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INTRODUCTION

During 1941 the E. W. Scripps made ten cruises off southern California, each covering the same area of about 80,000 square kilometers. The cruise plan consisted of a grid of approximately 40 stations. At each station a catch was made with the Allen five-liter closing bottle every ten meters from the surface to 60 meters. The catch was filtered through a net of No. 25 silk bolting cloth, and the diatoms so collected were later identified, counted and recorded as the number of diatoms per liter. The laboratory work was done by the late W. E. Allen, who had no opportunity to prepare more than a general report, which is now being edited for publication. For the purpose of this paper the number of diatoms per liter is taken as representing the number per square centimeter from the level at which the catch was made to the level of the next catch ten meters below. The sum of the seven catches at a station represents, according to this convention, the diatom population per square centimeter to a depth of 70 meters. Collections were not made at greater depths. However, the progressive reduction of the population down to 60 meters suggests that the diatoms below this depth would not change the totals sufficiently to affect the validity of the arguments presented here.

At each station, observations were made of temperature, salinity, and oxygen to a depth of 500 meters. Dynamic height anomalies (Sverdrup, 1947) are shown on all charts of this report as an indication of the character of the surface water and its horizontal movements. The general dynamic features of these waters have been discussed by Sverdrup and Fleming (1941), who showed that in the spring and early summer two types of surface water (down to about 100 meters) are present in this area: (1) “new” water which has been recently drawn to the surface by upwelling and (2) “old” water which has been

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1 Contributions from the Scripps Institution of Oceanography, New Series, No. 386.
at the surface for a relatively long time. New water is characterized by low temperature, high salinity, and a shallow thermocline. At this time of year there is typically in the western part of the cruise area and beyond it a south-flowing current of old water. Along its left-hand boundary one or more cyclonic eddies of new water appear, and inshore from these there may be a current of old water flowing northwesterly. Sverdrup and Fleming discussed the evidence for the theory that the two oppositely-directed currents represent two sides of a single large eddy. The pattern of circulation outlined above becomes less evident as upwelling of new water diminishes later in the year.

Michael (1921) showed, for a line of stations extending 125 miles out from Point Fermin, a negative correlation between the population density of the phytoplankton and the temperature of the surrounding water, indicating that large populations are, on the average, found in
Figure 2. Distribution of diatoms, Cruise 21. See Fig. 1 for description.

Figure 3. Distribution of diatoms, Cruise 23. See Fig. 1 for description.
recently upwelled water. Sverdrup and Allen (1939) found that large diatom populations in southern California waters were limited to new water, whereas water which had spent a long time on the surface was always characterized by a small diatom population.

**OBSERVATIONS**

For four cruises in 1941 Figs. 1 to 4 show the percentage contribution of each station to the cruise total of all diatoms. It is clear that the distribution of the diatom population is orderly and that the spacing of the stations is close enough to indicate the population at all points. In each figure, the area embracing all stations contributing at least 1% to the cruise total has been hatched. For convenience, the outline of this area will be called the one-per-cent contour.

**TABLE I. DISTRIBUTION OF DIATOMS OFF SOUTHERN CALIFORNIA IN 1941**

<table>
<thead>
<tr>
<th>Cruise</th>
<th>Month</th>
<th>Av. No. of diatoms per station (thousands per cm²)</th>
<th>No. of stations occupied</th>
<th>No. of stations with 1% or more of total population</th>
<th>% of total population at these stations</th>
</tr>
</thead>
<tbody>
<tr>
<td>17</td>
<td>March</td>
<td>1020</td>
<td>41</td>
<td>21</td>
<td>95.9</td>
</tr>
<tr>
<td>19</td>
<td>April</td>
<td>445</td>
<td>41</td>
<td>13</td>
<td>95.7</td>
</tr>
<tr>
<td>21</td>
<td>May</td>
<td>220</td>
<td>42</td>
<td>11</td>
<td>95.3</td>
</tr>
<tr>
<td>23</td>
<td>June</td>
<td>593</td>
<td>40</td>
<td>13</td>
<td>97.9</td>
</tr>
<tr>
<td>25</td>
<td>June</td>
<td>493</td>
<td>40</td>
<td>10</td>
<td>96.4</td>
</tr>
<tr>
<td>27</td>
<td>July</td>
<td>51</td>
<td>41</td>
<td>21</td>
<td>96.2</td>
</tr>
<tr>
<td>28</td>
<td>August</td>
<td>500</td>
<td>38</td>
<td>15</td>
<td>94.0</td>
</tr>
<tr>
<td>30</td>
<td>September</td>
<td>378</td>
<td>33</td>
<td>21</td>
<td>96.0</td>
</tr>
<tr>
<td>32</td>
<td>October</td>
<td>131</td>
<td>38</td>
<td>23</td>
<td>97.9</td>
</tr>
<tr>
<td>33</td>
<td>November</td>
<td>8</td>
<td>33</td>
<td>15</td>
<td>94.3</td>
</tr>
</tbody>
</table>

