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## **Floral patterns in the California Current: The coastal-offshore boundary zone**

by **E. L. Venrick**<sup>1</sup>

### **ABSTRACT**

This study quantified the vertical distributions of 294 taxa of phytoplankton from 112 samples in a vertical section across the California Current system off Southern California. The goal was to examine the relationship between coastal and offshore floras throughout the euphotic zone. The two associations were distinct throughout the upper 140 m. The coastal flora was found in water adjacent to and east of the Santa Rosa Ridge. The offshore flora occurred west of the California Current, and also at the station immediately east of the current, presumably the result of upstream entrainment across it. Both coastal and offshore floras were similar to the analogous floras described from the mixed layers in the springs of 1993 and 1995, in spite of different ENSO conditions prevailing during the three years.

There were two unexpected results. Although the hydrographic characteristics of offshore water had been strongly modified by mixing with California Current water, the offshore flora remained similar to that of a central Pacific study site, 3000 km to the west. Clearly, the maintenance of this species association is not directly dependent upon temperature or salinity. In contrast, even though the temperature-salinity relationship of the California Current fell within the envelop of T-S relationships of source water to the north, the floristic analyses identified no flora unique to the California Current. Absence of oceanic subarctic species in the Current may be related to upstream depletion of nutrients.

### **1. Introduction**

The California Current (the Current) is the eastern limb of the anticyclonic North Pacific Gyre. It meanders toward the equator, bringing cool, low salinity subarctic water south along the west coast of North America (e.g. Hickey, 1979; Bray *et al.*, 1999; Lynn and Simpson, 1987). The poleward-flowing California Undercurrent originates in the eastern tropical Pacific. Between Point Conception and the Mexican border, the California Current is separated from the coast by a region of complex bottom topography composed of a series of ridges and basins, some of which extend above the surface forming the Channel Islands. The most offshore of the Channel Islands is San Nicholas Island, which rises above the Santa Rosa Ridge. Near the California-Mexican border, a portion of the Current turns shoreward, forming the Ensenada Front, and merging with the cyclonic Southern Califor-

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nia eddy, which is centered approximately on San Nicholas Island (Bray *et al.*, 1999; Niiler *et al.*, 1989). The inshore limb of the Southern California eddy carries modified Current water mixed with relatively warm, saline water from offshore and/or the south. The eddy is most strongly developed during fall and winter and may be absent during the spring when the prevailing current direction is equatorward across the entire region (Bray *et al.*, 1999).

Thus, the California Current System is composed of waters of distinct sources: cool, low salinity subarctic water carried south by the California Current; warm, saline water from the central Pacific; and relatively warm, very saline water from the eastern tropical Pacific. In addition, cold, salty, subsurface water may be upwelled, especially in the vicinity of Point Conception and the northern Channel Islands (Hickey, 1979; Lynn and Simpson, 1987). The California Current System is also a mixture of faunal types. Many of the holoplanktonic zooplankton and larval fish species in this ecosystem have broader distributions, extending north into the subarctic Pacific, south into the equatorial Pacific, or west into the central Pacific (Berner, 1960; Brinton, 1960; McGowan, 1963; Moser *et al.*, 1987). These distributions correspond to the broader distributions of Current source waters. Although the relationships may be more complicated than direct advection (Roesler and Chelton, 1987) the association between zooplankton species and water types is strong, making changes in composition a useful marker of large-scale oceanographic change (Rebstock, 2002; Brinton and Townsend, 2003; Lavaniegos and Ohman, 2003). Equivalent information about the distribution and hydrodynamic relationships of phytoplankton species is lacking.

Much of our understanding of the hydrography and zoogeography of the California Current system has been provided by the California Cooperative Oceanic Fisheries Investigations (CalCOFI; <http://www.calcofi.org/>). Since 1984, CalCOFI has made quarterly surveys from Point Conception south to the Mexican border, and from less than 10 km from the coast to more than 600 km offshore (the “CalCOFI area”; Fig. 1). On the basis of four years of continuous near-surface hydrographic measurements and 12 years of discrete mixed layer chlorophyll measurements, both collected by CalCOFI, Hayward and Venrick (1998) defined four environmental regions within the present CalCOFI area. The low salinity core of the California Current divides offshore and coastal regions. Coastal waters are under the influence of episodic upwelling (Lynn and Simpson, 1987) and are cool, saline and relatively eutrophic. Offshore are the warm, saline oligotrophic waters of the central Pacific. The position of the boundary between coastal and offshore environments varies with time in response to the meandering of the Current, producing an “alley” of 50–200 km in width. At any point in time, the core of the Current and the boundary between coastal and offshore may fall anywhere within this alley. The fourth environmental region lies along the southern portion of the CalCOFI area where offshore water is carried toward the coast in the region of the Ensenada Front. These regions, which appear to be distinguished by different patterns of physical forcing and biological response, are local expressions of patterns previously defined by dynamic height characteristics (Lynn

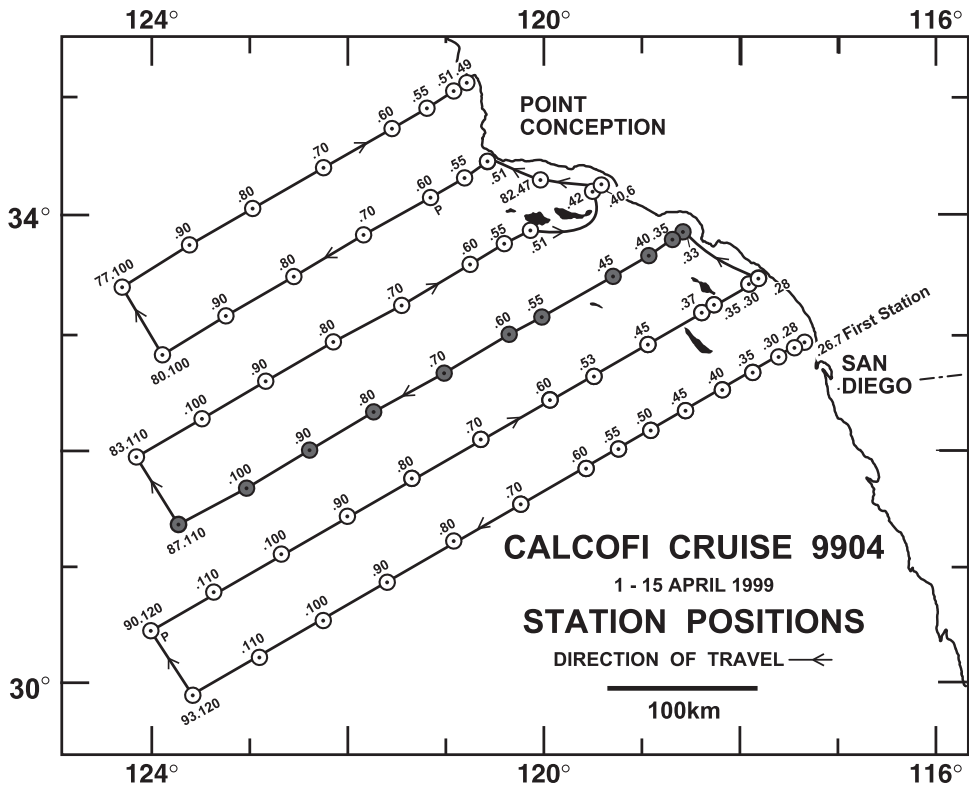


Figure 1. CalCOFI cruise pattern, April, 1999, showing station numbers; line numbers are given at the outer end of each transect. Solid circles indicate the stations used in this study (line 87).

and Simpson, 1987). The alley is analogous in position if not dynamics to the coastal transition zone extensively studied off central California (e.g. Chavez *et al.*, 1991).

