

PHYTOPLANKTON SPECIES IN THE CALIFORNIA CURRENT SYSTEM OFF SOUTHERN CALIFORNIA: THE SPATIAL DIMENSIONS

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ABSTRACT

This paper examines 16 years of microscopic information about phytoplankton taxonomic composition and abundances from each of four regions in the CalCOFI area. The NE region is approximately the region of the Southern California Bight; the SE region is the lower edge of the bight; the Offshore is the westernmost region; and the Alley is the path between the NE and the Offshore through which the California Current meanders.

The NE region and the Alley consistently had the highest phytoplankton abundances, dominated by diatoms. These two areas were most similar with respect to abundance fluctuations and species composition. The Offshore had the lowest abundances, dominated by coccolithophores. The SE region was intermediate with respect to both abundance and composition.

Temporal patterns of abundance and composition differed among regions. An increase in phytoplankton abundance was centered in the Offshore region, but was not accompanied by a change in phytoplankton composition. The only detectable effect of the ENSO cycle on phytoplankton abundance was an increase in abundance during La Niña events in the Offshore. However, a cycle of Offshore species composition with a period of five to eight years did not appear to be related to ENSO. Seasonal cycles were strongest in the NE and Alley. In both these regions, high abundances in spring during the early years of this study decreased and the annual abundance maximum appeared to migrate to summer and fall. These shifts may have been driven by decreases in the abundances of the diatom phytoplankton in the spring or by an interaction between the present cruise schedule and a gradual delay in the spring bloom.

INTRODUCTION

The region of the California Current off southern California is one of the best studied ocean areas in the world. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) has accumulated 65-year data sets of temperature, salinity, ichthyoplankton, and macrozooplankton and more than 30 years of data for nutrients and chlorophyll *a*. Based on these data, several

temporal cycles have been defined and studied, including the seasonal cycle (Lynn and Simpson 1987; Legaard and Thomas 2006); the El Niño–Southern Oscillation (ENSO; Chelton et al. 1982; Bograd and Lynn 2001); and two decadal cycles, the Pacific Decadal Oscillation (Ebesmeyer et al. 1991; Roemmich and McGowan 1995a, b; Mantua et al. 1997); and the North Pacific Gyre Oscillation (Bond et al. 2003; Di Lorenzo et al. 2008). Information on these scales of variability provides a background against which to evaluate longer period changes.

Routine sampling for phytoplankton species on CalCOFI cruises began in 1990. Prior to this, most phytoplankton studies in the California Current that were conducted on a taxonomic level had been relatively short term and/or local studies, difficult to extrapolate to a scale comparable to that of the CalCOFI studies (Allen, 1936, 1941, 1945a,b; Sverdrup and Allen 1939; Balech 1960; Beers 1986; Matrai 1986; Busse et al. 2006).

Using the routine CalCOFI samples, Venrick (2012) examined the influence of temporal scales of variability upon the abundance and taxonomic composition of phytoplankton collected from the mixed layer on CalCOFI cruises between 1990 and 2009. Spatial variability was removed by combining all counts for each taxon into a single mean value for each cruise. In addition to seasonal cycles, this time span encompassed three El Niño events and two La Niña events. It also included a period near the year 2000 in which a shift in the signs of the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO) may have occurred (Ebesmeyer et al. 1991; Bond et al. 2003; Lavaniegos and Ohman 2003; DiLorenzo et al. 2008). The exact natures of the interdecadal climate events are still open to debate (Bjorkstedt et al. 2012). These three scales and their influences upon the regional hydrography, chemistry and biology are summarized in some detail in Venrick (2012).

During the 1990–2009 study, there was a slow increase in both chlorophyll *a* and phytoplankton abundance, accompanied by a decrease in the number of phytoplankton species per cruise. There was no evidence

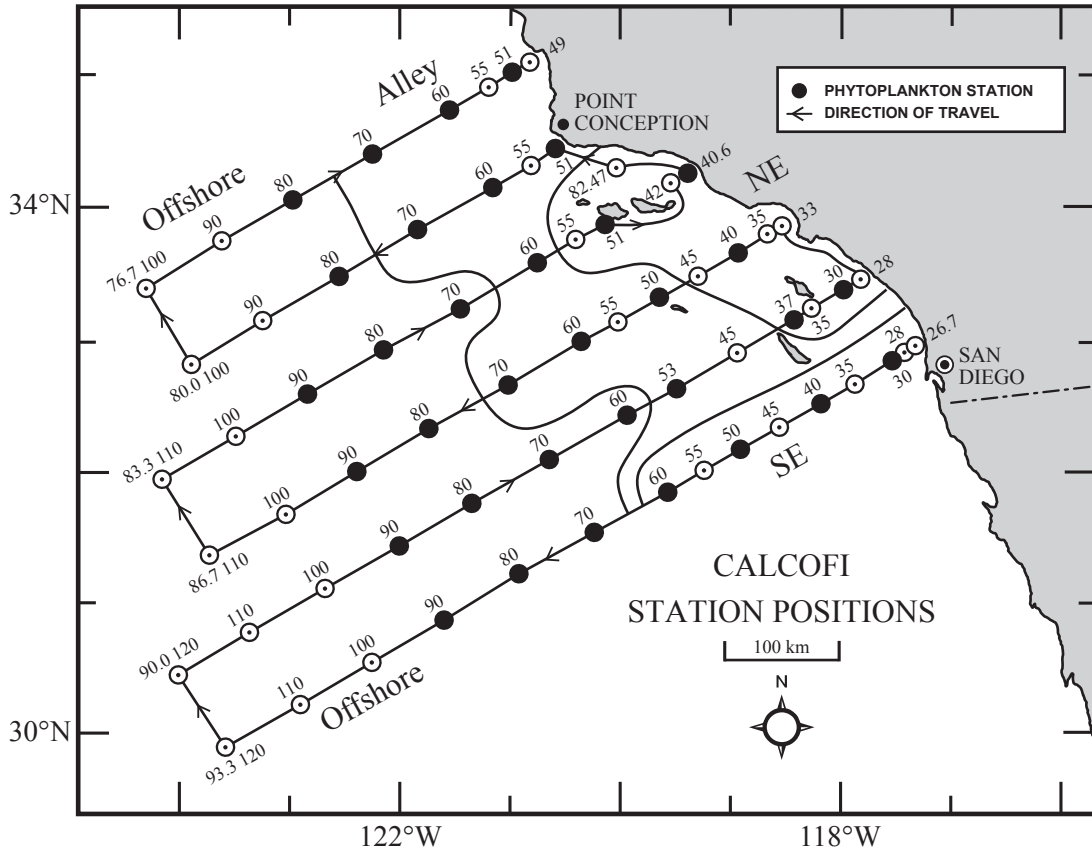


Figure 1. The basic CalCOFI station plan. Solid circles are stations from which phytoplankton samples were collected. Also indicated are the four environmental regions compared in this study.

for a major change in biomass or composition near the year 2000; however there was an unexplained increase in the temporal heterogeneity of phytoplankton composition after 2000.

During the 1990–2009 study, the response of phytoplankton abundance to ENSO events was similar to that of zooplankton, with reduced chlorophyll *a* and abundance during El Niño events and increased values during La Niña events. However, the relative magnitudes of changes were smaller than those of zooplankton. The effect of the ENSO cycle on phytoplankton abundance was not statistically significant.

During the 1990–2009 study, there was a clear seasonal cycle in both chlorophyll *a* and phytoplankton abundance. However, during the study period, the annual peak appeared to shift from spring to summer; this was accompanied by a change in composition of the peak, especially by a decrease in the abundance of hyalochaete species, a large subgroup of the diatom genus *Chaetoceros*. Venrick (2012) hypothesized that the shift reflected the change in nutrient source from wind-driven coastal upwelling in the spring to wind-stress-curl-driven upwelling in the summer (Ryckaczewski and Checkley 2008).

A weakness of this first study is the lack of spatial resolution. The CalCOFI area is a dynamic, heterogeneous system and it is not known whether the temporal patterns revealed in Venrick (2012) reflect the entire region or whether they are merely a composite of several dissimilar, smaller-scale patterns. The present paper extends the observations of temporal scales to the spatial dimension, using the four regions defined by Hayward and Venrick (1998; fig. 1). The Northeast region (NE) is approximately the region of the Southern California Bight (SCB). The Southeast (SE) region often contains the southern, shoreward-flowing limb of the quasi-permanent Southern California Eddy, which entrains both California Current water and Offshore water, moving them toward the coast at the southern boundary of the SCB. The Offshore region is the easternmost Central Pacific, which is influenced by the California Current. The Alley is the region between the NE region and the Offshore through which the southward-flowing California Current meanders and generates eddies; where it approaches the coast, as at Point Conception, it may entrain locally upwelled water.

