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Floral patterns in the California Current System off southern California: 1990–1996

by E. L. Venrick¹

ABSTRACT

In 1990, CalCOFI cruises began routine collection of samples for the enumeration of phytoplankton species. From each quarterly cruise, nearsurface samples from 34 stations are pooled into four regional samples prior to counting. This paper summarizes the first 6.5 years of the program in order to identify major large-scale patterns of species composition and fluctuations.

A total of 312 species were recognized during this study. Recurrent group analysis defines two major floral clusters. The first is composed of diatoms characteristic of enriched regions. This cluster is most abundant in the northeastern region and often attains maximum abundances in the spring. Seventy-two percent of the variability of chlorophyll is accounted for by the variability of these species. The second cluster is composed of species common in the offshore central North Pacific. These species have relatively low spatial and temporal variability in the study region. There is no detectable seasonality. In neither cluster can interannual variability be detected above seasonal variability, spatial variability and error.

These patterns differ from the geographic patterns of zooplankton species in the region, which are often dominated by fauna from the subarctic North Pacific and transition zone. The apparent absence of a similar subarctic flora is briefly discussed.

1. Introduction

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) began routine surveys of the California Current System (CCS) in 1949. From the onset, activities at each station have included measurements of temperature, salinity and oxygen and an oblique net tow for macrozooplankton and ichthyoplankton. Because of the lengths of the series, the hydrographic and zooplankton biomass data have provided unique information on ocean-atmosphere relationships on several scales, from seasonal (Hemingway, 1979; Roesler and Chelton, 1987) to interannual and interdecadal (Bernal, 1979; Chelton *et al.*, 1982; Roemmich and McGowan, 1995). Numerous studies of the zooplankton and ichthyoplankton samples have examined taxon-specific patterns of variability in more restricted data sets (e.g. Brinton, 1976, 1981; Colebrook, 1977; Mullin *et al.*, 1989; Moser *et al.*, 1987; Moser and Smith, 1993; Mullin, 1998) and two recent studies investigated taxonomic shifts over interdecadal scales (Lavaniegos and Ohman, 1999; Rebstock, 2001).

1. Integrative Oceanography Division, Scripps Institution of Oceanography, 9500 Gilman Drive, La Jolla, California, 92093-0227, U.S.A. *email: evenrick@ucsd.edu*

It was not until 1984 that chlorophyll and primary productivity became standard measurements on CalCOFI cruises. These are now of sufficient length to reveal some broad spatial and temporal patterns of variability in these phytoplankton parameters (Hayward and Venrick, 1998). However, phytoplankton studies at the species level have been sporadic and of short duration (Sverdrup and Allen, 1939; Allen, 1945a, b; Sargent and Walker, 1948; Balech, 1960; Matrai, 1986). Recent pigment-based studies in the CalCOFI region provide information at higher taxonomic levels (Goericke, pers. comm.). More extensive phytoplankton studies have been conducted independently of CalCOFI, most notably the studies of W.E. Allen off the end of the pier at Scripps Institution of Oceanography (SIO; Allen, 1936, 1941; Tont, 1976, 1981, 1987), those conducted under the auspices of the Food Chain Research Group of SIO (Beers, 1986; and references therein); and studies based on sediments and sediment traps in the Santa Barbara and San Pedro Basins (Lange *et al.*, 1987, 1990, 1997; Ziveri *et al.*, 1995). However, all of these lack the spatial and temporal scope of the core CalCOFI data set. Thus, our knowledge of the phytoplankton composition of the CCS and its scales of variability lags far behind comparable knowledge of zooplankton.

In the summer of 1989, a program to monitor the taxonomic composition and abundance of the larger phytoplankton was initiated. The goal is to establish a time series of phytoplankton data that will relate directly to the time series that exist for other physical, chemical and biological parameters. A necessary characteristic of a viable time series is that sample enumeration keep up with sample collection. On a standard cruise, 1225 water samples are collected, of which over half are of potential value to a study of phytoplankton. To reduce the number of samples sufficiently, vertical coverage is sacrificed and only the mixed layer is sampled. This layer (when it exists) has continuity across the entire cruise pattern, and the CalCOFI sampling protocol includes at least one sample at each station from the mixed layer. Also, this layer encompasses the full range of phytoplankton biomass and productivity in the region. As an additional compromise, individual samples are pooled into four regions before counting. This sampling strategy integrates small-scale spatial variability, but it provides data with which to evaluate regional and interannual changes in the near-surface layer. In addition, the time-series program provides an umbrella under which more specific small-scale studies can be conducted (e.g. Venrick, 1998).

This paper is a synopsis of the first 6.5 years of the time-series data. This data set is treated as a baseline interval with which to examine the numbers of species present, the existence of species associations and their seasonal and spatial variability. Because of the complexity of the CCS, the data set is still too short to reliably detect relationships with environmental variables or to resolve individual events, such as ENSO, above the spatial and intra-annual variability. Such analyses are deferred until a longer data set is available.

