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Summer phytoplankton assemblages and their environmental correlates in the Southern California Bight

by D. Goodman,[1] R. W. Eppley[2] and F. M. H. Reid[2]

ABSTRACT

Weekly observations of chemical and physical variables, and of phytoplankton abundances, were made over a 21-week period at three stations in the Southern California Bight. Principal component analysis was employed to resolve four phytoplankton assemblages among the 25 taxa with the highest variances for their log transformed abundances. Two of these components were described by the abundance of taxa characteristic of upwelling assemblages—both dominated by diatoms. A third assemblage was dominated by the "red tide" dinoflagellate, *Gonyaulax polyedra*, along with some small diatoms and a coccolithophorid.

Canonical correlation analysis of the four phytoplankton components against 13 environmental variables revealed distinct sets of temperature-salinity-nutrient conditions associated with periods of abundance of each assemblage. Two were interpretable, on physical grounds, as upwelling situations, and these were associated with periods of abundance of the phytoplankton assemblages that were identified, on floristic grounds, as upwelling assemblages. The "red tide" assemblage was associated with nonupwelling conditions.

The pattern of correlations of 89 other taxa, besides the 25 employed in the principal component analysis, with the four principal components and the four environmental canonical variates were also consistent with this interpretation. Comparison with phytoplankton assemblages described in other studies reveals substantial consistency in broad outline, but many differences in detail, especially with respect to the presence and absence of species.

The species assemblages defined by the principal components analysis exhibited episodes of abundance of a duration of 2–3 weeks at a given location. Current meter records, from nearby stations, but from another year, suggest that a persistence time of 2–3 weeks at a stationary site corresponds to a spatial patch scale of 20–40 km. These same current meter records show approximately 50% coherence in low-frequency currents at a separation of 25 km, indicating a possible common scale for spatial coherence of currents and spatial extent of phytoplankton blooms in this system.

Implications of the analysis are discussed in terms of hypotheses concerning the structure and dynamics of plankton communities.

1. Introduction

The dynamics of coastal marine phytoplankton communities are characterized by processions of species assemblages, associated, in time and space, with discernible

1. Biology Department, Montana State University, Bozeman, Montana, 59717, U.S.A.
2. Institute of Marine Resources, Scripps Institution of Oceanography, University of California San Diego, La Jolla, California, 92093, U.S.A.

features of their physical environment (cf. Smayda, 1980). It is believed that the phytoplankton species assemblages of lakes generally are not in equilibrium with their physical environment: transient species assemblages arise, persist only briefly, and then give way to a new assemblage (Richerson *et al.*, 1970; Allen *et al.*, 1977; Harris, 1978). The phytoplankton species assemblages of the central oligotrophic oceans, by contrast, display substantial temporal stability (Weiler, 1980; Beers *et al.*, 1982).

In this paper, we examine a 21-week record of changes in phytoplankton community composition and simulataneous changes in physical and chemical properties of the coastal water in the Southern California Bight off La Jolla. The analysis attempts to establish a statistically grounded relation between phytoplankton assemblages and specific temperature, salinity and nutrient conditions that prevail during the periods of their abundance. The strength of the association will be taken to reflect the contribution of spatial and temporal environmental heterogeneity to the species diversity and observed community dynamics, particularly with regard to the question whether an "equilibrium" or "nonequilibrium" view is appropriate.

Recent studies, in the same area, but not simultaneous with our sampling, have characterized the current regime along the narrow continental shelf between San Diego and Los Angeles (Winant and Olson, 1976; Hendricks, 1979; Winant, 1983; Winant and Bratkovich, 1981). The inocula for phytoplankton blooms, and the blooms themselves, are probably transported primarily by the longshore currents, so it may be that spatial structure of the current parcels (eddies) determines the characteristic time and length scales of coherent bloom events on the shelf. We speculate that the length scale of low-frequency longshore coherence in the currents is an indicator of the fundamental scale of the water parcels which bear the phytoplankton communities. Since each parcel of water moving along the shelf with a characteristic current structure will have experienced a particular history en route, a plankton record from a fixed station will exhibit variation which confounds successional processes within each water parcel and the movement, past the fixed station, of water masses with different histories. Even if the dynamics within each parcel were predominantly equilibrial, the variation in species composition recorded at the fixed station would appear to be dominated by transients.

2. Materials and methods

a. The data set. From mid-April to mid-September in 1967, the Food Chain Research Group, led by the late J. D. H. Strickland, recorded weekly observations of physical conditions, and concurrently collected plankton samples at three stations just north of La Jolla, California. During the period of the observations, there were three peaks in phytoplankton abundance, each associated with episodes of relative nutrient abundance (Eppley *et al.*, 1970).

The stations were 1.4, 4.6 and 12.1 km from shore. The water depths at these stations were 21, 175 and 175 m, respectively. In the following discussion, these

stations, in this order, will be referred to as stations 1, 2, and 3. The disproportionate depth at station 2, relative to its intermediate distance offshore, was owing to its position over the La Jolla Canyon.

Phytoplankton were collected in pump profiles which integrated from the surface to the "pigment layer depth," the depth at which *in vivo* chlorophyll fluorescence dropped essentially to zero. The phytoplankton samples were subsampled and species were identified, to the extent possible, and individuals were counted, using the Utermohl settling technique. Three different subsample volumes were examined, in order to obtain estimates for all size categories (Reid *et al.*, 1970).

Physical and chemical determinations were made at a variety of discrete depths. The analytical methods and subsampling procedure are described in Strickland *et al.* (1970). The physical properties we shall consider in this paper are temperature, density and salinity; the chemical properties are nitrate, phosphate and silicate concentrations. The physical and chemical properties will each be represented as two variables, corresponding to the value of that property at the surface and the value at the pigment layer depth. This set of twelve physical and chemical variables, in conjunction with the value for the depth of the pigment layer, will comprise the thirteen environmental variables that we submit to statistical analysis.

Use of values for physical and chemical measurements at two depths will allow the later analysis to establish associations with gradients (differences between values at the two depths) as well as with intensities (the values themselves).

b. Statistical treatment. In this study, we are concerned to determine the pattern of relationships between two subsets of variables in a collection of multivariate observations: the structure of associations between assemblages of phytoplankton taxa and physical syndromes of the water mass as defined by the thirteen environmental variables. This was investigated by means of canonical correlation analysis (Hotelling, 1935).

Canonical correlation analysis has not been used extensively in ecology. Pielou (1977) gives an introduction to the technique from an ecological perspective; most other treatments presume an application in the social sciences. Harris (1975) develops a description of canonical correlation as a kind of reciprocal multiple correlation between the two data sets. Tatsuoka (1971) introduces canonical correlation from the standpoint of discriminant analysis. A more abstract mathematical treatment is presented in Mardia *et al.* (1979).

Canonical correlation analysis identifies pairs of linear combinations of original variables in the two respective subsets such that the correlations between the new variables, called canonical variates, defined by these linear combinations, are maximal within each pair, while the correlation with the canonical variates that are members of other pairs is zero. The process is stepwise, in that the first pair of canonical variates represents the pair of linear combinations of original variables in the two respective sets

giving rise to the greatest correlation across the data. The second pair maximizes the correlation, subject to the constraint of zero correlation with both members of the first pair, and so forth.

Generally, the first few pairs of canonical variates will exhaust all the physically interpretable (or statistically significant) structure in the data. The vectors of coefficients (weighting factors in the linear combinations) that transform the original variables to the canonical variates will reveal the role each of the original variables plays in determining the value of each canonical variate. The values (scores) of the canonical variates may themselves be treated as a data set, whose spatial or temporal pattern can be scrutinized.

Our primary interest in the method of canonical correlation will be that it resolves a few constellations of variables that represent the bulk of the structure of the linear associations between two sets of variables (in this case phytoplankton species abundances and environmental variables), with no redundancy. The extent to which these constellations of variables coincide with actual coherent assemblages or physical factors will depend on the nature of the actual processes structuring the data. If the responsible mechanisms do result in linear relationships, and if the pairs of interacting complexes operate independently, then the canonical variates will represent physically real entities. If these conditions are not met, the variates themselves will be artificial constructs, but they still will be useful for economical description of the statistical relations between the two sets of original variables.

The statistical significance of a pair of canonical variates can be evaluated, after Bartlett (1947), according to the magnitude of the canonical correlation coefficient (the correlation between the pair of canonical variates). The null hypothesis is that the two sets of variables are independent. For the sorts of ecological data we have in mind, where there is bound to be some spatial and temporal serial correlation, and where some sort of causal interaction can reasonably be presumed, a null hypothesis of independence is not a strenuous one. Thus, in addition to some measure of statistical significance of a particular canonical correlation, we should also like to have a measure of the "strength" of the relation that is revealed.

One approach to this matter of strength of the relation, due to Stewart and Love (1968), measures the efficacy of one set of canonical variates in "predicting" (in the sense of a regression) the values taken by the complementary set of original variables. The measure, called the redundancy of the variables of the one data set, indicates what fraction of the variance in the original variables in that set is accounted for through canonical correlation with the second set of variables (eg., what fraction of variance in phytoplankton species abundances might be accounted for by canonical correlation with environmental variables). The redundancy can be calculated separately for each pair of canonical variates, and since the pairs are mutually uncorrelated, the total redundancy is obtained by summing the pair by pair values.

The redundancy measure for one of the sets of variables depends both on the value of

the canonical correlation coefficient between the two sets of variables and on the fraction of the variance in the original data set that is extracted by the canonical variates for that set of variables. It is the latter component of the measure that makes the redundancy a telling index of "importance" of a particular canonical correlation. In our studies, we shall be interested to learn what fraction of the variance in species abundances can be accounted for through canonical correlation with the environmental data. Since high-frequency variation, as well as sampling error, which is inevitably considerable in phytoplankton enumeration, will inflate the residual that cannot be accounted for by linear relationships with the environmental data, the redundancy measure will tend to be low even if there are reasonably coherent assemblages of species. If species respond more or less individually to the environmental variables, the redundancy will be lower yet.

