THE CHANGES IN THE PHYTOPLANKTON POPULATION OFF THE CALIFORNIA COAST[1]

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(Read by Francis T. Haxo)

Since the studies of the Scandinavian planktologists, particularly those of Cleve at the turn of the century, the microplankton have been recognized as potential indicators of the origin and characteristics of water masses. In the intervening years, the taxonomy of the more important phytoplankton constituents has been advanced and a number of studies have been published in which the distribution of phytoplankton has been carefully correlated with analyses of the chemical and physical features of the surrounding water masses.

Partcularly noteworthy are the studies of Hardy in the South Atlantic and Antarctic (Discovery Expedition), of Steeman Nielsen in the Pacific (Dana Expedition), of Peters and Käsler in the Atlantic Ocean (Meteor Expedition), of Gaarder in the North Atlantic (Cruises of the Michael Sars), and of Graham and Bronikowsky in both the Pacific and Atlantic Oceans (VII Carnegie Cruise). These have provided a great deal of carefully analysed data, especially concerning the dinoflagellates of the genus *Ceratium*. To these we can add my own studies, which have covered the following areas: the south of South America, the Antarctic seas, the Mediterranean, and the Atlantic littoral regions of France and the English Channel.

From these studies it is apparent that, within limits, the broad temperature realms of the oceans have a characteristic flora. While some species are fairly tolerant of wide ranges in temperature, others are restricted in their temperature distribution and are limited, for example, to tropical or to cold waters. Thus the species composition of a given water mass will reflect something of its present and/or previous temperature history. This is particularly valid when assemblages of indicator species are enumerated in characterizing a given water mass.

As background information on the area of present concern, the coastal waters of California, we have among others the studies of Allen extending over a period of more than twenty years, the studies on diatoms by Cupp, the investigation of Sargent and Walker on the relationships between diatom populations and water eddies, and the unpublished studies by Holmes on the phytoplankton of the North and Eastern Pacific. There are also the detailed studies by Kofoid, primarily of a taxonomic nature, on the dinoflagellates and tintinnids, a group of ciliate protozoans.

[1] Contribution from the Scripps Institution of Oceanography.

COMPARISON OF THE QUALITATIVE COMPOSITION OF THE PHYTOPLANKTON IN LA JOLLA DURING THE YEARS 1938-1939 (ALLEN'S COLLECTIONS) WITH 1957-1958

When in December 1957 it became evident that the planktonic populations in La Jolla were of an unexpected warm water, even tropical character, I began a comparative study of recent collections with Allen's samples from the nine month period August 26, 1938 through May 1939, when the water temperature averaged below the long-term mean with the corresponding recent collections in 1957-1958. For this study I have re-examined Allen's collections so that differences in species identification by different observers could be eliminated. Both collections were made from the end of the pier at the Scripps Institution (La Jolla).

Before presenting the results, some mention should be made of the differences in sampling methods employed. Allen was primarily interested in quantitative studies. For that reason he collected small volumes of sea water and the plankton were concentrated by settling. For my studies, the collections were made with a 62μ mesh net. The volume sampled was many times that of Allen for any given day. Because of these differences in methods and in volumes sampled, we can expect that the larger forms would be better represented in my collections. The smaller forms not retained by the net would be better represented in the plankton concentrated by Allen's settling technique. However, because of the greater frequency of Allen's collections (daily), the qualitative differences due to sampling methods might be expected to disappear when collections of a whole month are considered. Notwithstanding the difference in methodology, the differences in composition of the plankton described below were considered to be of real significance.