These four regions were initially defined on the basis of the similarity of temporal patterns of chlorophyll *a*

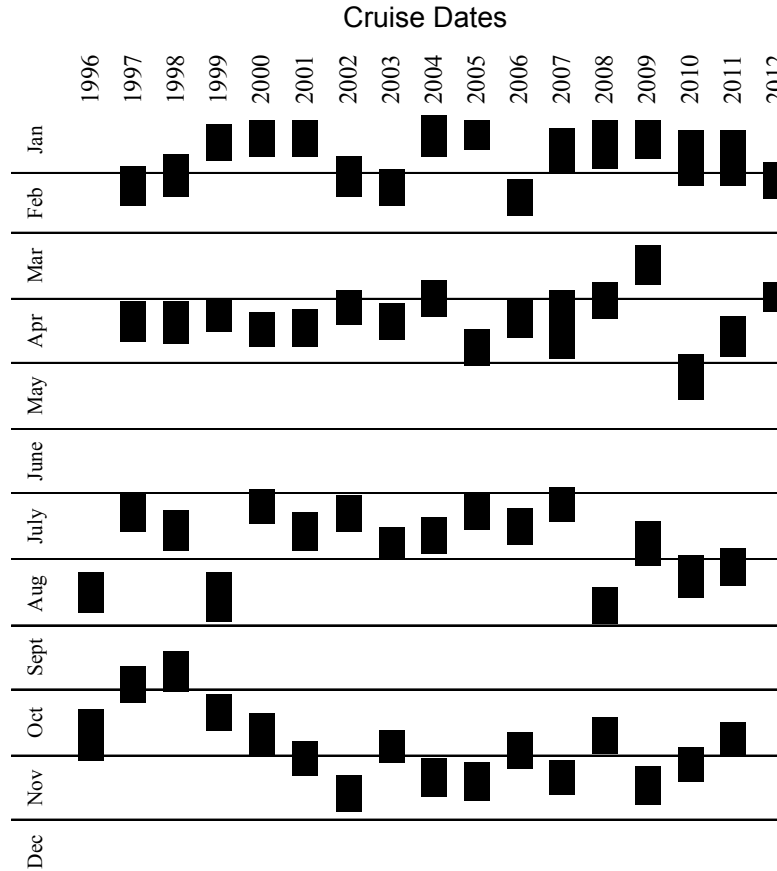


Figure 2. Cruise schedules, 1996–2012. Black bars indicate cruise dates.

at groups of stations between 1984 and 1996 (Hayward and Venrick 1998). Groups of stations with similar temporal patterns of chlorophyll were associated with similar physical forcing factors. Later, these groups of stations were shown to be characterized by different phytoplankton assemblages, with the exception of the Alley, which was characterized by the lack of a stable association (Venrick 1998a; Venrick 2009). The Alley appears to represent a meandering boundary between the NE and the Offshore. The phytoplankton assemblage in the Offshore, as defined here, has been shown to be more similar to that of the Central Pacific to the west than to that of the rest of the CalCOFI area (Venrick 1992, 2009).

The present study is based upon 16 years of quarterly data between summer 1996 and spring 2012 from each of the four regions; thus, there is a 13 year overlap with the previous study. The primary goal of this study is to add a spatial dimension to the temporal patterns and to examine on a regional basis the long-term increase in phytoplankton abundance, the phenological shift in the seasonal cycles, and compositional changes associated with both. In addition, these data may provide quantitative parameters of local phytoplankton that may be useful in future models of this region.

METHODS

CalCOFI Protocol

CalCOFI surveys have been conducted since 1949. Since 1984, cruises have occurred quarterly, and the basic sampling grid has consisted of 66 stations arranged in six lines spaced 40 nm apart (fig. 1). Within the quarterly framework, cruise dates and durations vary (fig. 2). In this study, seasons are defined as winter (Dec–Feb), spring (Mar–May), summer (June–Aug) and fall (Sept–Nov). A cruise is assigned to a season on the basis of its mid-date. Between 1996 and 2012, there were no cruises in June, or Dec, and only one in May.

Each station includes a large number of measurements and samples. These data and the methods by which they were acquired may be found on the CalCOFI website (<http://www.calcofi.org/>) and in individual data reports (<http://www.calcofi.org/ccpublications/calcofi-data-reports.html>).

Environmental Conditions

ENSO periods are defined as strong or moderate events lasting three months or longer based on the Oceanic Niño Index (ONI: <http://ggweather.com/>

TABLE 1
 Summary of El Niño and La Niña dates, sampling cruises, and general characteristics in the CalCOFI area.

Equatorial Event	Dates in CalCOFI region	Cruises	Comments	References
1997–98 El Niño	June 1997 to July 1998	9707 9709 9802 9804 9807	Conditions relaxed somewhat during the spring; in 1998, zooplankton biomass the lowest on record; chlorophyll not noticeably reduced in field samples but remote imagery indicated a reduction in the extent of eutrophic waters.	Lynn et al. 1998; Hayward et al. 1999; Hayward 2000; Kahru and Mitchell 2000; Bograd and Lynn 2001.
1998–00 La Niña	Nov 1998 to June 2000	9901 9904 9908 9910 0001 0004	Two La Niña pulses at the equator were not distinguishable in the CalCOFI area; record high chlorophyll values recorded during spring and summer 1999, subsequently returning to lower concentrations but generally continuing above the long-term mean; zooplankton biomass elevated throughout 1999, subsequently declining but remaining above low pre-1997 values.	Hayward et al. 1999; Bograd et al. 2000; Bograd and Lynn 2001; Durazo et al. 2001; Schwing et al. 2002; Venrick et al. 2003.
2002–03 El Niño	n.a.		A moderate equatorial El Niño did not significantly impact the CalCOFI area and is not considered in this study.	Venrick et al. 2003.
2007–08 La Niña	July 2007 to Feb 2009	0707 0711 0801 0804 0808 0810 0901	Cool conditions in the CalCOFI area appeared to precede this equatorial event by two months; most parameters did not respond strongly; satellite imagery indicated elevated chlorophylls, but these not apparent from the ship data.	McClatchie et al. 2008, 2009.
2009–10 El Niño	“Fall” 2009 to “Early” 2010	0911 1001	Strong impacts seen north of Pt. Conception; relatively weak in CalCOFI; SSH was elevated, but most physical and biological parameters near normal.	Bjorksted et al. 2010; Pacific Coast Ocean Observing System 2010.
2010–11 La Niña	July 2010 to Jan 2012	1008 1011 1101 1104 1108 1110	Strong impacts off Baja and inconsistently north of Pt. Conception; response in CalCOFI area mixed; SSH elevated and SST reduced but biological parameters near normal. Relaxation during summer 2011.	Bjorksted et al. 2011, 2012; Pacific Coast Ocean Observing System 2010 2011. Wells et al. 2013.

enso/oni.htm). The strength, timing, and influence in the CalCOFI area have been refined by local information (table 1).

Phytoplankton Sampling

Phytoplankton samples for this study were collected from summer 1996 through spring 2012. They were water samples collected from the second depth at 34 of the 66 standard stations, spaced approximately evenly across the grid (fig. 1). The CalCOFI protocol places the second sample within the mixed layer, whenever a mixed layer exists, generally between 5 and 15 meters. The samples were 30 ml water samples, preserved with 1% buffered formalin, and returned to the lab for enumeration. In the lab, equal aliquots from all samples from the same region were pooled into one sample, which was settled and counted under an inverted microscope. All larger cells were counted at 100X magnification; 17% of the sample was examined at 250X to enumerate the smaller cells. An attempt was made to count between 1,000 and 1,500 cells per sample. The volume of sample needed was determined by a relationship between

chlorophyll *a* concentration and number of cells, modified by practical constraints such as volume of sample available, settling chamber size, and available time. During this study settled volumes varied from 1 to 100 ml. There were no consistent changes in volumes settled or in number of cells counted.

Taxonomic Considerations

The phytoplankton taxa in this study include all cells that could be identified to a specific taxon. This criterion includes most phytoplankton larger than 2–3 in diameter, but excludes picoplankton. The data set consists of abundances of 364 taxa in ten major taxonomic categories: diatoms, thecate dinoflagellates, athecate dinoflagellates (including heterotrophic species), coccolithophores, and silicoflagellates. In addition, there are nine species in five categories which are very rare and which have been combined into a single “miscellaneous” category. Most taxa were species or small groups of similar species, but for completeness, unidentified species were included, lumped into the lowest taxa possible. The genus *Pseudo-nitzschia* was subdivided into two categories according to

TABLE 2
Regional abundances. Differences among regions are assessed by the magnitude of the χ^2 large sample approximation for the Friedman 2-way ANOVA statistic, which removes temporal variability. Subtending bars indicate median differences according to a Nemenyi a posteriori procedure.

