

SEASONAL AND BATHYMETRIC DISTRIBUTION OF THECATE AND NONTHECATE DINOFLAGELLATES OFF LA JOLLA, CALIFORNIA

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ABSTRACT

A one-year study of the spatial and temporal distribution of thecate and nonthecate dinoflagellates over 50 μm in length was carried out at two stations off La Jolla, southern California.

The survey revealed larger dinoflagellate populations at the Secchi level than at the surface, composed principally of nonthecate forms. The relative contributions of thecate and nonthecate dinoflagellates at three levels within the euphotic zone are presented, with special reference to autotrophic or heterotrophic characteristics of the leading species.

RESUMEN

Se realizó durante un año un estudio de la distribución espacial y temporal de dinoflagelados tecados y atecados de más de 50 μm de longitud, en dos estaciones frente a La Jolla, en el sur de California.

El reconocimiento reveló la presencia de poblaciones más grandes de dinoflagelados en la profundidad Secchi que en la superficie, compuestas principalmente por formas atecadas. Se presentan las contribuciones relativas de dinoflagelados tecados y atecados en tres niveles dentro de la zona eufótica, con atención a las características autotróficas o heterótrofas de las especies más abundantes.

INTRODUCTION

A one-year study, December 1976–December 1977, of both thecate (armoured) and nonthecate (naked) dinoflagellates was carried out at two stations off La Jolla, California.

Although the terms thecate and nonthecate are used throughout this contribution, the author is aware of differences of opinion among various investigators regarding these terms. The existence of platelike polygonal patterns observed on some of the "naked" species may be caused by membrane-lined cavities within the outer layer of the cells as discussed by Taylor (1976), who also reviews the work of other investigators in this respect.

The primary purpose of the present study was to

assess distribution patterns and the ratio of naked to armoured dinoflagellates with particular stress on the ability of the former to use phagotrophy as one method of heterotrophic nutrition. Although phagotrophy is not limited to nonthecate dinoflagellates, this form of nutrition is more common in members of this group. Many of them are devoid of photosynthetic pigments, and they must rely entirely on heterotrophic nutrition either by ingesting or otherwise absorbing dissolved or particulate organic matter.

There was more likelihood of detecting instances of phagotrophy in the larger forms of thecate and nonthecate dinoflagellates. However, the occurrence of large numbers of dinoflagellates smaller than 50 μm was noted.

The author became aware, at an early stage of the study, of the presence of a number of fairly large naked dinoflagellates in the live samples collected qualitatively by fine-mesh nets from the same stations or from the Scripps Institution of Oceanography (SIO) pier. Many of these dinoflagellate species, belonging chiefly to the genera *Gymnodinium*, *Gyrodinium*, and *Warnowia*, showed a variety of inclusions, both as food storage bodies as well as ingested particles. However, the presence of these organisms in the preserved samples collected at the same stations was often overlooked due either to distortion resulting from fixation or to disintegration. It is proposed to discuss further these large phagotrophic dinoflagellates in a separate contribution.

LITERATURE SURVEY

There are a number of contributions dealing with the occurrence of dinoflagellates off the coast of southern California, mainly in relation to those species causing red tides. The dinoflagellates considered are a fairly limited number of autotrophic bloom-forming species such as *Prorocentrum micans*, *Gonyaulax polyedra*, *Gymnodinium splendens*, and several species of *Ceratium*. The earlier works by Allen who monitored the occurrence of red tides in La Jolla Bay between 1917 and 1945, Lackey and Clendenning (1965), and other investigators were reviewed by Holmes et al. (1967). The latter authors confirmed Allen's (1941) findings that tides caused by *Prorocentrum micans* occurred before midsummer

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whereas those caused by *Gonyaulax polyedra* occurred after midsummer. An interdisciplinary approach to the plankton ecology of the area is to be found in a series of articles dealing with various aspects of this subject by members of the Food Chain Research Group in a publication edited by Strickland (1970).

The specific physiological ecology of *Gonyaulax polyedra*, among the dominant bloom-forming dinoflagellates mentioned above, has recently been analyzed by Eppley and Harrison (1974). These authors relate the local red tides caused by such organisms to nutrient enrichment via upwelling and consider the grazing by phagotrophic dinoflagellates, such as *Noctiluca miliaris*, *Polykrikos kofoidii*, and *Fragilidium heterolobum*, as one of the factors responsible for the decline of these local blooms.

Diurnal vertical migration of dinoflagellates as a function of the particular environmental conditions prevailing off La Jolla was considered by Eppley et al. (1968) in reference to *Ceratium furca* following a bloom off the California coast. This migration in some red tide dinoflagellates, particularly *Gonyaulax polyedra*, might serve as a survival mechanism enabling them to reach water depths where nutrients are available (Eppley and Harrison 1974).

The role of *Gymnodinium spendens*, an unarmoured dinoflagellate, as an important bloom-forming organism in Baja California and off the coast of California is described by Kiefer and Lasker (1975). This bloom seems to be limited to inshore waters, and the species constitutes an important food organism for anchovy larvae (Lasker 1975).