As shown on Table I, this contour encloses more than 90% of all the diatoms observed on each cruise. Fig. 5 shows that the use of either the half-per-cent or the two-per-cent contour would not greatly change the proportion of the population enclosed. For instance, the half-per-cent contour would enclose an additional 39 stations (four

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2 This outline can be defined precisely (on the assumption that the number of diatoms changes gradually from station to station) as the locus of all points such that if a station had been occupied at any one of them it would have contributed one percent to the cruise total. The cruise total is the sum of the station populations. The station population has already been defined as the population to 70 meters per cm² of surface. The cruise total multiplied by the average area represented by one station (about 2,000 km²) equals the total population in the whole area covered by the cruise.
stations per cruise) and would increase the enclosed population by about 5% per cruise. On the other hand, use of the two-per-cent contour would exclude 49 stations (five per cruise) included by the one-per-cent contour and would diminish the enclosed population by about 6% per cruise. Neither alternate line would affect the conclusion that nearly all of the diatom population during these cruises was found regularly in a single sharply defined area of limited extent.

During most of the 1941 cruises, particularly in the spring and early summer months, a moderately intense cyclonic eddy was present in the northern part of the cruise area. In Figs. 1 to 4, lines have been drawn through the centers of such eddies, in a direction parallel to the flow of the offshore current, or if this could not be determined, in a southeasterly direction. In most cruises these lines divided the populations in such a way that the larger part was on the offshore (southwest side) of the line. Except during cruises 27, 32, and possibly 30, over half of all the diatoms collected occurred in these very restricted patches (Table IIA). In the exceptional cruises the eddies were close to the outermost line of stations, so that it is likely that the area of densest population was not sampled at all. Thus, it appears that the cyclonic eddies in the northern parts of the area characteristically contained large diatom populations which were especially dense in the
offshore half of the eddies (Table IIIB). As this water flowed south-eastward the populations developed and then were scattered or destroyed. Whether the greatest development was reached before or after the water entered the cruise area from the northwest is unknown, but the rapid decay and almost total disappearance of the population within the local waters is shown by the paucity of diatoms just outside of the eastern, southern and western boundary to the productive area.

This pattern of population densities remained approximately constant throughout the year, although the total population varied from cruise to cruise (Table I) and although the species of diatoms involved varied in relative abundance from season to season. During several cruises a single species accounted for more than a quarter of the entire population, and in every cruise a dozen species or less comprised from one-third to nine-tenths of the population. Seasonal succession and other changes in the composition of the list of leading species shown on the charts (Figs. 1 to 4) are matters to be discussed at length elsewhere.
### TABLE II. Distribution of Diatoms in Cyclonic Eddies off Southern California