A second study examined mixed-layer phytoplankton species composition within the CalCOFI area in April, 1993 and April, 1995 (Venrick, 1998). Again, there was a clear separation of phytoplankton into coastal and offshore associations, the boundary between them falling within the alley defined by Hayward and Venrick. Offshore species were those typically found in the central Pacific, while coastal species were characterized by species that are known to dominate spring blooms over a wide geographical area. Neither the temporal biomass (chlorophyll) patterns nor species composition indicated relationships with subarctic or equatorial water sources such as are seen among zooplankton taxa. A third study looked at 6.5 years of near-surface samples collected quarterly and pooled into four broad regions before counting (Venrick, 2002). Again, coastal and offshore associations were identified.

These studies were based on near-surface parameters. While the coastal-offshore pattern seems robust in this layer, there remained uncertainty about floristic patterns and bound-

aries deeper in the water column. The present study addressed phytoplankton distributions beneath the mixed layer by examining the species composition along a coastal-offshore section across the CalCOFI area (CalCOFI line 87; Fig. 1). I determined the vertical persistence of the coastal-offshore separation of phytoplankton associations and characterized their vertical structure. In addition, I looked for evidence of advection of species from the north by the California Current.

## 2. Methods

### a. Field sampling

Samples were collected on CalCOFI cruise 9904 between 8–10 April, 1999, from the twelve stations along CalCOFI line 87 (Fig. 1). Station 33 is located off Long Beach Harbor, 7.5 km from the coast, in 56 m water. Station 50 is located in 75 m water on the Santa Rosa Ridge, just north of San Nicholas Island. Station 110 is 570 km offshore. At each station, up to twelve water samples were collected for phytoplankton. Simultaneous hydrographic and chemical data were collected by the CalCOFI program. Methods and data are available on the CalCOFI web pages ([http://www.calcofi.org/data/1990s/1999/9901\\_int.htm](http://www.calcofi.org/data/1990s/1999/9901_int.htm); and [http://www.calcofi.org/data/1990s/1999/9904\\_hyd.html](http://www.calcofi.org/data/1990s/1999/9904_hyd.html), resp.). Summaries of the oceanographic and biological results from CalCOFI 9904 have been published (Hayward *et al.*, 1999; Bograd *et al.*, 2000).

### b. Floristics

Phytoplankton samples were preserved with 1% buffered formalin (Thronsdon, 1978) and counted ashore with a phase-contrast, inverted microscope. The volume of material counted varied between 0.25 ml and 100 ml. Larger taxa were counted using a magnification of 100 $\times$ . For smaller, or more numerous taxa, every sixth row was counted at 250 $\times$ . Identification was facilitated by pipetting individuals to a slide for examination under a compound microscope at 1000 $\times$ .

Taxa were those that could be identified to species or genus under a light microscope: primarily diatoms, dinoflagellates, coccolithophores and silicoflagellates. No attempt was made to enumerate the picoplankton. The analyses in this paper were based upon single species or taxa containing a small group of similar species (e.g. robust *Pseudonitzschia* spp., a taxon which is usually dominated by *P. australis*; [Busse *et al.*, 2006]). Taxa containing many species were excluded (e.g. unidentified hyalochaetes). The final data base consisted of 294 taxa from 112 samples.

### c. Statistical procedures

This paper emphasizes patterns rather than probabilistic hypothesis testing.

*i. Similarity plots.* Floral similarity between stations was examined by calculating Spearman's correlation,  $\rho$  (Conover, 1999; Sprent, 1993) between all pairs of samples. Because

$\rho$  is based upon rank order of abundance, it is little influenced by the underlying population distribution and equally reflects changes in rare and abundant species. The resulting matrix contained correlations between 6216 station pairs, and the combined species list for a pair of stations (the sample size, or “n”) varied from 15 to 120 species. As a criterion for similarity or dissimilarity, the critical two-tailed value of a  $\rho$  at  $p = 0$  was used. This allowed one to account for unequal sample sizes. However, use of statistical tables does not imply probability. Because of the large number of correlations calculated (multiple testing) and their lack of independence, one cannot assign a precise significance level to any single  $\rho$ .  $\rho$  has been used only as an index of similarity, much as the percent similarity index is used. Pairs of stations with similar flora have been indicated visually with a straight line between them. This allows station relationships to be visualized directly in the dimensions of interest.

*ii. Recurrent group procedure.* Relationships between species were examined using the recurrent grouping procedure based upon the number of co-occurrences between pairs of species (affinity level, or  $\alpha$ ; Fager, 1957; Fager and McGowan, 1963). I used a value of 0.70 as the threshold level of affinity for grouping. This facilitated comparison with several earlier studies (e.g. Venrick, 1998, 1999, 2002). Instead of scores of presence and absence,  $\alpha$  was based on scores above/below the median value, which provides more realistic groupings of the most abundant species. For species present in less than half the samples (which included most species in the present study), this scoring becomes identical with presence/absence.

A recurrent group exists when all species in that group have an affinity (i.e.:  $\alpha > 0.70$ ) with all other species in that group. A species that does not belong to a group but that has an affinity with one or more group members is an associated species. Species within a recurrent group may have affinities with species in other groups. Clusters were defined on the basis of the number of such cross-group affinities. A cluster is composed of recurrent groups and associated species that are connected by cross group affinities. There were no cross group affinities between clusters, in the present study.

*iii. Comparisons with other floras.* The earlier studies in 1993 and 1995 defined coastal and offshore regions from near-surface samples (Venrick, 1998). Comparisons with these data required reduction of the 1999 data. Only the near-surface (second depth) sample from each station in 1999 was used. This reduced the number of samples in 1999 from 46 to 6 in the coastal region and from 31 to 3 in the offshore. Within each of the three years, data were pooled within coastal and offshore regions defined by that year’s analysis (Figs. 3 and 5 in Venrick 1998); thus the regions were not geographically identical. In pooling, abundances were weighted according to the area represented by the sample. However, no effort was made to interpolate over missing samples.

For comparison with floristic data from the central Pacific, data from the present study were integrated through the shallow layer and the deep layer. The transition between

shallow and deep associations was defined by the lowest correlation between vertically adjacent samples (Venrick, 1982). The transition depths were 99.5 m and 90.5 m at stations 100 and 110. At station 80, the transition was interrupted by California Current water; the shallow stratum was integrated from 0 to 65 m and the deep from 109 to 119 m.

*iv. Cumulative dominance curves.* The cumulative dominance curve provides information about similarities and differences of two or more floras by indicating where in the species lists the major sources of dissimilarity occur: among the dominant species, the rare species, etc. Curves were constructed by simultaneously considering the rank order of abundance of several data sets. Starting with the dominant species, the list was cumulated toward the rarer species. For each set of species in the data sets (e.g. the most abundant single species in every list [ $n = 1$ ], the most abundant 10 species [ $n = 10$ ], the most abundant 50 species [ $n = 50$ ]), the number of species in common to all lists was determined. For instance, if the same species dominated all species lists, the first data point was 1,1; otherwise it was 1,0. If there were three species that occurred in the top 10 species of each data set, the tenth point was 10,3. If the rank order of abundance of species is identical, the cumulative dominance plot has a slope of 1. Curves that are concave upward indicate less similarity among the dominant species than among the rare (e.g. the initial slope deviates from the 1 more than the end of the slope). Conversely, slopes that are concave downward indicate less similarity among the rarer species. Curves constructed from different numbers of data sets cannot be compared directly, as the null distributions will vary. Thus, the cumulative dominance curve for flora from the three offshore stations (1993, 1995 and 1999; Fig. 11) were not directly compared with the curve comparing the offshore CalCOFI flora with the central Pacific flora (1999 and 1996; Fig. 12).