The results are presented in a somewhat simplified way in figures 113 and 114, in which the more important indicator species of dinoflagellates, diatoms and tintinnidae are listed according to their appearance by months in the two periods under consideration. Such a simplified presentation can give only a rough approximation of the character of the plankton, since stress was placed here on the more persistent species and abundances are not indicated. Considera-

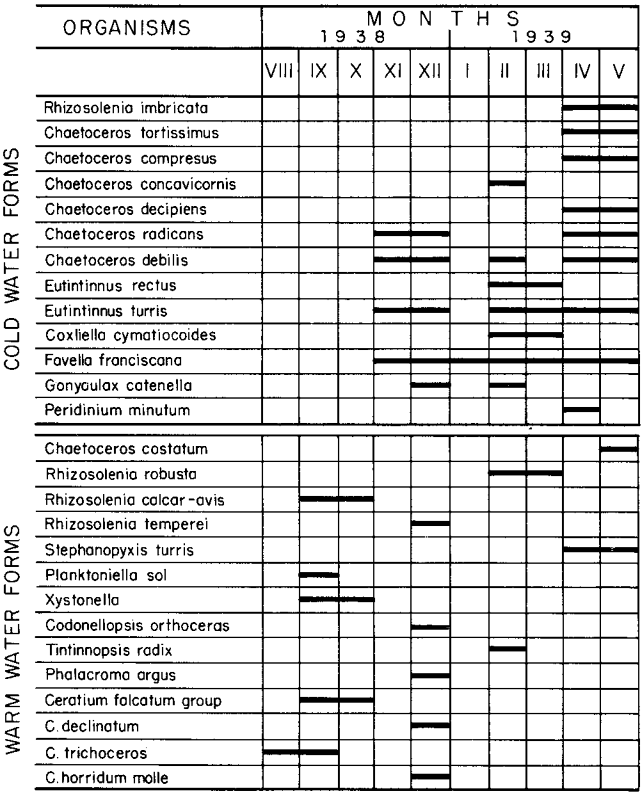

FIGURE 113. **Occurrence during 1938-1939 of dinoflagellates, diatoms and tintinnidae in the plankton at La Jolla.**

tion of the sporadically occurring species only sharpens the contrast between the two years. The figures do not bring out, for example, the significant differences observed in the planktonic populations of January through the first half of February 1958 and those of March 1958. While the former were relatively homogeneous, the latter showed considerable variability in composition.

The most important general conclusion is that the phytoplankton populations of 1957-1958 were atypical in that, on the one hand, warm water and tropical phytoplankton were abundantly represented (largely absent in 1937-1938) and, on the other hand, the appearance of cold water forms was delayed and restricted. No doubt this is a reflection of the warm water prevailing during the past year.

Looking at the two periods in greater detail, we note that Allen's samples collected during the summer of 1938 contained some warm water species but none of the more rare and tropical species, for example, *Ceratium carriense, C. lunula,* and *C. ranipes,* which are well represented in my pier samples of the past year. By late September of 1938 all but one quite tolerant tropical species of *Ceratium* had disappeared. By contrast, in 1957, many tropical species persisted throughout the first part of autumn. Furthermore, in December of 1957 there was an unexpected development. The planktonic population took on a most tropical character in spite of a relatively low water temperature. This was especially striking for the week of December 8-14, when two tropical species of *Ceratium* were collected for the first time. It is noteworthy that during the period December 19-22 of 1938 there was a slight indication of the same phenomenon in Allen's samples, but very much less marked and involving species less truly tropical in nature.

In the early weeks of 1958, as in 1939, the phytoplankton was not very abundant. In the 1958 samples, however, warm water plankton continued to dominate until the middle of February, at which time some changes were noted. We still found some tropical species, but many noted previously had disappeared. On the whole, the plankton showed a relative abundance of diatoms, including some that thrive in cold