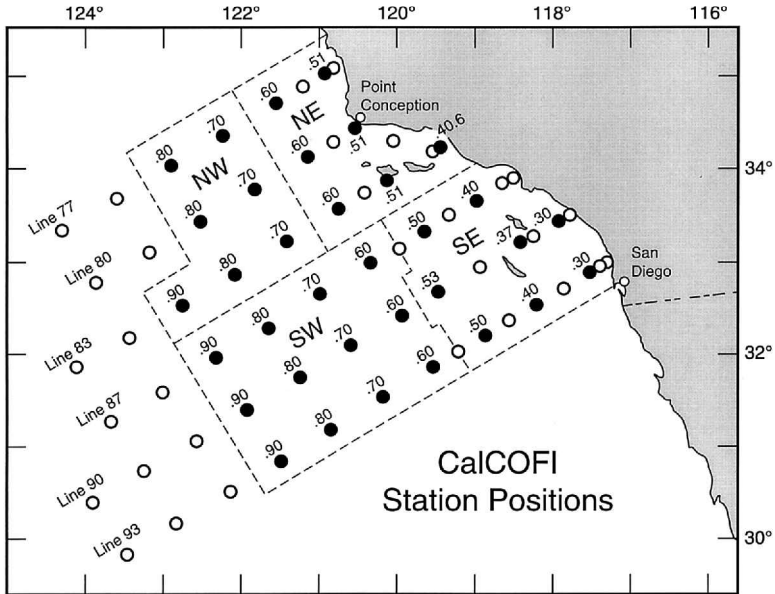


Figure 1. The CalCOFI station plan. Stations are occupied sequentially by line number: offshore along line 93, inshore along line 90, etc. Solid circles indicate stations from which phytoplankton samples were collected. Prior to counting, samples were pooled into the four regions indicated by the dashed lines.

2. Methods

a. Survey design

CalCOFI cruises are 2–3 week cruises conducted approximately quarterly. Cruises are designated by year and month; thus the mid-day of CC9004 fell in April of 1990. The data discussed in this study were collected between Jan. 1990 and April 1996 (26 cruises). Samples for the phytoplankton study are collected from 34 of the 66 regularly occupied stations (Fig. 1). These stations are separated by approximately 40 n mi (74 km). Western-most stations are not included because these stations are the most likely to be omitted when there are constraints of time or weather. Details of the station plan and data for individual cruises are available in data reports (SIO reference series) and through the CalCOFI web page (<http://www-mlrg.ucsd.edu/calcofi.html>).

b. Floristics

Phytoplankton samples were 30-ml water samples preserved with buffered formalin to a final concentration of 1% formaldehyde and a pH between 7.5 and 8 (Thronsdon, 1978). Samples were stored in the dark, at room temperature and were counted within four months of collection. Prior to counting, samples within each of the four regions were physically pooled, thereby condensing 34 samples into four. There are no regional counts from the

northeast or northwest regions of CC9004, leaving 102 samples in the data set. Pooled sample volumes of 0.57–100 ml were diluted or concentrated by settling and counted on a Zeiss phase-contrast inverted plankton microscope using the Utermöhl technique. The entire sample was counted at 100 \times for larger species, and every sixth row was counted at 250 \times for smaller species. Occasionally, very small and abundant species (*Emiliania huxleyi*, *Gephyrocapsa* spp., and/or a small form of *Nitzschia* cf. *bicapitata*) were counted along a single transect at 400 \times . Species identification was facilitated by transferring individual cells to an oil immersion microscope or to a scanning electron microscope. The nomenclature follows that given in Tomas (1997).

This study emphasizes the associations of species. Thus, data are limited to taxa with distinguishing morphology: most diatoms, coccolithophores and silicoflagellates, many thecate dinoflagellates, some athecate dinoflagellates and a few species in other taxa. The smallest taxa are about 5 μ in maximum dimension. Excluded are many of the small flagellates and the picoplankton, which may be quite important in the California Current System, but which require different techniques to quantify.

c. Statistical procedures

To identify species with similar distribution patterns, recurrent group analysis (Fager and McGowan, 1963) has been applied. This procedure utilizes a coefficient of affinity, α , calculated between all pairs of species. Alpha can vary from near 0 to near +1.0. In the original procedure, α was based upon scores of presence and absence, and an α close to 1.0 indicated two species that co-occurred often. Here, α is based on scores \geq the median abundance and $<$ the median abundance, where each species in each sample is scored relative to its median abundance over all samples. When a species is present in less than half of the samples, the median = 0 and scores of presence/absence are used. Calculated in this way, a high α indicates two species that tend to be more abundant in the same samples. The term “link” is used to indicate a coefficient of affinity greater than some pre-selected value. Species are formed into groups within which all species pairs are linked. A connection between two groups occurs when there are links between species in different groups. Associated species are those that have links with some but not all members of a group. Most of the analyses in this study are based on groups and associates formed at an affinity index of 0.55.

Emphasis is placed on nonparametric statistics: Spearman's correlation (ρ), Kruskal-Wallis one-way ANOVA, Friedman two-way ANOVA (Kendall's Concordance) and Theil's regression. Because the monthly timing of cruises is not constant, seasonality is examined by grouping cruises into January and February cruises (winter), March and April cruises (spring), July, August and September cruises (summer) and October and November cruises (fall). There are no data from December, May or June. Where several tests are done as a group, no correction is made for multiple testing because the important results are the relative strengths of the relationships rather than the significance of any one. When it is necessary to estimate actual or relative variance components, parametric procedures

Table 1. Comparison between the single count of a pooled sample and the mean count of individual samples. Also given are the total volumes counted. The correlation (Spearman's ρ) is the correlation between the rank order of n species' abundances in the two data sets.

Cruise and Region	Pooled sample single count		Individual samples mean count		Correlation	
	volume (ml)	# species	volume (ml)	# species	ρ	n
9304 NE	2.25	48	64.5	107	0.57	113
9304 NW	9.75	49	395	140	0.40	149
9504 NE	2.25	28	80.5	83	0.52	85
9504 NW	2.25	54	240	139	0.54	144

(ANOVA and regression) are used, but because the data are expected to be strongly non-normal, no probability values are attached to the results of these analyses.

d. Data validation

Two approaches have been used to investigate the degree to which these pooled samples represent the actual flora of the area. The first examines the information lost during the pooling of samples; the second examines the information lost because only a subset of the total flora is included in the study.