Many of the unarmoured dinoflagellates occurring off the coast of southern California may not be responsible for any of the red tides reported in the past but may well play a significant role in the food chain as active phagotrophs. The most notable contribution on this subject is in Kofoid and Swezy's (1921) monograph on unarmoured dinoflagellates. In this work, many of the large heterotrophic dinoflagellates also encountered in the present study have been described in detail, many of them showing ingested organisms. More recent references on phagotrophic nutrition by dinoflagellates are by Norris (1966), Norris (1969), Beers et al. (1975), who also review other reports of phagotrophic feeding, and by Kimor (1979) in relation to the predation of *Noctiluca miliaris* on *Acartia tonsa* eggs in the inshore waters of southern California.

MATERIALS AND METHODS

Location of the Stations (Figure 1)

Two stations, designated as 2 and 3, were occupied approximately every two to three weeks. Station 1, the

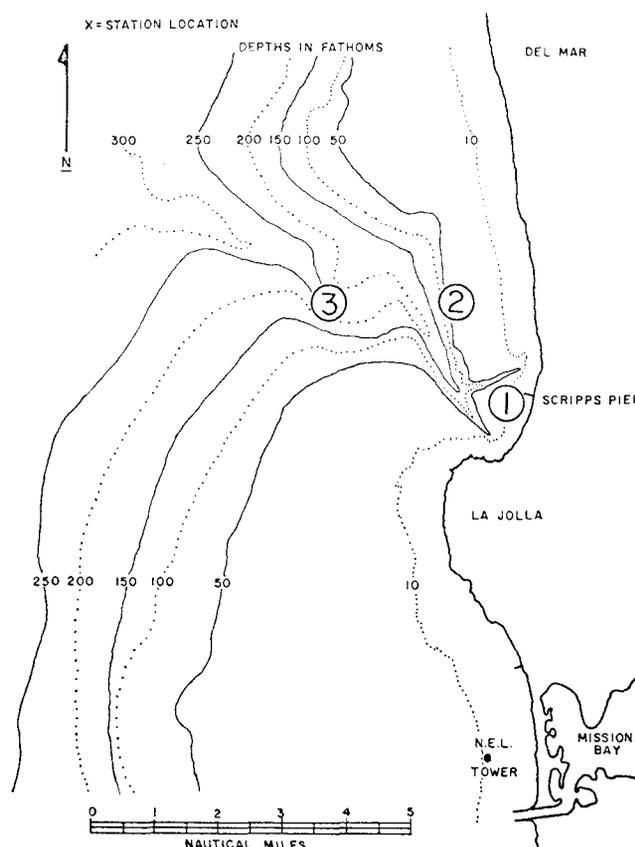


Figure 1. Location of Stations 1-3 (after Strickland 1970).

end of the SIO pier, was used extensively for the collection of living organisms and for records of temperature and salinity.

Station 2 was located at $32^{\circ}53.4'N$, $117^{\circ}16.5'W$, 1.6 km west of the coastline, in waters 72–90 m deep on a gradually sloping coastal shelf which drops rapidly to depths of over 360 m into the La Jolla Submarine Canyon to the west.

Station 3 was located at $32^{\circ}53.4'N$, $117^{\circ}18.6'W$, 5.3 km west of the coastline, in waters 470 m deep in a narrow depression in the La Jolla Submarine Canyon.

Drifting of the boats made it necessary to indicate the location of the two stations by circles, about 400 m in diameter (Figure 1). The coordinates listed above for the two stations refer to the center of the circles.

Sampling

a. Physical data. Transparency measurements (using a Secchi disk) were made routinely at the two stations (Figure 2). It is assumed that 20% of the surface illumination occurred at 1 x Secchi-disk depth (the shallowest depth at which the disk was no longer visible) and 1% at 3 x Secchi-disk depth, as outlined in Strickland et al. (1970), who also referred to the shortcomings of this method. However, technical

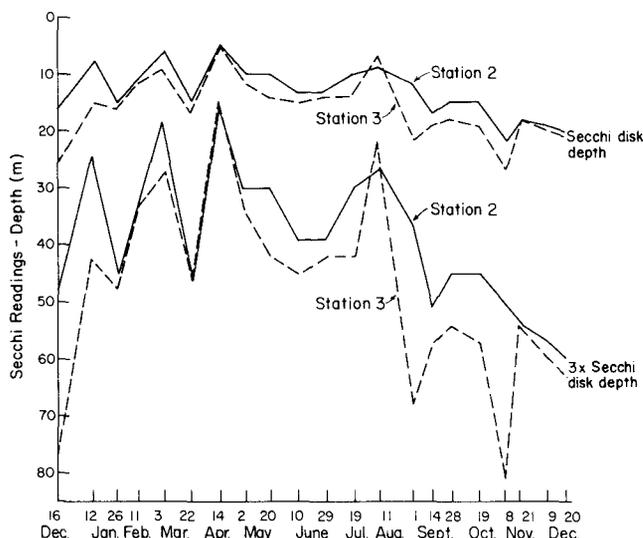


Figure 2. Secchi-disk and 3 x Secchi-disk depth readings at Stations 2 and 3 (December 1976-December 1977).

limitations in the available field work facilities of this investigation prevented the use of a more precise method for measuring the light profile. On four occasions temperature was determined at each of the three depths sampled (Figure 3). Otherwise only surface temperature was determined at both stations as measured by a bucket thermometer (Figure 3). Surface and bottom temperatures and salinities at the end of the SIO pier (Anonymous 1978) during the sampling days are also referred to in this report (Figure 4).

b. Niskin bottles (5 liters) were used to collect water for the preserved material and the chlorophyll samples. Bottles were deployed at the surface, the Secchi disk depth, and 3 x the Secchi-disk depth.

c. The plankton net used to collect live material was a ¼-m open-mouth net of 35- μ m mesh. The materials for live examination were stored in a styrofoam insulated box immediately after sampling.