3. Results

a. The phytoplankton taxa. One hundred forty seven phytoplankton taxa—many with very low abundances—were recorded in the 63 samples (21 weeks, 3 stations). At the times when a taxon was abundant, its numbers were briefly orders of magnitude greater than usual, giving rise to very skewed frequency distributions of abundance. In order to reduce the influence of these few episodes of extreme abundance, we log transformed the counts (natural logarithm of one plus the abundance expressed as cells per liter). This generated distributions that were more nearly normal, but it must be born in mind, for later, that, owing to the log transform, the linear combinations of phytoplankton-abundance variables must be interpreted as weighted products of abundances rather than weighted sums.

One hundred forty seven variables are, of course, an unwieldy number for multivariate statistics in a system of 63 observations (which probably are not genuinely independent, so the effective number of observations is even less). The number is particularly excessive for canonical correlation analysis: maximization of a correlation is independent of scale, so chance correlation of a few bizarrely distributed minor species with any pattern in the environmental variables might dominate the analysis. Accordingly, an objective, and directed, selection of a more manageable subset of the taxa is mandatory.

Of the 147 phytoplankton taxa, 114 were present in more than 10% of the samples. In Table 1, these 114 taxa are listed by name, ordered according to the mean of their log transformed abundances. Since, in this study, we are most interested in the variations in phytoplankton abundance, we selected for the multivariate analysis the 25 taxa with the highest variances in their log transformed abundances. These taxa are designated with an asterisk in the list in Table 1. Understandably, these 25 taxa were not uniformly the most abundant: they span about the top half of the rankings according to mean log-abundance.

Table 1. The 114 phytoplankton taxa present in more than 10% of the samples, ranked according to the mean of their log transformed abundances (augmented by 1.0). Also shown for each taxon are: the variance of the log transformed abundances, and correlations of the log transformed abundances with phytoplankton components I, II, III, and IV (PC), and with environmental canonical variates I, II, III, and IV (CV). Notation: micro = 5–20μ, small = 21–52μ, medium = 53–90μ, large > 90μ, [D] = dinoflagellate, [F] = flagellate, [O] = coccolithophorid, [S] = silicoflagellate, [C] = centric diatom, [P] = pennate diatom. The * designates a taxon that was among the 25 in the multivariate analysis.

Species (or group)	Mean	Variance	Fraction presence	CV I	CV II	CV III	CV IV	PC I	PC II	PC III	PC IV
[F] Monads (~2μ)	13.57	0.37	1.00	.35	−.26	.26	.42	.55	.29	−.39	.28
[F] Monads (~5μ)	11.54	2.67	.98	−.03	.18	.31	.17	.02	.53	.00	−.05
[F] Monads (~12μ)	10.13	5.89	.95	−.47	.22	.02	.26	−.28	.23	.35	.24
*[O] *Emiliania huxleyi*	10.08	8.51	.94	−.07	−.53	.38	−.04	−.07	.04	−.34	−.09
*[D] Naked dinoflagellates (micro)	7.93	19.07	.78	.48	−.25	.08	.61	.73	.17	−.10	.02
[P] *Nitzschia* spp (medium)	7.16	6.12	.95	.60	−.12	−.09	.29	.60	−.25	−.22	−.01
*[D] Thecate dinoflagel. (micro)	6.96	18.59	.73	.41	.12	.30	.31	.52	.34	−.00	.00
*[D] *Prorocentrum ovum*	6.18	21.33	.67	.48	−.17	.18	.22	.52	−.08	−.23	−.13
*[P] *Nitzschia closterium*	6.07	16.44	.75	.36	−.21	−.39	.47	.51	−.12	−.10	−.30
[P] *Nitzschia* spp (large)	5.67	7.77	.87	.52	.06	.13	.12	.51	.08	−.17	−.14
*[F] *Chilomonas marina*	5.43	21.17	.59	.34	−.18	.33	.48	.34	.26	−.13	.10
*[D] Naked dinoflagellates (small)	5.22	9.00	.79	.30	.12	.13	−.15	.12	−.05	−.10	−.19
[C] Centric diatoms (small)	5.11	6.68	.89	.57	−.11	−.13	−.28	.19	−.20	−.02	−.34
[D] *Scrippsiella trochoidea*	4.78	8.07	.83	.65	−.20	.15	.39	.66	.17	−.17	−.13
[P] Pennate diatoms (small)	4.30	7.98	.75	−.28	.12	.02	.12	−.10	.11	−.18	.06
*[C] Centric diatoms (micro)	4.24	21.40	.46	.62	.01	.05	−.11	.39	−.06	−.05	−.08
[P] Pennate diatoms (medium)	3.88	6.32	.76	.16	.36	.19	−.03	.02	.36	.19	−.30
*[C] *Skeletonema costatum*	3.64	15.12	.51	.81	.27	−.19	−.04	.57	−.16	.14	−.27
*[O] *Syracoshpaera pulchra*	3.47	19.92	.38	−.39	.10	.70	.05	−.31	.47	−.03	.01
[D] Naked dinoflagellates (medium)	3.45	6.65	.78	−.06	.06	.40	.19	−.14	.40	.02	.05
*[C] *Chaetoceros curvisetus*	3.37	16.59	.44	.60	.17	.11	−.47	.16	−.00	−.01	−.37
[D] *Ceratium furca*	3.28	6.81	.84	.61	.31	.39	.14	.48	.42	.09	−.19
[D] *Protoperid. depressum* (medium)	3.14	4.11	.84	.51	.04	.23	.08	.40	.35	−.06	−.10
*[P] *Nitzschia closterium* (small)	3.09	20.98	.32	−.30	.28	.48	−.27	−.32	.29	−.02	−.22
*[C] *Chaetoceros* spp	2.93	12.99	.43	.27	.43	.19	−.20	.12	.08	.15	−.17

Table 1. (Continued)

Species (or group)	Mean	Variance	Fraction presence	CV I	CV II	CV III	CV IV	PC I	PC II	PC III	PC IV
*[C] *Leptocylindrus danicus*	2.86	14.87	.43	.61	.30	−.01	−.09	.41	.08	.24	−.19
*[P] Pennate diatoms (micro)	2.80	16.73	.33	.62	.41	−.18	−.05	.33	−.16	.34	−.10
*[D] *Prorocentrum vaginula*	2.73	15.35	.35	.57	−.56	.14	−.07	.38	−.10	−.32	−.01
[D] *Protoperidinium globulus*	2.71	4.93	.68	.41	.02	.09	.07	.32	.21	−.11	−.06
*[C] *Chaetoceros costatus*	2.63	16.67	.32	.71	.41	−.01	.12	.60	.08	.24	−.34
*[C] *Chaetoceros debilis*	2.63	16.35	.33	.79	−.22	−.14	−.13	.48	−.24	−.13	−.12
[C] *Chaetoceros concavicornis*	2.62	5.46	.60	−.06	.25	−.45	−.20	−.11	−.35	.24	−.01
[D] *Dinophysis amygdala*	2.57	2.38	.84	.40	−.11	.29	.15	.40	.34	−.10	−.05
[C] Centric diatoms (medium)	2.57	3.45	.76	.49	.07	.31	−.10	.21	.05	.12	−.36
*[D] *Gonyaulax polyedra*	2.53	9.13	.54	.09	−.03	.72	−.10	−.14	.60	−.41	.06
[D] *Ceratium kofoidii*	2.44	3.28	.78	.32	.25	.41	.03	.16	.57	.16	−.08
[S] *Distephanus speculum*	2.42	3.65	.73	−.19	.37	.48	.21	−.16	.50	.12	.05
[D] *Ceratium divaricatum*	2.42	6.23	.59	.61	.28	.23	.28	.66	.32	.10	−.10
*[C] *Eucampia zoodiacus*	2.40	9.80	.43	.18	.48	.39	.21	.07	.50	.24	−.01
[D] *Dinophysis caudata*	2.36	3.24	.71	−.35	.35	.34	.09	−.30	.66	.02	.09
[D] *Dinophysis acuminata*	2.30	5.39	.60	.64	.09	.38	.04	.46	.37	−.07	−.23
[C] *Rhizosolenia alata*	2.23	4.80	.63	−.04	.06	.44	−.24	−.35	.40	−.02	−.06
[D] *Protoperid. depressum* (large)	2.10	2.88	.75	.65	−.05	.14	.09	.61	−.00	−.07	−.27
[D] *Gonyaulax spinifera*	2.07	2.70	.70	.02	.41	.09	.34	.23	.22	.17	−.05
[D] *Ceratium fusus*	2.03	4.18	.65	.26	.23	.57	.22	.20	.74	−.09	.07
[P] *Gyrosigma* spp	1.97	4.98	.54	.50	.04	.10	.06	.46	.20	−.22	.00
[D] *Protoperidinium* spp (small)	1.92	4.78	.51	−.01	.28	.22	−.04	.08	.27	.23	−.34
[D] *Prorocentrum gracile*	1.91	7.70	.35	.50	−.23	.28	.19	.47	.30	−.13	−.13
[C] *Chaetoceros didymus*	1.85	7.70	.32	.46	.49	.00	−.11	.17	.09	.39	−.19
*[O] *Cyclococcolithus leptoporus*	1.81	12.09	.22	−.10	.52	.16	.47	.09	.26	.26	−.00
[D] *Protoperidinium conicum*	1.79	3.82	.57	.55	−.08	.07	.07	.39	.19	−.12	−.18
[D] *Prorocentrum micans*	1.74	6.13	.38	.44	.11	.35	.21	.47	.40	−.06	.02
*[C] *Rhizosolenia delicatula*	1.69	10.47	.24	.79	−.33	.06	−.13	.49	−.28	−.21	−.24
*[O] *Acanthoica quattrospina*	1.67	10.30	.22	.70	−.26	.18	−.10	.44	−.10	−.23	−.22
*[C] *Rhizosolenia stolterfothii*	1.66	8.55	.29	.76	−.19	.05	−.18	.42	−.18	−.13	−.32