### 3. Results

#### *a. Environmental conditions*

*i. California Current ecosystem.* In winter, 1998, the California Current ecosystem underwent a dramatic shift from one of the strongest El Niños on record to an equally strong La Niña (Bograd *et al.*, 2000). At the time of sampling in April, 1999 both equatorward transport and upwelling off Point Conception were unusually vigorous (Bograd *et al.*, 2000). In the upper 100 m of the CalCOFI area, temperatures in April were approximately 1°C cooler than normal (Hayward *et al.*, 1999). The cruise mean chlorophyll ( $122 \text{ mg/m}^3$ ) was the highest seen since routine chlorophyll measurements began in 1984. Chlorophyll was elevated offshore, as well as in the region of wind-driven upwelling (Hayward *et al.*, 1999).

*ii. Line 87.* The low salinity California Current core was well offshore, entering the CalCOFI region at line 80 and crossing line 87 at stations 80 and 90 (Fig. 2, top left). The freshest water was centered at 86 m at station 80. The strongest southward flow was just



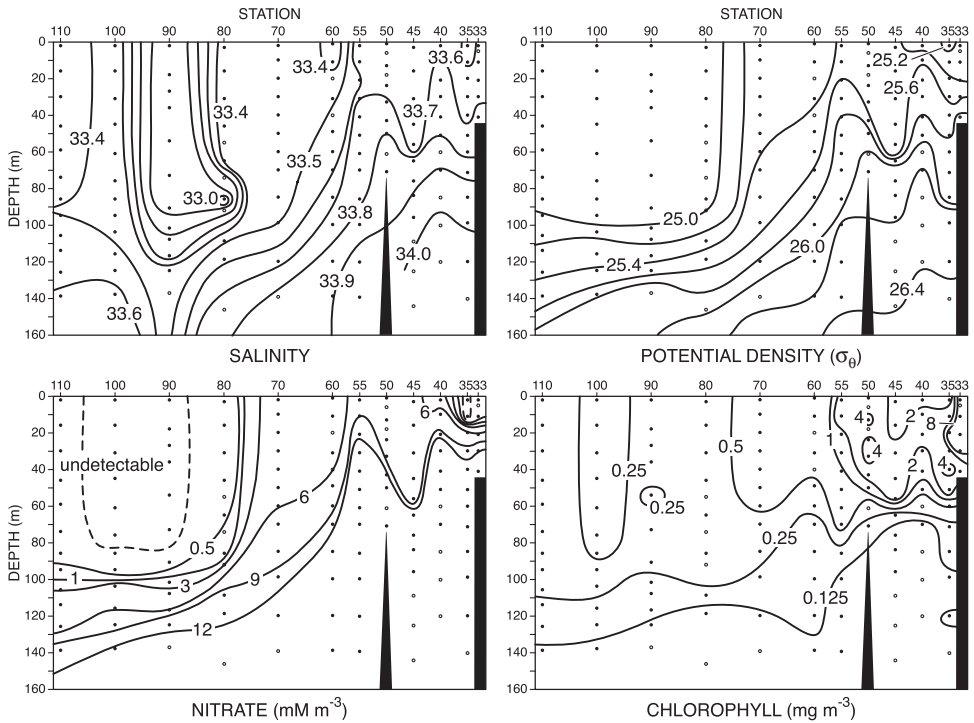


Figure 2. Sections of selected properties along line 87. Open circles indicate that no phytoplankton were enumerated from that sample.

east of station 80, along the shoreward edge of the Current core (Fig. 2 top right). The isobar topography above and inshore of station 55, where the track crossed the Santa Rosa Ridge, reflected both a weak cyclonic Southern California eddy and more local perturbations generated by bottom topography and local winds.

Nutrient concentrations were elevated east of the Santa Rosa Ridge where the topography of nutrient isolines followed those of potential density (Fig. 2, bottom left). Reduction of nitrate at the innermost stations was accompanied by supersaturated oxygen,  $>117.7\%$  at station 33, indicative of high productivity. Euphotic layer concentrations of all nutrients decreased rapidly west of station 70.

Mixed layer chlorophyll values (Fig. 2, bottom right), were consistently above the 20-year median, but only the outermost station, 110, established a long-term maximum of  $0.26 \text{ mg/m}^3$ , nearly three times the long-term median ( $0.09 \text{ mg/m}^3$ ). Concentrations of chlorophyll were generally elevated above and east of the Santa Rosa Ridge, consistent with the elevated nutrients in this region. The maximum concentration,  $15.9 \text{ mg/m}^3$ , occurred at 21 m depth, at the innermost station. Offshore of station 55, near-surface chlorophyll concentrations decreased rapidly and the depth of the maximum concentration deepened to approximately 100 m.



Temperature-salinity relationships along line 87 were bounded by the saline inshore waters and the relatively fresh California Current (Fig. 3). The five easternmost stations, inshore of the Santa Rosa Ridge (inshore stations: 33–50), were hydrographically similar. The three stations adjacent to the west (transition stations: 55–70) were somewhat cooler and fresher, and more heterogeneous, suggesting influence from the Current. The surface layer of station 60 was fresher than the surface layers of the adjacent stations. Station 90 had the cool, fresh water that characterizes the Current, as did station 80 between 74 and 92 m. Above 74 m, the T-S relationships of station 80 were similar to those of the two offshore stations, 100 and 110, suggesting entrainment of offshore water across the Current.

The T-S profile of water carried by the California Current across this section (seen at station 90 and between 74 and 92 m at station 80) fell within the envelope of T-S profiles that characterize the Westwind Drift, the southern limb of the subarctic Pacific and a source of the Current (Fig. 3). Offshore waters, however, were both cooler and more saline than typical central Pacific water, suggesting significant mixing with the Current (Lynn and Simpson, 1987).

#### *b. Phytoplankton*

The 294 taxa enumerated in this study included 136 diatoms, 89 dinoflagellates, 59 coccolithophorids, three silicoflagellates, and seven species from various other taxa. The most abundant species were the centric diatom *Chaetoceros debilis* (24% of the total number of cells), the coccolithophorid *Emiliana huxleyi* (22%) and the pennate diatom group “robust *Pseudo-nitzschia*” (15%). None of the remaining taxa contributed more than 10% of the total abundance. *E. huxleyi* was the most frequent species, occurring in 110 of the 112 samples.

*i. Station groups.* To identify phytoplankton associations and compare their distributions with the hydrographic regions, a similarity map was constructed (Fig. 4). The coastal-offshore discontinuity that characterizes near-surface phytoplankton persisted vertically through the euphotic layer. Floras shoreward of station 60 had no similarities with any offshore of station 60. The two-layered structure characteristic of central Pacific phytoplankton was evident at the two offshore stations, 100 and 110, where phytoplankton above and below the chlorophyll maximum tended to be dominated by different species (Venrick, 1982). However, the CalCOFI samples may not have extended deep enough to fully characterize the deep association. The flora of station 80, above and below the cold, fresh layer, was similar to the most offshore flora, consistent with the T-S signature. On the basis of these relationships, the flora of stations 33–55 have been defined as the “coastal” association and that of stations 110 and 100 to be the “offshore” association, along with the flora of station 80 except 86 m, the single phytoplankton sample from the cold, fresh layer at this station.