Sample Analysis

a. Chlorophyll *a* and phaeophytin. Seawater samples (250 ml) were filtered onto Whatman GF/C filters, placed in 90% acetone, extracted for 24 hours at 8–10°C in the dark, and read on a Turner model 110 Fluorometer according to the Strickland and Parsons (1968) method.

b. Preserved microplankton samples. To preserved samples, reagent grade formaldehyde was added to 1-quart prescription bottles so as to produce a final 5% concentration after the addition of the sample. A sub-sample (100 ml) was removed for subsequent reference if necessary, and the remainder was allowed to settle for about 48 hours. The supernatant fluid was removed by vacuum aspiration. The resulting con-

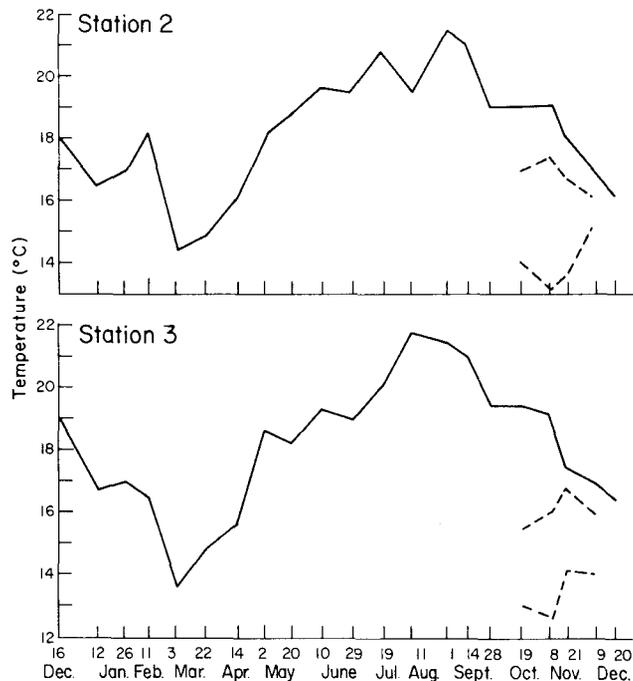


Figure 3. Temperatures at Stations 2 and 3 (December 1976-December 1977).

centrated sample had a known volume between 75–100 ml.

Aliquots (25-50 ml) from the concentrated sample were allowed to settle for at least 24 hours in 9.2-cm-tall cylinders, after which the numerical abundance of the dinoflagellates larger than 50 μ m in length was determined. An inverted microscope at 100 and 200 magnification was used for the counts by the Utermöhl (1932) method. Thecate and nonthecate dinoflagellate species were counted, and instances of inclusions were recorded. The results are expressed as numbers per liter at the species and group level.

The live samples collected from net hauls were examined within an hour of their collection. Photo-

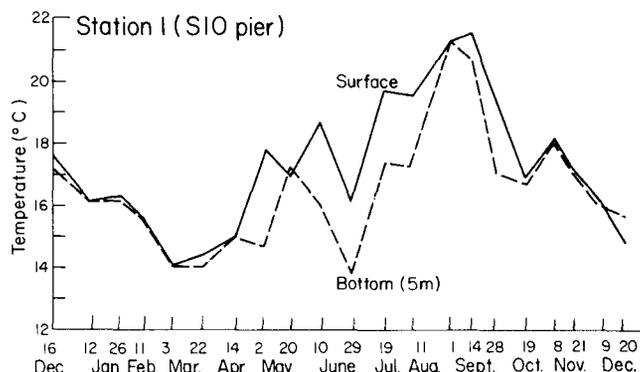


Figure 4. Surface and bottom temperatures at SIO pier (December 1976-December 1977).

graphic records were made, particularly of those forms that showed easily identifiable ingested organisms.

RESULTS AND DISCUSSION

The Environment

The area chosen for investigation is known for its highly variable hydrographic and biological properties (Strickland et al. 1970). The environmental data taken during the present study tended to confirm this variability, with the exception of salinity. The fluctuations of surface salinity recorded at the end of the SIO pier were small, with a minimum of 33.37‰ in August and a maximum of 34.15‰ in July. The differences in the data recorded at the same station at 5-m depth were insignificant (Anonymous 1978).

Temperature records (Figure 4) for the SIO pier (Anonymous 1978) at surface and bottom (5 m) levels indicated a minimum of 14°C in March and a maximum of 21.5°C in September at the surface for the year of this study. Bottom temperatures were roughly 2°C lower during the period April to August 1977, approaching the surface values during the following months.

Surface temperatures at the study sites (Figure 3) showed the same general pattern at both stations.

Temperature records for Secchi and 3 x Secchi depths at Stations 2 and 3, taken during four consecutive cruises between October 19 and December 9, 1977, indicate a decrease in temperature with depth, which might impact on the spatial distribution of the dinoflagellates (Figure 3).