The critical value of χ^2 under the assumption of the null hypothesis at $p = 0.05$ is 7.82. Were the assumptions fulfilled, the result would be highly significant.				
χ^2 (observed) = 86.3				
	Region			
	Alley	NE	SE	Offshore
abundance (cells/ml)				
median	243	210	95	57
mean	369	331	158	72

whether cell width exceeded four microns. Both “slim *Pseudo-nitzschia*” and “robust *Pseudo-nitzschia*” are composites of several species, some overlapping. The athecate dinoflagellate species were more poorly resolved taxonomically than the species of the other major taxa, giving the “unidentified athecate” category a disproportionate weight in analyses of individual taxa. Consequently, athecate dinoflagellates have been retained only in the discussion of major taxa.

The absence of picoplankton data will produce a negative bias in the total number of cells, especially in the more oligotrophic regions. To the extent that picoplankton fluctuations are not coherent with fluctuations of other taxa, the results of this study will be biased toward larger taxa.

Statistical Procedures

Most statistical procedures in this study are nonparametric, which do not assume that the data are from a normal distribution, and which use the median as a measure of central tendency (Tate and Clelland 1957; Sprent 1993; Conover 1999). I present the mean as well as the median, because of its general familiarity. The difference between the median and the mean is an indication of the skew of the population distribution. Trend lines are least squares fits. As descriptive tools, neither the mean nor the least squares line assumes normality.

Procedures used include Spearman’s nonparametric correlation (ρ), the Kruskal-Wallis one-way analysis of variance (ANOVA), and Friedmann’s 2-way ANOVA. A significant ANOVA suggests that samples are not all from the same population. Following a significant result, a posteriori tests may indicate samples, or groups of samples that are likely to be from distinct populations (Nemenyi 1963; Sokal and Rohlf 1969). A posteriori results are indicated in tables by bars linking samples from the same

population. Two nonoverlapping bars (table 2, Offshore and SE) indicate samples likely to be from two discrete populations; a bar under two or more samples (table 2, NE and Alley) indicates that discrete populations cannot be detected.

The study is focused on the strength of the relationships between the different regions. Correlation matrices are used where, under other circumstances, a single concordance test might be more appropriate.

Principal component analysis (PCA) was used to decompose the variability of the abundance data of the major taxa and to examine the importance of different scales. Input data were the log-transformed and normalized abundance data of four major taxa in each sample. To determine the acceptance criterion for the principal component, I ran 600 Monte Carlo simulations on the data, with the observed counts of the taxa associated randomly with samples (modified from Ledesma and Valero-Mora 2007). Resulting eigenvalues are more conservative than the commonly accepted value of 1.0.

With more than 350 taxa, examination of species composition and changes over time requires extreme reduction of data. I have used species correlation profiles, which plot the similarity of species composition of all pairs of samples as a function of their separation in time. Similarity was measured by Spearman’s correlation (ρ) between rank orders of abundance. A correlation profile is analogous to a variogram through time using a measure of similarity rather than a measure of variance. Like a variogram, it detects temporal pattern. Unlike a variogram, peaks of a correlation profile represent greater similarity rather than greater variance (dissimilarity). To remove variability at the smallest scales, curves were smoothed with a 21 point running average. This represents an average interval of 26 days.

This study compares and contrasts characteristics of phytoplankton in four regions at three time scales. The resulting labyrinth of tests (“multiple testing”) and statistical interdependencies negate the use of classical hypothesis testing. However, tabulated probability levels correct for sample size and give a yardstick for comparisons, even though the underlying assumptions have been violated. In the following study I present statistics and classical alpha errors (critical values) at $p = .05$ and indicate in bold, results that exceed critical values. The results, however, must be judged on the basis of the magnitude and consistency of the patterns over all analyses.

RESULTS

Phytoplankton Abundance

Regional patterns. Cruise-mean abundances were consistently higher in the Alley and NE, lower in the SE region and lowest in the Offshore (table 2, fig. 3).

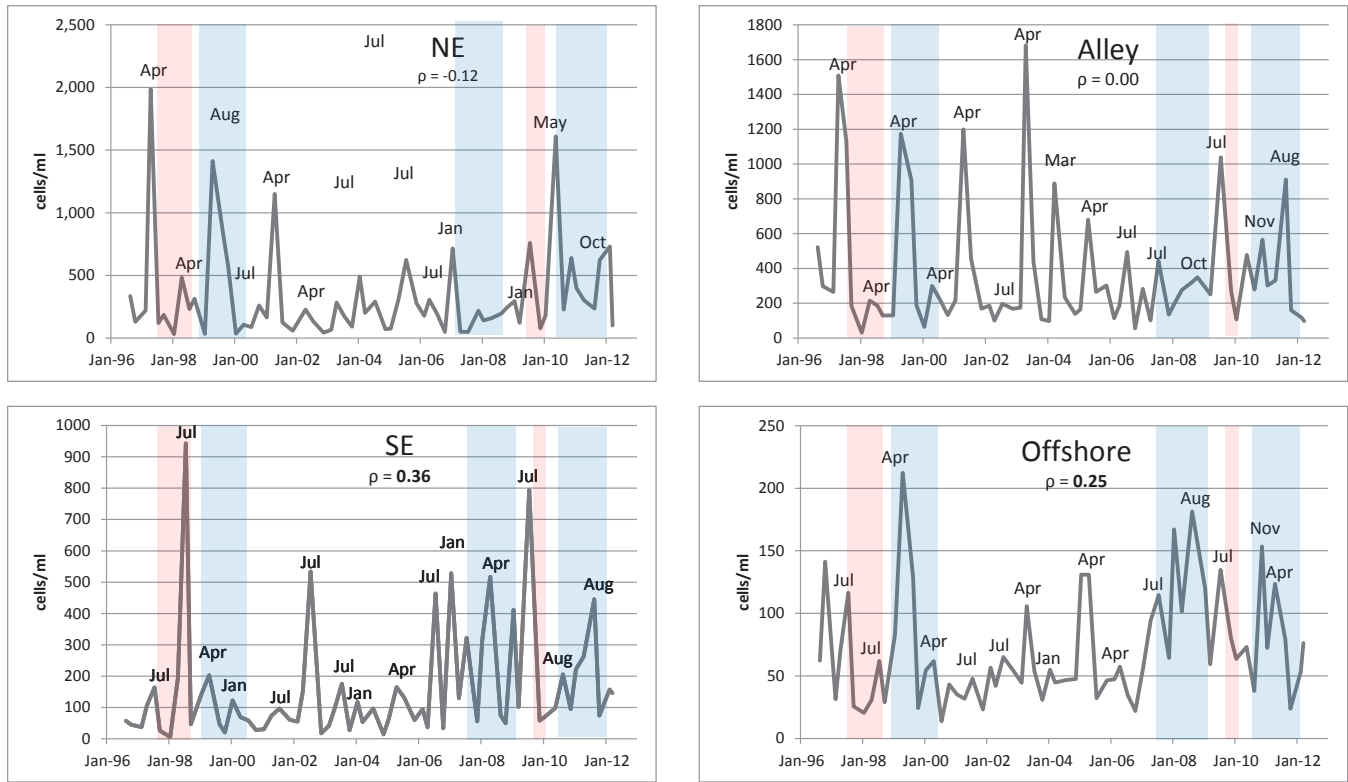


Figure 3. Temporal changes of phytoplankton abundance (excluding athecate dinoflagellates) in the four regions of the CalCOFI area. El Niño periods are shaded red; La Niña periods are shaded blue. Months of maximum annual abundance are indicated. Values of ρ indicate correlations of abundance and time (increase or decrease in abundance). The critical value of the statistic under the assumptions of the null hypothesis at $p = 0.05$ is 0.25. Were all assumptions fulfilled, the bold statistics would be significant.

TABLE 3
Pair-wise comparison of phytoplankton abundances. Values are Spearman's nonparametric correlation (ρ). Values above the diagonal are correlations across all samples; values below the diagonal have had the seasonal cycle removed.

Critical values of ρ under the assumptions of the null hypothesis at $p = 0.05$ are 0.25 ($n = 64$; above diagonal) and 0.52 ($n = 15$; below). Were assumptions fulfilled, bold correlations would be significant.

		Region				
		NE	Alley	SE	Offshore	
seasonal cycle removed	NE		0.46	-0.12	0.11	all data
	Alley	0.60		0.32	0.44	
	SE	-0.02	-0.35		0.42	
	Offshore	0.32	0.31	0.38		

Four of the six correlations between regions, over all data (table 3), were strongly positive, suggesting that abundance fluctuations in most regions were related. The only regions that appeared independent were the NE and SE regions and the NE and the Offshore. Most of the overall concordance among regions was driven by similar seasonal cycles. When the seasonal cycle was removed (table 3), most correlations decreased. Longer-period fluctuations remained correlated only in the NE and Alley.