In April 1993 and 1995, in addition to the regionally pooled samples, samples from all the individual stations in the inshore regions were counted (Venrick, 1998). Since both sets were drawn from the same preserved samples, any differences between counts reflects only error introduced in the laboratory: subsampling, pooling and counting errors. Nonparametric correlations (Spearman's ρ) between the rank order of abundance (ROA) of species enumerated in the NE and SE pooled counts and the ROA of the counts averaged over the individual stations were calculated. The four correlations vary between 0.40 and 0.57 (Table 1). All are significant ($p \ll 0.001$). Much of the discrepancy from perfect correlation is due to that fact that the total volume of water enumerated for the pooled samples was much less than the total for the individual samples. As a consequence, there are 2–3 times as many species recorded from the individual stations. It is concluded that, while the pooled samples under-represent the rarer species, the pooling of samples does not appear to introduce intolerable inaccuracies into the data.

An independent, if imperfect, index of phytoplankton biomass is obtained from the concentration of chlorophyll in the phytoplankton samples. This is compared with the total number of cells enumerated from the same samples to give an indication of the degree to which variations of the counts in this study reflect variations in the entire phytoplankton standing crop (Fig. 2). This correlation is significant ($\rho = 0.77$; $p < 0.001$). When the total number of unidentified cells is added, the correlation increases slightly ($\rho = 0.78$). The magnitude of $1 - \rho$ reflects sampling and counting error and variable concentrations of chlorophyll per cell, as well as the unenumerated fraction of the flora. Although it is possible that a majority of the phytoplankton cells were counted, this seems unlikely, since

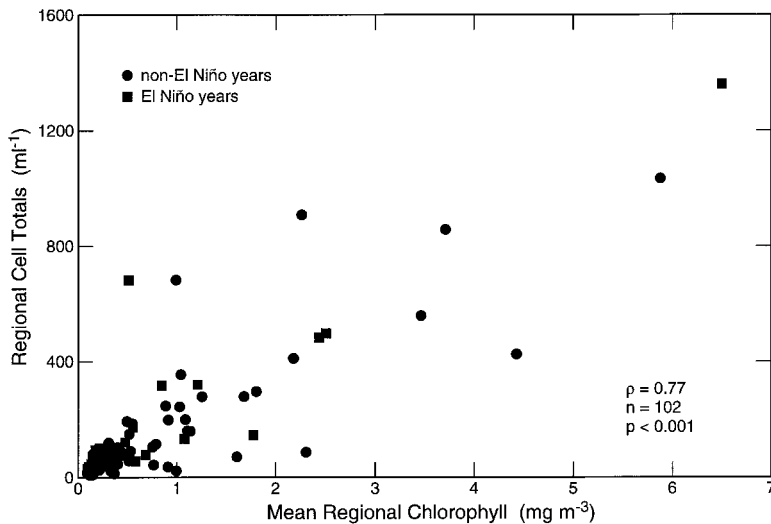


Figure 2. The relationship between chlorophyll (mean value per region per cruise) and the total number of identified cells (samples pooled by region).

the picoplankton are expected to be important, at least in some areas at some times (Putt and Prézelin, 1985). Thus, the relatively high correlation suggests that the uncounted taxa were responding to the environment in the same way as those that were counted, or that the biomass of the uncounted taxa was relatively constant. It is concluded that patterns in the data used in this study are representative of the floral patterns as a whole.

2. Environmental background

Hayward and Venrick (1998) describe the major spatial patterns of the CalCOFI survey area (Fig. 3). The California Current carries cool, fresh water from the subarctic Pacific and northern transition zone toward the equator. The current meanders past the California coast, often moving shoreward near the Mexican border along the Ensenada Front. As it approaches the coast, some portion turns northward, entering the Southern California eddy, the rest continues south along the coast of Baja California. The low salinity jet of the current defines an inshore and an offshore regime. Inshore, upwelling of subsurface nutrients (driven by geostrophy and wind) leads to phytoplankton growth and increased chlorophyll concentrations, especially in the north during the spring months (Fig. 3). Offshore conditions are more consistently oligotrophic, resembling those of the eastern central Pacific. Because of the meandering of the current, some stations fluctuate between inshore and offshore conditions. Within the inshore region, the highest chlorophyll values are in the north. Southern inshore stations are often oligotrophic, influenced by the onward sweep of offshore water.

The 6 ½ year period of this study is embedded in a period of warming of the upper

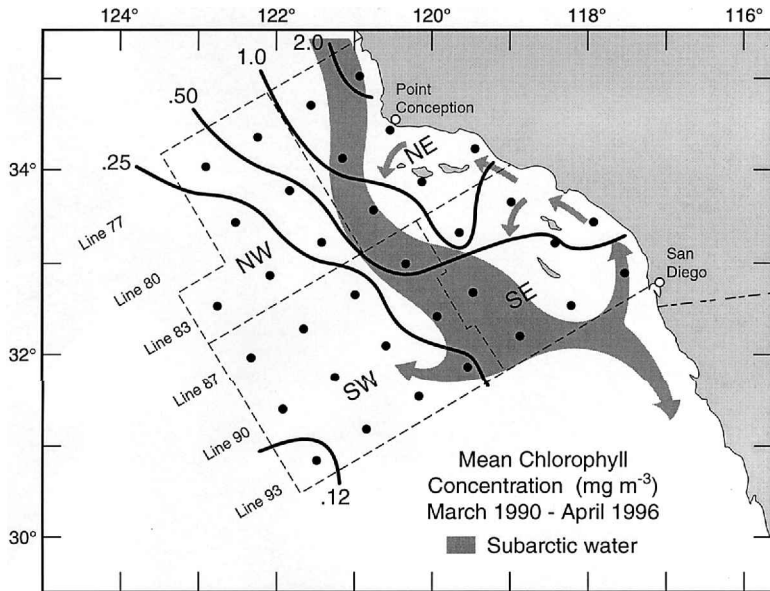


Figure 3. Schematic presentation of the flow patterns in the California Current system and the distribution of mean chlorophyll (Jan 1990–April 1996) superimposed upon the CalCOFI station plan. The subarctic/transition zone water that forms the core of the California Current is indicated by shading.

waters of the California Current System that has been accompanied by a strong decrease in macrozooplankton biomass (Roemmich and McGowan, 1995). These trends appear to have originated with the North Pacific climate shift of 1976–77, and they have persisted at least through this study period. Data since 1986 indicate a concomitant change in the avian fauna, marked primarily by a decrease in numbers of sooty shearwaters (Ainley *et al.*, 1995; Veit *et al.*, 1996, 1997).