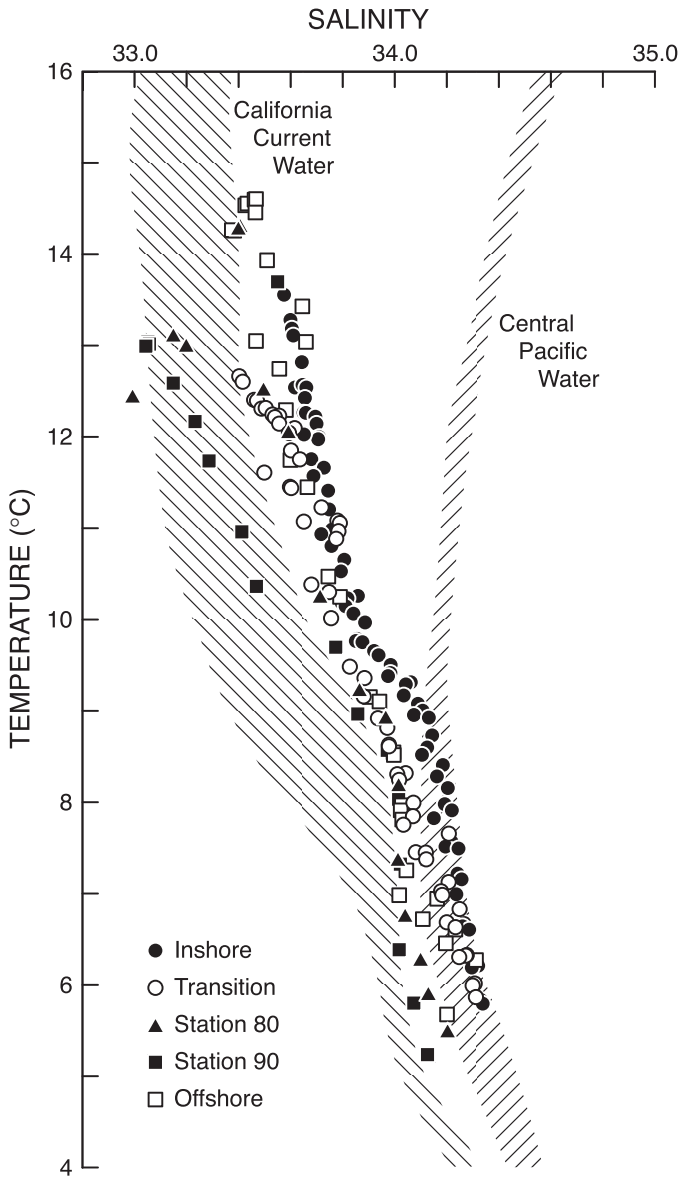


Figure 3. Temperature-salinity relationships of stations sampled in this study, 0–500 m. Individual data points for stations are grouped by hydrographic characteristics: inshore stations: 33–50, transition stations: 55–70; offshore stations: 100 and 110. Station 90 is California Current water, as is station 80, 74–92 m. Station 80 above 74 m is central Pacific water. Also shown are the envelopes (mean  $\pm$  1 standard deviation) of T-S profiles for the central Pacific quadrant centered on 28°N 155 °W (Emery and Wert, 1976) and the for California Current origin in subarctic/transition waters (area 19, Emery and Dewar, 1982).

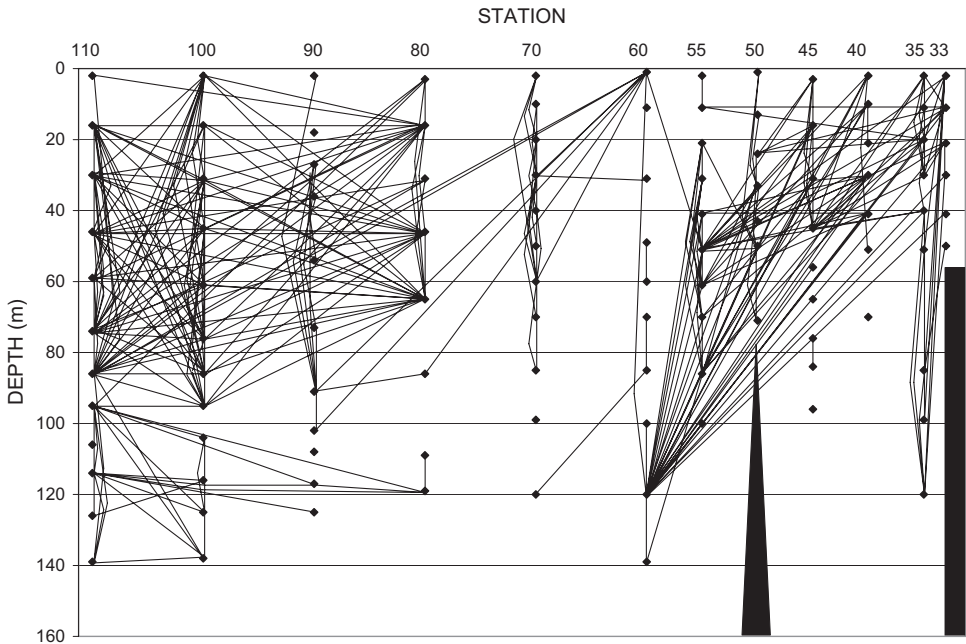


Figure 4. Similarity diagram of flora along line 87. A line connects pairs of similar samples: those whose correlation coefficient equal or exceed the tabulated two-tailed critical value of  $\rho$  at  $p = 0.01$ .

The flora of station 90, the core of the California Current was similar to only the flora of the cold, fresh layer of station 80 (86 m) and the surface sample of station 60. Thus, the distribution of flora in the Current reflected the hydrographic patterns. The flora of station 70 was relatively homogeneous in the upper 90 meters but was distinct from the flora of any other station. At station 60, the flora had little vertical coherency, but the sample from 120 m had unexpected similarities to shallower samples from more coastal stations. The composition at 120 m may have resulted from transport and sinking of near-surface populations, possibly mediated by the deepening density isopleths along the west side of the Santa Rosa Ridge (Fig. 2). The original count sheet noted unexpected near-surface abundances and recorded many apparently healthy cells, consistent with aggregation and sinking. Rapid sinking may also have been a factor in the species composition of 120 m at station 35, which was more similar to the shallow flora at stations 35 and 33 than to flora at intermediate depths.

The distinction between offshore and coastal flora was reinforced by negative correlations. There were 320 strong positive similarities plotted in Figure 4. There were 761 equally strong, negative correlations (Fig. 5). Of these, 530 were dissimilarities between coastal and offshore stations. There were no dissimilarities among coastal stations and only seven within and among the offshore stations, all reflecting floral discontinuity above and

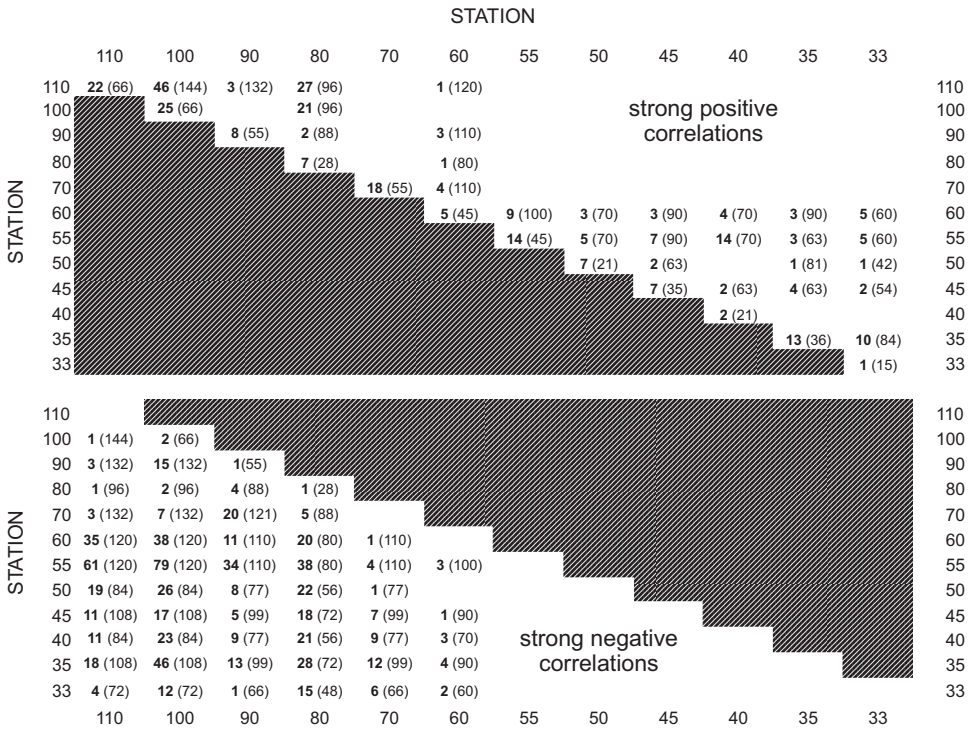


Figure 5. Floristic similarity and dissimilarity of species rank order of abundance in samples from stations along line 87. A strong positive or negative correlation is one whose absolute value equals or exceeds the tabulated critical value of  $\rho$  at  $p = 0.01$ . Data are the number of strong correlations between all possible pairs of samples within a station, or between two stations. The total possible number of correlations is a function of sample number and is given in parentheses. Blank cells indicate zero strong correlations.

below 90 m. The remaining strong dissimilarities involved the intermediate band between coastal and offshore flora.