Transparency measurements as indicated by Secchi depth showed strong temporal fluctuations at both stations throughout the year with higher transparencies reported for the outward station during most of the cruises. This trend proved particularly obvious during the latter part of 1977 (Figure 2).

The chlorophyll data for the total phytoplankton population at the two stations cannot be directly related to the standing crop of the portion of the dinoflagellate population considered here (Figure 5). This may be attributed to the difficulty in determining the contribution of photosynthetic dinoflagellate species relative to other autotrophs, notably diatoms, present in the plankton at the same time, location, and depth. For this reason we cannot be sure whether the fairly prominent peak in chlorophyll *a* values recorded at Station 3 in April 1977 was caused mainly or solely by the photosynthetic dinoflagellate *Peridinium trochoideum*. This species was noted as abundant at that time, although it was not counted in the samples since it is smaller than 50 μm . Similarly, the abundance of *Prorocentrum micans*, also a photosynthetic, bloom-forming thecate dinoflagellate, was over 1,400

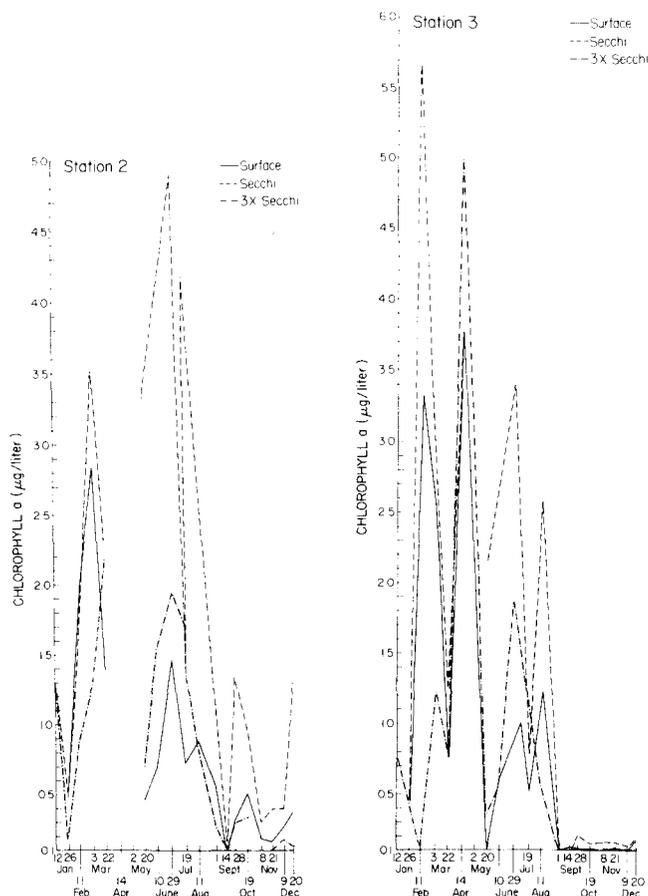


Figure 5. Chlorophyll *a* concentrations (surface, Secchi, and 3 x Secchi) at Stations 2 and 3 (December 1976-December 1977).

cells/liter in the surface layer. This species, together with *Ceratium dens* listed in Table 1, may have contributed to the 29 June 1977 peak at Station 2 (Figure 6).

In general, with the exception of the March peak in surface and Secchi-depth chlorophyll concentrations at both stations, the chlorophyll fluctuations during the latter months did not seem to coincide at the two sites either in time or in depth, suggesting the existence of significant differences in the environment even over this comparatively short distance.

Species composition

Sixty-three taxa of thecate and twenty-eight taxa of nonthecate dinoflagellates were encountered in the course of this investigation. However, in the following sections, reference will only be made to those taxa considered most important on the basis of their numerical abundance or their possible significance as ecological indicators.

Table 1 summarizes for each station and depth the abundances of six dominant thecate species and three dominant nonthecate species recorded in the study. Heterotrophic species are indicated.

TABLE 1
 Dominant Thecate and Nonthecate Dinoflagellates¹ at Stations 2 and 3, December 1976-December 1977.

