoflag. Total Cells >20%	Dinoflag. Total Cells <20%	Red-water Samples	<i>Gonyaulax</i> Culture
Chl a : cell	32.8 (31) 9.26	14.7 (84) 8.4	33.0; 28.0	48.0
C: cell	3,656 (25) 2,622	1,390 (67) 958	5,600; 2,000	3,500
C: N	9.20 (15) 3.50	6.41 (36) 2.77	6.1; 7.1	

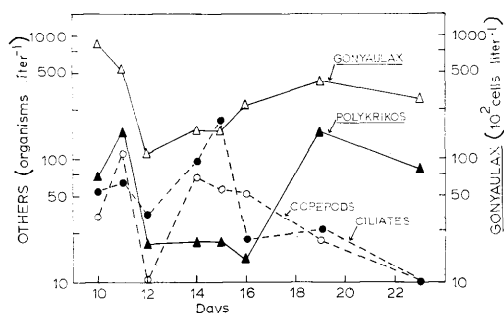


Fig. 5. Time distribution of mean average over upper 40 m of *Gonyaulax polyedra* and *Polykrikos kofoidii*, copepods, and ciliates.

total cells was higher than 10%, we find that dinoflagellates were the main primary producers.

Distribution of microzooplankton—During this study phagotrophic dinoflagellates, ciliates, and copepodites were also counted in the phytoplankton samples. All three groups of organisms are possible grazers of dinoflagellate blooms and may have been responsible for the disappearance of certain blooms. Two phagotrophic dinoflagellates were observed: *Noctiluca scintillans* and *Polykrikos kofoidii*. The first was present only in some samples and in very low numbers; the second was almost always present, with maximum concentration following with a small lag the maximum concentration of *G. polyedra* (Fig. 5). However, the concentration of *P. kofoidii* was 10^3 times lower than that of *G. polyedra*.

The average concentration of ciliates at the sea surface was $1,300 \text{ liter}^{-1}$. This value is similar to those reported for other areas (Margalef 1963, 1973; Beers and Stewart 1969), and higher than the value given by Beers and Stewart (1967) for the California Current. The maximum density, $6,000 \text{ liter}^{-1}$, found at station 20, is lower than the maximum observed in other regions and also lower than the maximum observed in the same region on a cruise the following year. The mean ratio in the euphotic zone for the phytoplankton cells to ciliates was ten times higher than the ratio reported by others; the mean ratio for *G. polyedra* : cili-

ates was 100 : 1. With the exception of the holotrich *Tiarina fusus*, observed at all the stations, almost all the ciliates belonged to the group of small ($40 \mu\text{m}$) oligotriches without lorica. When we consider that the dominant ciliates observed during this study were similar in size to *G. polyedra*, that their abundance was low, and that the relationship between the distribution of the two organisms was not significant (Fig. 5), it seems reasonable to assume that the ciliates were not feeding primarily on *G. polyedra*.

Of course, 50-ml samples are not adequate for counting copepods; nevertheless, the mean value for the whole period, $35 \text{ organisms liter}^{-1}$, provides a lower-bound estimate of the importance of the copepod population in the area. The concentration was highest in the beginning of the first week; later the population declined (Fig. 5). Nauplii and copepodites were the most numerous organisms seen. Based on the ratio of *G. polyedra* cells to copepods, a growth rate for the phytoplankton population of 0.8 doubling per day, and the assumption that all the phytoplankton production was consumed by the copepods, we can estimate a mean ingestion rate of about 90 cells per hour per organism. Paffenhöfer (1971) gave the mean ingestion rate over the whole developmental period for *Calanus helgolandicus* feeding on *Gymnodinium splendens* as 92 cells per hour per organism. Since *G. splendens* and *G. polyedra* are similar in size and since the phytoplankton concentration used in Paffenhöfer's experiments is similar in range of those found during this cruise, it seems likely that copepods controlled the phytoplankton production during this period.