<table>
<thead>
<tr>
<th>Cruise</th>
<th>No. of stations inside 1% contour and in southwestern half of cyclonic eddy</th>
<th>% of total population at these stations</th>
<th>Av. % of total population at each station inside 1% contour</th>
<th>Av. % of total population at each station inside 1% contour and in southwestern half of eddy</th>
</tr>
</thead>
<tbody>
<tr>
<td>17</td>
<td>10</td>
<td>64.1</td>
<td>4.6</td>
<td>6.4</td>
</tr>
<tr>
<td>19</td>
<td>8</td>
<td>79.0</td>
<td>7.4</td>
<td>9.9</td>
</tr>
<tr>
<td>21</td>
<td>4-5</td>
<td>50.3-65.0</td>
<td>8.7</td>
<td>12.5</td>
</tr>
<tr>
<td>23</td>
<td>9-10</td>
<td>51.3-73.7</td>
<td>7.5</td>
<td>5.7</td>
</tr>
<tr>
<td>25</td>
<td>7</td>
<td>80.5</td>
<td>9.6</td>
<td>11.5</td>
</tr>
<tr>
<td>27</td>
<td>8</td>
<td>16.4</td>
<td>4.6</td>
<td>2.1</td>
</tr>
<tr>
<td>28</td>
<td>7-8</td>
<td>51.3-60.8</td>
<td>6.3</td>
<td>7.3</td>
</tr>
<tr>
<td>30</td>
<td>3-6</td>
<td>23.6-52.3</td>
<td>4.6</td>
<td>7.9</td>
</tr>
<tr>
<td>32</td>
<td>8</td>
<td>37.3</td>
<td>4.2</td>
<td>4.7</td>
</tr>
<tr>
<td>33</td>
<td>11</td>
<td>81.1</td>
<td>6.3</td>
<td>7.4</td>
</tr>
</tbody>
</table>

The point to be made here is that, although the composition of the population changed, the pattern as a whole bore a remarkable constant relationship to the hydrography.

In the present report we will describe in detail only the observations made during the spring months when conditions were most clearcut and uniform from cruise to cruise. Therefore, discussion will be limited to those observations, and especially to those of cruise 19, which was representative of the spring cruises.

A number of the individual species observed during cruise 19 were distributed in patterns as clearly related to the hydrography as that of the diatom population as a whole. Figs. 6 to 11 show the distribution of six separate species during this cruise. As in previous charts, the hatching covers those stations contributing at least one per cent to the cruise total for the species. It is clear that Nitzschia seriata (Fig. 6) and Chaetoceros radicans (Fig. 7) had essentially the same distribution as the whole diatom population, as did C. lorenzianus, N. longissima, and several minor species. The boundaries of the area of high population were not determined, then, by a single preponderant species. As suggested by Michael, a whole group of species appears to be controlled in the same way by the same set of factors.

A second type of distribution is that of C. socialis (Figs. 10, 14). This species and C. compressus (Fig. 11), C. debilis (Fig. 15) and C. didymus were very similar in being restricted essentially to a few sta-
Figure 6. Distribution of Nitzschia seriata, Cruise 19. At each station (indicated by a dot), phytoplankton catches were made every ten meters from the surface to 60 meters. Figures at stations show percentage contribution of each station to cruise total of the species. Hatched area includes all stations contributing at least one per cent to cruise total.

Within the one-per-cent contour. Of these four species, all but C. didymus represented important fractions of the total diatom population, as shown in Fig. 1. At station 24 (Lat. 33° 25' N, Long. 119° 43' W) more than two-thirds of the cruise total for each of these species was collected, and they were also abundant at station 46 (Lat. 32° 29' N, Long. 119° 26' W). These species were common only in the neighborhood of these two stations, and in general they were not observed at all outside of the one-per-cent contour for all diatoms.

A radically different kind of distribution is that of Rhizosolenia alata (Fig. 8). The distribution of this species, as well as Dactylosolen antarcticus (Fig. 9), Rhizosolenia hebetata, Chaetoceros dadayi, C. atlanticus and C. messanensis, is complementary to that of the main group. On the whole, diatoms of these six species were few or absent at populous stations but were relatively numerous at many stations outside the populous areas.

Thus, many of the species collected during cruise 19 can be divided into groups according to their distribution as follows:

1. Common, occurring at most stations in the eddy but rarely elsewhere. Chaetoceros radicans, etc.
Figure 7. Distribution of Chaetoceros radicans, Cruise 19.

Figure 8. Distribution of Rhizosolenia alata, Cruise 19.
Figure 9. Distribution of Dactyliosolen antarcticus, Cruise 19.

Figure 10. Distribution of Chaetoceros socialis, Cruise 19.
2. Restricted, occurring at only a few stations in the cyclonic eddy. *Chaetoceros socialis*, etc.