Included in the study period is a moderate El Niño event that affected the CCS in 1992 and 1993. This was characterized by a one to two degree warming of sea-surface temperatures, unusually strong poleward coastal currents and a delay in the start of upwelling (Lynn *et al.*, 1995). During both years, however, the El Niño characteristics relaxed during late spring, when circulation returned to more normal patterns and supported upwelling in the northern inshore region (Hayward, 1993; Hayward *et al.*, 1994). Except for these spring months, chlorophyll concentrations in the CalCOFI region were depressed.

During the first four months of 1995, a massive red tide, primarily *Lingulodinium (Gonyaulax) polyedra* occurred in the southeastern portion of the survey area, possibly stimulated by unusually heavy precipitation (Hayward *et al.*, 1995). Off the SIO pier, the bloom peaked at 2 million cells l^{-1} in the second week of March, corresponding to surface chlorophyll values exceeding 500 $\mu g\ chl\ a\ l^{-1}$. During the January CalCOFI cruise surface

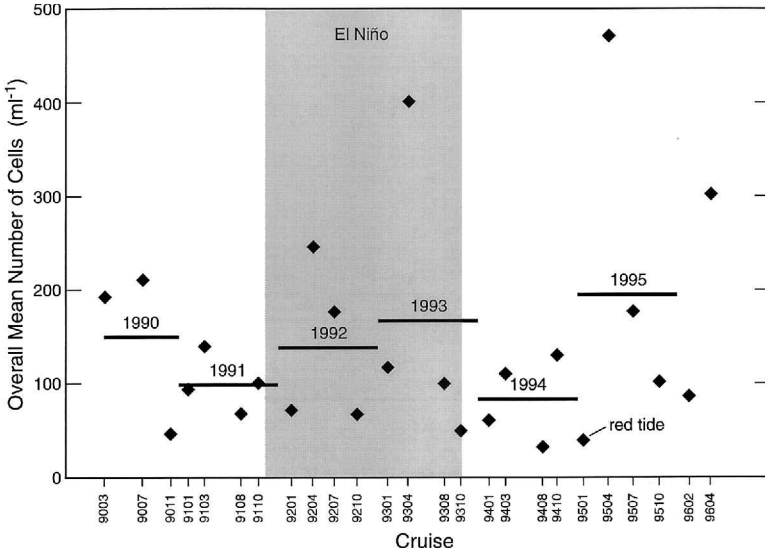


Figure 4. The temporal variability of the total number of enumerated cells. Values are the mean values per cruise. Annual mean values are shown as solid horizontal bars. Major events are indicated.

chlorophyll values at the pier ranged from less than 2 $\mu\text{g chl } a \text{ l}^{-1}$ to more than 30 $\mu\text{g chl } a \text{ l}^{-1}$.

Conditions during the remaining portions of this study were more normal than not, although the concept of normalcy in the CCS is a chimera. Details of the system since 1991 have been summarized in a series of reports (Hayward, 1993; Hayward *et al.*, 1994, 1995, 1996).

3. Results

a. Floral characteristics

The mean number of cells per cruise varies an order of magnitude, between 33 and 470 cells ml^{-1} (Fig. 4). No temporal trend is apparent. Nor is there an obvious signal from the moderate El Niño event of 1992–93. The more oligotrophic conditions associated with El Niño in the California Current System are expected to increase the proportion of smaller cells. A large change in the fraction of uncounted cells (including picoplankton) should be apparent in the relationship between total cells counted and chlorophyll (Fig. 2). This is not the case. The relationship between total cells and chlorophyll is similar during El Niño years and non-El Niño years. The massive red tide in early 1995, was too near shore to affect the total number of cells on the broad spatial scale of this study.

A total of 312 species were identified during this study. These include 133 diatoms, 119 dinoflagellates, 49 coccolithophores, 3 silicoflagellates and 8 from other taxa (Fig. 5). The

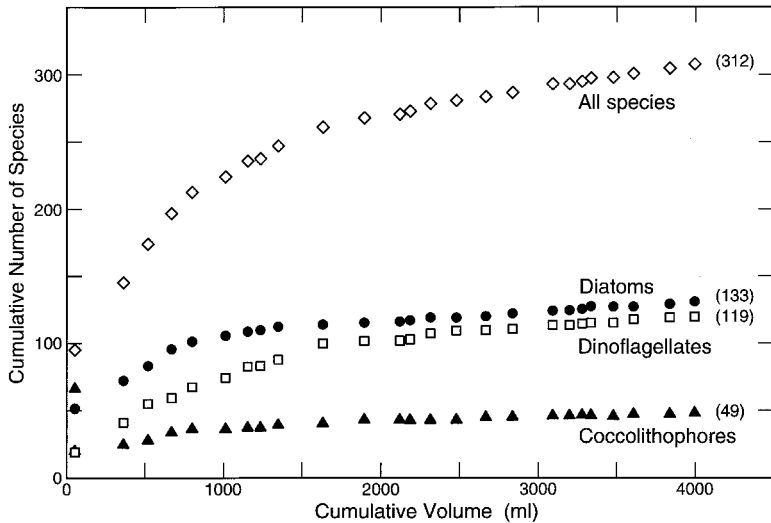


Figure 5. Species-volume curves for all enumerated species and for the three major taxa.

last 12 samples (3 years) of the cumulative species-volume curve suggest a nearly linear increase in the number of species, with approximately three species being added for each additional cruise (Theil's regression, $b = .018$ species ml^{-1}). Diatoms and dinoflagellate species are increasing at similar rates, somewhat more rapidly than are coccolithophores. Interpretation of this increase is confounded by an increasing ability to recognize species. A review of the last twelve species added to the list suggests that four of them are cryptic enough to have been present but overlooked in previous samples; eight probably represent species not previously encountered. Additional samples will indicate whether a horizontal asymptote is being approached by any or all of the taxa.