Discussion

Earlier workers concluded that dinoflagellates were typical organisms of oligotrophic areas or were characteristic of the terminal assemblage in the succession of a phytoplankton community. Eppley et al. (1968) and Eppley and Harrison (1975) observed that dinoflagellates were associated with upwelling, but only when the

nutrient enrichment did not reach the surface and where a shallow but steep thermocline was maintained. The results presented here indicate that dinoflagellates are able to outcompete diatoms even in more extreme conditions. The largest population of dinoflagellates was observed when the $\text{NO}_3\text{-N}$ concentration at the surface was highest, when significant temperature gradients were absent, and when the stability of the water column was relatively low. The discrepancy between these results and the previous idea of the role of dinoflagellates suggests that a different analysis of the phenomenon observed might be fruitful. The persistence of a dinoflagellate bloom results not only from its successful development but also from its successful maintenance. Usually these two processes are considered together, but a clearer analysis may follow if they are treated separately. The 20-day longevity of the bloom is easily explained by the competitive advantages of dinoflagellates once a threshold cell density has been achieved: their ability to migrate into zones with optimum levels of light and nutrients; their freedom from sinking losses; and their potential for excreting products inhibitory to other phytoplankton groups (Hasle 1950, 1954; Eppley et al. 1968; Wyatt and Horwood 1973). Certain hydrographic conditions are prerequisite for the dinoflagellates to exploit these advantages, but despite the vast amount of existing information the thresholds of these hydrographic conditions have not yet been defined. During this cruise, the dinoflagellate population underwent a clear diel vertical migration (Walsh et al. 1974), suggesting that although upwelling was in progress, these organisms were able to exercise their characteristic advantages.

Although the duration of the bloom can thus be explained, it is more difficult to explain its development, especially in view of the character of upwelling water. Laboratory experiments with dinoflagellates (Kain and Fogg 1960; Seliger et al. 1971; Sweeney 1975) have shown that dinoflagellates have lower division rates than diatoms and that their growth requirements are more spe-

cific. It is evident that in order for them to outcompete a diatom population some environmental criteria must be met, for example, a nutrient-depleted shallow mixed layer, a steep shallow thermocline, or the presence of discrete water masses (Slobodkin 1953; Margalef 1960; Eppley and Harrison 1975). Since none of these conditions was present during the cruise, it appears that the dinoflagellates must have been introduced into the area by the downstream flow of surface water. Supporting this suggestion is the parallelism in the distribution of dinoflagellates and low salinity water.

Sources of the initial dinoflagellate population could have been a red tide on the southern coast of California or a seeding mechanism associated with Vizcaino Bay. The hydrographic characteristics of this bay (north of the area studied) suggest that it might provide an optimum environment for the development of dinoflagellate blooms. The water in Vizcaino Bay moves slowly alongshore in a clockwise eddy, pours out of the bay south of Cedros Island, and converges with the main flow of the California Current (Dawson 1952; Willie 1961). There is no available information on the phytoplankton of the bay, but if a red tide had occurred there during this study, part of it would have been washed out and would have provided a continual seed supply for the water around Punta San Hipólito. As for the first possibility, given a downflow stream of $20\text{--}25\text{ cm s}^{-1}$ (Walsh et al. 1974), a dinoflagellate bloom lasting 20 days off Punta San Hipólito would require a pre-existing red tide extending 300 to 400 km along the Baja California coast from San Hipólito to San Diego. Such a red tide of *G. polyedra* extending for 300 km along the California coast from Santa Barbara to San Diego was observed by Torrey (1902). Unfortunately, samples were not taken in the regions north of Punta San Hipólito. However the observation of Sweeney (1975) that red tides off San Diego occur later in the season suggests Vizcaino Bay as the most probable source in the present case.

Finally, the possibility that dinoflagellates can be as important as diatoms in the upwelling phytoplankton community is a new factor in our understanding of the trophic relations of coastal upwelling ecosystems. Since these groups have completely different physiological and biological characteristics and chemical composition, both must be considered in predictions of production in these regions.

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