Interannual changes. Phytoplankton abundances in both the SE region and the Offshore increased during the study period, in spite of one very high early value in each (fig. 3). In the Offshore, this peak occurred during the spring of the 1998–2000 La Niña, a period with record high chlorophyll *a* across most of the CalCOFI area (table 1). In the SE, however, the peak was earlier, more closely associated with the 1997–98 El Niño, and it appears to have been a more local phenomenon. Phytoplankton abundances in the two eutrophic regions were more stable during the study period.

ENSO effects. The ENSO signal was greatest in the Offshore (table 4). However, this was driven only by high abundances during La Niña conditions; reduction of abundances during El Niños was undetectable. Although the ENSO signal was weaker in other regions, they showed the expected pattern of abundances with abundances lower during El Niños and higher during La Niñas. An influence of ENSO cannot be disproved with these data, but the effects on phytoplankton abundance were relatively weak.

Seasonal patterns and phenological changes. Only the Alley and the SE region had consistent (detectable) seasonal cycles (table 5). In spite of differences in the

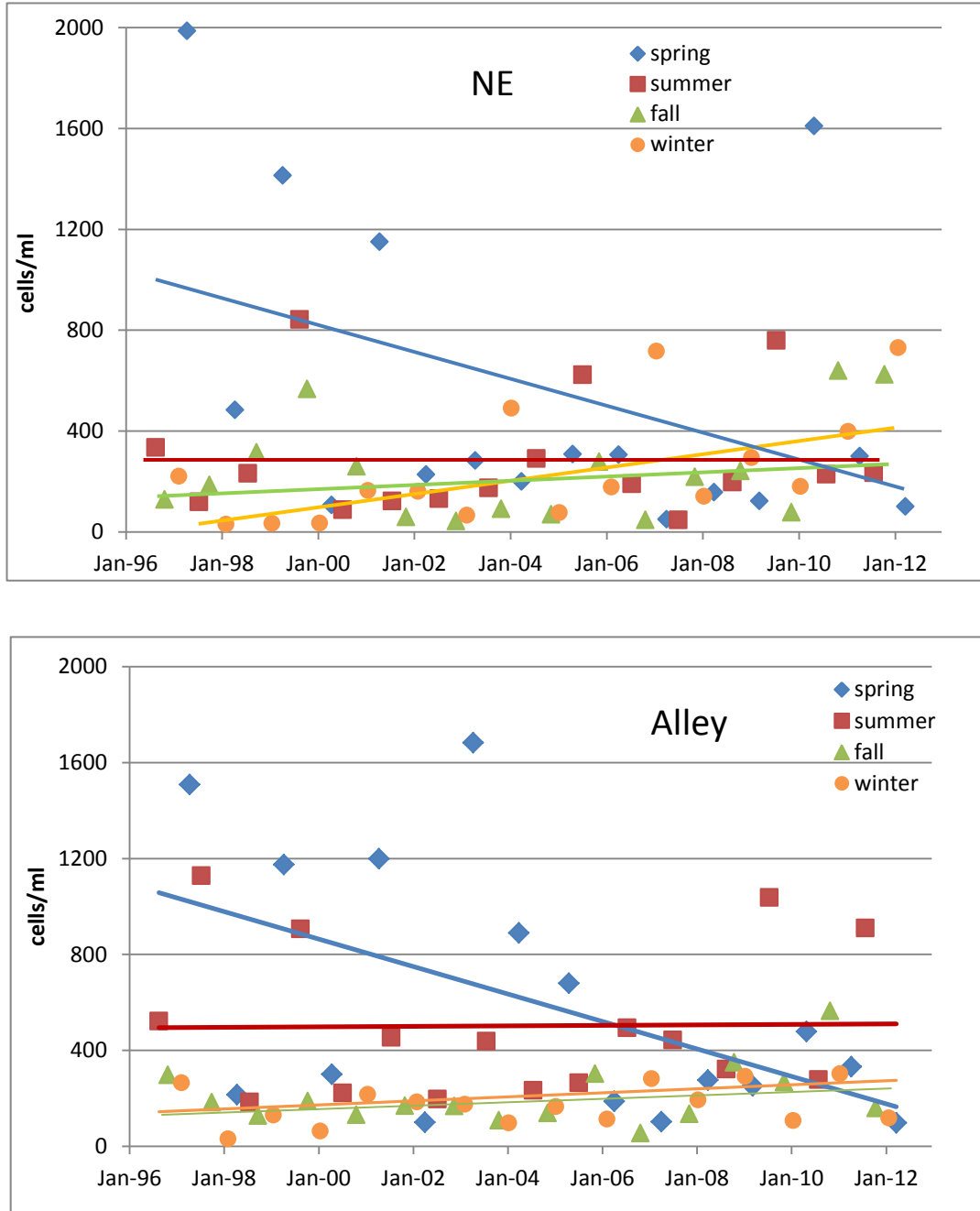


Figure 4. The long-term changes of annual peak abundance in the NE region and the Alley. Regression lines describe abundance trends within seasons.

amplitudes of the cycles, all four regions showed agreement in that higher abundances tended to occur in summer or spring and lower abundances in winter or fall.

During the study, the timing of the annual peak in the NE and Alley regions shifted toward later months (fig. 3). In the NE, before 2004, all annual peaks but one occurred in spring becoming irregular thereafter. In the Alley, before 2006, every peak except one

occurred in the spring; after 2006 peaks occurred in summer and fall.

These shifts in the timing of the annual peaks resulted from interaction between a decrease in abundance in spring samples and changes in other seasons (fig. 4). In the NE, the spring decrease was accompanied by increases in fall and winter abundances. At the start of the study, spring abundances exceeded those of other

TABLE 4

Summary of the changes of the total number of cells in the three ENSO states. Changes are assessed by the magnitude of the Kruskal-Wallis 1-way ANOVA (H). Subtending bars indicate differences according to a Nemenyi a posteriori test.

The critical value of H under the assumptions of the null hypothesis at $p = 0.05$ is 5.99. Were assumptions fulfilled, the bold statistic would be significant.

Region	H (observed)	Abundance (cells/ml)	Enso State		
			La Niña	Neutral	El Niño
NE	1.62	median	235	196	181
		mean	354	346	187
Alley	2.75	median	301	220	195
		mean	366	375	303
SE	3.82	median	143	83	70
		mean	192	103	209
Offshore	10.31	median	102	62	50
		mean	103	57	58

TABLE 5

The seasonal variability of phytoplankton abundances. Changes are assessed by the magnitude of the χ^2 large sample approximation for the Friedman two-way ANOVA. Subtending bars indicate differences according to a Nemenyi a posteriori procedure.

The critical value of χ^2 under the assumptions of the null hypothesis at $p = 0.05$ is 7.8. Were assumptions fulfilled, the bold statistics would be significant.

Region	χ^2 (observed)	Abundance (cells/ml)	Season			
			Spring	Fall	Summer	Winter
NE	6.20	median	300	218	197	164
		mean	580	249	286	212
Alley	14.84	median	439	332	175	168
		mean	625	501	204	175
SE	24.2	median	176	105	95	47
		mean	304	150	150	44
Offshore	6.92	median	71	62	56	43
		mean	83	77	69	55

seasons and the annual maximum was stable. Decreasing spring abundances progressively fell into the range of abundances in other seasons, and the timing of the annual maximum became variable, no longer a predictable cycle. A similar interaction can be seen in the Alley.

TABLE 6

Summary of principal component analysis on major phytoplankton taxa. Input data are the abundances of each major taxa in each sample. Only the eigenvalue of the first component exceeds the critical value (estimated from Monte Carlo simulations).

Principal component	Eigenvalues	Cumulative %	Critical eigenvalues ($p = 0.05$)
PC1	2.44	61.0	1.17
PC2	0.714	78.9	1.02

Loadings of major taxa on principal component 1

Taxon	Loading
coccolithophores	0.53
athecate dinoflagellates	0.53
diatoms	0.46
thecate dinoflagellates	0.41

As declining spring abundances approached and overlapped those of summer, the regular spring peaks shifted to peaks in summer and occasionally autumn. In both regions, the abundance declines in spring were offset by increases during the other seasons, so the annual average remained stable.

Major Taxa

The most abundant major taxa were diatoms, thecate and athecate dinoflagellates, coccolithophores, and silico-flagellates; the first four taxa were present in at least one region on 63 or 64 of the 64 cruises. In addition there was a small category composed of nine infrequent species that belong to various other major groups.

The abundances of all major taxa were least in the Offshore region (fig. 5). Diatoms dominated the flora in the NE, Alley, and SE; coccolithophores dominated in the Offshore. This result changes very little when abundances are expressed as percentages of the total.

