RED TIDES I HAVE KNOWN

Beatrice M. Sweeney

Department of Biological Sciences
University of California
Santa Barbara, California 93106

ABSTRACT

Quantitative data for the species composition of dinoflagellate red tides which I have observed during the last 25 years in southern California and elsewhere are presented. One species is usually markedly more plentiful than any other. *Gonyaulax polyedra* and *Prorocentrum micans* have been the dinoflagellates responsible for red water along the coast of southern California. Near Madang, in New Guinea, I observed red tides of *Gonyaulax polygramma*, *Pyrodinium bahamense* f. *compressa* Bohm, and the blue-green alga *Trichodesmium*, and at Oyster Bay, Jamaica, red water caused by *Pyrodinium bahamense*.

Red water typically is restricted in its distribution, both vertically and laterally. Water collected within a red patch containing large numbers of *Prorocentrum* was shown to have growth-promoting properties for this species in culture, while water from outside this patch did not. The vitamin B_{12} content of both samples by *Euglena* bioassay was identical, 0.02 mμg ml^{-1}, and *Prorocentrum* cells from these water samples both contained 0.7 mμg mg^{-1} dry weight. Sea water collected at a time when there was no red tide contained much smaller amounts of vitamin B_{12}, as did *Prorocentrum* cultured in medium made up with this sea water. Thus *Prorocentrum* may accumulate this and perhaps other organic micronutrients in excess of immediate requirements. No evidence was obtained for toxicity of *Gonyaulax polyedra*, either in red water or in culture.

INTRODUCTION

"Red tides" are spectacular phenomena when the sea turns the color of tomato soup because of the presence of large numbers of organisms, often dinoflagellates,containing orange or red pigment. When the species responsible produces a toxin, aquatic animals may be killed. The longest series of observations of red tides in the world is probably that at La Jolla, California. Between 1924 and 1945, Allen (1-5) documented 5 red tides there, two caused by *Prorocentrum micans* in 1924 and 1933, and three caused by *Gonyaulax polyedra* in 1938, 1942 and 1945. My observations of this interesting phenomenon at La Jolla began in 1949 and continued until 1961. I have also been privileged to see red tides in Oyster Bay, Jamaica and near Madang in New Guinea, and, since 1967, in the vicinity of Santa Barbara, California. After my departure from Scripps Institution of Oceanography, others continued observations of red tides there (9).

QUANTITATIVE DATA WITH REGARD TO DATE, LOCATION AND SPECIES COMPOSITION

Cell counts of the red tides which I have observed personally (Table I) show clearly that only a single dinoflagellate is responsible for the discoloration of the sea at any one time. The only exception to this generalization was in 1961.

Table I

Red tides observed by the author

Date	Location	Organism Responsible	Number of cells ml^{-1} in Surface Water: Most Plentiful Dinoflagellate	Other Dinoflagellates	Others
7/11/52	La Jolla, Ca.	*Prorocentrum micans*	2470	36	34
3/9/54	"	"	12000	40	-
4/26/54	"	"	2080	12	-
4/21/55	"	"	1430	330	-
6/17/58	Ensenada, B.C.	*Gonyaulax polyedra*	15400	25	-
7/4/58	"	"	1900	82	2
7/21/58	Imperial Beach, Ca.	"	7510	-	-
8/15/58	La Jolla, Ca.	"	22200	43	-
4/13/61	"	*Prorocentrum micans*	880	122(95 *Gonyaulax*)	-
4/28/61	"	*Gonyaulax polyedra*	3780	1710 (1350 *Prorocentrum*)	-
1/13/66	Oyster Bay, Jamaica	*Pyrodinium bahamense*	590	16	-
10/13/69	Bostrem Bay, New Guinea	*Gonyaulax polygramma*	3440	-	-
10/4/70	Santa Monica, Ca.	*Gonyaulax polyedra*	13180	200	-
7/30/71	"	"	20000	0	-
8/4/71	Rinçon, Ca	"	8060	435	-
8/7/71	"	"	12610	75	-
8/16/71	Goleta Bay, Ca.	"	9330	0	-
8/18/71	"	"	5310	125	-
9/8/72	"	"	5160	0	1
9/15/72	"	"	7000	63	-
10/22/73	"	"	1440	1	-
8/2/74	Long Beach, Ca.	"	7540	9	-
8/10/74	Ventura, Ca.	"	3720	13	25
8/19/74	Rinçon, Ca.	"	11200	28	3

The dominant organism was accompanied by a mixture of other dinoflagellates, relatively few in number. It is remarkable that only two dinoflagellates, *Gonyaulax polyedra* and *Prorocentrum micans*, have been responsible for every red tide I have seen off Southern California, yet the nutritional requirements of photosynthetic dinoflagellates, as determined in culture, appear to be similar, and no special features distinguish either *Gonyaulax polyedra* or *Prorocentrum micans*, as far as we know. Indeed, accompanying organisms are almost exclusively dinoflagellates (Table I), in California a mixture of *Ceratium dens, C. furca, C. fusus, Gymnodinium splendens* and a number of species of *Peridinium*, which suggests that conditions are generally favorable for the growth of dinoflagellates at times when a red tide develops.