Table 1. (Continued)

Species (or group)	Mean	Variance	Fraction presence	CV I	CV II	CV III	CV IV	PC I	PC II	PC III	PC IV
[P] *Thalassiothrix mediterranea*	1.66	6.70	.37	.75	−.20	.06	−.10	.51	−.21	−.14	−.36
[D] *Protoperidinium* spp	1.65	4.18	.48	−.01	.11	.11	−.25	−.16	−.01	−.08	−.28
[C] *Chaetoceros affinis*	1.65	8.37	.27	.15	.65	.18	.09	.17	.31	.40	−.02
[P] *Thalassiosira rotula*	1.54	4.16	.44	.53	.27	−.27	.06	.47	−.15	.26	−.12
*[C] *Chaetoceros radicans*	1.44	8.50	.21	.33	.71	−.09	.07	.29	.10	.35	−.14
[D] *Oxytoxum sceptrum*	1.43	4.57	.35	.21	−.12	.54	.20	.21	.57	−.38	.03
[C] *Hemiaulus sinensis*	1.43	7.74	.22	.75	−.18	.05	−.09	.47	−.06	−.09	−.26
[D] *Protoperidinium oceanicum*	1.39	2.71	.49	.57	−.11	.39	.05	.38	.44	−.15	−.11
[D] *Ceratium pentagonum*	1.35	2.29	.49	−.36	.06	.51	−.23	−.58	.58	−.07	.07
[C] Centric diatoms (large)	1.28	2.47	.49	.48	−.09	−.27	.12	.57	−.30	−.04	−.11
[P] *Thalassiothrix frauenfeldii*	1.27	3.89	.35	−.31	.23	−.03	−.45	−.45	.02	.11	.00
[D] *Ceratium tripos*	1.26	2.38	.56	.04	−.25	−.05	.21	.25	−.06	−.13	−.08
[C] *Dactyliosolen mediterraneus*	1.24	4.77	.25	−.32	.16	.16	−.49	−.54	.07	.05	−.07
[D] *Ceratium macroceros*	1.23	1.41	.62	−.29	.29	.22	.19	−.22	.37	.03	−.04
[C] *Rhizosolenia fragilissima*	1.19	6.37	.19	.29	.42	.11	.28	.33	.40	.38	.03
[O] *Helicosphaera carteri*	1.18	5.83	.21	.21	−.22	−.02	.18	.26	−.14	−.01	.04
[C] *Lithodesmium undulatum*	1.10	3.55	.30	.64	.02	−.00	−.13	.45	−.08	−.07	−.39
[C] *Schroderella delicatula*	1.01	3.81	.25	.49	.17	−.08	−.13	.32	−.14	.17	−.20
[P] Pennate diatoms (large)	.98	3.28	.30	−.23	.14	−.04	−.24	−.37	.03	.12	.08
[D] Naked dinoflagellates (large)	.97	2.33	.38	.28	−.01	.20	.06	.02	.25	.07	.15
[D] *Prorocentrum* sp C	.89	2.98	.29	−.16	−.06	.37	.07	−.23	.48	−.03	.32
[C] *Bacteriastrum delicatulum*	.87	3.38	.21	−.15	.31	.28	−.45	−.41	.09	.02	−.16
[P] *Asterionella japonica*	.85	3.86	.18	.21	.62	.01	−.03	.16	.21	.26	−.21
[C] *Cerataulina bergonii*	.84	3.41	.21	.05	.59	.11	−.14	.00	.23	.25	−.11
[D] *Ceratium bucephalum*	.82	.87	.48	.04	.04	.10	−.24	−.03	−.03	−.03	−.19
[C] *Ch. atlanticus var. neopolitana*	.82	4.23	.34	−.23	.22	−.12	−.54	−.56	−.07	.22	−.19
[C] *Chaetoceros convolutus*	.79	2.58	.21	.07	−.25	−.36	.09	.36	−.28	−.03	.04
[D] *Protoperidinium steinii*	.77	1.65	.33	−.23	.24	.22	−.28	−.40	.19	.19	.07
[P] *Thalassionema nitzschioides*	.75	2.70	.19	−.04	.35	.07	−.06	−.16	.00	.18	−.15
[P] Pennate diatom sp A	.75	2.21	.24	−.39	.23	−.03	−.43	−.54	−.00	.26	−.08

Table 1. (Continued)

Species (or group)	Mean	Variance	Fraction presence	CV I	CV II	CV III	CV IV	PC I	PC II	PC III	PC IV
[C] *Rhizosolenia hebetata*	.72	1.61	.30	−.11	.41	.07	−.13	−.14	.09	.21	−.14
[D] *Ceratium extensum*	.71	1.09	.36	−.37	−.04	.20	−.14	−.44	.21	.00	.16
[S] *Dictyocha fibula*	.70	2.52	.25	−.23	−.02	.23	−.18	−.42	.31	−.19	.12
[C] *Rhizosolenia styliformis*	.69	1.82	.27	−.23	−.04	−.11	−.04	−.22	−.09	.18	.11
[D] *Ceratium horridum*	.69	.88	.41	−.05	−.10	−.12	.05	.01	−.09	−.16	.22
[P] *Pseudoeunotia doliolus*	.68	1.46	.27	−.18	.06	−.11	−.07	−.18	−.23	.22	.06
[D] *Pronoctiluca spinifer*	.66	2.11	.19	−.18	.20	−.06	−.08	−.28	−.04	.09	−.11
[C] *Rhizosolenia setigera*	.62	1.51	.25	.12	.50	−.21	−.08	.08	−.02	.21	−.11
[D] *Dinophysis tripos*	.60	1.04	.32	.14	.16	.28	.29	.16	.25	.09	−.11
[D] *Dinophysis fortii*	.59	1.19	.25	.17	.04	.45	.08	.18	.38	−.15	−.08
[C] *Chaetoceros messanensis*	.56	1.97	.16	−.27	.24	−.09	−.45	−.49	−.04	.19	−.23
[D] *Protoperidinium pellucidum*	.50	1.25	.21	.14	.12	−.04	.28	.34	.06	.27	.03
[C] *Stephanopyxis turris*	.45	1.34	.16	.63	.25	.15	.02	.47	.08	.21	−.25
[D] *Gonyaulax digitale*	.44	1.11	.18	.20	.61	−.07	.18	.25	.15	.30	.06
[D] *Gonyaulax polygramma*	.44	.78	.22	−.32	.27	−.05	−.32	−.46	−.04	.24	−.11
[D] *Protoperidinium divergens*	.43	1.87	.13	−.11	−.17	.29	.10	−.15	.40	−.10	.35
[D] *Podolampas palmipes*	.35	.72	.18	−.12	−.07	.25	.07	−.18	.42	−.06	.29
[D] *Protoperidinium granii*	.33	1.10	.14	−.09	−.14	.33	.14	−.10	.41	−.10	.40
[D] *Protoperidinium ovum*	.33	.66	.16	−.32	−.09	.17	−.20	−.42	.19	−.09	−.01
[P] *Nitzschia longissima*	.29	.84	.11	−.22	.18	−.21	−.41	−.44	−.09	.27	−.13
[D] *Dinophysis hastata*	.28	.55	.16	−.03	.23	.24	.10	−.05	.34	−.10	.21
[D] *Protoperidinium pyriforme*	.27	.50	.16	−.26	−.05	.10	−.07	−.33	.27	−.07	.24
[C] *Planktoniella sol*	.22	.27	.18	−.20	.01	−.13	−.36	−.42	−.11	.25	.01
[C] *Rhizosolenia robusta*	.22	.28	.16	.18	−.33	−.24	.01	.20	−.33	.04	.10
[D] *Oxytoxum scolopax*	.21	.47	.13	−.12	−.08	.29	−.08	−.24	.26	−.08	.17
[D] *Podolampas spinifer*	.21	.35	.13	−.11	−.04	.18	−.07	−.25	.31	−.06	.23
[P] *Thalassiothrix longissima*	.19	.33	.11	−.18	.02	.08	−.36	−.36	.00	.10	−.11
[D] *Oxytoxum elegans*	.16	.19	.14	−.19	.31	−.05	−.32	−.38	−.07	.20	−.09
[D] *Phalacroma cuneus*	.15	.18	.14	−.19	−.08	.06	−.14	−.32	.04	−.10	.07

To an algal ecologist, the short list of 25 taxa is something of a disappointment. The short list contains a disproportionate number of categories of small plankton forms that are not readily identifiable to species level. Some of the classifications are merely on the basis of size and general taxonomic group. Furthermore, the short list omits many of the species that might be thought more typical of the coastal habitat. Nevertheless, the working list was the result of a selection criterion motivated by a specific ecological question, and to this extent it addresses a specific ecological question. For this reason, the short list was retained for the central multivariate analysis. In order to compare with known results concerning more commonly selected taxa, and in order to explore questions concerning the pattern of participation of the list of 114 taxa with the structure revealed in the analysis of the short list of 25, we shall later consider correlations of all these species with the taxon assemblages and environmental complexes identified in the multivariate analysis. These correlations are listed in Table 1, but discussion of them will be deferred to a concluding section of the paper.

b. A strategy for preliminary clustering. On our first application of canonical correlation to the two sets of variables (the 13 environmental variables and the log transformed abundances of the 25 phytoplankton taxa) the redundancy of the sets of taxon abundances in the canonical correlations was very low, despite very high, and significant, values for the canonical correlation coefficients. The low redundancy resulted from a peculiar structural relation between the canonical variates and the original phytoplankton abundance data: each canonical variate was influenced strongly by only a very few taxa. It was almost as if canonical correlations were establishing environmental associations with one species at a time, rather than with species assemblages, so the amount of total variance of the 25 taxa that was involved in each of the canonical variates remained small. This pattern is interesting in its own right, and will be discussed in a later section, but it does not satisfy our initial intention to discover the manner in which species assemblages are associated with physical states of the water.