Species	Depth	Dec 16	Jan 12	Jan 26	Feb 11	Mar 3	Mar 22	Apr 14	May 2	May 20	Jun 10	Jun 29	Jul 19	Aug 11	Sep 1	Sep 14	Sep 28	Oct 19	Nov 8	Nov 21	Dec 9	Dec 20
Station 2.																						
A. Dominant thecate dinoflagellates																						
<i>Ceratium cf. dens</i>	surface				13			96			29	1379	1012	271	27			22				
	Secchi				2			258	13					342			25					
	3 x Secchi							1570														
<i>Ceratium furca</i>	surface	34		24	245	62	1722	2765	57		12	819		1671	22		456	1490	180		166	67
	Secchi					32	51	3914	31				18	949	46	227	628				13	27
<i>Ceratium fusus</i>	3 x Secchi				6			2667														
	surface				27		15	16					200	13	38	38	41	50	222	51	52	18
<i>Dinophysis fortii</i>	Secchi						77							13			13		11			
	3 x Secchi																					
<i>Peridinium depressum</i> ²	surface						95					331	43		22							
	Secchi								31				282	760		38			11			13
<i>Peridinium divergens</i> ²	3 x Secchi								32		13											
	surface						382						115	13								6
<i>Peridinium depressum</i> ²	Secchi					13	109	67					28	24	23	24	21					
	3 x Secchi						13															
<i>Peridinium divergens</i> ²	surface	17			13						12	51	964	23	92	89			222	48		
	Secchi	30		16							11		94	253			25	61	86			
<i>Peridinium divergens</i> ²	3 x Secchi			2	14			126														
	surface																					
<i>Cochlodinium catenatum</i> ²	Secchi					3209	131	21						101		6	264	110				
	3 x Secchi					4119	3388							51	1116	5877	1500				179	
<i>Gyrodinium spp. >65µm</i> ³	surface							21					21									
	Secchi				21		57	43			830	89	94	25	59	10	63					
<i>Torodinium robustum</i> ²	3 x Secchi				12		60				103	21	44					10	10			
	surface											17	12			38	41	44		18		
<i>Torodinium robustum</i> ²	Secchi							56					447	114	42	13		11	13	10		
	3 x Secchi							32							26							
Station 3.																						
C. Dominant thecate dinoflagellates																						
<i>Ceratium cf. dens</i>	surface						41	409						311	27			6				
	Secchi							244						292								
	3 x Secchi							45						11								
<i>Ceratium furca</i>	surface				21	80	937	3117						85	11		45	24		43	23	43
	Secchi					118		2438	6				11		15		124	23				12
<i>Ceratium fusus</i>	3 x Secchi							1796														
	surface			21	21		26							29	27	28	10	98	17			8
<i>Dinophysis fortii</i>	Secchi													146	5		12		6	37		
	3 x Secchi																					
<i>Peridinium depressum</i> ²	surface						118	142						11	5			5		7		
	Secchi					7		105	6				90	785	49			6	8		14	
<i>Peridinium depressum</i> ²	3 x Secchi							60														
	surface						134			6												
<i>Peridinium divergens</i> ²	Secchi						28							11								9
	3 x Secchi																		3			
<i>Peridinium divergens</i> ²	surface				21			53						187	141	5	33	18				10
	Secchi							122						146				12	7			8
<i>Peridinium divergens</i> ²	3 x Secchi	13						30						6		16						3
	surface																					
<i>Cochlodinium catenatum</i> ²	Secchi					1340		18									22	335	110		106	40
	3 x Secchi					3397		35						67	1990	9444	65			88	22	
<i>Gyrodinium spp. >65µm</i> ³	surface														27		5	6				
	Secchi														29	20	61					
<i>Torodinium robustum</i> ²	3 x Secchi						12	30					11	11							10	21
	surface																					
<i>Torodinium robustum</i> ²	Secchi													34	314	20	37		11	17		
	3 x Secchi							10							5		9					

¹In cells/liter. ²Heterotrophic. ³Mostly heterotrophic.

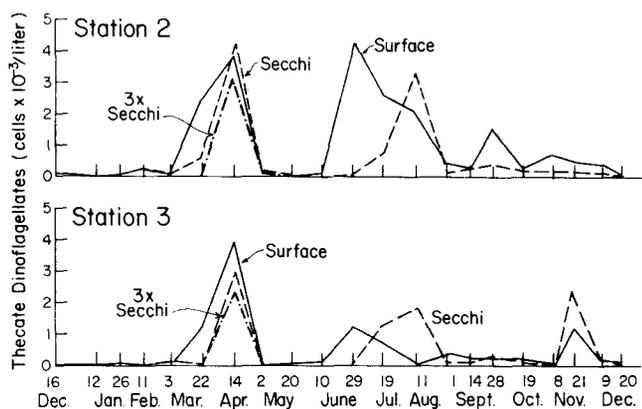


Figure 6. Spatial and temporal abundances (cells $\times 10^{-3}$ liter) of thecate dinoflagellates (December 1976-December 1977).

Spatial and Seasonal Distribution of the Dinoflagellates in the Study Area

The seasonal progression of thecate and nonthecate dinoflagellates at both stations consisted of alternating peaks composed of species belonging to either of the two groups. This pattern, although similar in its general trends at both stations, varied in intensity and species composition (Figures 6 and 7).

For a better assessment of the contribution of the leading species to the total standing crop of dinoflagellates larger than $50 \mu\text{m}$ at any time and depth, as presented in Figures 6 and 7, the abundances of six dominant thecate species and of three nonthecate species are listed in Table 1 by station and depth. One criterion for selecting these species was their general perennial distribution at the two sampling stations. However, other species, such as the photosynthetic *Gonyaulax polyedra*, produced a short-lived peak in November 1977 at Station 3 with 960 cells/liter in the surface sample and 2377 cells/liter at the Secchi-disk depth. At Station 2, it showed more moderate abundances, with 317 cells/liter at surface and 158 cells/liter at Secchi-disk depth (Figure 6).

Additional species of *Peridinium* occurring in low concentrations, such as *P. conicum*, *P. oceanicum*, and *P. steinii*, considered to be heterotrophic (Reid et al. 1970) would add to the heterotrophic component of the dinoflagellate populations if included with the *Peridinium* species listed in Table 1. *Peridinium trochoideum*, recorded as very abundant at both stations in the April 1977 samples and known as one of the few photosynthetic species belonging to this genus, is excluded here as it is less than $50 \mu\text{m}$.