Principal component analysis (PCA) was used to examine the relative importance of spatial and temporal variability to the composition of major taxa. Descriptors are abundances of the four most frequent taxa: diatoms, thecate dinoflagellates, athecate dinoflagellates, and coccolithophores. A single meaningful component emerged, which explains 61% of the variability (table 6). The first principal component is highly correlated with chlorophyll *a* (Spearman's $\rho = 0.59$; critical value [0.05] = 0.12; data not shown) and may be viewed as an abundance axis. The most important attribute separating samples along component 1 is the regional abundance; this is followed by seasonal abundance and interannual abundance (table 7). The ENSO scale is relatively weakly expressed. Samples with high scores along this principal axis are summer samples from the Alley and NE regions. Among the highest

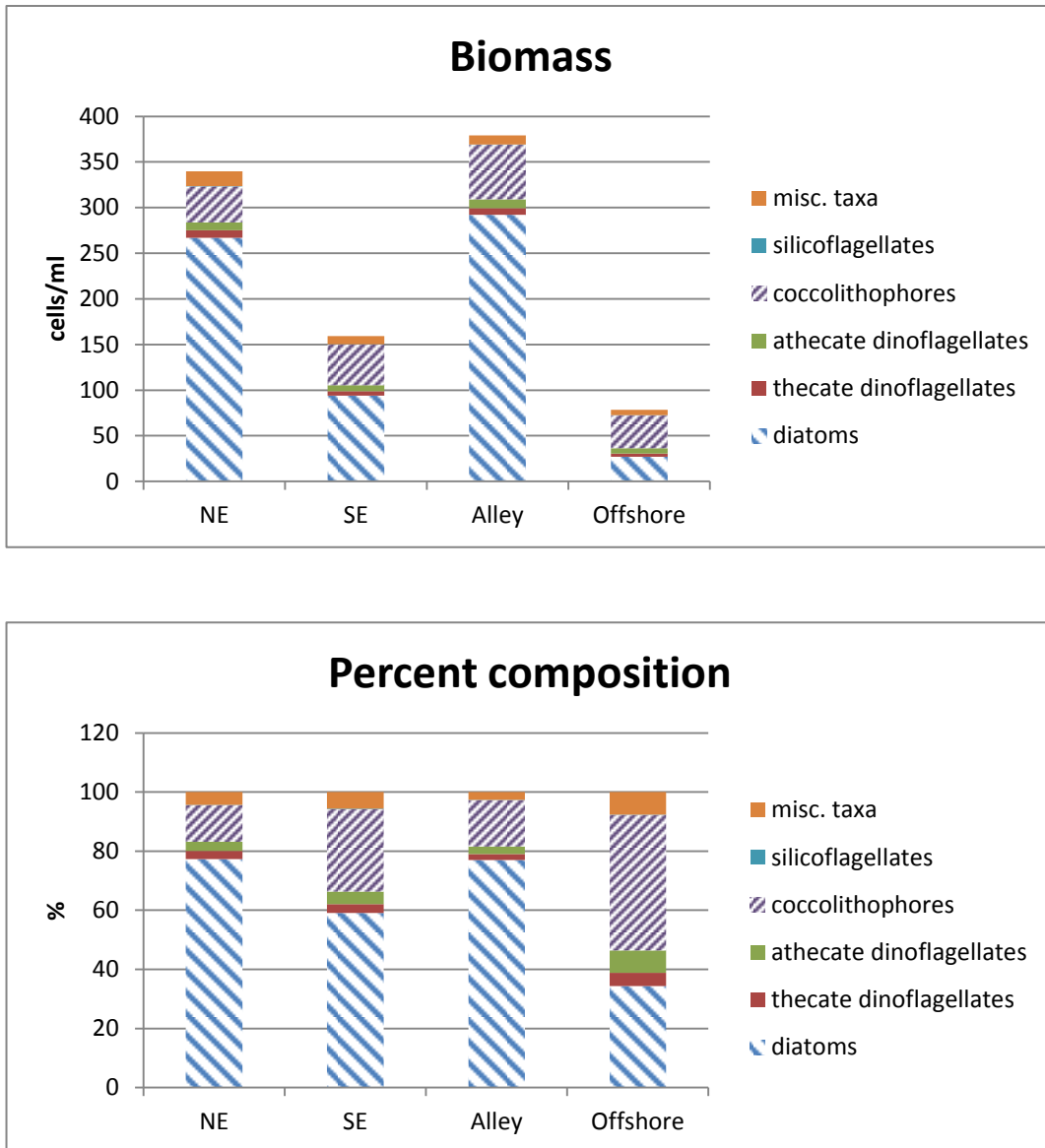


Figure 5. Regional composition of major taxonomic categories as means and percent composition.

25% of the scores, there are no samples from the Offshore. Samples with low scores along the axis are samples from the SE and Offshore regions.

All taxa have positive loadings on the first component, indicating that fluctuations of the four major taxa were correlated. This concordance is unexpected. Several characteristics of phytoplankton tend to sort along a eutrophic-oligotrophic axis, including taxonomic affiliation and cell size (Margalef 1978; Malone 1980; Goericke 2011), predicting a greater separation between, for instance, diatoms and dinoflagellates; or between small-celled groups, such as coccolithophores; and predominantly large-celled groups such as diatoms. Instead, the first component appears to express one large scale of

variability that affects all taxa similarly through time and across the CalCOFI area.

Single Taxa

Over the entire study, there are 364 taxonomic categories. Athecate dinoflagellates were excluded from the following analysis because of their low taxonomic resolution, leaving 165 diatoms, 115 thecate dinoflagellates, 55 coccolithophores, three silicoflagellates, and nine species from five other taxonomic groups. Total numbers of species and abundances per cruise were inversely related, with more species found in the SE and Offshore regions (table 8a). Approximately half of the taxa (193) were found at least once in all four regions, while only

TABLE 7

Influence of four sources of variability in the scores of samples along principal component 1. Differences are assessed with the Kruskal-Wallis one-way ANOVA (H). Subtending bars indicate differences according to a Nemenyi a posteriori test.

Also shown is the critical value of H under the assumption of the null hypothesis at $p = .05$; c.v. (0.05). Were the assumptions fulfilled, the bold statistics would be significant.

	Region			
	H = 52.7 ; c.v. (0.05) = 7.81			
	NE	Alley	SE	Offshore
median score	0.59	0.47	-0.45	-0.82
mean score	0.76	0.50	-0.50	-0.77

	Season			
	H = 24.1 ; c.v. (0.05) = 7.81			
	Summer	Winter	Spring	Fall
median score	0.40	-0.05	-0.18	-0.71
mean score	0.93	-0.17	-0.19	-0.58

	Years			
	H = 23.1 ; c.v. (0.05) = 7.81			
	2008-12	2004-08	1996-00	2000-04
median score	0.38	-0.13	-0.28	-0.77
mean score	0.52	0.06	-0.24	-0.34

	ENSO State		
	H = 6.23 ; c.v. (0.05) = 5.99		
	Neutral	El Niño	La Niña
median score	-0.39	-0.06	0.16
mean score	-0.11	-0.10	0.25

79 were found in a single region. The highest numbers of species unique to a single region were found in the Offshore and SE regions (table 8a), which were the lower biomass regions (table 2). Comparisons of species composition between regions (table 8b) suggest the taxonomic compositions of the NE region and the Alley were similar, as were those of the SE region and the Offshore. Least similar were the compositions of the NE region and the Offshore. The top ten dominant species in all four regions consisted of 17 taxa (table 9); four taxa were dominant in all regions, but two of these, slim *Pseudo-nitzschia* spp. and hyalochaete species in the genus *Chaetoceros* are taxa with many similar species, and the dominant species may have changed among the regions.

Interannual patterns. A decline in the number of species per cruise was observed between 1990 and 2009 (Venrick 2012). This decline continued between 1996 and 2012 and was strongest in the Offshore (table 8a), coincident with the greater increase in abundance there (fig. 3). To look for interannual changes in taxonomic composition, the Offshore species composition, averaged

TABLE 8

Overview of the phytoplankton parameters in the CalCOFI area.

a) General statistics: total numbers of species, mean numbers of species per cruise (n), the number of species unique to each region, and the changes of the number of species over time (p). The critical value of Spearman's ρ under the assumption of the null hypothesis at $p = 0.05$ is 0.25. Were the assumptions fulfilled, the bold correlation would be significant.

	NE Region	Alley	SE Region	Offshore
total	269	246	296	293
n	48	47	56	59
number unique	18	10	25	26
change over time (p)	-0.01	-0.10	-0.02	-0.26

b) Correlations between species compositions of different regions. Values are the mean correlations (ρ) between each pair of the 64 cruises. There are no critical values tabulated for mean statistics.

	Alley	SE	Offshore
NE	0.32	0.17	0.09
Alley		0.15	0.16
SE			0.25

over 2000 and 2001, was compared with the average of 2010 and 2011. The earlier period was used to minimize the influence of the preceding El Niño and La Niña events. Offshore phytoplankton abundance increased from a mean of 42.4 cells/ml to a mean of 87.2 cells/ml, while the number of species decreased from 173 to 155. As predicted by the principal component analysis (table 6), all major taxa increased in abundance. Relative to their abundances in 2000-01, diatoms, athecate dinoflagellates and the miscellaneous category increased by about 150%; thecate dinoflagellates by 85%; and coccolithophores by 60%. Eight of the ten dominant species were common to both periods. There were no major shifts in abundance other than the expected general increase. There is no evidence that a significant species change accompanied the interannual abundance increase.