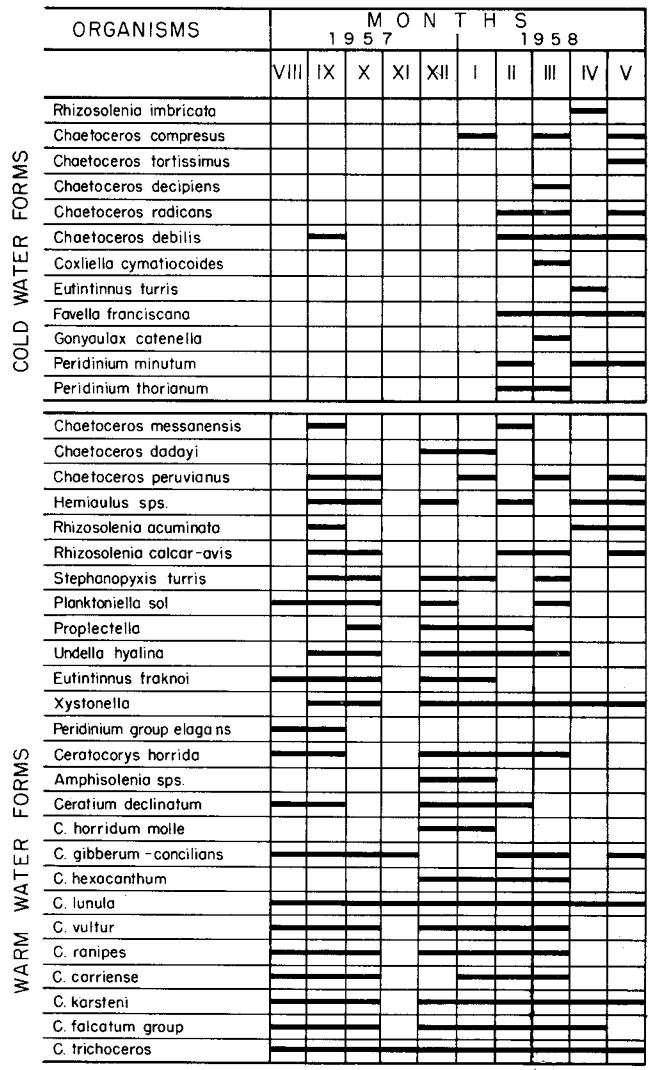

FIGURE 114. **Occurrence during 1957-1958 of dinoflagellates, diatoms and tintinnidae in the plankton at La Jolla.**

water. Present also were several other protists (*Peridinium* and tintinnidae) that seem to prefer cold and temperate waters. During the last part of the month there were noticeable fluctuations in the character of the plankton from a population typical of warm water to a mixed one, with several northern species. By contrast, in 1939, warm water species were not found in January and the plankton of February was dominated by tintinnidae, generally cold and temperate or cosmopolitan species, a situation which continued through April of that year.

Of particular interest is the characteristic presence in the February 1939 collections, as well as those of December 1938, of chains of *Gonyaulax catenella* and its presence in only a single sample of the 1957-1958 collections (a single chain of two in a sample of March 13). From laboratory experience it is known that this dinoflagellate has markedly lower temperature preferences for growth than other *Gonyaulax* species commonly found in the La Jolla area.

In March of 1958 the collections for the first time showed many common features with those of 1938. In general, the plankton were of a mixed and fluctuating character, dominated by zooplankton, especially larvae, with several of the same cold water species of tintinnidae, diatoms and dinoflagellates.

April 1958 showed a regular increase of temperature but not a very great change in the composition of the plankton. However, some typical warm water species were again present, but these were in general poorly represented.

May 1958 showed significant changes by the middle of the month, with a dominance of dinoflagellates, especially *Gonyaulax polyedra* and *Diplopeltopsis minor,* a truly cosmopolitan species. There were several cold or temperate species of diatoms, but the most conspicuous elements of the plankton are widespread species. Also present was a typical warm water diatom, *Hemiaulus membranacea.* By contrast, May 1939 showed plankton with little changes from that of the preceding month. The last half of May 1939 was dominated by *Prorocentrum micans.*

From all this we gain a strong impression of marked difference in phytoplankton composition in the years under comparison. The difference attenuated after 15th February but did not disappear, as shown by the persistence in 1939 of the typical cold water forms and the almost total absence of warm water species so much in evidence in 1958. The greatest anomaly embraced the period, December to the middle of February.

An interesting feature of the plankton studies is that an invasion of warm water in the San Diego region seems normal for December. This feature was also observed in plankton samples for December 1953, available in the Marine Botany Laboratory at the Scripps Institution of Oceanography. These were largely dominated by *Prorocentrum micans,* but samples of December 17 and 18 contained some typical warm water species. On the whole, the plankton composition was very similar to that of December 1938 and quite different from that of December 1957.