Among the nonthecate dinoflagellates, a number of species of known phagotrophic capability were recorded sporadically in the samples, generally in low numbers. Of these, most common were *Achradina sulcata*, *Erythroopsis minor*, *Kofoidinium* sp., *Noc-*

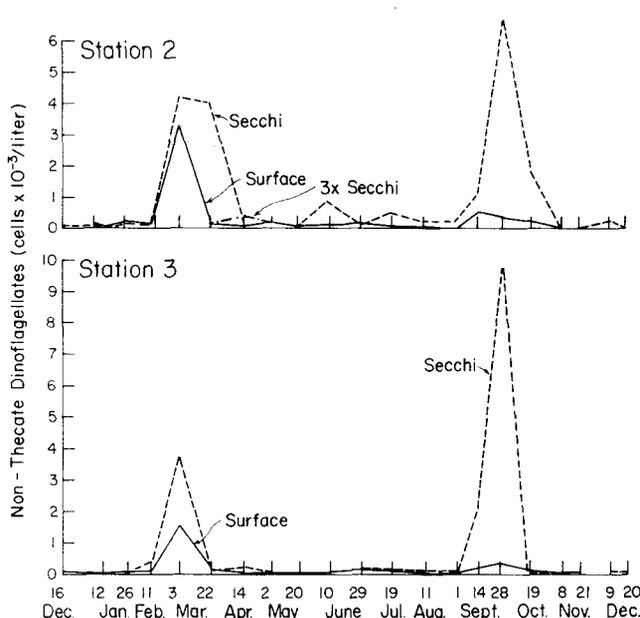


Figure 7. Spatial and temporal abundances (cells $\times 10^{-3}$ liter) of nonthecate dinoflagellates (December 1976-December 1977).

tiluca miliaris, *Polykrikos kofoidii*, *Pronoctiluca pelagica*, and *P. spinifera*. These species were generally preserved in adequate condition to be enumerated. Other species among the nonthecates devoid of photosynthetic pigments, belonging to the genera *Balechina*, *Gymnodinium*, *Gyrodinium*, and *Warnowia*, were recorded principally in live samples collected at Stations 2 and 3 and off the SIO pier and examined soon after being brought to the laboratory. As these species disintegrated completely or lost their shape beyond recognition soon after fixation, they could not be included in the counts.

In some species, such as *Balechina coerulea*, both chromatophores as well as ingested food bodies were detected, suggesting myxotrophic nutrition.

The data, as summarized in Table 2 and Figure 8 on a cruise-by-cruise basis, clearly indicate that the total

TABLE 2
 Yearly Averages¹ of Total, Thecate and Nonthecate
 Dinoflagellates at the Two Stations

Depth	Total	Thecate	Non-thecate	% thecate	% Non-thecate	Whole euphotic zone
<i>Station 2</i>						
Surface	1253	993	260	79	21	
Secchi	1512	542	970	36	64	1100
3 x Secchi	227	176	51	35	65	
<i>Station 3</i>						
Surface	688	529	159	77	23	
Secchi	1601	508	1093	32	68	980
3 x Secchi	187	125	62	67	33	

¹in cells/liter.

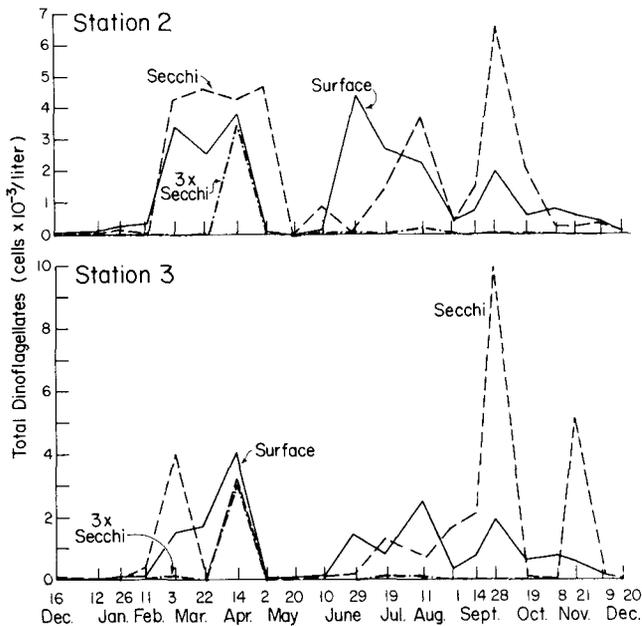


Figure 8. Abundances (cells $\times 10^{-3}$ liter) of total dinoflagellates (December 1976-December 1977).