In order to force an analysis that would focus on assemblages of bloom species, we transformed the taxon abundance variables to principal component scores. Then the scores for the first four components were used to represent intensities of development of respective assemblages, and these four variables were submitted along with the 13 environmental variables for canonical correlation analysis.

Inasmuch as principal components are necessarily orthogonal, this treatment imposed a new and special structure on the matrix of correlations within the set of "floristic" variables in the canonical correlation analysis. Nevertheless, this structure need not drive the outcome of the canonical correlation analysis, for the fact that two floristic variables are uncorrelated within the data set does not determine the correlation between the environmental variables with which they are correlated in turn. Of course, there cannot be correlation coefficients of one between two of the

floristic variables and the same set of environmental variables; but as long as the correlations are imperfect, two orthogonal floristic variables may be correlated with the same environmental variables.

As it turned out, the phytoplankton components were, for the most part, each correlated with different sets of environmental conditions, but this was a result, not a tautology. On the other hand, the principal components did filter out that portion of the original variance which could not readily be organized into linear relationships, so it was to be expected that substitution of the components in place of the original taxon abundances in the canonical correlation analysis would increase the value of the redundancy measure—and indeed this is what occurred.

c. Orthogonal components. The eigenvectors defining the first four principal components of the log transformed phytoplankton abundances are presented in Table 2. Altogether, the four components accounted for a little more than half the variance in the 25 taxa. For convenience, we will designate those eigenvector elements which comprise the largest one third, in absolute value, within a component as the core of that component. These values are printed in bold type in the table.

The first component was dominated by a large number of positive contributions. In a very rough way, therefore, we would expect this to be a measure of biomass. The core of this component consisted primarily of centric diatoms—the exceptions being a category of unidentified pennate diatoms, the coccolithophorid *Acanthoica quattrospina*, and the dinoflagellate *Prorocentrum vaginulum*.

The second principal component was dominated by positive contributions from two centric diatoms, *Chaetoceros radicans* and *Eucampia zoodiacus*, and the coccolithophorid *Cyclococcolithus leptoporus*, with negative contributions from *Emiliania huxleyi* and *P. vaginulum*.

The third component was dominated by the dinoflagellate *Gonyaulax polyedra*, a coccolithophorid *Syracosphaera pulchra*, and a small form of the pennate diatom *Nitzschia closterium*. There were no negative elements in the core of this component.

The fourth component was dominated by very small unidentifiable non-thecate dinoflagellates, the flagellate *Chilomonas marina*, the coccolithophorid *C. leptoporus*, larger cells of *N. closterium*, and a negative contribution from *Chaetoceros curvisetus*.

d. Phytoplankton assemblages. The values (scores) taken on by components I, II, and III, at each station, over time, are graphed in Figure 1. The components appear to persist at a given location for a variable time, with periods of abundance generally lasting from 1 to 4 weeks.

The diatoms involved in the core of component I comprise a typical warm water upwelling assemblage, comparable to those described for the Gulf of Panama (Smayda, 1963), the California Current off Baja California (Smayda, 1975) and

Table 2. Eigenvectors defining principal components of log transformed phytoplankton abundances, scaled so that the largest element of each is 1.0 in absolute magnitude. Elements of absolute value greater than 0.667 are in bold type.

	Eigenvector			
Taxon	I	II	III	IV
Skeletonema costatum	**1.000**	.382	−.180	−.062
Chaetoceeros debilis	**.981**	−.315	−.190	−.206
Rhizosolenia delicatula	**.974**	−.470	.088	−.210
Rhizosolenia stolterfothii	**.939**	−.267	.068	−.288
Chaetoceros costatus	**.890**	.575	−.020	.195
Acanthoica quattrospina	**.874**	−.370	.258	−.167
Centric diatoms (micro)	**.771**	.019	.063	−.182
Pennate diatoms (micro)	**.768**	.575	−.250	−.082
Leptocylindrus danicus	**.761**	.420	−.018	−.152
Chaetoceros curvisetus	**.742**	.239	.153	**−.768**
Prorocentrum vaginulum	**.707**	**−.788**	.198	−.112
Prorocentrum ovum	.600	−.236	.245	.358
Non-thecate dinoflagellates (micro)	.600	−.346	.110	**1.000**
Thecate dinoflagellates (micro)	.510	.174	.415	.498
Nitzschia closterium	.452	−.291	−.540	**.758**
Chilomonas marina	.423	−.255	.460	**.790**
Chaetoceros radicans	.403	**1.000**	−.121	.120
Non-thecate dinoflagellates (small)	.377	.174	.188	−.251
Chaetoceros spp	.329	.609	.268	−.331
Eucampia zoodiacus	.223	**.673**	.544	.341
Gonyaulax polyedra	.107	−.186	**1.000**	−.159
Emiliania huxleyi	−.087	**−.745**	.526	−.064
Cyclococcolithus leptoporus	−.129	**.733**	.227	**.768**
Nitzschia closterium (small)	−.377	.389	**.669**	−.444
Syracosphaera pulchra	−.487	.143	**.982**	.086
Cumulative percent of total variance	27	38	47	54

earlier investigations at the site of our study (Balech, 1960). *Skeletonema costatum* characteristically is abundant at the inception of the spring bloom in temperate inshore waters, and various *Chaetoceros* species follow it (Smayda, 1958). *Leptocylindrus danicus, S. costatum* and *Rhizosolenia stolterfothii* are cosmopolitan species. The *Chaetoceros* species of component I are temperate, except for *Ch. costatus* which has warmer water affinities though it is often abundant along with the temperate forms off southern California (Smayda 1958; Reid unpubl.).

Many of the diatoms in component I tended to be more abundant in samples from our most inshore station, compared to offshore. There were four episodes when component I took on relatively high values: during weeks 1–4, 8–11, 14–16 and on week 20. These peaks were seen to some degree at all three stations (Fig. 1). As

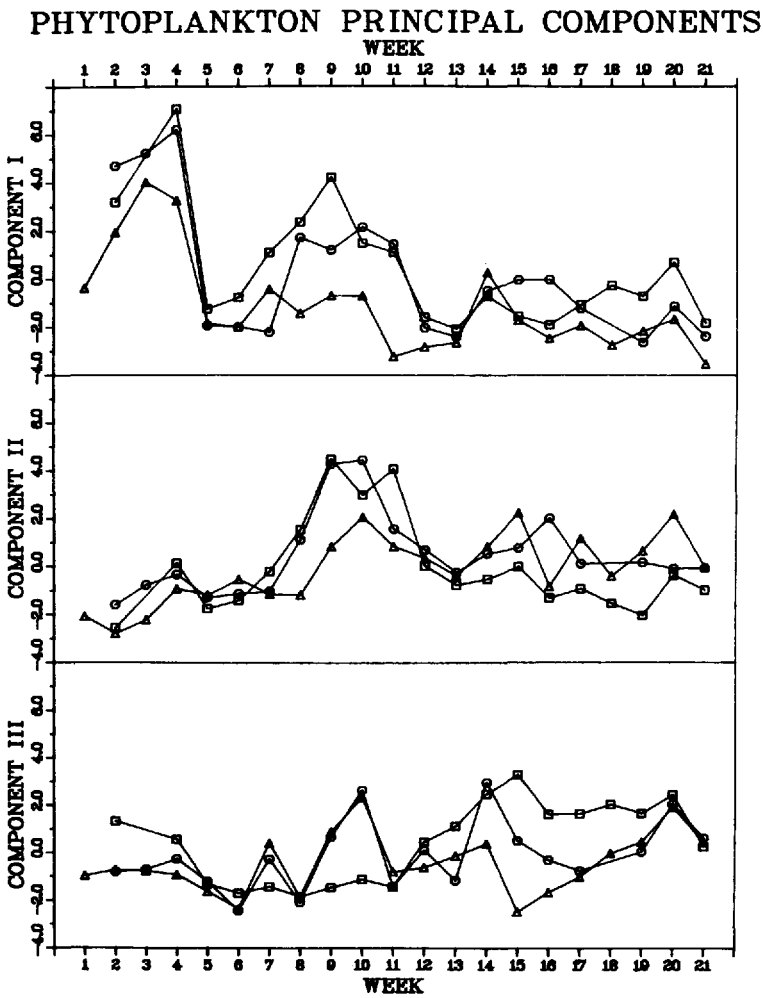

Figure 1. Principal component scores for phytoplankton components I, II and III, plotted for each observation at each station. Week 1 begins on April 26, 1967. Station labels: □ station 1; △ station 2; O station 3.

anticipated from the nature of component I as a "biomass" component, the trends in values for component I and the record of total plant carbon were similar (see Fig. 3).

The dominant diatom in component II was *Ch. radicans*, which is also a temperate upwelling species, but one which did not contribute importantly to component I. Sargent and Walker (1948), in their survey offshore of our study area, found that *Ch. radicans* was abundant in samples wherever diatoms were numerous, whereas a second group, including *Chaetoceros debilis* (which was important in our component I), was

restricted to samples that apparently corresponded to foci of very recent, intense upwelling. For this reason, it is believed that there are at least two floristic phases of the upwelling diatom assemblage (Smayda, 1963).