The similarity analysis confirmed the separation of coastal and offshore flora throughout the euphotic zone, but it gave little information about the nature of the transition between them. The unique T-S relationships at station 90, and in the stratum between 74 and 92 m at station 80, together with the floral similarity of these samples, suggested possible injection of an additional flora by the Current. The similarity plot also suggested a distinct flora at station 70, although a unique hydrographic origin was not indicated by the T-S relationship there.

ii. *Recurrent species groups.* Recurrent group analysis was performed both to characterize the dominant species in the coastal and offshore floral groups, and to seek unique flora in the region between them. Twenty-six species were grouped into ten groups with five

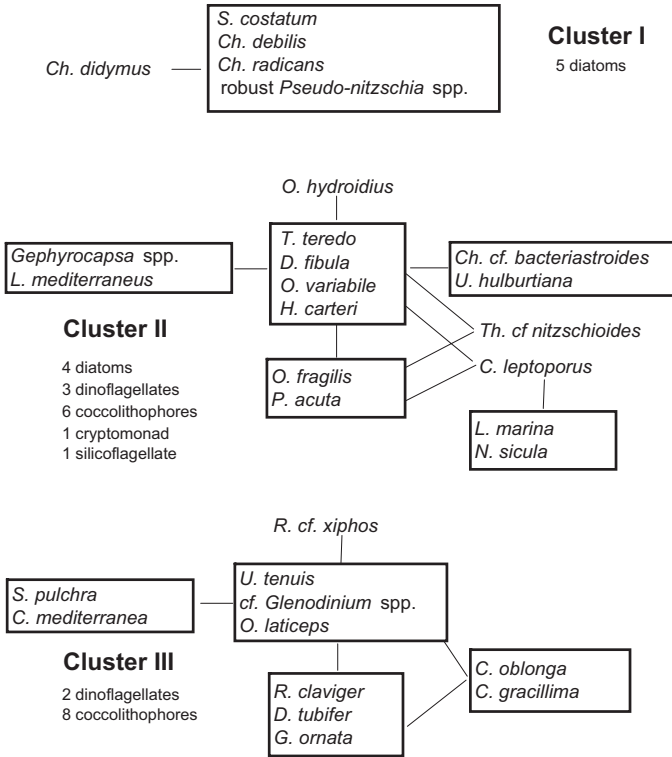


Figure 6. Results of recurrent group analysis,  $\alpha = 0.70$ . Species of a recurrent group are enclosed in a box; associated species are not. One or more affinities between species in different groups, or between associated species and species in a group are indicated by straight lines. The taxonomic composition of each cluster is given.

associated species. The groups, in turn, were inter-connected into three clusters which had no cross connections (Fig. 6). Cluster I was a single recurrent group of four diatoms with one associated diatom. This group included the first and third most abundant species, *Chaetoceros debilis* and robust *Pseudo-nitzschia* spp. Cluster I was a coastal assemblage (Figs. 7, 8). The summed abundance of the five component species exceeded 1,000 cells/ml in the 20 m samples of stations 33 and 35, and abundances were consistently elevated above 50 m inshore of station 55. When the samples with elevated abundances of Cluster I were plotted in T-S space (Fig. 9), the relationship with coastally upwelled water was evident; elevated abundances were restricted to relatively cool water (<13.2°C) with salinities greater than 33.6.

Cluster II consisted of fifteen species associated into five interrelated recurrent groups and three associated species (Fig. 6). Cluster II was the most diverse cluster, including four diatoms, three dinoflagellates, five coccolithophorids, one silicoflagellate and one cryptomonad. Cluster III consisted of two dinoflagellates and eight coccolithophorids (Fig. 6).

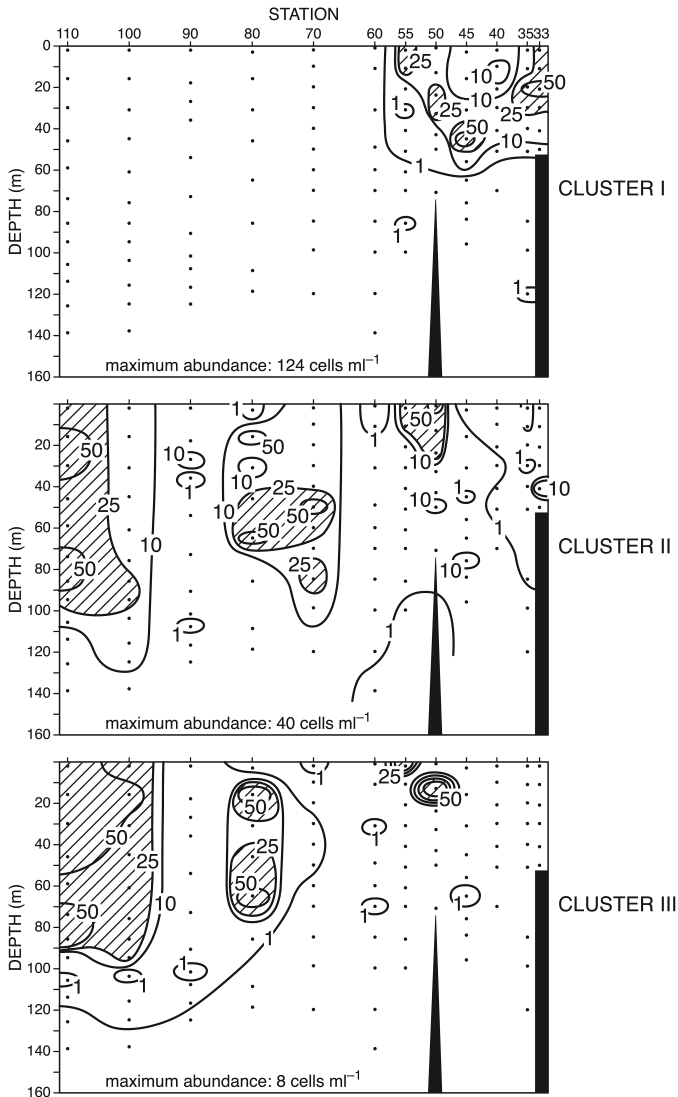


Figure 7. Distributions of clusters of recurrent groups and associated species along line 87. Contours are given as percent of maximum abundance. Shading indicates abundances  $> 25\%$  of maximum abundance.