GENERAL SURVEY OF THE CALIFORNIA PLANKTON IN APRIL 1958

Although it was not possible to extend observations during the period of greatest anomaly at La Jolla, opportunity was presented during April of this year to incorporate microplankton collections into the CCOFI cruise program. These were made by vertical and horizontal tows with a 62μ net at stations on the MLR grid extending from Baja to Northern California. Very rough weather restricted the planned coverage, particularly north of San Francisco.

Based upon preliminary examination of the collections, the general character of the plankton distribution is shown in figure 115, that of selected warm water dinoflagellates in figure 116, and that of the genus *Ceratium* in particular, in figure 117. It was indeed found that tropical to warm water forms were commonly present as far north as the 15°C isotherm and in some cases extended to the 14°C isotherm. According to previous investigations, species included

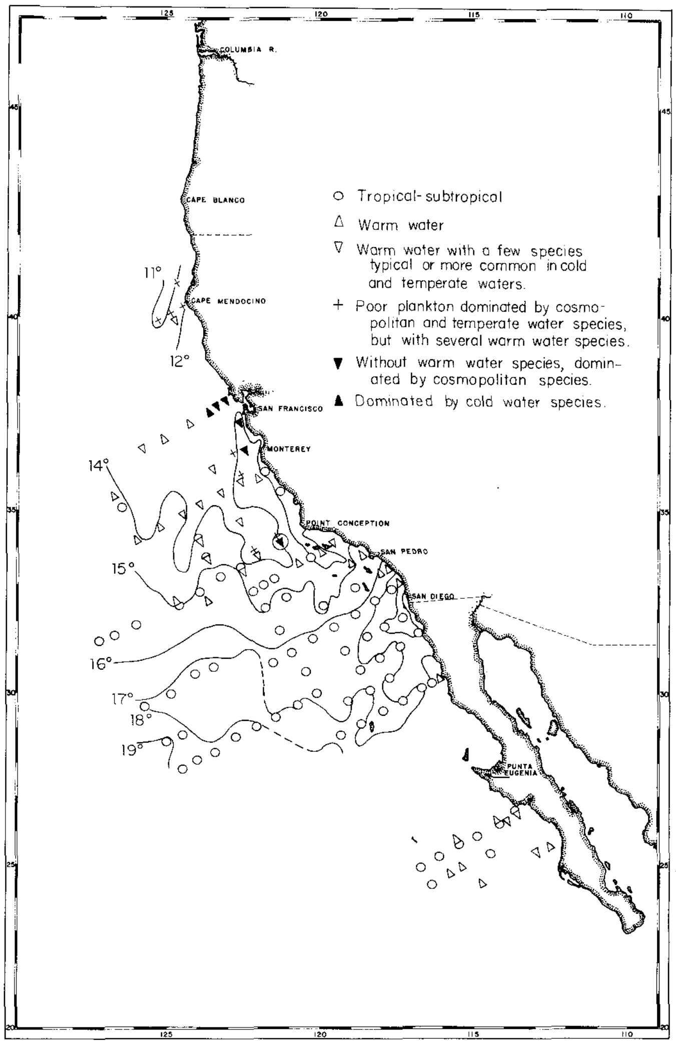

FIGURE 115. Distribution of micro-nannoplankton, March 29-April 28, 1958 (CCOFI Cruise 5804).