Over all samples, the Shannon' entropy index (Legendre and Legendre, 1983) is 3.1 and the evenness index is 0.54 (Table 2). This varies little between regions, although, unexpectedly, the highest diversity occurs in the most eutrophic area, the NE region. There is significant concordance of species structure among all regions. Of the ten dominant species in the pooled samples, all rank in the top ten in the NE region, eight are in the top

Table 2. Entropy and evenness by region.

Region	# species	Entropy (H)	Evenness (H/H max)
NE	207	3.01	0.56
NW	232	2.81	0.52
SE	225	2.93	0.54
SW	241	2.83	0.52
Overall	312	3.1	0.54

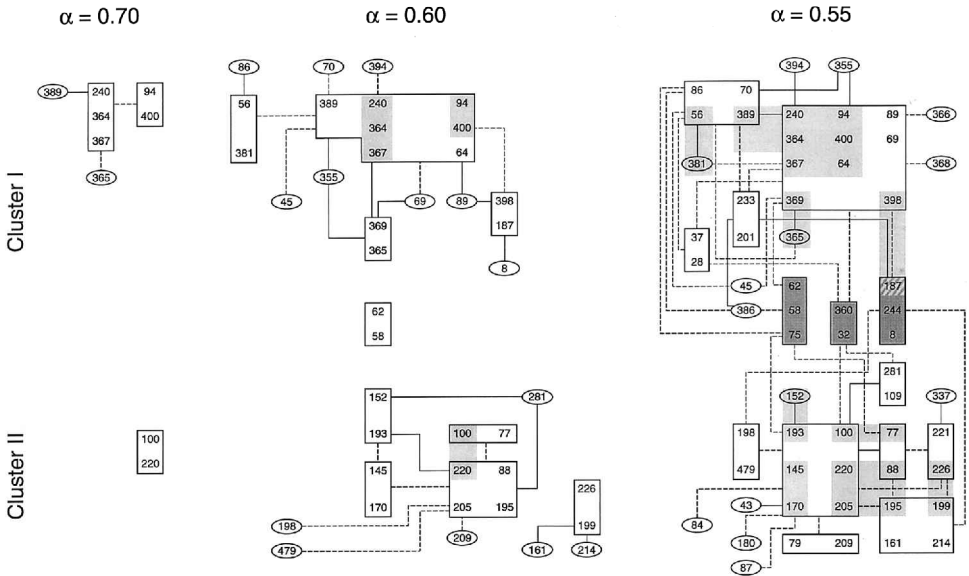


Figure 6. The recurrent groups distinguished with three levels of affinity: $\alpha = 0.70, 0.60$ and 0.55 . Species codes are identified in Table 3. Boxes enclose recurrent groups. Ovals enclose associated species. Links between groups, and between groups and associated species are indicated by straight lines, where a solid line indicates that more than half of the possible number of links are realized. At each level of α , the light shading indicates the major groups formed at the next higher level of α . Darker shading indicates transition groups between clusters.

ten in the NW and SE regions and five are in the top ten in the SW region. The overall dominant species, *Emiliania huxleyi*, is the regional dominant in all regions except the SE region, where it ranks second. The greatest change in rank is seen with *Chaetoceros socialis* that ranks first in the SE region and is absent from the SW region. However, none of the regions achieves a full complement of 312 species. Even after 6.5 years there is still considerable spatial autonomy.

b. Recurrent groups

Recurrent group analysis based upon an affinity index of 0.70 groups 9 species into three groups with two associated species. Two groups are related by links between groups (Fig. 6). When α is reduced to 0.60, the single group and the interrelated pair of groups become the nucleus for two larger clusters of groups and associated species. Within each cluster, there are links among groups; but there are no links across clusters. In addition, there are two species pairs without relationships with other groups. As the affinity is further lowered, the initial clusters enlarge. It is not until an affinity of 0.55 that links appear between the two clusters. However, these links are indirect, involving one of three “transition” groups that have links with both cluster I and cluster II. There are no links

Table 3. Composition of clusters defined by recurrent grouping, taxonomic affinities and mean abundances. diatom: dt; dinoflagellate: dn; coccolithophore, c; silicoflagellate: s