3. Complementary, occurring seldom within the eddy, but generally elsewhere. *Rhizosolenia alata*, etc.

Species intermediate in character between those of groups 1 and 2 are to be expected, and it is not unlikely that an extensive study would show that the distribution of some species changes with, for instance, the seasons. However, all species listed above retained their characteristic distribution throughout the spring cruises of 1941. Many other species observed are not readily fitted into this scheme. In particular, some were so scarce that it is only possible to conclude that they did poorly over the entire cruise area.

![Figure 11. Distribution of Chaetoceros compressus, Cruise 19.](image)

If data for other years substantiate this division, each of the groups can be considered as belonging to a “plankton element” defined by Gran (1902: 74 ff) as an assemblage having similar ecological requirements. Since Gran’s paper, many such ecological requirements have been discovered and elucidated, particularly by Harvey (1947, and papers referred to therein).
Figure 12. Surface temperatures, Cruise 19.

Figure 13. Surface temperatures, Cruise 21.
INTERPRETATION

A close relationship existed between these groups of plankton and the circulation features of the water. It is inconceivable that the small differences in temperature observed, or possible small differences in average insolation, could account for the distribution of the diatoms. The depth of the mixed layer, which increased with distance from shore, as Sverdrup and Fleming observed, could not by itself account for the distribution. Rather, it is necessary to look for a complex of physical, chemical and biotic factors whose individual values and combined effect varied from day to day and from point to point. The over-all effect is that freshly upwelled water is more fertile than old water, as pointed out by Michael (1921) and by Moberg (1928). The details of the distribution of the diatoms during the spring of 1941 can be related to this phenomenon as follows.

Freshly upwelled water entered the area of observations from the northwest intermittently, and its concentration in some areas was higher than elsewhere as indicated by low temperatures in the centers of the cylonic eddies (Figs. 12, 13). In these areas, as at stations 24 and 46 in cruise 19, large populations occurred, with species in groups one and two predominating. From the fact that the very densely populated stations, which were also the only stations at which group-two diatoms were found in appreciable numbers, often occurred singly or in pairs, it can be inferred that the diameter of the areas of highest concentration of upwelled water were close to the station grid interval of 20–30 kilometers. Surrounding these areas was a larger one in which the concentration of new water diminished with increasing distance from the centers of population, as indicated by higher temperatures and lower salinities. This area supported a large population in which the species of group one were conspicuous, while diatoms of group two were rare or absent. The remainder of the area covered by the cruises was, on the whole, occupied by water which was of high temperature and low salinity and therefore had probably been on the surface for some time. The diatom population was small, but species of group three were found in their greatest abundance here.

The diminution in population density was probably controlled by different combinations of factors in different parts of the eddy system. Toward the east, that portion of the upwelled water which was carried around the eddy, except near its periphery, had little opportunity for mixing with old water, and the diminution of the population in the inshore half of the eddy must have resulted from processes occurring within the water body, such as exhaustion of nutrients, increase of grazing, etc., which produced combined effects as shown by Braarud
Figure 14. Distribution of Chaetoceros socialis, Cruise 21.

Figure 15. Distribution of Chaetoceros debilis, Cruise 21.
(1935) and Fleming (1939). To the west, intense lateral mixing with offshore water which was both infertile and barren (Sverdrup and Fleming, 1941: 331) would reduce both the concentration of nutrients and the density of the population, and, in combination with the other processes, produce the steep population gradient on the offshore side of the eddies.

SUMMARY

In waters off southern California in 1941, the diatom population was concentrated at any one time in one or a few relatively small patches. These patches were closely related to cyclonic eddies of freshly upwelled water entering the area of observation from the north (particularly in the spring when upwelling was strongest). The population was most abundant in the offshore halves of the eddies where the upwelled water, judged by its low temperature and estimated path of travel, was most concentrated and had been present on the surface the shortest time. Populations in water which had apparently travelled some distance around the eddies were less abundant, presumably because of exhaustion of nutrients, grazing, and other biological processes. Abundance diminished more sharply to the west than to the east because, in addition, there was intense lateral mixing with barren infertile offshore water.

Four plankton elements, in the sense of Gran, could tentatively be identified: (1) a group of species, mostly very abundant, found only where the upwelled water was most concentrated; (2) a group, some very abundant, found at almost all stations within the well marked patches of generally high population density; (3) a group of species, none of which reached great abundance but which were relatively more abundant in water which had been on the surface a long time; and (4) a group of species rare throughout the cruise area.

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