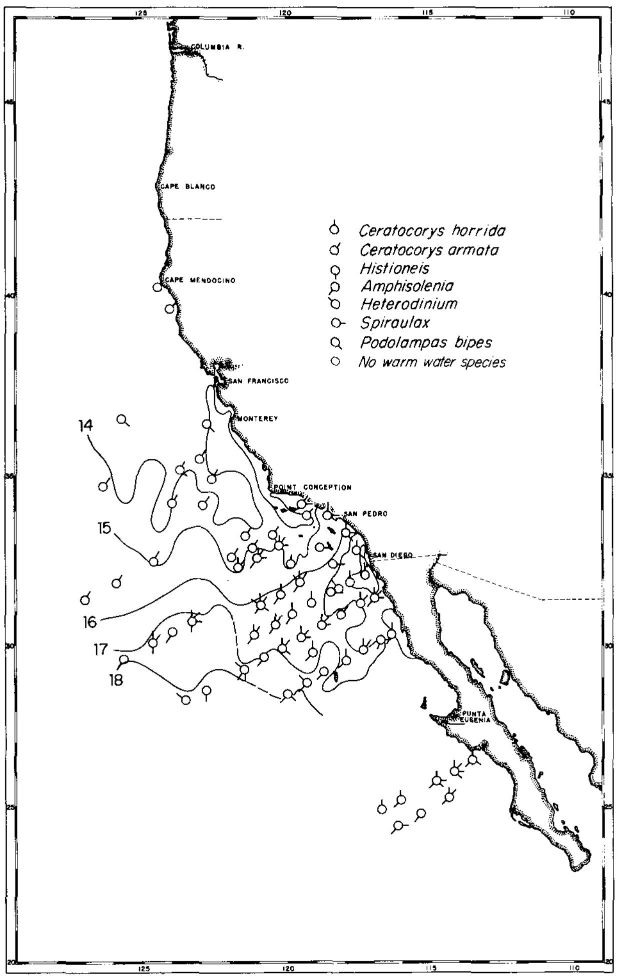

FIGURE 116. Distribution of some warm water dinoflagellates, March 29-April 28, 1958 (CCOFI Cruise 5804).

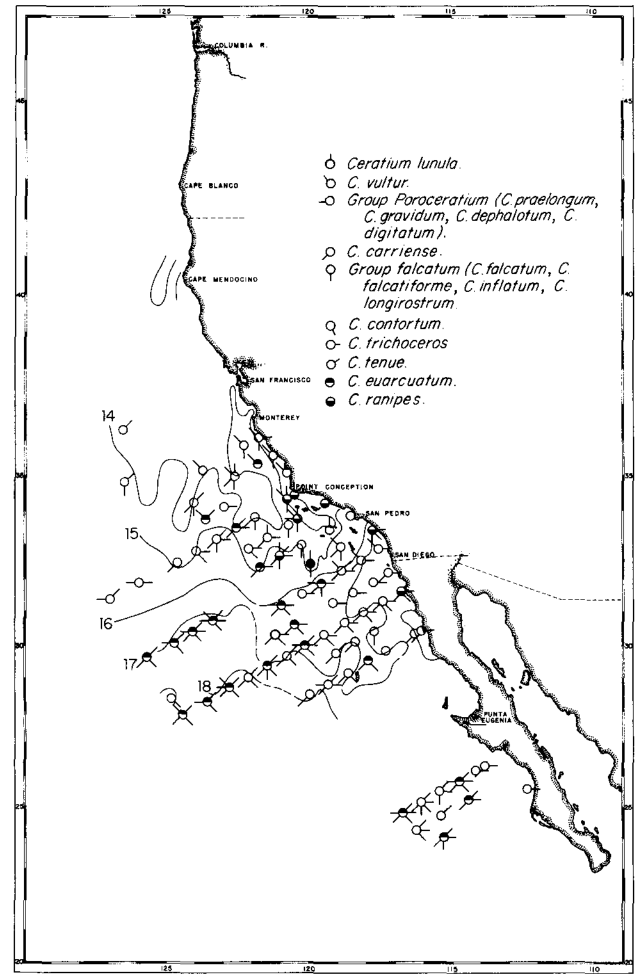

FIGURE 117. Distribution of Ceratia, March 29-April 28, 1958, (CCOFI Cruise 5804).

in this designation are not normally found in waters cooler than 18-19°C.

Looking to the north off San Francisco and Monterey, we see a different situation. Here the populations are dominated by cold water species; tropical or warm water species were not observed. The collections made farther north off Cape Mendocino, where the temperature was between 11° and 12°, present a surprising picture. Here we note the occurrence of several warm water species of *Ceratium*. Although all of these are tolerant species, they have never previously been found in such cold waters. Perhaps the drift bottle data may shed some light on this anomaly.

In the intermediate area largely delimited to the south by the 14° isotherm, the planktonic populations were of a mixed character. This is probably a reflection of the strong mixing of the water masses.

In conclusion, one is impressed with the striking change in the character of the planktonic populations from south to north and the far northward extension of typically warm water forms. Considering the normal temperature tolerance of these warm water species, it is tempting to ascribe this abnormal distribution to an active transportation to the north and a strong mixing of the waters.