Correlation profiles provide a means for detecting long-term changes and repeating patterns of species composition. The profile incorporates changes in species number, but is independent of total abundance. In all regions, the correlation profiles show a decrease in the similarity of species composition of sample pairs separated by longer time intervals, evidence for a slow evolution of species composition and/or dominance order (fig. 6).

Changes in species composition across the postulated interdecadal shift in 2000 were examined by partitioning the species correlation profiles into three sets: comparisons between samples before 2000, comparison between samples after 2000, and comparisons across the shift. A species shift would appear as a lower correlation between pairs of samples that span the shift.

TABLE 9

Dominant species in the regions of the CalCOFI area. Species are listed according to their median abundances.

NE region	median (cells/ml)	mean (cells/ml)	SE region	median (cells/ml)	mean (cells/ml)
slim <i>Pseudo-nitzschia</i> spp.	24.6	74.1	<i>Emiliana huxleyi</i>	16.2	24.9
<i>Emiliana huxleyi</i>	23.0	31.7	slim <i>Pseudo-nitzschia</i> spp.	5.0	32.6
<i>Chaetoceros</i> spp. (hyalochaetes)	15.4	42.2	unidentified coccolithophores	4.8	9.5
<i>Chaetoceros radicans</i>	12.0	19.2	<i>Fragilariopsis pseudonana</i>	4.4	7.4
<i>Fragilariopsis pseudonana</i>	11.0	17.3	<i>Chilomonas marina</i>	3.4	4.9
cf. <i>Nitzschia closterium</i>	6.4	17.4	cf. <i>Nitzschia closterium</i>	3.0	7.8
unidentified coccolithophores	5.6	13.2	<i>Gephyrocapsa</i> spp.	1.0	2.5
robust <i>Pseudo-nitzschia</i>	2.8	16.8	<i>Chaetoceros</i> spp. (hyalochaetes)	0.8	15.9
<i>Chaetoceros socialis</i>	0.3	18.2	<i>Mastogloia woodiana</i>	0.1	3.9
<i>Chaetoceros debilis</i>	0.1	42.3	<i>Phaeocystis pouchetti</i>	<<0.1	3.6

Alley	median (cells/ml)	mean (cells/ml)	Offshore	median (cells/ml)	mean (cells/ml)
<i>Emiliana huxleyi</i>	31.1	38.6	<i>Emiliana huxleyi</i>	12.7	19.0
slim <i>Pseudo-nitzschia</i> spp.	24.1	62.3	unidentified coccolithophores	5.3	8.8
<i>Chaetoceros</i> spp. (hyalochaetes)	15.8	46.4	<i>Chilomonas marina</i>	3.4	4.7
unidentified coccolithophores	10.9	14.1	slim <i>Pseudo-nitzschia</i> spp.	2.5	8.3
cf. <i>Nitzschia closterium</i>	5.5	11.2	cf. <i>Nitzschia closterium</i>	1.6	3.2
<i>Chaetoceros debilis</i>	5.2	42.9	<i>Fragilariopsis pseudonana</i>	1.2	2.1
robust <i>Pseudo-nitzschia</i>	4.5	16.2	<i>Umbilicosphaera hulburtiana</i>	0.7	1.4
<i>Chaetoceros radicans</i>	2.8	18.5	<i>Gephyrocapsa</i> spp.	0.6	2.1
<i>Dactylosolen fragilissima</i>	1.2	12.4	<i>Chaetoceros</i> spp. (hyalochaetes)	0.2	2.4
<i>Chaetoceros socialis</i>	0.3	14.2	cf. <i>Phaeocystis</i> sp.	<<0.1	2.6

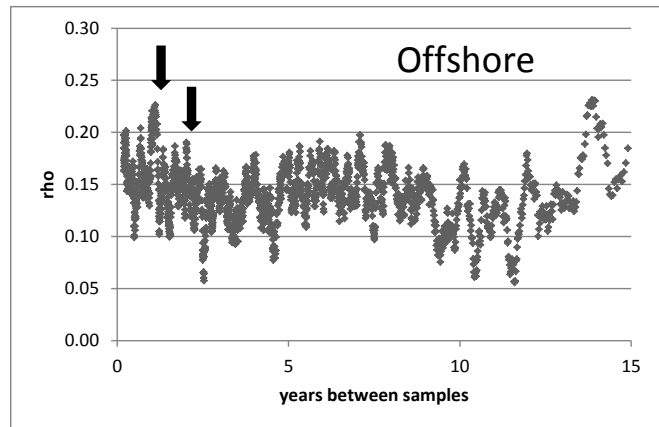
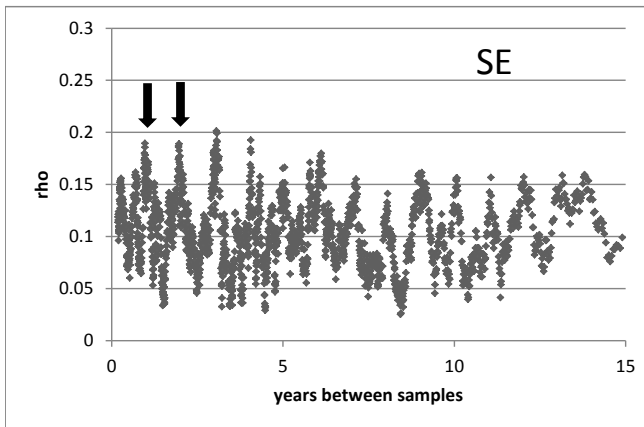
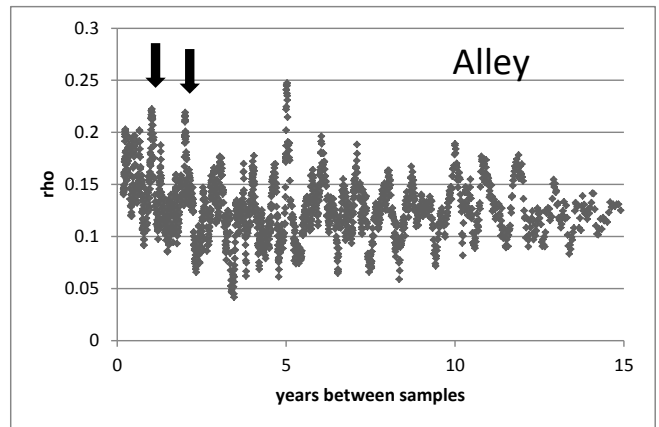
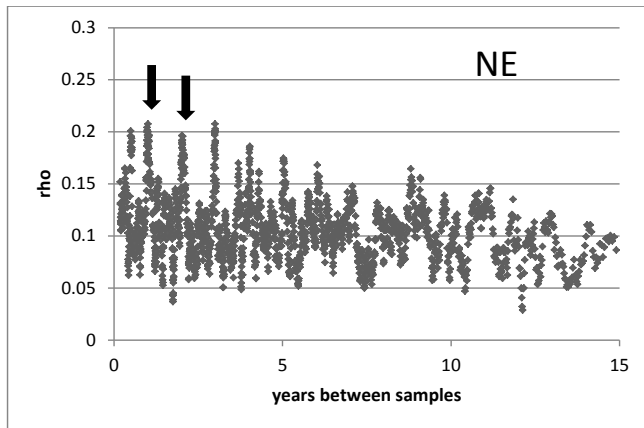


Figure 6. Correlation profiles for the four regions. Each plot is the correlation of rank order of abundance of species composition (ρ) between sample pairs as a function of their separation in time. Points are 21-point running means. Arrows indicate the first two annual peaks.