Cluster I			Cluster II		
Code	taxon	Mean (cells ml ⁻¹)	Code	taxon	Mean (cells ml ⁻¹)
94	dt <i>Pseudo-nitzschia</i> spp. (small forms)	16.58	479	c <i>Umbilicosphaera hurburtiana</i>	0.79
367	dt <i>Chaetoceros debilis</i>	12.80	161	dn <i>Oxytoxum</i> cf. <i>variabile</i>	0.73
355	dt <i>Skeletonema costatum</i>	8.02	88	dt cf. <i>Nitzschia bicapitata</i>	0.67
240	dt <i>Chaetoceros radicans</i>	7.02	100	dt cf. <i>Nitzschia bicapitata</i> (minute)	0.66
400	dt <i>Pseudo-nitzschia</i> spp. (large forms)	5.77	220	c <i>Umbellosphaera tenuis</i>	0.47
	<i>P. australis</i>		77	dt <i>Mastogloia woodiana</i>	0.43
	<i>P. multiseriis</i>		205	c <i>Rhabdosphaera claviger</i>	0.36
398	dt <i>Fragilariopsis pseudonana</i>	5.52	195	c <i>Gephyrocapsa ornata</i>	0.35
89	dt <i>Cylindrotheca closterium</i>	4.73	145	dn <i>Glenodinium</i> cf. <i>danicum</i>	0.29
364	dt <i>Chaetoceros compressus</i>	2.41	221	c <i>Umbilicosphaera sibogae</i>	0.20
394	dt epiphytic cylinder	1.77	109	dn <i>Prorocentrum</i> cf. <i>balticum</i>	0.19
381	dt <i>Hemiaulus sinensis</i>	1.64	193	c <i>Discosphaera tubifer</i>	0.17
56	dt <i>Leptocylindrus danicus</i>	1.46	214	c <i>Syracosphaera pulchra</i>	0.15
365	dt <i>Chaetoceros constrictus</i>	1.43	199	c <i>Helicosphaera carterae</i>	0.15
389	dt <i>Dactyliosolen fragilissimus</i>	1.14	198	c <i>Helladosphaera</i> spp.	0.13
28	dt <i>Bacteriastrium delicatulum</i>	0.95	226	s <i>Dictyocha fibula</i>	0.11
369	dt <i>Chaetoceros didymus</i>	0.85	281	c <i>Sphaerocalyptra</i> sp.	0.07
69	dt <i>Thalassionema nitzschioides</i>	0.54	209	c <i>Sphaerocalyptra gracillima</i>	0.06
70	dt <i>Thalassionema frauenfeldii</i>	0.44	170	dn <i>Oxytoxum laticeps</i>	0.05
64	dt <i>Dactyliosolen phuketensis</i>	0.42	152	dn <i>Torodinium</i> sp.	0.05
37	dt <i>Chaetoceros affinis</i>	0.17	79	dt <i>Mastogloia rostrata</i>	0.01
86	dt <i>Haslea wawriakae</i>	0.14			
Transition Groups					
62	dt <i>Rhizosolenia</i> cf. <i>hebetata semispina</i>	0.07	187	c <i>Emiliania huxleyi</i>	37.37
58	dt <i>Proboscia alata</i>	0.07	244	dt <i>Nitzschia tenuirostris</i>	1.31
75	dt <i>Lioloma mediterranea</i> + <i>delicatula</i>	0.07	8	dt <i>Liriogramma</i> sp.	0.11
360	dt <i>Chaetoceros concavicornis</i> + <i>convolutus</i>	0.20			
32	dt <i>Chaetoceros atlanticus</i>	0.08			

among transition groups. There are no links directly between groups in cluster I and groups in cluster II.

The fact that the composition of the recurrent groups merges and splits as the affinity level is altered suggests that it is the clusters of groups, rather than the individual groups that are statistically robust and more likely to reflect ecological relationships. Thus, the two clusters of groups formed at $\alpha = 0.55$ are used (Table 3). An associated species is included as a member of a cluster only if it has half or more of the total possible links with one or more groups in that cluster. The three groups that have affinities with members of both clusters ("transition groups") are excluded as is one species pair within cluster that has a greater proportion of possible affinities with transition groups than it has with other groups in cluster I. The excluded pair consists of the coccolithophore *Ophiaster hydroides* (#201) and the chromophyte *Chilomonas marina*, (#233), two species that are common both in the central Pacific and the inshore California Current System. The resulting clusters consist of 20 and 21 taxa, respectively (Table 3). Cluster I is composed entirely of diatoms. Cluster

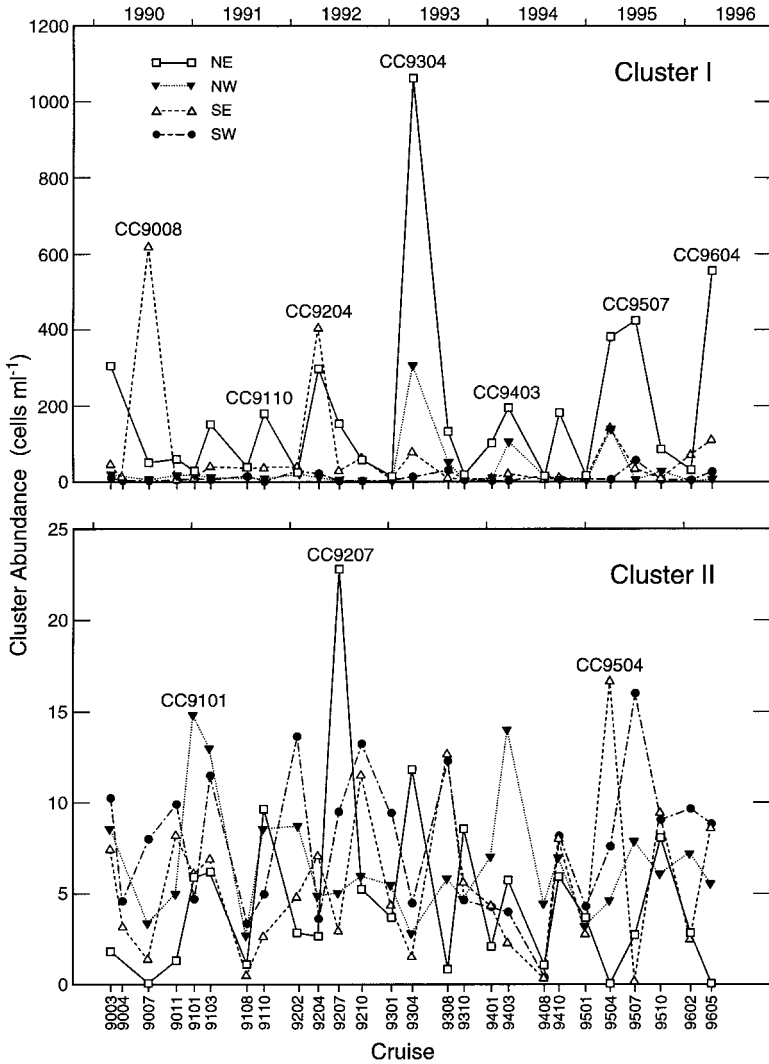


Figure 7. The summed abundances of species in cluster I and cluster II, by region. Major peaks are identified by cruise.