Although there have been exceptions (9), red tides typically occur in the summer in S. California, *Prorocentrum* red tides somewhat earlier than those in which *Gonyaulax* is the dominant organism. In Oyster Bay, Jamaica, red water persists during the entire year, and the organism responsible for the discoloration of the water, and incidentally for brilliant displays of bioluminescence, is *Pyrodinium bahamense*. In New Guinea on Kranket Island near Madang, large numbers of a similar *Pyrodinium bahamense* f. *compressa* Bohm[1] were seen in October, 1969, during the "Alpha Helix" expedition to New Guinea. The more open Bostrem Bay near by developed a deep orange color at the same time, but here *Gonyaulax polygramma* was responsible. In the open sea off Madang, a third red tide was observed, due to large numbers of *Trichodesmium* sp. This organism is a red blue-green alga, not a dinoflagellate. All the red tides observed in California and in New Guinea (Table I) occurred during the dry season, so run off from the land does not seem to be an important factor in the development of a red tide.

In 1958, 1971 and 1974, red water appeared first in the southernmost part of the California coast, as far south as Ensenada, Baja California in 1958, and progressed northwestward up the coast over a period of several months. Although water generally moves north along the Southern California coast, it is not known whether the organisms or only the favorable conditions moved northward. However, in La Jolla in 1952, plankton samples were collected from Scripps pier every day. Samples for each week were combined and the number of *Prorocentrum* in these samples was counted after a red tide of *Prorocentrum* occurred in July (Fig. I). The increase in the number of this dinoflagellate between May 26 and July 10th could be accounted for by a growth rate of 0.3 divisions day $^{-1}$ (broken line, Fig. 1), in good agreement with growth rates measured in culture. Thus it is not impossible that the red tide developed by cell division of the local *Prorocentrum* population.

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1 The author is indebted to Dr. Enrique Balech for the identification of the *Pyrodinium* and *Gonyaulax* from New Guinea.