The remaining diatom in the core of component II was *E. zoodiacus*, a south temperate species. The two coccolithophorids in the core of this component, *Emiliania huxleyi* and *C. leptoporus,* are both cosmopolitan species; though of the two, *E. huxleyi* has a somewhat broader range (extending into colder water) and tends to be much more abundant (McIntyre and Be, 1967).

In component II, as in I, there was general positive correlation among stations. All stations showed a peak around weeks 8–11 (there was a simultaneous peak in component I); and at stations 2 and 3 there were spikes at weeks 16 and 15 respectively. The event at week 20 was evident in component II only as a peak at station 3; the event at weeks 1–4 appeared as a minimum at station 3.

Except for a peak in week 20 for all three stations, there was not marked agreement between stations for component III, which was dominated by *G. polyedra.* At stations 1 and 2 there was a maximum at week 14–15, but at station 3 week 15 was a minimum. There was a spike at week 10 at stations 2 and 3, but at station 1 the period from weeks 5–11 was marked by a sustained minimum in component III. At stations 2 and 3 there were depressions in component III in week 6 and week 8.

No coherent spatial or temporal pattern was evident for component IV.

e. Taxonomic patterns in the phytoplankton assemblages. The correlation coefficients of each of the list of the 114 taxa (which were present in at least 10% of the observations) with the scores of each of the first 4 phytoplankton principal components are given in Table 1. Trivially, the correlations for those 25 taxa which were involved in the principal component analysis will recapitulate the eigenvectors to a scale factor dependent on the associated eigenvalue. The correlations for the remaining 89 taxa, however, are new information which will bear on the taxonomic composition of the assemblages identified initially on the basis of the principal components.

The 114 taxa consisted of 34 centric diatoms (29.8%), 19 pennate diatoms (16.7%), 50 dinoflagellates (43.9%), 5 coccolithophorids (4.4%), 4 flagellates (3.5%) and 2 silicoflagellates (1.8%). The relation between these groupings and the phytoplankton principal components is shown in Table 3, where each taxon is located in a contingency table according to the number of the principal component with which it had the correlation of greatest absolute value, stratified by sign of the correlation.

The distribution of associations is markedly nonrandom. Disproportionate numbers of taxa are correlated most strongly, with specific signs, with certain of the principal components (I+, II+, III+, IV-). The prevalence of positive signs for the correlations with the first 3 components indicates that the periods of abundance for the bulk of the 114 taxa were at times when one of these three phytoplankton components was abundant, giving greater credence to the biological reality of the components.

Table 3. Contingency table relating the taxonomic grouping to the number of the phytoplankton principal component (I through IV) with which the taxon had the correlation with the highest absolute magnitude, broken down by sign of the correlation, for all 114 taxa.

		Centric diatom	Pennate diatom	Dinoflagellate	Coccolithophorid	Flagellate	Silicoflagellate
I	[−]	1	2	7		1	1
	[+]	15	6	17	1		
II	[−]	1		1	2		
	[+]	9	3	4	1		
III	[−]	2		1			
	[+]	1	1	14	1	1	1
IV	[−]	5	5	4			
	[+]		1	3		2	

Furthermore, even with the left marginal of the contingency table fixed, the distribution is significantly nonrandom. Using the log-linear method for this sparse table (Bishop *et al.*, 1975), the statistical interaction between taxon group and principal component association could arise by chance only at the $p \sim 0.01$ level.

We note that subsets of both groups of diatoms, and the dinoflagellates, tend to be associated positively with component I, in ratios not dissimilar from their total representation. Dinoflagellates, by contrast, are under-represented in the taxa associated positively with component II, though the ratios of centric to pennate diatoms are not far from expected. Dinoflagellates are overwhelming in the set associated positively with component III. Diatoms, especially pennate diatoms, are somewhat over-represented in the taxa associated negatively with component IV. The patterns reinforce our preliminary interpretation of component I as a generalized upwelling bloom, component II as a second, distinct phase of an upwelling diatom bloom, and component III as a dinoflagellate assemblage (which we would expect, therefore, to be associated with conditions of stronger stratification).

f. Canonical variates. The eigenvectors which transform the principal component scores of the 25 taxa and the values of the 13 original environmental variables into the four floristic and four environmental canonical variates are listed, in arbitrarily scaled form, in Table 4. Here, for convenience, we designate those elements which make up the largest half, in absolute value, within a vector, as the core of that canonical variate, and these are printed in bold type.

By Bartlett's test, the first three canonical correlations are significant ($p < 0.05$), and the fourth is not. Altogether, the first four canonical variates based on the

Table 4. Eigenvectors defining the canonical variates, scaled so that the largest element of each is 1.0 in absolute magnitude. Elements of absolute value greater than 0.5 are in bold type.

	Canonical variate pair			
	I	II	III	IV
Phytoplankton component:				
I	**1.000**	−.165	−.171	**−.753**
II	−.096	.388	**1.000**	−.356
III	−.096	**1.000**	−.477	−.438
IV	**.663**	.459	.171	**1.000**
Environmental variable:				
Pigment layer depth	**−.918**	**.546**	−.124	.250
Temperature (surface)	**−.781**	**1.000**	−.296	−.193
Temperature (pigment layer bottom)	.082	**.740**	.247	**−.796**
Salinity (surface)	.000	−.039	.086	−.239
Salinity (pigment layer bottom)	**.644**	.234	−.235	−.318
Sigma t (surface)	−.493	.416	−.037	**.557**
Sigma t (pigment layer bottom)	**1.000**	−.312	.296	**−1.000**
Nitrate (surface)	−.137	.078	−.049	**−.546**
Nitrate (pigment layer bottom)	.411	.078	**1.000**	−.102
Phosphate (surface)	.192	−.169	.049	−.023
Phosphate (pigment layer bottom)	−.247	.364	−.370	.375
Silicate (surface)	.041	.013	−.321	−.011
Silicate (pigment layer bottom)	**−.932**	**−.779**	**−.531**	**−.625**
Canonical correlation coefficient	.88	.75	.63	.44
Cumulative redundancy	.20	.34	.43	.48

environmental variables account for slightly less than half the variance in the first four components of the phytoplankton abundances.

g. Environmental conditions and floristic associations. The first pair of canonical variates shows a weighted sum of phytoplankton components I and IV (with I more heavily weighted) correlating positively with the following set of circumstances: shallow pigment layer; low surface temperature; and, at the pigment layer depth, high salinity, high density, and low silicate. Except for the dearth of silicate, these clearly correspond to upwelling conditions.

Phytoplankton component IV is involved positively with component I in canonical pair I, which suggests a degree of co-occurrence of the two plankton assemblages during times of upwelling. Phytoplankton component IV is also strongly involved with component I in canonical pair IV, where, however, the two phytoplankton components have opposite signs, suggesting that the environmental conditions defined by the environmental variables in canonical variate IV favor one of the plankton assemblages while depressing the other. Conditions which would predict high values for phytoplank-

ton component IV and low values for phytoplankton component I are: high density and low nitrate at the surface, and low temperature, low density and low silicate at the pigment layer depth, generally suggestive of midsummer conditions.

The second pair of canonical variates shows component III dominating the phytoplankton contribution, correlated with the following environmental circumstances: shallow pigment layer; low silicate at the pigment layer depth; and high temperatures both at the surface and the pigment layer depth. This suggests a late season nonupwelling situation, consistent with our conjecture that component III, dominated by *G. polyedra*, was not an upwelling assemblage.

The third pair of canonical variates shows component II dominating the phytoplankton contribution, while the environmental variate is dominated by a high concentration of nitrate relative to silicate at the pigment layer depth. The high nitrate bespeaks upwelling, consistent with our interpretation of component II as an upwelling assemblage, but (as with canonical pair I), the meaning of the relative depletion of silicate at the pigment layer depth is not clear. It is interesting that the two independent upwelling assemblages resolved by the principal components were individually correlated with different indices of upwelling, one marked by a temperature and salinity signal, the other by the availability of nitrate.

h. Involvement of other taxa in the pattern of correlation. The correlation coefficients of each of the 114 taxa with the scores of each of the 4 environmental canonical variates is given in Table 1. As before, the correlations involving taxa that were elements of the principal components that were then submitted to the canonical correlation analysis are a foregone conclusion, whereas the correlations for the remaining 89 can reveal the extent to which other taxa participated in the pattern suggested by the canonical correlation analysis.

In Table 5, the relations between phytoplankton assemblage affinities and environmental conditions, for the 89 taxa that were not included in the principal component analysis, are displayed in contingency table form. Each taxon is assigned to one cell of the table, according to which environmental canonical variate and which phytoplankton component it correlated with most strongly, stratified by sign of the correlation.

The distribution of associations is markedly nonrandom. A test for interaction between the two classifiers (correlation with phytoplankton component and correlation with environmental canonical variates) is consistent with the null hypothesis of chance association only at a $p \ll 0.001$ level. The associations confirm that the pattern of canonical correlation extends to the taxa that were not included in the multivariate analysis.

Five cells, in the contingency table of Table 5, account for the correlation patterns of 71% of the taxa. Twenty one taxa showed their strongest correlations as positive with phytoplankton component I and positive with environmental canonical variate I. These, accordingly, are a taxonomic extension of the generalized upwelling assemblage

Table 5. Contingency table, for the 89 taxa that were not submitted to the principal component analysis, relating the number of the phytoplankton principal component (I through IV, signed according to the sign of the correlation) with which the taxon had the correlation of greatest absolute magnitude, to the number of the physical canonical variate (I through IV, signed according to the sign of the correlation) with which it had the correlation of greatest absolute magnitude. The counts shown are the numbers of taxa in each category.