dinoflagellates showed the highest numerical abundance at the Secchi-disk level. This depth is at about 20% of the surface radiation (Lorenzen 1970) and it often coincided with the chlorophyll maximum within the euphotic zone. However, at both stations the thecate dinoflagellates showed a decrease in numbers with depth, which was more abrupt at Station 2, wherever the nonthecates considerably increased in numbers at the Secchi level relative to the surface values (Figures 6 and 7). This is also reflected in the ratio of thecate to nonthecate dinoflagellates at the three levels (Table 2). In the surface layer at both stations, the thecates predominated (79% and 77% of the total population at Stations 2 and 3, respectively; Table 2 and Figure 9). At the Secchi-disk depth, the ratio was reversed with the nonthecates prevailing at both stations (64% and 68% at Stations 2 and 3, respectively). At both stations there was a marked decrease in numerical abundance at 3 x Secchi, suggesting that light may be a limiting factor, at least for autotrophs, except for a few dark-adapted species. Among the species currently recorded at this depth level, generally in low numbers (with the exception of *Ceratium furca* in April 1977), were species of *Ceratium* and *Peridinium*, *Pyrophacus horologicum* and *Gyrodinium* spp., *Noctiluca miliaris*, *Polykrikos kofoidii*, *Torodinium robustum*, and occasionally *Cochlodinium catenatum*. Many of these species are either facultative or obligate heterotrophs, and some are proven phagotrophs (Steidinger and Williams 1970). On the whole it seems evident that the non-

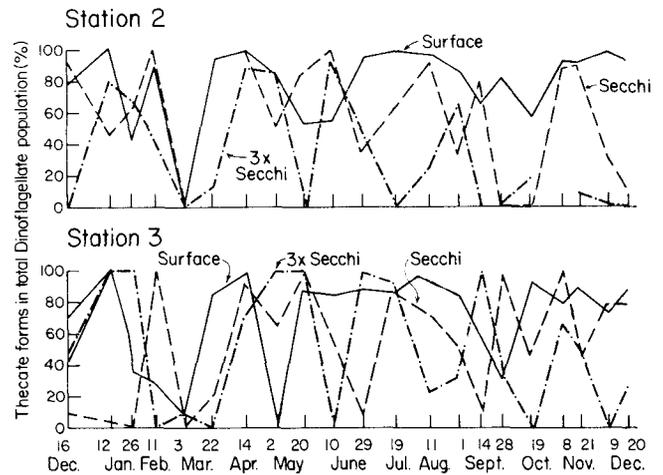


Figure 9. Percentages of thecate forms in total dinoflagellate population (%) (December 1976-December 1977).

thecate dinoflagellates, which include many heterotrophic forms, are better adapted to "shade conditions" as prevailing at and below the Secchi-depth zone.

Characteristics of the Dinoflagellate Community off La Jolla

In this study, 91 taxonomic categories were recorded, most of them identified to the species level. Of the 91 taxa, 63 were thecate forms. The most abundant among these species proved to be *Ceratium furca*, recorded as perennial at Station 2 and particularly common in the upper water layers of both stations. This is in agreement with the biogeography of this euryhaline species, which is considered to be neritic and epipelagic in other parts of the world (Kimor 1972, 1975). Of the 63 thecate taxa, about 20% are considered nonphotosynthetic on the basis of data from literature (Steidinger and Williams 1970) and from personal observations. These supposedly nonphotosynthetic thecate dinoflagellates include among others most of the *Peridinium* forms, with the exception of *P. trochoideum* (F.J.R. Taylor, personal communication). These *Peridinium* species, although present at most times, were not abundant constituents of the plankton during this period. On the other hand, although the genus *Ceratium* as a whole is considered photosynthetic, some of the species, particularly those occurring at the base of the euphotic zone such as *C. setaceum*, seem devoid of photosynthetic pigments and may thus add to the heterotrophic component.

Of the 28 nonthecate taxa within the size class being considered, about 50% are nonphotosynthetic. Some genera, such as *Noctiluca*, *Polykrikos*, *Gyrodinium*, *Warnowia*, and some species of the genus *Cochlodinium*, are typical phagotrophs. Their presence in the

plankton, often in high numbers relative to other members of the dinoflagellate community, makes them an important factor in the structure of the food web.

A survey of the organisms with visible inclusions (whether as accumulation bodies or phagocytized organisms) showed that most were nonthecate species. Among the thecate dinoflagellates, such inclusions were seen in several *Ceratium* species, notably *C. cf. dens* and *C. massiliense*, both with a *Gymnodinium*-like cell inside, *C. pentagonum*, *Dinophysis fortii*, and *D. caudata*. Among the nonthecate dinoflagellates, evidence of phagotrophy was clearly recorded in *Noctiluca miliaris*, *Polykrikos kofoidii*, *Cochlodinium* spp., *Gyrodinium* spp., *Gymnodinium* sp., and *Balechina coerulea*. Dinoflagellate species bearing such inclusions were recorded at all three depths sampled, at both stations. However, most of the species showing accumulation bodies (whether thecate or nonthecate species) were recorded in the surface layer, whereas those species (mostly nonthecate) with phagocytized cells were recorded at the Secchi and 3 x Secchi levels, i.e. toward the base of the euphotic zone.

SUMMARY

1. The seasonal and bathymetric distribution of thecate and nonthecate dinoflagellates greater than 50 μm in length at the surface, Secchi depth, and 3-x-Secchi depth has been described over a one-year period at two stations off La Jolla, southern California.

2. In general, thecate dinoflagellates showed a decrease in abundance with depth, whereas the nonthecates showed a marked increase at the Secchi-disk level.

3. The seasonal peaks in numerical abundance showed an alternation between species belonging to thecate and nonthecate forms, although the occurrence of such peaks did not always coincide for both stations at a given time and depth.

