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Variability of diatom species populations: From days to years

by Sargun A. Tont[1]

ABSTRACT

Based on over 300,000 individual measurements, temporal and spatial variations in diatom abundances and related atmospheric and oceanic variables have been investigated for two locations near the coast of southern California. Time scale of periods investigated ranged from days to 10 years; variability over centuries can be reconstructed from climate records. The results of principal component analysis based on weekly averages indicated that eigenvectors at Scripps and Pt. Hueneme piers, nearly 200 km apart, were similar; removal of seasonal cycles (by calculating anomalies) did not significantly alter these eigenvectors. Principal components derived from matrices based on weekly averages of 20, 23, and 65 species of diatoms have significant inverse correlations with sea-surface temperature anomalies. Based on 3-month (seasonal) averages, the abundance of several species of diatoms respond to climatic fluctuations as defined by changes in sea-surface temperature, air temperature, sea level and alongshore wind stress.

1. Introduction

Earlier studies based on a segment of the time series used in this study found that part of the variability of total diatom populations off the coast of southern California was due to a combination of local upwelling and climate-induced changes in the circulation patterns of major water masses (Tont, 1976; Tont and Platt, 1979; Tont, 1981). In this paper, I report the results of further studies which are based on the analysis of the individual species of diatoms sampled by the late Prof. W. E. Allen and his colleagues at two locations near the coast of southern California (Fig. 1). Although several hypotheses can be tested using this data set (see below), the major focus in this paper is on long-period (climatic) changes and their possible effects on individual species of diatoms.

Compared to terrestrial studies, literature dealing with the climatic component of long-term fluctuations in marine populations have been few in number (Tont and Delistraty, 1980). Recently, however, there has been a growth of such studies in which effects of climate either directly or indirectly have been implicated in biological changes. Longhurst *et al.* (1972) and Glower *et al.* (1974) attributed the instability of oceanic populations to natural, environmental, and anthropogenic factors. Climatic

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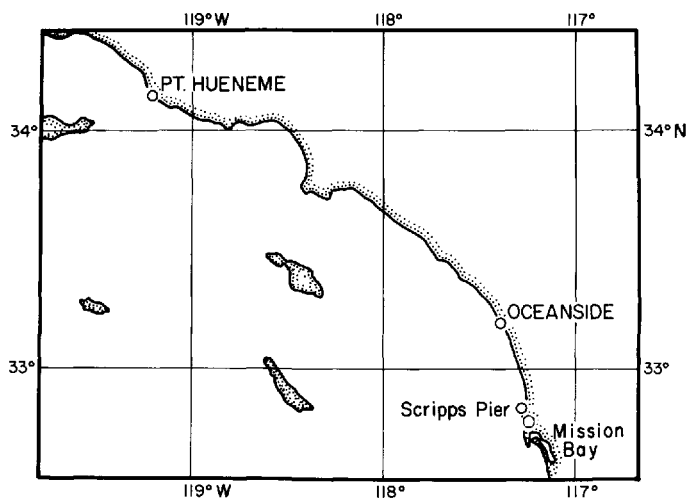
Figure 1. Locations discussed in the text.

variables figure prominently in the works of Lasker (1978), and Johnson and Seckel (1977). Several investigators have discussed the relationship between climatic (density independent) and biological (density dependent) variability in the marine environment (Walford, 1931; Sette, 1960; Cushing, 1975; Cushing and Dickson, 1976; Parrish and MacCall, 1978). A major conference instigated by the onset of the 1957–1958 El Niño was one of the very first interdisciplinary examination of a major climatic event related to the marine environment (Sette and Isaacs, 1960). Smith and Eppley (1982) have shown that Scripps pier temperature anomalies, which are indicative of large-scale climatic changes, and day length can be used to hindcast primary production in the California Bight. An intensive analysis of the biological consequences of El Niño events which occur off the coast of South America can be found in Walsh (1978). The 1982–1983 El Niño, which occurred in both hemispheres of the Pacific Ocean, has been studied in more detail than any similar event of that kind (Barber and Chavez, 1983; Reid *et al.*, 1985; and Wooster and Fluharty, 1985).