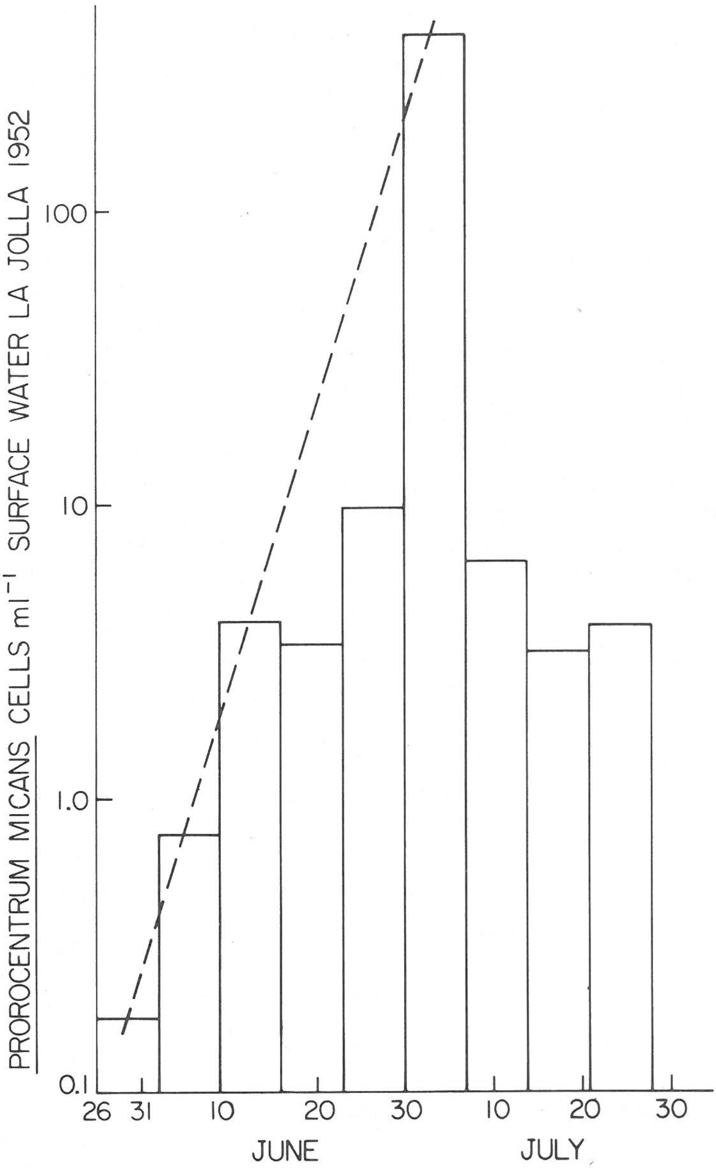

Figure 1: The number of *Prorocentrum micans* in water samples collected from the pier at Scripps Institution of Oceanography in May-July, 1952. Samples were collected daily. One ml samples for each day of a week were pooled and counted to give the average number of cells for that week. Red water was observed on July 7-11, 1952. The dotted line is the calculated growth rate of 0.3 divisions day^{-1}.

The organsims collected during red tides were motile and appeared to be in good condition. The number of bacterial colonies growing on plates inoculated with red water collected aseptically by Donald Lear at La Jolla, 7/26/54, was not higher than usual: less than 50 bacteria ml^{-1}. During the last few days of red water on several occasions in Santa Barbara, large numbers of resting spores of *Gonyaulax* were observed.

DISTRIBUTION

Red water is usually restricted to discrete patches, the edges of which are so distinct that it is possible to locate them even from a small boat. The same organism is found outside as well as inside these patches but in much lower numbers (Table II). On three occasions when samples were collected from different depths in a red patch during the day, large numbers of the organism responsible for the discoloration of the water were only found in the top few meters (Fig. 2). Dinoflagellates other than the most common species were evenly distributed with depth, down to 10-15 m. In laboratory cultures, *Prorocentrum micans* and *Gonyaulax polyedra* are only weakly phototactic, but there is evidence for their vertical migration in the sea (7, 8). Red patches have been observed to disperse at night and reform in the morning (9), possibly through phototaxis. However, the sharp horizontal boundaries cannot be explained by phototaxis and may mark the separation of two distinct water masses.

Table II

Prorocentrum micans, cells ml^{-1} in surface water inside and outside red water patches, La Jolla, California

Date	Cells ml^{-1} Inside red patch	Cells ml^{-1} Outside red patch
7/10/52	1350	240
7/11/52	2456	440
7/21/52	800	260
7/26/54	2080	150

BIOLOGICAL PROPERTIES OF RED WATER

During the red tide of 1952, water samples from inside and outside a red patch were tested for promotion of the growth of *Prorocentrum micans* in culture. Both sea water samples were filter-sterilized and then added as a supplement to mineral-enriched aged sea water medium. Water collected