4. Most of the nonthecate heterotrophic dinoflagellates (in the size class considered) were recorded at the Secchi depth during the 3 May 1977 peak, with the partial exception of *Cochlodinium catenatum*.

5. Phagotrophic inclusions, as distinct from food storage bodies, were noted in a few thecate species of the genus *Ceratium* and in a number of the larger nonthecates such as *Noctiluca miliaris*, *Polykrikos kofoidii*, and *Gyrodinium* spp.

6. Examination of live samples collected from different depths at the survey site and at the end of the SIO pier revealed the presence of a number of non-preserved fragile dinoflagellates, most of which contained phagocytized inclusions. Among the species

noted were *Balechina coerulea*, *Warnowia cf. purpurata*, *W. maxima*, and *Gymnodinium* spp.

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LITERATURE CITED

- Allen, W.E. 1941. Twenty years statistical studies of marine plankton dinoflagellates of southern California. *Amer. Midl. Nat.*, 26:603-635.
- Anonymous. 1978. Data report. Surface water temperatures at shore stations. United States West Coast, 1975-1976. SIO Ref., 78-5: 80 p.
- Beers, J.R., F.M.H. Reid, and G.L. Stewart. 1975. Microplankton of the North Pacific Central Gyre. Population structure and abundance, June 1973. *Int. Revue Ges. Hydrobiol.*, 69(5):607-638.
- Eppley, R.W., and W.G. Harrison. 1974. Physiological ecology of *Gonyaulax polyedra*, a red water dinoflagellate of southern California. In V.R. LeCicero (ed.), *Proc. 1st Int. Conf. on Toxic Dinoflagellate Blooms*, Nov. 1974, M.S.T.F., Wakefield, Mass. p. 11-22.
- Eppley, R.W., O. Holm-Hansen, and J.D.H. Strickland. 1968. Some observations on the vertical migration of dinoflagellates. *J. Phycol.*, 4(4):333-340.
- Holmes, R.W., P.M. Williams, and R.W. Eppley. 1967. Red water in La Jolla Bay, 1964-1966. *Limnol. Oceanogr.*, 2(3):503-512.
- Kiefer, D.A., and R. Lasker. 1975. Two blooms of *Gymnodinium splendens*, an unarmored dinoflagellate. *Fish. Bull.*, U.S. 73(3):675-678.
- Kimor, B. 1972. The Suez Canal as a link and barrier in the migration of plankton organisms. *Israel J. Zool.* 21(3-4):391-403.
- . 1975. Euryhaline elements in the plankton of the Bardawil Lagoon (northern Sinai). *Rapp. Comm. P.-Reun. CIESM* 23(3):119-120.
- . 1979. Predation of *Noctiluca miliaris* Souriray on *Acartia tonsa* Dana eggs in the inshore waters of southern California. *Limnol. Oceanogr.* 24(3):568-572.
- Kofoid, C.A., and O. Swezy. 1921. The free-living unarmoured Dinoflagellata. Univ. Calif. Press, Berkeley. 562 p.
- Lackey, T.B., and K.A. Clendenning. 1965. Ecology of the microbiota of San Diego Bay, California. *Trans. San Diego Soc. Nat. Hist.* 14:9-40.
- Lasker, R. 1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and the successful first feeding. *Fish. Bull.*, U.S. 73(3):453-462.
- Lorenzen, C.J. 1970. Surface chlorophyll as an index of the depth, chlorophyll content, and primary productivity of the euphotic layer. *Limnol. Oceanogr.* 15(3):479-480.
- Norris, R.E. 1966. Unarmoured marine dinoflagellates. *Endeavor* 25(96):124-129.

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- Norris, D.R. 1969. Possible phagotrophic feeding in *Ceratium lunula* Schimper. *Limnol. Oceanogr.* 14(3):443-449.
- Reid, F.M.H., E. Fuglister, and J.B. Jordan. 1970. Phytoplankton taxonomy and standing crop. *In* J.D.H. Strickland (ed.), *The ecology of the plankton off La Jolla, California, in the period April through September, 1967*. Univ. Calif. Press, Berkeley. p. 51-66.
- Steidinger, K.A., and J. Williams. 1970. Dinoflagellates: memoirs of the Hourglass cruises. *Mar. Res. Lab. St. Petersburg, Florida* 2:251 p.
- Strickland, J.D.H. (ed.) 1970. *The ecology of the plankton off La Jolla, California, in the period April through September, 1967*. Univ. Calif. Press, Berkeley, 103 p.
- Strickland, J.D.H., and T.R. Parsons. 1968. A practical handbook of seawater analysis. *Bull. Fish. Res. Board Can.* 167:311 p.
- Strickland, J.D.H., L. Solorzano, and R.W. Eppley. 1970. General introduction, hydrography, and chemistry. *In* J.D.H. Strickland (ed.), *The ecology of the plankton off La Jolla, California, in the period April through September, 1967*. Univ. Calif. Press, Berkeley. p. 1-22.
- Taylor, F.J.R. 1976. Dinoflagellates from the International Indian Ocean Expedition. E. Schweizerbart'sche Verlags., Stuttgart, 234 p. + 46 plates.
- Utermöhl, H. 1932. Neue Wege in der quantitativen Erfassung des Planktons. *Verh. Int. Ver. Limnol.* 5:567-595.