It must be pointed out that these works differ in emphasis on the role of climate as a regulatory agent on marine populations. There is no clear-cut agreement as to what causes climatic fluctuations. Regardless of uncertainty about an 'ultimate' cause of climatic change, however, the mechanics of ocean-atmosphere coupling as a primary agent in climatic change is well understood. Understanding variability of biological populations is important not only for its intrinsic scientific value but also for practical applications. It is difficult, for example, to evaluate the impact of man-induced changes in the environment if we do not have a clear understanding of the natural variability of the environment. Such understanding may also help us in attempts to predict the temporal variations of biological populations.

2. Materials and methods

a. Data set. This study uses diatom counts from the 25,000 samples collected and processed by the late Prof. W. E. Allen and his colleagues. The original counts are deposited in the archives of the Scripps Institution of Oceanography, La Jolla, California, and a data report based on these records has been recently completed and is available on request (Tont, 1986). During 1920–1929, the surface samples were collected every day with a 2-gallon galvanized pail at the Scripps Pier and Pt. Hueneme Pier (Fig. 1). The samples then were filtered through a conical net (mesh size 50-100 μm), and counted. Starting in 1930, a settling method was instituted for samples collected at Scripps Pier where organisms were settled out of one liter of water and cells from a known fraction of sample were counted in a Sedgwich-Rafter counter. Although samples were taken daily, in the majority of cases only the weekly averages calculated by Allen were found; regrettably, part of the records had been misplaced or lost prior to this study. The most complete data set for 98 diatom species was for Scripps Pier (weekly averages for the period 1930–1939), followed by Pt. Hueneme (1930–1938). Weekly totals (all the species combined) are available for 1920–1939 for Scripps Pier and 1920–1938 for Pt. Hueneme Pier.

The diatom taxonomy used by Prof. Allen and his coworkers was checked by Carina Lange of the Scripps Institution of Oceanography. Among the abundant species (23 species account for over 95% of total counts) only one name change—*Asterionella japonica* Cleve to *Asterionella glacialis* Castracane—was necessary. Name changes at the genus and species levels were also made for the remaining species. Each species was identified by a four letter code to conserve space and to facilitate quick understanding of the presented material. The first two letters refer to genus and the last two letters to species; e.g., CHSO for *Chaetoceros socialis*. And the coding for species identified only at the genus level are represented by two last letters as OO; e.g., CHOO for *Chaetoceros* spp. The names of all 98 species identified at Scripps and Pt. Hueneme piers and their rankings both by abundance (based on total number of organisms for the period, the most abundant is ranked first) and frequency of occurrence (the number of times the species was observed) are shown in Table 1. There were 65 species common to both locations; species observed only at one site usually ranked low by either abundance or occurrence criteria. The ranking of species common to both sites shows some similarity, but species such as *Nitzschia longissima, Navicula* spp., *Pleurosigma* spp., *Licmophora abreviata* deviate from this rule. Unlike most of the other diatoms, these four species do not form chains (Venrick, pers. comm.) and thus would be less likely retained by the filtering method used at Pt. Hueneme as compared to the settling method used for Scripps samples.

Sea-surface temperature and salinity records (in Scripps archives) were obtained from daily bucket samples. The atmospheric and sea level data used were obtained from the National Oceanic and Atmospheric Administration, U.S. Dept. of Commerce, Washington D.C. Wind data were recorded at Lindberg Airport, San Diego,

Table 1. Ranking by abundance (RA) and occurrence (RO) of W.E. Allen's diatom collections taken at Scripps Pier (SIO) and Pt. Hueneme Pier (PTH), 1930–1938. Diatoms are coded according to genus (first two letters) and species (the last two letters) and are listed in alphabetical order; those identified only at genus level are placed at the end of that particular group, e.g., BAOO follows BAVA. Species when not present are designated by two hyphens.