	Physical canonical variate							
	I−	I+	II−	II+	III−	III+	IV−	IV+
I−	7		1	2	1	1		
I+		21		2			2	
II−		2	1					
II+	1	1		2		8	1	
III−		1	1					1
III+	1			15				
IV−	12						2	
IV+		2		1				

associated with the temperature-density signal. They included numbers of centric diatoms, pennate diatoms and dinoflagellates, in proportions similar to their representation in the total pool of taxa, and these spanned the gamut of abundant and rare taxa (in terms of their frequency of occurrence in this study).

Fifteen taxa showed their strongest correlations as positive with phytoplankton component III and positive with environmental canonical variate II. These are a taxonomic extension of the *G. polyedra* warm water assemblage. They included only 1 diatom taxon (*Rhizosolenia alata*), the flagellate category "monads ($\sim 5\mu$)", and 1 silicoflagellate (*Distephanus speculum*), the remaining 12 being dinoflagellate taxa, about half of which were very rare in our set of samples.

Eight taxa showed their strongest correlations as positive with phytoplankton component III and positive with environmental canonical variate II. These are a taxonomic extension of the *Chaetoceros radicans* upwelling assemblage which correlated with a nitrate signal. With the exception of one dinoflagellate (*Gonyaulax digitale*) they were all diatoms (2 pennate, 5 centric): *Chaetoceros didymus, Ch. affinis, Asterionella japonica, Cerataulina bergonii, Thalassionema nitzschioides, Rhizosolenia hebetata*, and *Rh. setigera*. These taxa were moderately rare to rare in our samples.

Twelve taxa showed their strongest correlations as negative with phytoplankton component IV and negative with environmental canonical variate I. These are a complement of the component IV upwelling assemblage which correlated positively in canonical pair I. In other words this was an assemblage that probably was relatively

Table 6. Within-station correlations between scores of environmental canonical variates and scores of phytoplankton principal components that were highly weighted in the eigenvectors defining the associated phytoplankton canonical variate.

Environmental canonical variate	Phytoplankton component	Station 1	2	3
I	I	.81	.76	.69
II	III	.57	.70	.69
III	II	.67	.62	.49
IV	IV	.59	−.09	.30
IV	I	−.29	−.32	−.14
I	IV	−.11	.46	.71

abundant at times when the general upwelling assemblage was rare, and water was warm and of low density (it is not clear how to interpret phytoplankton component IV itself, since this included one eigenvector element with a very substantial negative value). These taxa forming a complement to the component IV assemblage were predominantly diatoms (5 pennate, 5 centric) and 2 dinoflagellates, all of which were rare to very rare in our set of samples. These were similar in their associations to the seven taxa which showed their strongest correlations as negative with phytoplankton component I and negative with environmental canonical variate I. This group was predominantly dinoflagellates (5), with 1 silicoflagellate and 1 centric diatom, all of which were very rare in our samples.

i. Correlation over time and space. The principal component analysis, and canonical correlation analysis, as we employed them, did not distinguish among stations, nor did they take account of the time sequence of the observations. We now inquire whether the canonical correlations were based on variability attributable to consistent differences between stations (these were at different distances offshore), or whether they were based on changing conditions experienced at all the stations, and if the latter, what was the degree of simultaneity.

In Table 6 we show the correlation coefficients between the four environmental canonical variates and the phytoplankton principal components that made up the core of the associated floristic canonical variate, stratified by station, where each correlation coefficient, therefore, is based on 21 pairs of observations. For the most part, we find strong correlations, with the expected signs, at all three stations, indicating that the correlations were based on changing conditions, not differences between stations. The few combinations that did not maintain a consistent correlation over the three stations involved phytoplankton component IV, which we have noted, on other grounds, did not manifest a coherent spatial or temporal pattern, and which did not yield readily to interpretation.

In order to quantify the temporal persistence of the phytoplankton assemblages (this was treated visually in Fig. 1), we computed Euclidean distance (based on the 25 taxa submitted to the principal component analysis) for all pairs of samples, at each station. Then the mean Euclidean distance for each lag (number of weeks separating the observations), at each station, was graphed against the magnitude of the lag (Fig. 2). The mean distance increased approximately linearly with the time separation for 5 or 6 weeks. The time for a 50% change in the mean Euclidean distance, obtained from linear regression over the interval that appeared linear, was 2–3 weeks. This degree of serial correlation in the data, of course, compromises the attempts to apply conventional significance tests to our correlation analyses, though it constitutes a major observation in its own right.

j. Other indices. More usual indices of phytoplankton crop (measured as total weight carbon), upwelling (measured as depth to the 1 μM nitrate level), and stratification (measured as the gradient in sigma *t* over the water column) generally agree with our interpretation of the canonical correlations and the serial correlation in phytoplankton community composition. Values of these indices, at each station, over time, are graphed in Figure 3.

Gradual seasonal changes in the physical parameters over the duration of the 21-week study are reflected in the general upward trend with time for both the intensity of stratification and the depth to the nitracline, indicating a progressive stratification and depletion of surface nutrients. The longer term changes were punctuated by sharp minima in stratification, most notable at week 6, evident also at week 11, week 20, and possibly week 1.

The first 3 of these demarcations were associated with sounding of the nitracline, so even though they indicate a breakdown of stratification near the surface, they do not correspond to "upwelling" events, nor are they fully accounted for simply by strong wind-mixing. These events probably marked changes in water parcels passing the stations. The late season disturbance of stratification (in week 20), during which the stratification remained high compared to the earlier portion of the season, did coincide with a slight shoaling of the nitracline at the most offshore station, but was not associated with a deflection of the trend for depth of nitracline at the other stations. This event was marked by the most extensive development of a bloom of the phytoplankton assemblage which was dominated by dinoflagellates. The prior three demarcations coincided with distinct depressions in phytoplankton abundance.

The minimum in stratification at week 6 separates the first two diatom blooms. Phytoplankton component II was not stongly represented in the first bloom, but did appear afterward. The first high-nutrient episode (weeks 1–4) was associated with higher salinity at the pigment layer depth compared to the second high nutrient episode (weeks 8–11) suggesting upwelled water of more southerly origin for the first (Reid *et al.*, 1958).

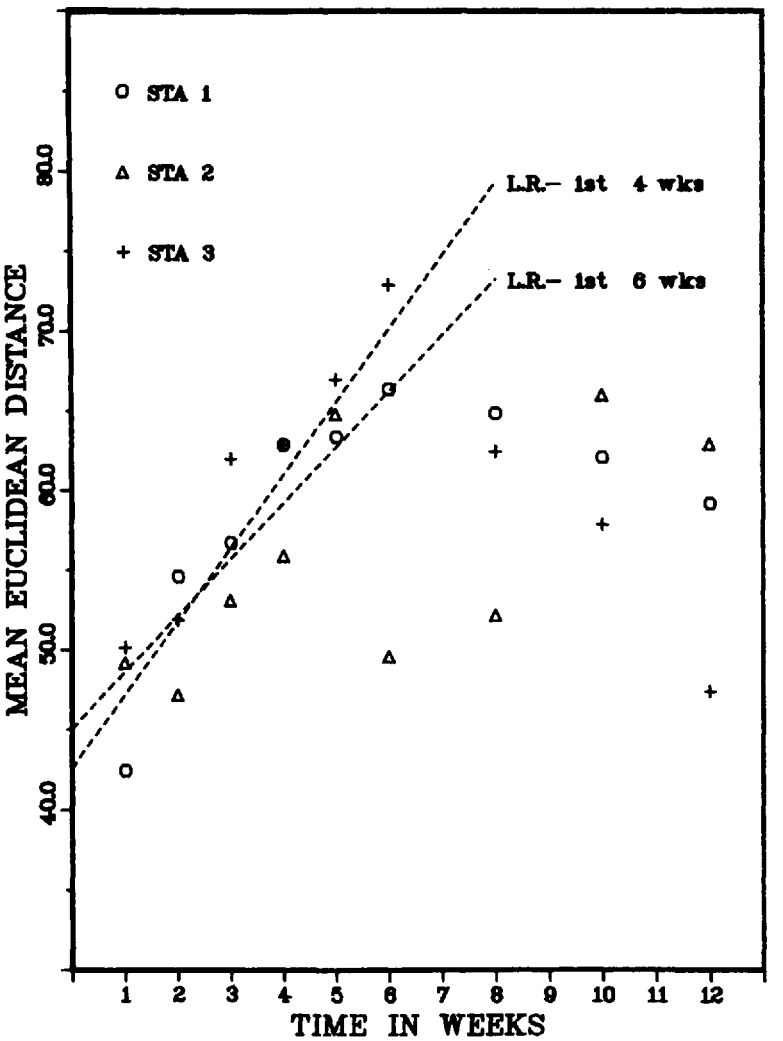

Figure 2. Mean Euclidean distance of the phytoplankton composition of sample pairs as a function of the time separating the samples, for the sets of samples at each station. The points for all stations were used in computing the linear regressions.