Clusters II and III were offshore assemblages reaching maximum abundances at stations 100 and/or 110 with isolated patches of elevated abundance at station 80 (Figs. 7, 8). Both had patches of elevated abundance above 20 m at stations 50 and 55, which were due to “blooms” of only one or two species in the cluster. Offshore clusters tended to be less abundant at station 90, the Current core, than at adjacent stations. Members of both

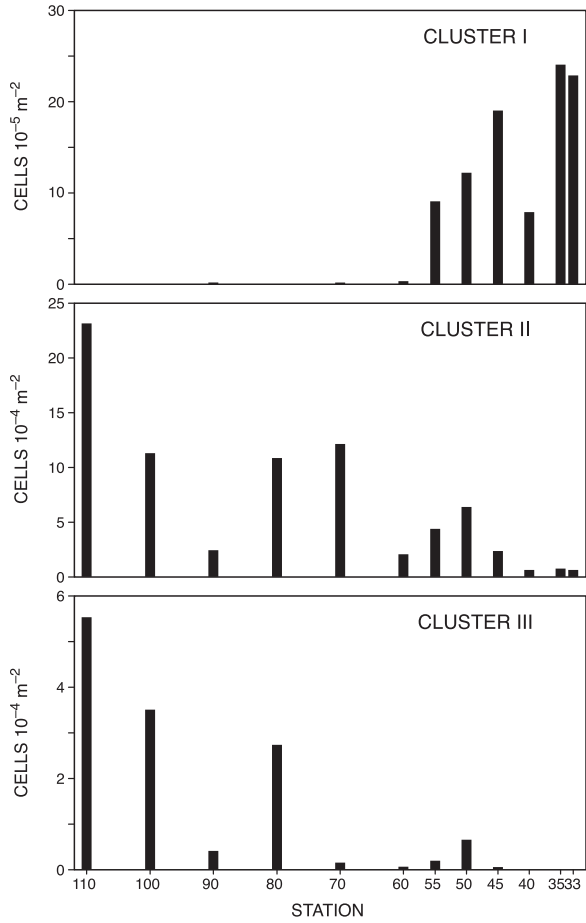


Figure 8. Integrated abundances of three clusters of three recurrent groups and associated species along line 87.

offshore clusters were totally absent in near-surface waters east of station 40. When samples of elevated abundances were plotted in T-S space (Fig. 9), the samples from the very warm, relatively fresh offshore waters were uniformly characterized by elevated abundances of Cluster II and/or Cluster III. The major difference between the distributions of Clusters II and III was the broader distribution of Cluster II, which extended further eastward and somewhat deeper in the water column.

Recurrent group analysis defined no set of species unique to either station 70 or station 90. *Emiliania huxleyi*, the most frequent species in this study, strongly dominated the California Current water (station 90 and 86 m at station 80) where it accounted for 73% of the total number of cells enumerated. None of the other 142 species present in the Current accounted for more than 4% of the total. However, *E. huxleyi* also dominated several other



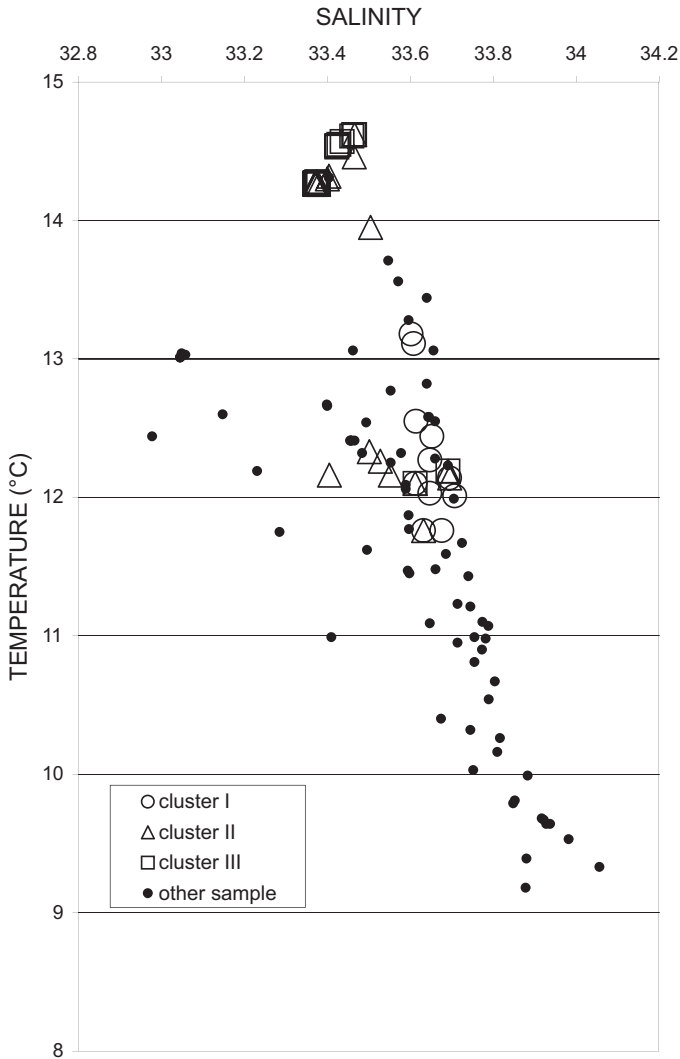


Figure 9. Samples with elevated abundances of three clusters of recurrent groups plotted in T-S space. Elevated abundances are those  $> 25\%$  of the maximum abundance (given in Fig. 7). Note: data points plotted in Figure 3 that were not accompanied by phytoplankton samples are not plotted here.

stations, accounting for more than half the cells at stations 60 and 70 and less than half at stations 45, 80 and 110. The maximum abundance of *E. huxleyi* occurred at the surface of station 50 where it accounted for 63% of the total cells (Fig. 10). Thus, the center of abundance and dominance pattern suggested *E. huxleyi* to be a transition, or opportunistic species, and the importance of the Current in transporting this species into the region is

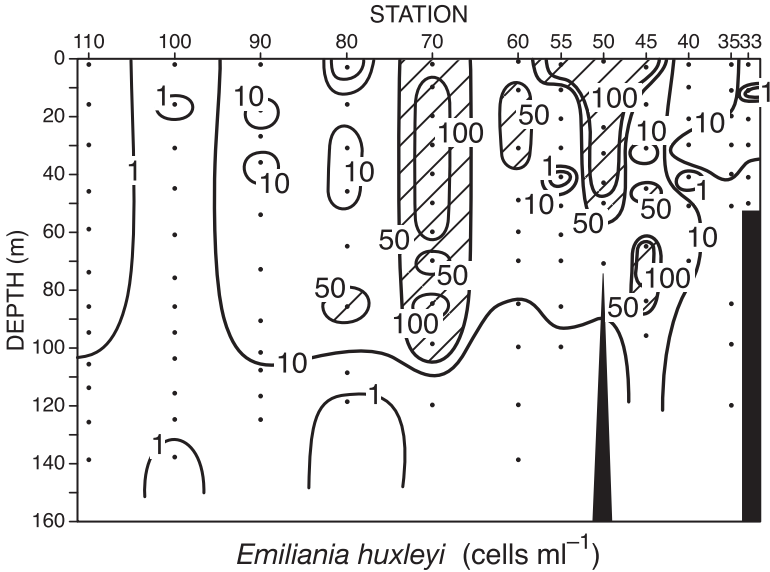


Figure 10. Distribution of *Emiliana huxleyi* (cells/ml) along line 87.

unclear. From these observations, *E. huxleyi* does not appear to be an indicator of subarctic flora transported south by the California Current.

iii. *Interannual variability within the CalCOFI area.* To examine the interannual variability of the coastal and offshore flora, I have compared the mixed layer flora of the present study with coastal and offshore floras described from the mixed layer in April 1993 and April 1995 (Venrick, 1998). The hydrographic data are available at: <http://www.calcofi.org/newhome/data/1990s.htm>.