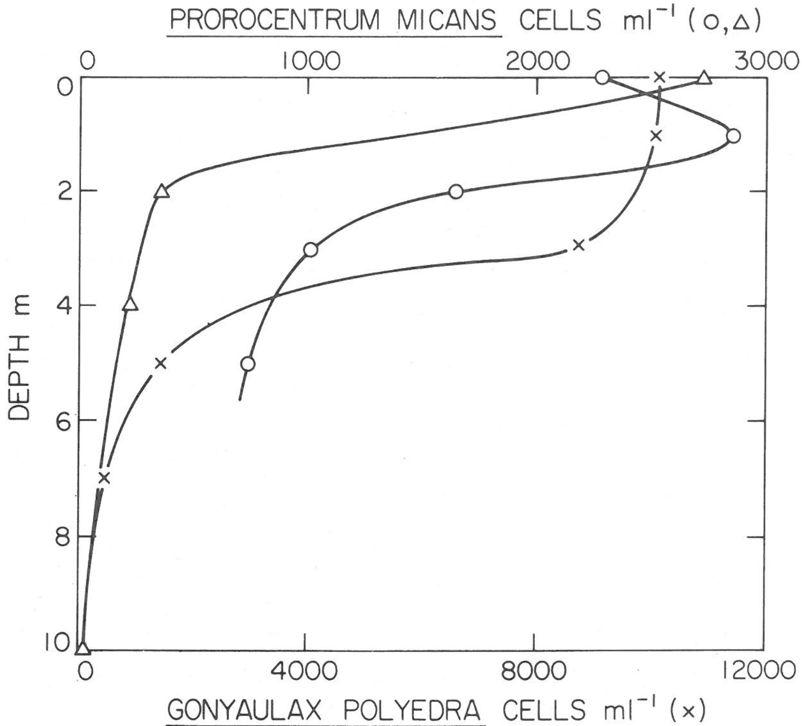

Figure 2: The distribution of red tide organisms with depth: *Gonyaulax polyedra*, Ensenada, B.C. 6/18/58 (X); *Prorocentrum micans*, La Jolla, Ca. 7/10/52 (0), and 7/11/52 ( ). Accompanying dinoflagellates: on 7/10/52 *Ceratium dens.* 100 ml^{-1}, *C. furca*, 100 ml^{-1}, *Peridinium* sp, 100 ml^{-1}; on 7/11/52, *C. dens*, 10 ml^{-1}, *C. furca*, 10 ml^{-1}, *Peridinium* sp, 10 ml^{-1} at all depths. Samples were collected during the day.

inside a red patch promoted the growth of the *Prorocentrum*, while water from outside this patch was only slightly growth-promoting (Table III). Boiling the water samples abolished all activity.

Since dinoflagellates require an external source of vitamin B_{12}, the possibility that this vitamin was responsible for the growth-promoting activity of water from the red patch was explored. Vitamin B_{12} was detected by *Euglena* bioassay in sea water from both inside and outside the red patch, but both samples contained the same amount of vitamin B_{12}, 0.02 mμg ml^{-1}. *Prorocentrum* cells, removed by filtration from the two water samples, were also similar with respect to their content of vitamin B_{12}, 0.7 mμg mg^{-1} dry weight or about 3 mμg in 10^6 cells. This value was kindly corroborated by independent assay carried out by Dr. David Hendlin of Merck and Co. No vitamin B_{12} could be detected in the aged sea water collected before the red tide, and very little in bacteria-free *Prorocentrum micans* grown in medium

Table III

Growth promotion of *Prorocentrum micans* in culture by filter-sterilized sea water from inside and outside a red water patch, 7/10/52.

Basal medium: aged sea water supplemented with nitrate, 2 mM, phosphate, 0.2 mM, $FeCl_3$, 0.05 mM, EDTA, 1 mg. l^{-1} and micronutrients (Arnon's A_4B_7). Natural illumination, 20°C. Inoculum: 0.05 ml; medium : 5 ml.

Supplement:	0	4% soil extract	5% sea water from *inside* red patch	5% sea water from *outside* red patch	5% sea water from *inside* red patch, *boiled* 1 min	5% sea water from *outside* red patch *boiled* 1 min.
Yield, cells ml^{-1}	0	19670	16000	150	200	0

made up using this sea water, 0.13 mμg in 10^6 cells in one culture (assayed 3/31/53) and none in another (assayed 2/9/53).

Considered together, these observations point to the existence of a growth-promoting substance or substances, present in the red patch and absent outside it. It is unlikely that inorganic macro- or micronutrients were responsible for the growth promotion observed, since the assay medium contained P, N, Fe and micronutrients. Vitamin B_{12} does not seem a likely candidate, since there was no difference with respect to this vitamin either in water samples or cells from inside and outside a red patch. However the higher vitamin B_{12} content of *Prorocentrum* from the red tide, as compared with the same species in culture, suggests that these cells can accumulate an excess of this and perhaps also of other organic micronutrients. The accumulation of growth factors in excess of immediate needs and the observed progression of red water northward along the coast of California raise the possibility that the initiation of a red tide may be distant, both in time and in space, from its realization.

THE QUESTION OF TOXICITY

Since *Gonyaulax catenella* is known to produce saxitoxin (6, 10, 11), the possibility that *Gonyaulax polyedra* might be toxic was examined, although no mass mortality of any kind was observed during any of the red tides listed in Table I. Samples (1 1/2 or 2 liters) of the *Gonyaulax* red tide in June and July, 1958, were transferred to Fernbach flasks in the laboratory at Scripps

Institution of Oceanography, and aerated gently. Sea water collected during the previous winter and laboratory cultures of *Gonyaulax polyedra* served as controls. Two anchovies or two red crabs [2] (*Pleuroncodes planipes*) were introduced into each flask, and the behavior and survival of these animals were observed for several days. Neither the naturally occurring nor the cultured *Gonyaulax polyedra* showed any evidence of toxicity under these conditions.

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[2] The author wishes to acknowledge the collaboration of Carl Boyd in these experiments.

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