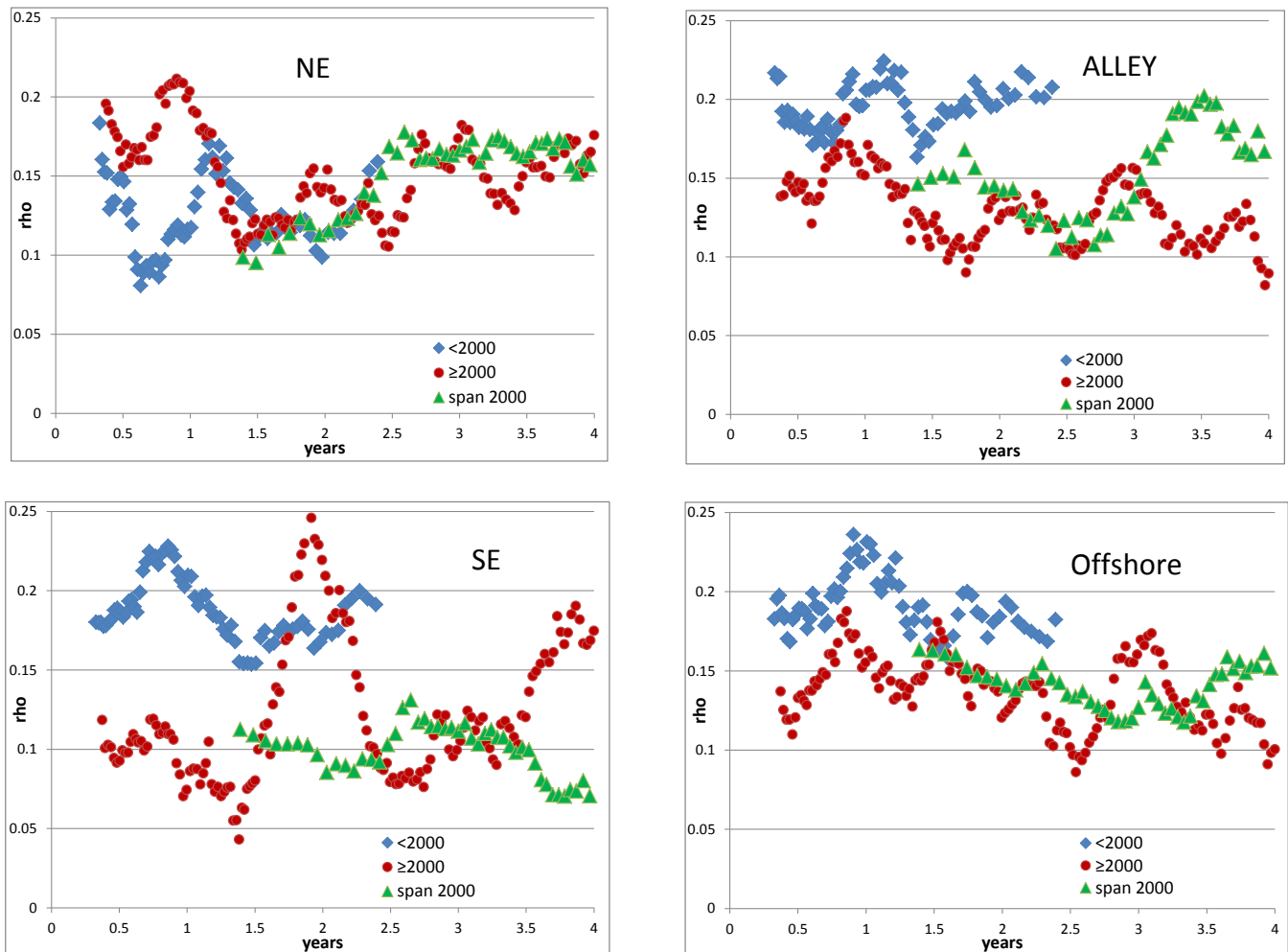


Figure 7. As for Figure 6 but data are divided into comparisons between sample pairs collected before 2000, comparisons between sample pairs collected during or after 2000, and comparisons between sample pairs one before 2000, one during or after 2000.

There is no evidence for a shift in composition within any of the regions near the year 2000 (fig. 7). An increase in heterogeneity after 2000 can be seen in the Offshore, the Alley, and in the SE region (where it is partially masked by a strong peak at a two-year interval). In contrast, the stability of species composition in the NE region was unchanged, apparently buffered from whatever changes occurred near the year 2000.

ENSO effects. The Offshore correlation profile (fig. 6) suggests a periodicity of species composition of about five to eight years. There appears to be a trough at 2.5–3.5 years, a broad peak between five and eight years, and a trough between 9.5–12.5 years, a periodicity of approximately 5 to 7 years. An echo of this pattern is apparent in the SE region. The periodicity of the ENSO cycle varies between three and seven years. However, there is no direct evidence that ENSO is the underlying driver. If the peaks represent pairs of samples from El Niño periods, or La Niña periods, this should

be apparent from the makeup of the individual points. Instead, the highest 5% of the points defining the Offshore peak at five to eight years includes no sample pairs between two El Niño or two La Niña periods. Moreover, the points defining the trough at 2.5–3.5 years have more low correlations between two El Niño samples and two La Niña samples than low correlations between one of each. More data is needed to verify this pattern and determine causal mechanisms. At present, these data show no evidence for a shift in species composition directly related to the ENSO cycle.

Seasonal cycles and phenological shifts. All four correlation profiles show an annual peak indicative of a seasonal cycle of species composition (fig. 6). In all regions the magnitude of the annual peaks decreased over time and their regularity tended to erode. The cycle of species composition was most regular in the SE and least regular in the Offshore, consistent with the seasonal cycle of abundance (table 5).

TABLE 10

Composition of spring flora in 1997 and 1999 (the annual peak) and spring flora in 2011 and 2012 (not the annual peak). Also shown are the abundances of the *Chaetoceros* subgenus *hyalochaete*.

NE Region		early spring (peak)				recent spring (not a peak)			
		1997	1999	mean (cells/ml)	(%)	2011	2012	mean (cells/ml)	(%)
major taxa									
diatoms		1954	1282	1618	94.7	144	38	91	42.7
(hyalochaete <i>Chaetoceros</i>)		(358)	(746)	(552)	(32.3)	(37)	(9)	(23)	(10.8)
coccolithophores		7	120	64	3.7	104	50	77	36.2
thecate dinoflagellates		4	0	2	0.1	40	7	24	11.3
athecate dinoflagellates		11	5	8	0.5	9	17	12	5.6
other taxa		22	11	16	0.9	13	5	9	4.2
all species		1997	1418	1708		310	117	213	
dominant taxa									
slim <i>Pseudo-nitzschia</i> spp.		1073	161	617	36.1				
<i>Chaetoceros debilis</i>		95	278	186	10.9	46	28	37	17.3
<i>Dactyliosolen fragilissimus</i>		343	1	172	10.1	50	19	34	16.0
<i>Chaetoceros radicans</i>		57	271	164	9.6	63	5	34	16.0
<i>Chaetoceros</i> spp. (hyalochaete)		95	121	108	6.3	7	19	13	5.6
<i>Skeletonema costatum</i>		4	169	86	5.0	9	17	13	5.6
						19	2	10	5.0
major taxa									
diatoms		1353	1097	1225	91.1	276	36	156	70.9
(hyalochaete <i>Chaetoceros</i>)		(170)	(736)	(435)	(33.7)	(211)	(15)	(106)	(48.0)
coccolithophores		134	54	94	7.0	34	60	47	21.3
thecate dinoflagellates		5	5	5	0.4	5	3	4	1.8
athecate dinoflagellates		1	16	9	0.7	1	13	7	3.1
other taxa		16	6	11	0.8	11	1	6	2.7
all species		1509	1178	1343.5		327	113	220	
dominant taxa									
slim <i>Pseudo-nitzschia</i> spp.		521	133	327	24.3				
<i>Dactyliosolen fragilissimus</i>		538	1	270	20.1	153	10	82	37.2
<i>Chaetoceros debilis</i>		52	284	168	12.0	20	38	29	13.2
<i>Chaetoceros radicans</i>		35	209	122	0.0903	36	5	21	9.5
<i>Chaetoceros</i> spp. (hyalochaete)		26	135	80	0.0598	13	19	16	7.2
<i>Emiliana huxleyi</i>		112	44	78	0.0576	14	3	8	3.6
						13	19	7	7.4

Data from both the NE and the Alley suggest phenological shifts in abundance (figs. 3, 4). Between 1990 and 2009 (Venrick 2012), a long-term shift in the season of the annual peak abundance was accompanied by a shift in the dominant species, especially a decrease in the hyalochaete species of the genus *Chaetoceros*. To examine this within regions, the taxonomic composition of two early spring samples in the NE region and the Alley (1997 and 1999, skipping the depressed El Niño spring of 1998), were compared with the composition of the two most recent springs, 2011 and 2012. In both regions, the decrease in abundance was due to decreases

in the abundances of diatom species (table 10), which underwent an 18-fold decrease in the NE and an 8-fold decrease in the Alley. In the NE, the diatom decrease was dominated by decrease of hyalochaete species. This was not the case in the Alley where hyalochaete *Chaetoceros* species decreased less than diatoms as a whole. The high variability between the two early spring samples and between the two recent spring samples may mask long-term changes in the other phytoplankton components. Because of the reduction in the diatom abundance, the compositions in recent years tended to shift toward a greater dominance of coccolithophorid taxa.

SUMMARY AND DISCUSSION

This study evolved from a study of the temporal variability of phytoplankton in the CalCOFI area (Venrick 2012), which covered the period 1990 to 2009 but lacked information about regional differences within that area. The present study between 1996 and 2012 includes the same stations but partitions the phytoplankton into four regions to address the question of regional heterogeneity and to examine temporal patterns within and across regions.