II consists of eleven coccolithophores, five dinoflagellates, four diatoms and one silicoflagellate.

The mean abundance of cluster I species (75 cells ml⁻¹) is roughly half that of the total numbers of cells counted (157 cells ml⁻¹). The species of cluster II are less abundant (mean = 6 cells ml⁻¹). The abundances of the two clusters are plotted by region (Fig. 7). In all but the SW region, the abundance of cluster I was consistently greater than that of cluster II. Both clusters have significant differences between

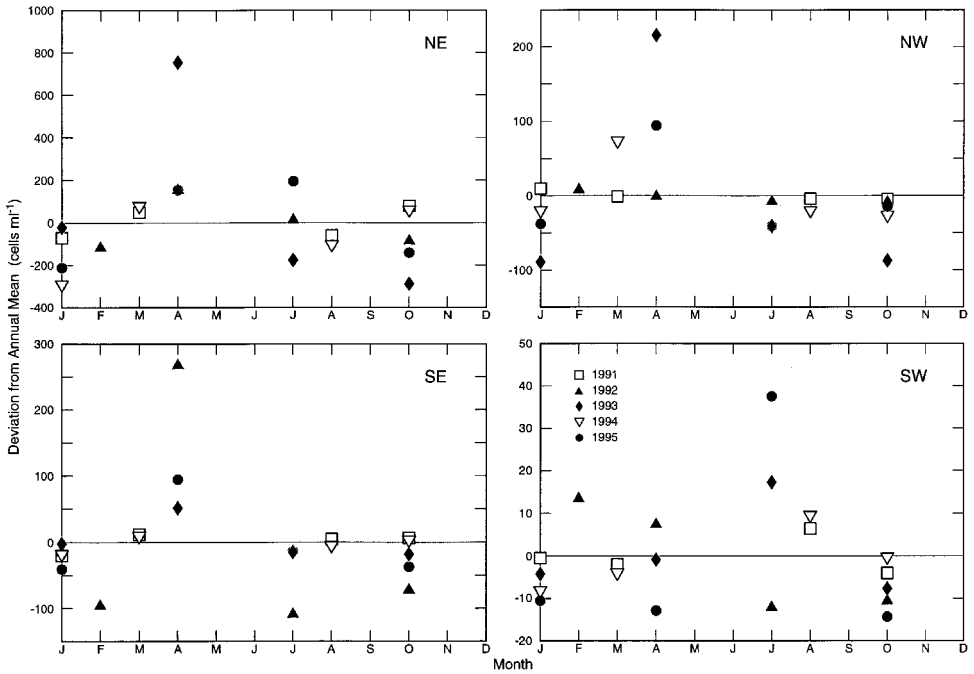


Figure 8. The seasonal variability of the summed abundance of species in cluster I, by region. Values are deviations from the annual mean value. Seasonality (concordance) is significant in all regions except the SW.

regions (Friedman 2-way ANOVA, $p < .01$). The maximum abundances of cluster I occur in the NE region, lowest abundances in the offshore regions. The abundances of cluster II are generally highest in the SW region, although maxima are reached in other regions.

Cluster I has significant seasonality in all regions except the SW region (Fig. 8; Kendall's concordance $p < .05$). Abundances are maximal in March and April and minimal in January and February. The seasonal variability of cluster I is of the same order of magnitude as the spatial variability, but together they account for only half of the total variance (Table 4). Interannual variability cannot be detected in this data set.

The total variance of cluster II is nearly three orders of magnitude less than that of cluster I (Table 4). Neither temporal nor spatial variability is resolved above the residual error.

The picture that evolves from these analyses is of an inshore group of abundant species with a seasonal cycle. This group reaches maximum abundances in the NE region in the spring, almost certainly responding to the increased nutrient concentrations that typically occur there in the spring (Hayward and Venrick, 1998). A second group of species is less abundant and less variable in space and time. These species tend to be more abundant in the

Table 4. Relative sources of variability of cluster abundances.

Source	Variance	% variance
Cluster I		
Between regions	0.77×10^8	27
Between years	≈ 0	0
Between seasons	0.65×10^8	22
Error	1.47×10^8	51
Cluster II		
Between regions	≈ 0	0
Between years	≈ 0	0
Between seasons	≈ 0	0
Error	1.96×10^5	100

offshore regions. The low variability of this second group suggests that these species are a background assemblage upon which the fluctuations of cluster I are superimposed. This pattern can be quantified by examining the parametric multiple regression of chlorophyll on the total abundances of clusters I and II. Seventy two percent of the variability of chlorophyll is accounted for by the variability of cluster I. The contribution of cluster II is negligible (1%). Interestingly, the variations of cluster I account for the same fraction of the variability of chlorophyll as do all the enumerated cells (73%) even though the species of cluster I account for only half of the total abundance. Analysis of pigment concentrations from the CalCOFI region suggests the same pattern: a relatively small number of pigments account for a disproportionate fraction of the variability in chlorophyll (Goericke, pers. comm.). The pattern is similar to the dichotomy between large and small phytoplankton reported from several regions (e.g. Malone, 1971; Joint *et al.*, 1993). In the present case, however, there is an overlap in the sizes of the species of cluster I and those of cluster II. For instance, *F. pseudonana* of cluster I is similar in size and shape to *N. bicapitata* of cluster II (Table 3), and *M. rostrata* (cluster II) is distinctly larger than *H. wawriakae* (cluster I).