4. Discussion

The canonical correlation analysis allowed us to associate causally sensible complexes of physical and chemical conditions with the waxing and waning of the major phytoplankton assemblages observed during the course of the 21-week survey. Of the four plankton assemblages identified, two were quite distinct with respect to the conditions which favored their abundances, and the remaining pair co-occurred under

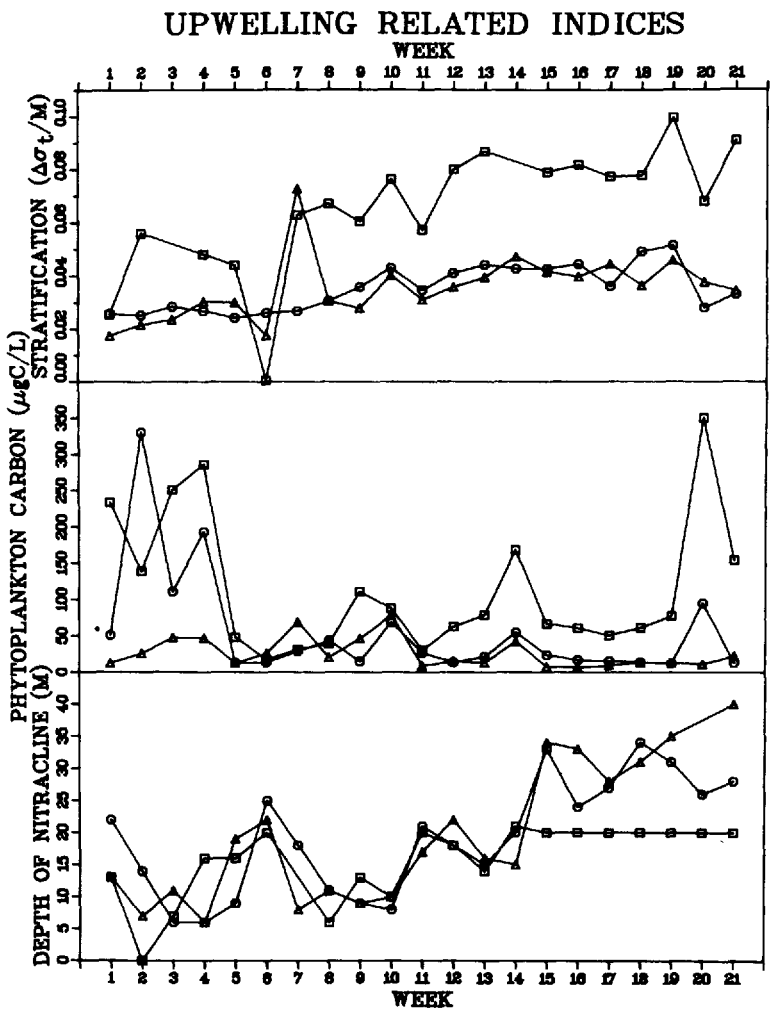

Figure 3. Water column stratification, phytoplankton carbon, and depth to the 1 μM nitrate level, plotted for each observation date at each station. Water depth was 21 m at station 1, truncating the depth-to-nitracline values there as nitrate became depleted toward the end of the study period. Roughly, the phytoplankton carbon tends to be high when depth of the nitracline is small and stratification is relatively intense. Station lables: □ station 1; △ station 2; ○ station 3.

one identified set of environmental circumstances, whereas they were discriminated by another defined set of circumstances.

a. Consistency of phytoplankton assemblages. A number of previous studies have described phytoplankton communities in the southern California Current system, and

three of these (Reid *et al.*, 1978; Estrada and Blasco, 1979; Cullen *et al.*, 1982) employed principal component analysis to resolve the taxon assemblages. A few persuasive generalizations emerge from comparing results among these studies, but they are rather broad and impressionistic.

The studies concur in the distinctness of major dinoflagellate blooms and major diatom blooms, and the latter are associated with conditions more suggestive of "upwelling." There is agreement that more than one sort of diatom bloom may be in evidence during the course of a study of relatively short duration, and these respective assemblages can be associated with detectable differences in the water mass, e.g.: the "foci" of upwelling, vs. "old" upwelled water described by Sargent and Walker (1948), or the distinction between temperature- salinity- and nitrate-characterized "upwelling" observed in our study and by Estrada and Blasco (1979).

Similarities with respect to the details of the species composition of the different assemblages are tantalizing, but not uniformly compelling. Thus, in one cruise (Mescal I) Estrada and Blasco observed a dinoflagellate bloom (their component I), dominated by *G. polyedra*, and associated with conditions of low salinity and high nutrients, reminiscent of our component III. Of the 17 taxa which we categorized as correlating with component III and environmental canonical variate II, 11 are not to be found in the list of 60 taxa considered by Estrada and Blasco, 5 do appear among the taxa with large values in the eigenvector defining their component, and 1 is among the taxa that had low values in their component.

In another year (Mescal II) these authors found a second and quite different dinoflagellate assemblage, associated with low salinity, but with no appreciable overlap with our component III. In that same cruise, Estrada and Blasco observed an "upwelling" diatom assemblage which agreed with our group of taxa correlating positively with our phytoplankton component I and environmental canonical variate I to the extent that *Rhizosolenia delicatula, Rh. stolterfothii, Leptocylindrus danicus* and *Ceratium divaricatum* (=*dens*) were among the taxa heavily weighted in their eigenvector; but there were two dinoflagellates in our assemblage which had negative weightings in their eigenvector, 1 dinoflagellate and 1 diatom which had negligible weightings in their eigenvector, and 24 taxa we identified in this assemblage which were not among the 60 considered by Estrada and Blasco.

The second principle component resolved by Estrada and Blasco for Mescal I, though it was a bloom associated with a nitrate signal (like our component II), had essentially no floristic equivalent among our phytoplankton components.

The 3 diatom assemblages identified by Sargent and Walker, on the basis of graphically determined spatial patterns, do overlap to an extent with the list of taxa considered in our analysis, but agree only partially with assemblages we resolved. Sargent and Walker found that *Chaetoceros radicans* and *Nitzschia longissima* were among those taxa present wherever diatoms were abundant, but in our study these were allied more closely with the more restricted phytoplankton component II. The

group that Sargent and Walker assigned to foci of upwelling included *Chaetoceros debilis*, which was at the core of our generalized upwelling component (I), and *Ch. didymus* which indeed correlated most strongly with our phytoplankton component II. The group Sargent and Walker described as minor species which were only present when most diatoms were rare or absent included 4 species from our study (*Rhizosolenia alata, Rh. hebetata, Chaetoceros atlanticus,* and *Ch. messanensis)* which, were indeed relatively rare in our study, and had in common negative (but not strong) correlations with our component I and positive (but not strong, except for *Rh. hebetata*) correlations with our component II. The strongest correlation of the set was a positive correlation of *Rh. alata* with our dinoflagellate component III; and further this species, like others in this dinoflagellate component, correlated moderately positively with our environmental canonical variate II.

Reid *et al.* (1978) observed a dinoflagellate dominated component, which was abundant at some stations in the chlorophyll maximum layer, that had at its core 6 taxa, of which 3 were included in our study. Two of these three (*Ceratium kofoidi* and *Prorocentrum* sp "C") were clearly identified with our dinoflagellate assemblage that correlated with phytoplankton component III and with environmental canonical variate II). The third, *Eucampia zoodiacus*, despite affinities with our upwelling assemblage I, did correlate strongly with environmental canonical variate II (like the dinoflagellate assemblage) and did exhibit a moderate correlation with the dinoflagellate assemblage, component III.

Reid *et al.* (1978) resolved a second component, diatom dominated, which corresponded more to horizontal than to vertical variability in the samples. Of the six species at the core of this component, five were represented in the present study: three (*Skeletonema costatum, Hemiaulus sinensis,* and *Leptocylindrus danicus*) clearly were associated with the generalized upwelling assemblage, correlating with phytoplankton component I and environmental canonical variate I, one (*Thalassiothrix frauenfeldii*) showed essentially the reverse of this pattern, and one (*Rhizosolenia fragilissima*) showed broad associations with several of the canonical variates.

Cullen *et al.* (1982) studied a synoptic set of samples from a comparatively small area (a grid approximately 40 km longshore and 15 km cross-shelf), so the nature of the variability in the samples is somewhat different from that in the studies which included several bloom events. This study resolved 2 principal components among its highest variance taxa, and another 2 assemblages (rotated principal components) for a set of less variable taxa. The observed pattern was stronger in the vertical dimension (surface compared to chlorophyll maximum layer) than horizontally. Of the four assemblages, three do not have obvious parallels among the components in our study (either for lack of substantial overlap in taxa, or for lack of similarity in the correlation patterns of the taxa that are in common). One assemblage, their factor B for the "low variance" taxa, has three heavily weighted taxa in common with our study: the dinoflagellates *Ceratium furca, Prorocentrum micans* and *Prorocentrum gracile,*

which are similar in all having strong affinities with our generalized upwelling assemblage and moderate affinities with our warm water dinoflagellate assemblage.

At least as striking as these points of similarity among studies, are the overwhelming qualitative differences owing to species that are important in one study but not recorded at all in the other. Even accounting for differences in collection (especially depth), vagaries of identification, and differences in data treatment (eg., Estrada and Blasco carry out their principal component analysis on a correlation matrix, whereas we, for reasons stated in Reid *et al.* (1978), operate on the covariance matrix), the differences in detail between the assemblages reported in this handful of studies suggest that the sample space of phytoplankton assemblages off Southern California involves a far richer variety of assemblages than has been adequately characterized. Further, it appears from this comparison, and from our observations regarding serial correlation, that the basic sampling unit is the "bloom event" rather than the tow or station "sample," with the consequence that an adequate statistical evaluation will require an enterprise of staggering scale.

b. Canonical correlation with species abundances. The fact that our analysis resolved differences in the environmental conditions associated with the plankton assemblages prompts brief reconsideration of the canonical correlation analysis of the log transformed abundances of the 25 individual taxa and the 13 environmental variables. The eigenvectors transforming the 25 taxon abundances to canonical variates showed large weightings for only a few taxa each; generally one to three elements in each were in the range 1.0 to 0.66 times the largest. We may now take this to imply that the analysis actually was resolving sets of environmental conditions that correlated strongly with individual groups, of one to three taxa each, and which were uncorrelated amongst themselves.