	SIO		PTH		
CODE	RA	RO	RA	RO	
1 AEHP	--	--	49	50	*Asteromphalus heptactis* (Brebisson) Ralfs
2 AMOO	73	66	65	59	*Amphora* spp.
3 ASGL	10	16	17	18	*Asterionella glacialis* Castracane
4 ASTE	--	--	58	54	*Actinoptychus senarius* Ehrenberg
5 BADL	69	67	--	--	*Bacteriastrum delicatulum* Cleve
6 BAEL	62	63	--	--	*Bacteriastrum elongatum* Cleve
7 BASL	--	--	74	84	*Bacteriastrum solitarium* Mangin
8 BAVA	48	56	--	--	*Bacteriastrum varians* Lauder
9 BAOO	18	29	10	17	*Bacteriastrum* spp.
10 CCOO	--	--	85	83	*Cocconeis* spp.
11 CEPE	51	45	41	37	*Cerataulina pelagica* (Cleve) Hendey
12 CEOO	74	68	--	--	*Cerataulina* spp.
13 CHAF	15	25	12	21	*Chaetoceros affinis* Lauder
14 CHCI	--	--	36	43	*Chaetoceros concavicornis* Mangin
15 CHCN	21	32	11	29	*Chaetoceros constrictus* Gran
16 CHCO	4	13	9	8	*Chaetoceros compressus* Lauder
17 CHCS	19	30	7	15	*Chaetoceros costatus* Pavillard
18 CHCU	8	12	15	9	*Chaetoceros curvisetus* Cleve
19 CHDA	--	--	83	81	*Chaetoceros danicus* Cleve
20 CHDC	36	41	30	36	*Chaetoceros decipiens* Cleve
21 CHDE	7	10	1	4	*Chaetoceros debilis* Cleve
22 CHDI	16	28	14	16	*Chaetoceros didymus* Ehrenberg
23 CHDM	--	--	50	62	*Chaetoceros diadema* Gran
24 CHLA	20	26	19	19	*Chaetoceros laciniosus* Schutt
25 CHLO	29	34	18	12	*Chaetoceros lorenzianus* Grunow
26 CHNE	65	71	--	--	*Chaetoceros atlanticus* var. neapolitana (Schroder) Hustedt
27 CHPD	--	--	73	70	*Chaetoceros pendulus* Karsten
28 CHPE	56	51	28	53	*Chaetoceros peruvianus* Brightwell
29 CHRA	5	15	5	7	*Chaetoceros radicans* Schutt
30 CHSO	1	9	4	6	*Chaetoceros socialis* Lauder
31 CHSX	--	--	77	80	*Chaetoceros simplex* Ostenfeld
32 CHTS	--	--	63	68	*Chaetoceros teres* Cleve
33 CHVA	13	43	25	51	*Chaetoceros vanheurcki* Gran
34 CHOO	2	4	3	1	*Chaetoceros* spp.
35 COGR	--	--	82	79	*Coscinodiscus granii* Gough
36 COOO	26	3	16	2	*Coscinodiscus* spp.
37 CXCP	--	--	81	77	*Corethron criophilum* Castracane
38 CYCL	64	69	61	65	*Cylindrotheca closterium* (Ehrenberg) Reimann et Lewin

Table 1. (Continued)