4. Discussion

The temporal spacing (quarterly) of samples and their pooling into large regions obscures small-scale events. For instance, there is no signal from the very visible red tide that occupied the coastal band in the spring of 1995, although it was sampled at the innermost CalCOFI stations. Events that are regionally restricted and of short duration are relatively unimportant in the broad scale context of the entire CCS.

The patterns that do emerge from this analysis are robust—large scale and temporally persistent. The significance of these patterns becomes clear when they are compared with the results of studies conducted in April 1993 and April 1995 (Venrick, 1998). These were the first of a series of studies specifically designed to investigate the smaller-scale

Table 5. Comparison between the species of clusters I and II, this study, and the first two recurrent groups identified from samples collected from the CCS during April 1993 and 1995 (Venrick, 1998).

	Number of species				
	This study	1993	In common	1995	In common
Onshore species	cluster I	group 1		group 1	
Diatoms	20	11	11	12	8
Offshore species	cluster II	group 2		group 2	
Diatoms	4	1	0	1	1
Dinoflagellates	5	5	3	3	2
Coccolithophores	11	3	3	0	0
Silicoflagellates	1	0	0	1	1
Total	21	9	6	5	4

information that is lost by the coarse sampling design of the time-series program. Mixed layer samples were enumerated from individual stations in the CalCOFI grid, giving two “snap shot” pictures of species distributions in space. Recurrent group analysis with $\alpha = 0.70$ produced, in each year, two major recurrent groups, one with maximum abundances (>500 cells ml^{-1}) in the region of Pt. Conception, the other with maximum abundances (>1 cell ml^{-1}) offshore. The first two recurrent groups formed at $\alpha = 0.60$ are used to compare with the present results. The compositions of the groups in 1993 and 1995 correspond closely with the two clusters defined in the present study (Table 5). The smaller sizes of recurrent groups found in the 1993 and 1995 studies result from the higher level of affinity used in the earlier analyses.

The inshore species of both studies are quintessential diatoms of spring blooms (Venrick, 1998). They are centered nearshore and respond to local enrichment. Most of the offshore species are characteristic species of the central Pacific. For instance, in a comparison between the species of cluster II in the present study and the key species identified from the shallow flora in the central Pacific, 1000 km north of Hawaii (Venrick, 1988), more than half of the species are common to both data sets (Table 6). Previous comparisons have had similar results (Venrick, 1992, 1998). Thus, it is concluded that the

Table 6. Comparison between the species of cluster II and key species defined from the central Pacific environment (Venrick, 1988).

	# species		
	CCS cluster II	Central Pacific key species	in common
Diatoms	4	7	4
Dinoflagellates	5	3	3
Coccolithophores	11	8	5
Silicoflagellates	1	0	0
Total	21	18	12

species of cluster II have populations that extend well offshore to the west. In the 1993–1995 study (Venrick, 1998), the transition region between inshore and offshore groups clearly reflected the location of the core of the California Current. Since this core meanders onshore and offshore through time, the location of the transition between inshore and offshore groups is also expected to vary. In the present study, much of the abundance fluctuations of a cluster within regions may reflect the onshore-offshore variations in the boundary between clusters, rather than actual abundance changes.

The spatial resolution provided by the spring study (Venrick, 1998) reinforces the conclusion of the present study: the nearsurface layer of the CalCOFI region is occupied primarily by two distinct flora, one offshore, one inshore. In contrast, the assemblages of zooplankton and ichthyoplankton in the region are clearly represented by species from four different habitats (Moser *et al.*, 1987; Moser and Smith, 1993; Brinton, 1960, 1962). The most abundant and widespread zooplankton species are contiguous with large populations in the subarctic and transition domains. Other zooplankton and ichthyoplankton species are contiguous with populations to the south in the eastern tropical Pacific and to the west in the central Pacific. In addition, there are resident shelf species that do not connect directly to larger populations (Moser and Smith, 1993). Changes in the abundance and range of zooplankton species have been related to changes in climate and the major circulation features of the region (Roesler and Chelton, 1987; Moser *et al.*, 1987; Brinton, 1981).

The phytoplankton species of cluster II are analogous with the central Pacific fauna. There are also similarities between the phytoplankton species of cluster I and local shelf fauna. Even though a well defined subarctic flora exists across most of the northern Pacific (Venrick, 1971; Honjo, 1977; Reid *et al.*, 1978), it does not appear to be represented by a well-defined surface flora in the CCS. This is a major difference between flora and fauna.

It is possible that a subarctic flora is present in the CCS but is centered below the mixed layer and is not well sampled in this study. Since the cold, low salinity water that defines the subarctic core of the current is at or near the surface throughout the study region, this would indicate subsidence of the cells relative to the transporting water. Evidence that this is not the case comes from two vertical sections across the Ensenada Front, just south of the present study area. Although samples there were taken vertically through the California Current core, no flora appeared to be related to it (Venrick, 2000). To examine this question more specifically, a vertical section of 137 samples was collected along line 87 during CalCOFI 9904. Enumeration of these samples is underway.

There are other potential explanations for the lack of a signal from the subarctic flora, including the possibility that it is, in fact, absent. All of these alternative explanations however, imply that the subarctic species in the CCS are not organized into a single flora and that, as a group, their importance to the phytoplankton is less than implied by analogy with the zooplankton. This could have important implications for reconstruction of past circulation patterns from diatoms and coccolithophores in the sediments. Until additional data are available, it is premature to speculate further.

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