April 1999 was one of the strongest La Niña events in CalCOFI history. In contrast, April 1993 was imbedded in a moderate El Niño event, and April 1995 in ENSO-neutral conditions. In spite of the apparent climatic contrast, environmental conditions were rather similar in all three springs. In each case, the California Current was stronger than usual, even for spring, and upwelling was vigorous in the north. In 1993, as in 1999, the core of the Current crossed line 87 at station 90, where minimum salinities were below 33.00. In 1995 the current was further inshore, crossing the study section at stations 55 and 60 with slightly higher minimum salinities. In all three years, along line 87 the stations with inshore flora, as defined by the similarity maps, occurred above and inshore of the Santa Rosa Ridge (station 50 and inshore). The distribution of coastal flora may be strongly influenced by bottom topography. In contrast, the location of offshore floristic stations may be influenced by the position of the Current. In 1995, when the Current was closer to shore, the offshore flora along line 87 extended inshore to station 60, with a much narrower area

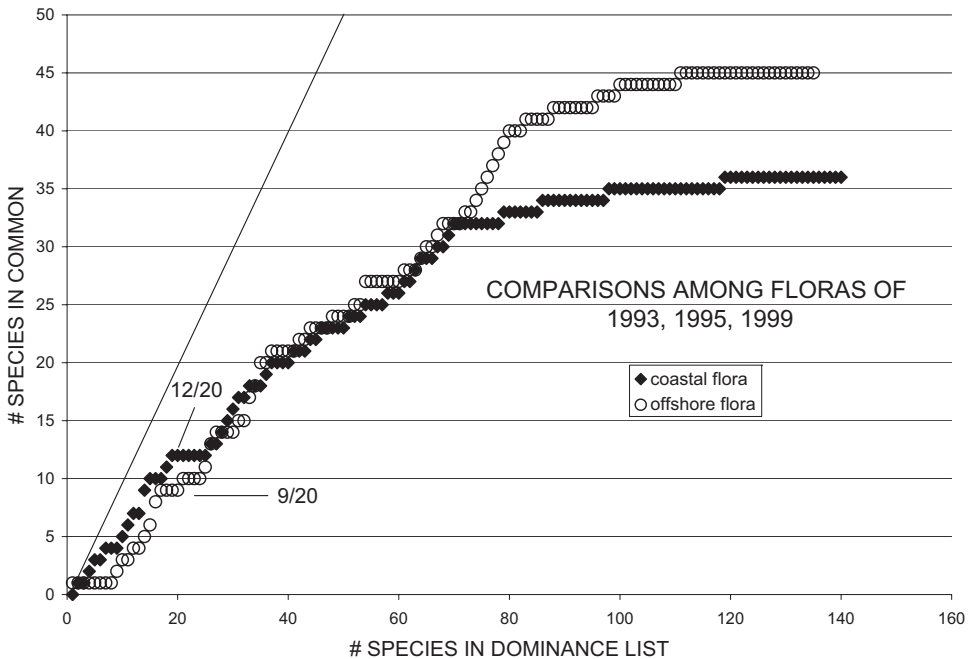


Figure 11. Cumulative dominance curves for the coastal flora, and for the offshore flora, 1993, 1995 and 1999. Line is 1:1 line (identical rank order of abundance).

of transition. Unfortunately, the sampling in 1993 extended only out to station 80 and the offshore flora was not well defined by that study.

Chlorophyll concentrations in all three years were anomalously high for spring values. The cruise mean concentration in 1999 was approximately 30% greater than in 1993 or 1995, but, as noted previously, this was due largely to elevated values in the offshore region. Inshore chlorophyll concentrations were similar in 1995 and 1999; they were somewhat lower in 1993. Thus, we might expect any floristic differences among these years to be more pronounced in the offshore region.

When coastal phytoplankton samples from the three years were pooled within years, correlations across years decreased from 0.52 to 0.41 over a six year period. The cumulative dominance plot was concave downward indicating greater stability among the dominant species than among the rare (Fig. 11). Although a different species dominated each year, one species (*Chaetoceros debilis*) was one of the two most abundant species in each of the three years, and three species (*Ch. debilis*, *Ch. radicans*, and *small Pseudo-nitzschia spp.*) were consistently one of the top five dominant taxa (Table 1). In contrast, only 36 species, 21% of the total species list, were found during all three years.

As suggested by the chlorophyll data, interannual stability was lower among the pooled samples of the offshore stations, decreasing from 0.43 between 1993 and 1995, to 0.23 and 0.25 when the comparison included 1999. In contrast, the median similarity between

Table 1. Species common to the top 20 species of the 1993, 1995 and 1999 samples pooled from the coastal CalCOFI region and from the offshore CalCOFI region. Rank 1 is the dominant species.

Coastal Regions: sta. 33–55		Offshore Regions: sta. 80 (in part), 100, 110	
Lowest rank	Species	Lowest rank	Species
2	<i>Chaetoceros debilis</i>	1	<i>Emiliania huxleyi</i>
4	slim <i>Pseudo-nitzschia</i> spp.	9	<i>Oxytoxum variabile</i>
5	<i>Ch. radicans</i>	10	<i>Gephyrocapsa</i> spp.
7	<i>Nitzschia Americana</i>	12	<i>Gephyrocapsa ornata</i>
10	<i>Emiliania huxleyi</i>	14	<i>Discosphaera tubifer</i>
11	<i>Ch. compressus</i>	15	<i>Leucocryptos marina</i>
12	<i>Ch. socialis</i>	16	<i>Umbellosphaera tenuis</i>
14	robust <i>Pseudo-nitzschia</i> spp.	16	cf. <i>Glenodinium</i>
14	<i>Ch. didymus</i>	17	<i>Umbilicosphaera hulburtiana</i>
15	<i>Skeletonema costatum</i>		
18	<i>Gephyrocapsa</i> spp.		
19	cf. <i>Cylindrotheca closterium</i>		

coastal and offshore flora over all periods was  $-0.06$ , emphasizing the distinctness of the two associations. The cumulative dominance plot for offshore flora again indicated greater stability among the dominant species than among the rare, but, relative to the coastal flora, there was less stability among the dominants. (Fig.11). Although one species (*E. huxleyi*) was dominant in all three data sets, it was the only species common to the top eight dominants (Table 1). Forty-five species (25%) occurred in all three data sets. In general, both the coastal and offshore floras exhibited more interannual stability than variability, in spite of the different ENSO conditions. These data illustrate the difficulty of predicting the precise local consequences of an ENSO cycle.

*iv. Spatial-temporal variability within the central Pacific flora.* A series of studies was conducted over a 23-year period in the central Pacific environment, near  $28^{\circ}\text{N}$ ,  $155^{\circ}\text{W}$  (Venrick, 1999). These allowed objective comparison of the flora in the offshore California Current ecosystem with flora within the central Pacific. Over the 23-year study period, correlations between the rank order of abundance of species in samples from the shallow stratum of the central Pacific varied between 0.72 and 0.32 with a relatively stable long-term correlation about 0.40 (Venrick, 1999). Over the same period, the structure of the deep flora was somewhat less stable with correlations varying between 0.72 and 0.14. For comparison with the present data, data from the most recent central Pacific samples, collected in July 1996, were used. These were separated from the present data by 2.8 years and 3000 km. The correlations between shallow floras of offshore California Current system and the central Pacific stations varied between 0.30 and 0.40, with a mean of 0.34. These values overlapped the lower edge of the range of correlations between shallow central Pacific flora over a similar time period. The correlations between deep floras varied