Spatial Patterns

On the largest scale, there is connectivity across the entire CalCOFI region that is seen in the positive correlations among regional phytoplankton abundances (table 3), in the positive loadings of all major taxa on the first axis of the PCA (table 6), in the high number of taxa abundant in all regions (table 9), and in the positive correlations of species composition between regions (table 8b).

The large-scale concordance indicated by these observations, however, tends to mask rather than negate regional differences. A principal component analysis, with the abundances of the major taxa as input variables, suggests that the spatial dimension was the strongest source of variability. Throughout this study, the NE region and the Alley have been more similar to each other and least similar to the Offshore. The NE region and the Alley were the most eutrophic regions, with highest abundances (table 2), fewest species (table 8a), and most similar species composition (table 8b). Both regions were dominated by diatoms (77%) with coccolithophores making up an additional 12%–16% (fig. 5). Neither region showed evidence for an increase in abundance over the study period (fig. 3). Neither region showed a response to the ENSO cycle (table 4). Initially, the two regions had clear seasonal cycles of abundance with high values in spring. Data from both regions indicate a progressive decline in the magnitude of the spring maximum and a deterioration of the regular cycle (figs. 3, 4).

The Offshore was the most oligotrophic region with the lowest abundances (table 2) and a high number of species (table 8a). There was an increase in abundance during the study (fig. 3), accompanied by a decrease in the number of species (table 8a). The Offshore was dominated by coccolithophores, which accounted for 46% of the total cells; diatoms accounted for an additional 34% (fig. 5). The Offshore was the only region with a detectable response to the ENSO cycle (table 4); this may reflect a relatively low level of local variability in the Offshore, making ENSO perturbations more easily detected, or it may indicate something fundamental about ENSO effects on phytoplankton in the CalCOFI area. The species correlation profile in the Offshore suggests a cycle of species com-

position with a period of five to eight years, which does not appear to be related to the ENSO cycle and remains unexplained. A seasonal cycle of abundance is not apparent (table 5), although there was some repetition of taxonomic composition on an annual scale (fig. 6).

The SE region was sometimes similar to the Offshore, and other times intermediate between the Offshore and the more eutrophic NE and Alley. The SE had the highest number of species (one more than the Offshore) but no evidence for a decrease in species number over time (table 8a). Abundances in the SE region were intermediate (table 2), and increased during the study (fig. 3). The SE had a clear seasonal signal (table 5), but there was no evidence for a phenological change. Like the NE and Alley it was dominated by diatoms and coccolithophores although the proportion of diatoms was lower (59%) and that of coccolithophores was higher (28%) (fig. 5).

These four regions were initially defined by temporal averages of cruise-derived parameters (Hayward and Venrick 1998). The geographical correspondence between the regional boundaries and the local currents suggest that the boundaries are strongly influenced, perhaps defined, by the currents. However, the currents are not static, and the use of mean regional boundaries has resulted in an unknown amount of hybridization of regional characteristics across boundaries. The differences that have emerged from this study are strong enough to be detected in spite of that hybridization. Ideally regions should be defined in real time not by long-term averages so that the regions would more accurately reflect in situ conditions.

Temporal Patterns

Two of the temporal patterns will not be discussed further: the five to eight year repetition of species composition in the Offshore (fig. 6), and the increase in variability of composition in all regions except the NE after the postulated interdecadal climate shift near the year 2000 (fig. 7). Explanations for these patterns are not immediately forthcoming, but should similar patterns in other parameters appear, the phytoplankton data can be revisited.

Two temporal patterns warrant further consideration: the long-term increase in the phytoplankton abundance seen in the SE region and the Offshore, and the changes in the timing of the annual peak seen in the Inshore region and the Alley.

Interannual changes. An increasing trend in average chlorophyll *a* concentration in the CalCOFI area has been recognized for more than a decade (Schwing et al. 2002; Goericke et al. 2005), and several physical mechanisms have been proposed to explain this increase, either in the CalCOFI area (Aksnes and Ohman 2009; Rykaczewski and Checkley 2008; Rykaczewski and Dunne 2010) or directly north, from where it is potentially

linked by advection (Garcia-Reyes and Largier 2010; Bograd et al. 2015).

Regional differences in chlorophyll *a* trends in the CalCOFI area were identified in 2011 (Bjorkstedt et al. 2011). Shipboard chlorophyll *a* extractions, integrated through the water column, indicated an increase in chlorophyll *a* in the offshore stations and in the California Current, but a decrease in the nearshore stations. Although neither sampling scale nor spatial subdivisions are identical to those used here, those chlorophyll trends are consistent with the trends of phytoplankton abundance.

On the other hand, satellite observations have been pooled into a time series from late 1996 through 2011 (Kahru et al. 2012). In this case, the chlorophyll *a* increase was highest near the coast—the opposite of the abundance trends. Analysis of CalCOFI secchi disk depth estimates from 1969 to 2007 (Aksnes and Ohman 2009) showed a decrease in euphotic zone depth across the entire CalCOFI area, implying an increase in chlorophyll and phytoplankton abundance both inshore and offshore. A long-term increase in nearshore chlorophyll *a* has been documented off the end of the Scripps pier (Kim et al. 2009) and a diatom increase is implicated in the recent increase in export of biogenic silica in the Santa Barbara Channel (Krause et al. 2013). Thus, a long-term increase in phytoplankton has been documented from several perspectives, but there is little consensus about regional patterns or the geographical center of phytoplankton increase.

Phenological changes. On a coarse temporal scale, there were seasonal cycles of phytoplankton abundances in all regions except the Offshore. However, in the NE and Alley, the annual peaks, initially in spring, appeared to shift progressively later in the year (figs. 3, 4), apparently driven by a strong decrease in the diatom component of the spring flora (table 10), which greatly reduced the spring amplitude of the cycle. Venrick (2012) hypothesized a change in nutrient source from coastal wind-driven upwelling in the spring to wind-stress-curl-driven upwelling in the summer (Rykaczewski and Checkley 2008). Coastal upwelling is maximal during the spring in the NE region and the Alley. Wind-stress-curl-driven upwelling is centered further offshore and later in the year. Evidence for a shift in importance of the two mechanisms would be decreasing phytoplankton abundance in the spring in the NE region and the Alley and an increase in abundance in the Alley later in the year.

Results of this study are partially consistent with the original hypothesis. Spring abundances decreased in both the NE and Alley, but increases in summer abundances were small, if present at all (fig. 4). Thus the relative but not the absolute magnitudes of spring and summer abundances have changed in the direction predicted.

An alternate explanation for this phenological shift is an increasing mismatch between a rather static CalCOFI

cruise schedule and a slowly shifting seasonal peak. During the study, 12 of the 16 spring cruises were centered in April, three in March, and only one in May (fig. 2). It is possible that the seasonal peaks in abundance have not diminished but have shifted a few weeks earlier or later in the season, outside the sampling window. In this case the phenological change may be due only to a shift in time and may not involve decreasing peak abundances.

Some evidence for this hypothesis comes from the NE region. The latest spring cruise (May 7, 2010) directly followed the earliest spring cruise (March 16, 2009; figs. 2, 3). In the NE region, the May abundance was the second-highest spring abundance (and fourth-highest annual abundance) in the entire series (fig. 3), while the March cruise had the fourth-lowest spring value. This is consistent with a spring peak delayed slightly beyond the usual cruise schedule. Not sampling a delayed abundance peak could cause the CalCOFI data to underestimate the mean annual phytoplankton abundance and might resolve the discrepancy between the long-term increase in chlorophyll *a* shown in satellite data and in ship-based data. However, the data from the Alley are less supportive. The May 2010 abundance in the Alley was higher than that of March 2009, but both values were near the middle of the data set and did not indicate a relationship between abundance and sampling date.

Predictions of the effects of climate change, suggest that spring productivity will move earlier, not later. Most evidence from the marine environment supports this. (Poloczanska et al. 2013; Edwards and Richardson 2004). However, based on direct examination of along-shore wind stress between 1967 and 2007, Bograd et al. (2009) estimated significant variability in both onset and duration of wind driven upwelling in the California Current large marine ecosystem (33°–48°N). A delay in upwelling was detected in the northern part of the area. Although a change was not detected in the vicinity of the NE region, a mechanism for a progressive delay in the seasonal cycle has been identified.

A shift in phenology, whether driven by a decrease of the spring abundance or a delay in peak date, has implications both for the subsequent responses of the zooplankton and fish as well as for our understanding of the physics and chemistry of the nutrient input into the euphotic layer and predictions of climate change. It is important that this ambiguity be resolved. If our sampling schedule has become uncoupled from the seasonal cycle, we risk misinterpreting the system entirely.

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The paper is dedicated to Jerry Fecht, who knows neither *Calanus* nor *Chaetoceros*, but who encourages and inspires nonetheless.

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