The redundancy levels in the analysis on the individual taxa were inauspicious, in that no single correlation accounted for more than 9% of the total variance in the phytoplankton abundances (the first two accounted for 5% and 0.5% respectively), and the cumulative redundancy attributable to all thirteen canonical correlations was 34%. This corroborates the impression that the canonical correlation between the environmental variables and the individual taxon abundances was emphasing aspects of pattern in which the taxa tended to behave independently or in small groups, as contrasted with correlations across major assemblages.

With the present data set, it would be presumptious to interpret the list of environmental canonical variates as the "niche centers" of the respective taxa or groups of two or three taxa, for the data cannot provide this degree of resolution. We saw that our data set really encompassed just a few events. If a considerably more extensive data set revealed a similar pattern, the biological interpretation of the canonical correlations with individual taxa would be warranted.

c. Physical structure and scale in the coastal waters. The predominant water motions on the shelf off the southern California coast are low-frequency longshore currents. Mean longshore current velocities at frequencies less than one/day are generally in the range 1–3 cm/sec, varying over depth in spring and summer, and directed either north, or more usually south (Winant and Bratkovich, 1981). There is a characteristic structure to these currents (Hendricks, 1979; Winant, 1983). Furthermore, the structure is of a sort that could organize the appearance of phytoplankton species assemblages as they are carried past a point of observation on the shelf.

If currents are measured along an isobath at different locations on the shelf, the correlation between the low-frequency currents declines with the distance separating the stations. Hendricks (1979) observed that the currents are highly correlated at a 15 km separation; Winant (1983) found that the correlations decline to 50% at a longshore separation of about 25 km. These observations suggest that the water is moving along the shelf as identifiable parcels (eddies), each with a characteristic energy in its low-frequency current components.

There is evidence of persistence of phytoplankton blooms on time or space scales commensurate with those of the water parcels. Tont (1976, 1981) analyzed records of diatoms, collected daily off the Scripps pier during the period 1920–1939 by the late W.E. Allen. Comparison of diatom abundance with sea level, surface water temperature and salinity records suggests that episodes of diatom abundance were associated with "upwelling" events. These episodes were of various time durations, typically one to three weeks, similar to the time scales of persistence of diatom-dominated phytoplankton assemblages in our present study.

Dinoflagellate blooms of various time and length scales have also been recorded in the area, though synoptic studies of the phytoplankton species assemblages are rare. A few of the blooms, such as that reported by Torrey (1902) appear to have had length scales of greater than 100 km. More frequently, the blooms are more local in extent (Sweeney, 1975). Two to three weeks seems to be a typical time scale for the local dinoflagellate blooms.

Two recent studies of the spatial extent of coastal phytoplankton species assemblages (Reid *et al.*, 1978; Cullen *et al.*, 1982) showed appreciable longshore variation in community composition over distances of a few tens of kilometers, and cross-shelf variation over much smaller distances. The latter study had sufficient spatial resolution to reveal distinct "boundaries" between assemblages. Phytoplankton studies have not yet been extensive enough, or sufficiently synoptic, to reveal fully the characteristic length scale of species assemblages along the shelf. Satellite images of the Southern California Bight, with respect to both surface chlorophyll distributions (Smith and Baker, 1982) and surface temperature (Lasker *et al.*, 1981), show additional complexities in the circulation, with eddies and jets moving offshore, and intrusions of offshore water onto the shelf.

Thus the coherence and structure of the currents may serve as causal factors which

influence the structure of the phytoplankton communities which they carry. If the longshore currents lose coherence at spatial scales of the order of 25 km, then this may be related to the length scale of the phytoplankton species assemblage eruptions along the shelf (and both may be related to the longshore time and length scales of upwelling events, revealed in the temperature records, for example).

Some rough approximations of the longshore length scale of the eruptions can be arrived at by converting time scales (as in the present study) to length scales, using the low-frequency current velocities recorded from current meters. Winant and Bratkovich (1981) found the longshore low-frequency currents varied with depth in the water column, with depth of the bottom, and with season. Typical velocities at 10 m depth may be 1 to 2 cm/sec in spring and summer (contrasting with considerably greater velocities in winter).

The 25 km length scale and 1 to 2 cm/sec velocity of the low-frequency longshore current, suggest that a water parcel would pass a given station in 10 to 20 days, consistent with the observation that eruptions of major species assemblages in our study were of 1 to 4 weeks duration. This time span is also typical of the duration of upwelling events (Tont, 1976). Thus, this time scale does not allow us to differentiate between the time of passage of a water parcel and an "event." There may be physical reasons for the congruence of these time scales, if both are causally related to meteorological phenomena, notably local winds.

d. The role of history in determining phytoplankton assemblages. While the cause of diatom blooms clearly is "upwelling" of nutrients, and the dinoflagellate eruptions are perhaps less directly tied to nutrient enrichment, the species inoculum of the enriched water is not necessarily uniform at all bloom locations along the coast of the Southern California Bight. We presume that the inoculum, which seeds enriched water to initiate a bloom population, is transported primarily with the longshore currents, and at slower velocities with the cross-shelf currents.

In order to explain the implications of this speculation more fully, we can simply ask whether each water parcel would be expected to transport the same species assemblage. The answer is probably not, as each would experience different events as it moved along the shelf. Upwelling at headlands is typical of this stretch of coastline (Armstrong *et al.*, 1967) and is so limited in duration that one parcel might be enriched while the adjacent parcels might not. Vertically migrating herbivores could be transported beneath one parcel and not another, as the currents at different depths often are not identical—at times they are even in quite disparate directions (Winant and Bratkovich, 1981). Bottom scouring by bores associated with internal tides (Winant, 1974) might differentially inoculate the upper waters with diatom resting spores or dinoflagellate cysts resuspended from the sediments.

Thus, if the low-frequency currents account for the water moving along the shelf as discrete parcels, there is reason to expect that each parcel may contain, as a result of its

unique history, a distinct assemblage of phytoplankton. The spatial structure of the phytoplankton assemblages may reflect the physical structure of the water parcels—analogous, in part, to the older idea of water mass indicator species (see Balech, 1960; Kimor *et al.*, 1978).

Purely temporal "events" such as upwelling, may result primarily in the increased growth and biomass of species which chanced to be transported to the site of the upwelling as inoculum. There is, as yet, ambiguity in resolving the respective roles of inoculum composition and environmental conditions in determining details of the phytoplankton community structure. For example, Dunstan and Menzel (1971) observed the blooming of essentially all the dominant species present in an inoculum of coastal phytoplankton, upon enrichment in the laboratory. Nevertheless, diatoms should be favored by turbulence and nutrient enrichment to a greater extent than dinoflagellates (Margalef, 1978), but these relative dynamic processes operate against a background of the qualitative effect of the composition of the seed inoculum in a local situation.

Certainly, gross changes in the dominant species of a mixed assemblage in the laboratory can be brought about by altering the nutrient regime either in terms of constant nutrient concentration (Thomas *et al.*, 1980) or in terms of the temporal pattern of nutrient availability (Turpin and Harrison, 1979). And, of course, it must be true that a species cannot participate in a bloom if it is not present.

e. Community organization. The role of spatial and temporal variability in determining the dynamics and composition of plankton communities may be represented according to two opposing extreme hypotheses. One, an equilibrium view, treats the gradients of environmental conditions as essentially accessible to all species. The gradients simply define a quantitative differentiation of a resource spectrum. Coexistence of competitors, then, would be thought to depend upon quantitative conditions on the extent of overlap of resource utilization. This hypothesis, as it applies to plankton, has recently been reviewed by Allen (1977).

The second view, a nonequilibrium model, treats the separation of species in resource time-space as virtual. Observed overlap in occurrence is interpreted merely as a kind of spillover from the respective species' centers of abundance—a coincidental phenomenon, contingent upon spatial and temporal transients. In this model, the persistence of the community, as we observe it, depends very much on scale. Locally, competitive exclusion might be the rule governing the dynamics; on a medium scale transient dynamics would predominate; on a larger scale yet, a pattern of regularity in the community's characteristic gestalt may appear if the observations span a sufficient number of foci, in time and space, of the different species abundances, but the community composition will be governed as much by the distributional statistics of the environmental correlates of these foci of abundance as by the purely interactive dynamics between species.

Both points of view recognize the reality of environmental change and spatial heterogeneity. The essential difference between the two models is that the equilibrium view suggests that the community's response to environmental driving may be represented as a moving equilibrium, so that the community composition at any moment in any place is largely determined by the interplay of intrinsic biological properties of the species, as modulated by the local conditions; whereas the nonequilibrium view suggests that the community, at any given moment in any given place, is far from biological equilibrium, even with respect to the current state of the environment, and that the community composition is importantly influenced by past environmental conditions and spatially distant events that are not necessarily reconstructable from information about the present, local state of the environment.

Our discussion of possible physical spatial structuring of the water bearing the phytoplankton communities off the southern California coast implies a nonequilibrium interpretation at the level of resolution of species composition observed at a fixed station. From the perspective of a hypothetical time sequence of observations within a single water parcel, during the course of its journey, the qualitative effects of presence and absence of taxa, owing presumably to accidents of history, would still imply a nonequilibrium interpretation at the level of resolution of particular species abundances; but at the level of resolution of relative abundances of gross taxonomic groups (eg., "upwelling diatoms" vs. "red tide dinoflagellates") in this parcel, an equilibrium interpretation would be consistent with the observed correlations with environmental variables and with the pattern of very broad (but not detailed) regularities in taxonomic composition of blooms. Neither the present study, nor any of the other analyses reviewed here, suffice to indicate how large a spatial and temporal scale of observation would be necessary to give an appearance of equilibrium dynamics in the phytoplankton species dynamics off the California coast.

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