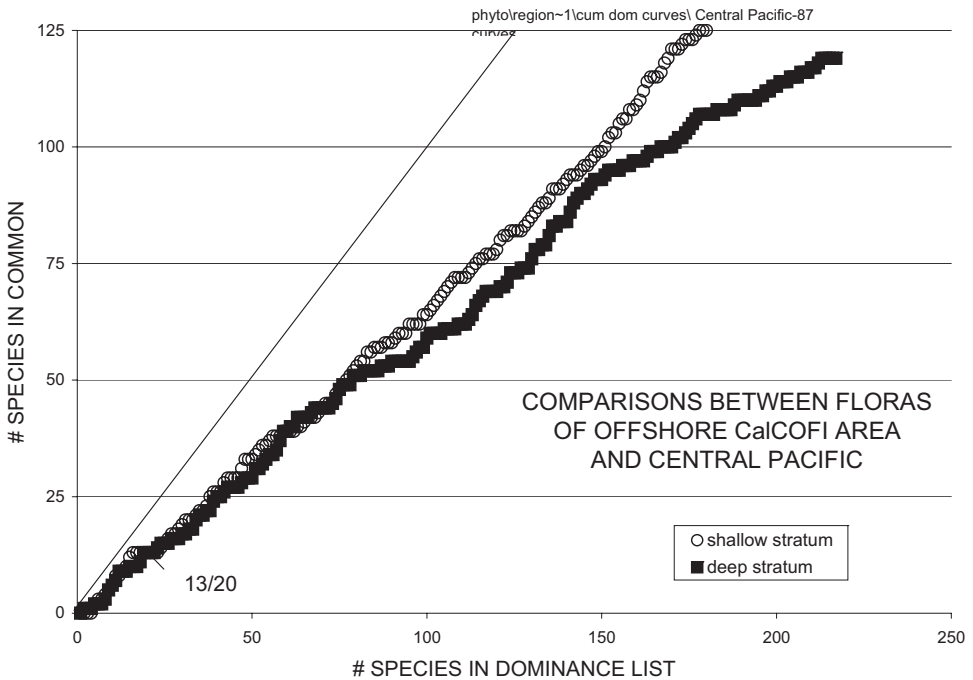


Figure 12. Cumulative dominance curves for the offshore California Current flora, 1999 and the central Pacific flora, 1996. Line is 1:1 line (identical rank order of abundance).

between 0.20 and 0.30, and were slightly outside the range of comparable correlations among central Pacific deep flora. These differences may reflect some seasonal and interannual changes, but are expected to be primarily spatial. The important result, however, is not that differences in floral composition could be detected, but that the differences were small compared with the marked hydrographic changes that occurred over the same distance (Fig. 3).

After pooling all shallow or deep data within 1996 and within 1999, the cumulative dominance curves were relatively straight, indicating that dominant species are neither more nor less variable than rare species. Both shallow and deep strata shared 13 of the top 20 dominants (Fig. 12; Table 2). There were 132 species common to the shallow strata of the central Pacific and offshore CC (54% of total list), and 119 species (72%) common to the deep strata.

#### 4. Discussion

The initial goal of this study was to characterize floral patterns in a section across the California Current system, in order to determine the persistence of the coastal and offshore associations first described from mixed layer data. It appears that these two associations

Table 2. Species common to the top 20 species of the pooled samples from the offshore CalCOFI region in 1999 and the central Pacific in 1996. Rank 1 is the dominant species.

Shallow Stratum		Deep Stratum	
Lowest rank	Species	Lowest rank	Species
5	<i>Emiliania huxleyi</i>	2	<i>Emiliania huxleyi</i>
5	<i>Umbellosphaera tenuis</i>	5	<i>Florisphaera profunda</i>
6	<i>Leucocryptos marina</i>	8	cf. <i>Thalassionema nitzschioides</i> .
8	<i>Oxytoxum variabile</i>	9	Slim <i>Pseudo-nitzschia</i> spp.
9	<i>Gephyrocapsa ornata</i>	9	<i>Gephyrocapsa</i> spp.
10	<i>Gephyrocapsa</i> spp.	10	<i>Leucocryptos marina</i>
11	<i>Ophiaster</i> spp.	11	<i>Oxytoxum variabile</i>
11	<i>Discosphaera tubifer</i>	12	<i>Ophiaster</i> spp.
13	cf. <i>Cylindrotheca closterium</i>	12	cf. <i>Cylindrotheca closterium</i>
14	<i>Rhabdosphaera clavigera</i>	15	<i>Leptocylindrus mediterranea</i>
15	slim <i>Pseudo-nitzschia</i> spp.	19	<i>Umbellosphaera tenuis</i>
15	<i>Calyptrorphaera oblonga</i>	20	cf. <i>Glenodinium</i> spp.
16	cf. <i>Glenodinium</i> spp.	20	<i>Gephyrocapsa ornata</i>

remain distinct throughout the euphotic layer, at least in the spring. The boundary between them was approximately 300 km wide (160 n mi) and included the core of California Current. The species composition (rank order of abundance) of both coastal and offshore flora are relatively stable over several years, or they recur annually in the spring.

As noted in earlier publications, the coastal association is dominated by species that characterize wind-driven upwelling systems through a great range of latitudes—spring-bloom species. Off northern California, Hood *et al.* (1990) described two distinct biological regimes. Although phytoplankton assemblages were not quantified, the inshore flora was often dominated by *Skeletonema* and various *Chaetoceros* species, as well as *Pseudo-nitzschia* spp. and *Thalassiosira* spp., an assemblage resembling the coastal assemblage described in the present paper. Recurrent group analysis of phytoplankton from the continental shelf off Kodiak Alaska in August, 1964 defined three related groups, all distinct from the adjacent oceanic flora of the subarctic Pacific (Venrick, 1971). Three diatoms in this study, *Ch. debilis*, *S. costatum* and *Ch. didymus* were members of these Alaskan groups. Other members of the Alaskan groups included *Ch. compressus*, *Ch. decipiens*, *Bacteriastrum delicatulum*, *Thalassionema nitzschioides* and *Thalassiosira rotula*, all found in coastal CalCOFI flora. Thus, it appears that a coastal flora similar to the one defined in the present study extends around the northeastern Pacific, adjacent to and distinct from both central and subarctic oceanic assemblages.

The offshore flora of the CalCOFI region is closely related to the flora of the central Pacific, from which it is derived. A similar association was identified from the offshore Ensenada Frontal region (Venrick, 1992). It seems likely that these species extend throughout much of the eastern central Pacific and are thus analogous to many of the

central Pacific larval fish and zooplankton species that are common in the CalCOFI regions. The oligotrophic central Pacific flora persists in spite of extensive modification of hydrography. It is possible that the species composition and vertical structure are determined by the oligotrophic nutrient regime independent of either temperature or salinity directly.

In these data, there was no assemblage closely related to oceanic subarctic flora to the north. This has been noted in previous studies (Venrick, 2002) but because earlier studies examined near-surface phytoplankton only, I could not eliminate the possibility of subsurface transport of a coherent subarctic association. The vertical coverage provided here seems to confirm the absence of a floral analog to the subarctic zooplankton species, in spite of the fact that the low salinity core of the California Current was little modified from its source waters to the north. Upstream nutrient depletion may be a factor. Roemmich (1989) calculated a mass balance nutrient budget for the CalCOFI region. The greatest source of nutrients in the euphotic zone is through Ekman transport. Advection provides a detectable source of nutrients and, of the advective sources, a small near-surface source can be associated with the California Current. However, there is considerable seasonal and interannual variability in this transport (Bograd *et al.*, 2001). In April 1999, nitrate was present in the core of the California Current when it first entered the CalCOFI region (from offshore at line 80). Virtually all nutrients had disappeared by the time the Current crossed the study section along line 87 (Fig. 2 and [http://www.calcofi.org/data/1990s/1999/9904\\_hyd.html](http://www.calcofi.org/data/1990s/1999/9904_hyd.html)). Samples north of the present study area were recently collected (April and October, 2008) to determine if the disappearance of oceanic subarctic flora from the California Current is related to nutrient depletion.

To date, the studies that have specifically focused on coastal and offshore floral patterns have all been based on April samples. Spring is the season in which wind-driven upwelling is maximal, the coastal flora is expected to be most fully developed and the contrast with offshore flora is expected to be the greatest. Spring and summer are the seasons when the flow of the California Current is strongest and the Current may provide a more effective boundary at this time. The recently collected October samples will permit me to examine seasonal changes in the coastal-offshore pattern during a period of more relaxed Current flow.

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