DISCUSSION

Reid: Can you tell if the warm water species are from the south or from the west?

Haxo: I have raised the same question myself, but I believe that Dr. Balech's data do not permit distinguishing between these two alternatives.

Johnson: I am glad that he did not say that this actually established a transport. You are dealing with biological groups which respond to temperature conditions, and they reproduce in large numbers when the factors are favorable. You will notice throughout his paper he indicates the presence of warm water forms in cold water areas, or vice versa, which means that the seed material is really there, and where he speaks of temperature tolerance of a species, this does not necessarily mean that the species cannot get outside those temperature tolerances, but instead, these are the temperature tolerances within which it reproduces in large numbers. I believe we have to think of this when we interpret these things. If the water warmed up sufficiently off Cape Mendocino, we would have many more of these tropical and subtropical forms than are showing up there now. Not because they were carried in, but simply because the conditions became favorable for rapid reproduction; as you know, these organisms reproduce at a geometrical rate, so in a very short time propagate a considerable population. This does not mean that they have not been carried in, but that you have to think of the two things at the same time.

Haxo: Yes, one cannot look at the phytoplankton as simple drift bottles, which they certainly are not. All you need is a basic seed population, and if conditions are suitable for growth the population will increase in size. However, the source of the seed population, whether resident or transported, might be difficult to determine on the basis of present qualitative data. Perhaps the answer will be forthcoming when the collections have been more fully analyzed.

Hubbs: You did mention a few species that have not been found here before, such as tropical species of *Ceratium*. These are examples of temperature restricted distributions, in this case to warm water. The opposite situation is seen in the case of *Gonyaulax catenella,* a cold water form which actually cannot survive in warm water.

Haxo: This is certainly true. Unfortunately, information on temperature restrictions or tolerances is still largerly subjective. It would be very helpful if we had more extensive laboratory information on temperature tolerances of California coastal phytoplankton.

Sette: When you speak of temperature tolerance, do you mean mere survival, or, in addition, the ability to reproduce and maintain a population?

Haxo: Dr. Balech's approach has been that of a phytogeographer. His temperature designations are derived from information obtained at sea from other cruises from which it becomes known that certain species are to be found only in certain temperature realms. Therefore, based on this kind of information, they are thought to have certain temperature requirements and tolerances, presumably for survival and growth. This will remain an uncertain point until more exacting information is available. It is of interest that Dr. Balech has already encountered a number of dinoflagellates four or five degrees colder than previously reported.

Sette: In other words, these are tolerances as they are found to exist in the field.

Haxo: Yes, the tolerances are based upon observed distributions correlated with temperature.

Johnson: In a very few laboratories, cultures have been subjected to experiments to elucidate much of this kind of problem. There has been some work in Braarud's laboratory in which they studied a fair number of dinoflagellates for temperature tolerances. Some were also found to have different salinity tolerances, which may sometimes tend to have a reciprocal influence.

Haxo: Yes, these important studies have provided interesting examples of the complexities in the interaction of environmental factors on the growth of marine organisms and further indicate the desirability of extending efforts to cultivate phytoplankton under controlled laboratory conditions.

Hubbs: A suggestion (I think it is probably true of many of the invertebrates) is that when we have a seeming incursion of the southern forms, (we seem to be certain that it is an actual incursion) they will come up in a warm period and then tend to stay here even if the conditions are so bad that they die during the winter. Some of these that may have come up from the south are now living in water that they would not normally have reached simply because it has turned colder. The second point is a question regarding the 1939 data.

Haxo: The two periods were compared from late August through May. The temperatures of the 1938-1939 series were markedly lower (—0.85°C to —1.89°C) than those of the long term means (1917-1955) only during the months of October, November, February and March.

Johnson: I might mention here I had not realized to what extent Balech was looking at some of Allen's old samples which were concentrated by settling techniques. I have collections made with a No. 20 net which he might look over for some of these rare forms which he did not see before. I am quite sure that Allen did not pay much attention to rare forms, for his opinion was that it was the dominant forms that were important biologically, but they may not be the ones most important from the point of indicating changes in the oceanographic conditions.

Brinton: The phytoplankton reflects rather shallow environment compared to zooplankton forms, so that you can probably define depthwise the environments of these organisms better than you can many zooplankton samples. I seem to recall that Balech did find some forms relatively near to shore which he felt fairly certain were related to tropical waters. How did this compare to offshore?

Haxo: The general distribution of warm water dinoflagellates is brought out by figure 116. *Ceratocorys horrida* is an especially good indicator of tropical conditions and in April was found inshore as far north as San Pedro and far offshore from San Diego at the outermost station made along the 17°C isotherm.

Could I re-emphasize one point? Dr. Balech has dealt in all cases with assemblages of species, single members of which might be absent from adjacent stations. Assemblages of a half dozen or more species were used to indicate a given oceanographic condition.

ADDENDUM BY DR. BALECH

(Prepared following his reading of the transcript of the discussion)

We do not know actually how many species of marine dinoflagellates form cysts, although there is a general belief—far from proven—that most can do so. However, I should stress that these "seed" forms would give active forms with the approach of the conditions most suitable for each species. Thus, for warm water organisms, the main (evidently not the only) factor would be the increase of temperature. In this connection, it is well to remember that there exists what I call "ecological inertia" which delays the development of a population even after the onset of favorable conditions and the disappearance of a population after conditions become unfavorable.

Let us apply what is stated above to the situation at La Jolla during the past year. The theory of the appearance of the warm water population by reproduction (excystment and growth) *in situ* of a seed population requires a very noticeable and protracted increase of temperature, which had not happened. The water temperature at the surface at La Jolla was about 19-20°C. in September. In October it oscillated between 17.5°-18°. In November it was between 16-17°C. and by then the impoverishment of the warm water plankton was plainly noticeable, *i.e., Ceratium vultur, C. ranipes, C. carriense, C. karsteni, C. horridum molle* and the species of the falcatum group were not found in this month. It was the same for some of the most conspicuous warm water tintinnidae. But in December, with the temperature *still decreasing,* all these species plus some others such as *C. hexacanthum,* appeared again and were found consistently from the middle of December to March.

All this supports the conclusion that the populations observed at La Jolla did not arise locally but were transported from a center of subtropical or even tropical water. Whether this center was situated to the south or to the west of La Jolla, we cannot tell.

We tried to get some supplementary information from the samples of the April 1958 cruise (CCOFI Cruise 5804). From the distribution charts we cannot make any clear distinction between a possible southerly or westerly origin of the plankton. However, the distribution of *C. lunula, C. trichoceros* and *Spiraulaux jollifei,* species also found at that time in La Jolla, seems to give some support to a possible west northwest origin. It seems that these species were pushed against the southern coast and then, caught by a current from the south, carried northward, along with forms coming from the south. This explanation seems to fit especially such species as *C. lunula, C. hexacanthum, C. platycorne,* that prefer oceanic oligotropic waters, as shown by distribution data (Steemann Nielsen, Graham and Bronikowsky, and Peters).

The same mechanism, *i.e.,* transportation to the north, may account for the presence of several warm water species near Cape Mendocino, notwithstanding the low temperature of that region. When these species were found in cold waters, they were never far removed from currents having temperatures of at least 16° C.

All these species found near Cape Mendocino are tolerant. By this is meant that under unfavorable conditions, they are able to maintain at least an impoverished population. The species found near Cape Mendocino seem unable to maintain a population if the temperature is below 15°C. These data are derived from the collection studied all over the world. As pointed out by both Dr. Haxo and Dr. Johnson, we have very few data from laboratory experiments. All attempts to cultivate these warm water species have failed as far as I know.

Unfortunately quantitative data on the plankton distribution are not available. However, populations were designated as consisting of warm water plankton only if *many* warm water species were present. The somewhat simplified presentation in the graphs and charts of distribution do not bring forth the full weight of the evidence. For instance, in most of the samples taken at La Jolla in December through February, no less than 25 very definite warm water species were recorded including very intolerant forms such as *Ceratocorys horrida.* Dr. Haxo pointed out the interesting information derived from the distribution of this species.

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