CODE	SIO RA	SIO RO	PTH RA	PTH RO	
39 DIBR	54	55	42	26	*Ditylum brightwellii* (West) Grunow ex V. Heurck
40 DIOO	67	59	--	--	*Ditylum* spp.
41 DUPU	37	48	40	49	*Detonula* pumila (Castracane) Schutt
42 EUZO	9	18	2	14	*Eucampia zoodiacus* Ehrenberg
43 FROO	44	38	54	52	*Fragilaria* spp.
44 GRMA	40	22	67	69	*Grammatophora marina* (Lyngbye) Kutzing
45 GROO	49	47	--	--	*Grammatophora* spp.
46 GUFL	75	72	70	67	*Guinardia flaccida* (Castracane) H. Peragallo
47 HEHA	39	40	24	42	*Hemiaulus hauckii* Grunow
48 HESI	47	53	--	--	*Hemiaulus sienesis* Greville
49 LAAN	--	--	72	75	*Lauderia annulata* Cleve
50 LCLY	32	8	78	72	*Licmophora abbreviata* Agardh
51 LPDA	11	21	22	34	*Leptocylindrus danicus* Cleve
52 LPME	43	46	62	57	*Leptocylindrus mediterraneus* (H. Peragallo) Hasle
53 LTUN	35	27	38	31	*Lihodesmium undulatum* Ehrenberg
54 NAOO	17	1	26	5	*Navicula* spp.
55 NILO	23	5	39	20	*Nitzschia longissima* (Brebisson) Ralfs
56 NISE	3	2	8	3	*Nitzschia seriata* Cleve
57 NIOO	--	--	80	76	*Nitzschia* spp.
58 ODAU	52	37	47	25	*Odontella aurita* (Lyngbye) Agardh
59 ODLO	55	50	46	28	*Odontella longicruris* (Greville) Hoban
60 ODMO	70	70	51	30	*Odontella mobiliensis* (Bailey) Grunow
61 ODOO	57	42	55	44	*Odontella* spp.
62 PASU	60	73	--	--	*Paralia sulcata* (Ehrenberg) Cleve
63 PKSI	--	--	75	71	*Planktoniella sol* (Wallich) Schutt
64 PLOO	31	7	48	23	*Pleurosigma* spp.
65 PSDO	42	35	52	45	*Pseudoeunotia doliolus* (Wallich) Grunow
66 RHAL	22	20	34	22	*Rhizosolenia alata* Brightwell
67 RHCV	72	75	71	64	*Rhizosolenia calcaroavis* Schultze
68 RHDA	12	17	21	33	*Rhizosolenia delicatula* Cleve
69 RHFR	24	19	37	40	*Rhizosolenia fragilissima* Bergon
70 RHIM	63	64	79	74	*Rhizosolenia imbricata* Brightwell
71 RHRB	--	--	88	88	*Rhizosolenia robusta* Norman
72 RHSE	28	23	45	35	*Rhizosolenia setigera* Brightwell
73 RHST	25	14	27	27	*Rhizosolenia stolterfothii* H. Peragallo
74 RHSY	53	54	84	82	*Rhizosolenia styliformis* Brightwell
75 RHOO	30	33	29	41	*Rhizosolenia* spp.
76 SKCS	6	11	6	11	*Skeletonema costatum* (Greville) Cleve
77 SPME	71	74	--	--	*Stauroneis membranacea* Cleve
78 SRTH	66	61	68	61	*Streptotheca thamensis* Shrubsole
79 STOO	68	58	53	48	*Stephanopyxis* spp.

Table 1. (Continued)

CODE	SIO		PTH		
	RA	RO	RA	RO	
80 SUOO	59	52	69	58	*Surirella* spp.
81 THAN	--	--	76	78	*Thalassiosira anguste* Olineata (A. Schmidt) Fryxell et Hasle
82 THBU	--	--	43	56	*Thalassiosira bioculata* (Grunow) Ostenfeld
83 THCD	34	31	23	32	*Thalassiosira condensata* Cleve
84 THDC	50	62	32	38	*Thalassiosira decipiens* (Grunow) Jorgensen
85 THGR	27	44	44	46	*Thalassiosira gravida* Cleve
86 THNO	--	--	56	66	*Thalassiosira nordenskioldii* Cleve
87 THPA	--	--	31	60	*Thalassiosira pacifica* Gran et Angst
88 THRO	41	36	13	13	*Thalassiosira rotulla* Meunier
89 THSU	45	60	59	73	*Thalassiosira subtilis* (Ostenfeld) Gran
90 THOO	46	49	66	85	*Thalassiosira* spp.
91 TIOO	--	--	57	47	*Triceratum* spp.
92 TLAC	33	24	33	24	*Thalassiothrix acuta* Karsten
93 TLFN	--	--	86	86	*Thalassiothrix frauenfeldii* Grunow
94 THLE	38	39	35	39	*Thalassiothrix heteromorpha* Karsten
95 TLLO	58	57	60	55	*Thalassiothrix longissima* Cleve et Grunow
96 TLPF	--	--	87	87	*Thalassiothrix mediterranea* var. pacifica Cupp
97 TNNI	14	6	20	10	*Thalassionema nitzschioides* Grunow
98 TROO	61	65	64	63	*Tropidoneis* spp.

California, located approximately 20 km south of Scripps Pier; sea level measurements were taken from a station located approximately 30 km south of the Scripps Pier.

b. Data analysis. Unless otherwise noted all the statistical techniques discussed here can be found in Legendre and Legendre (1983). Because linear regression and principal component analysis require that variables used follow normal distribution, the first step in the analysis of the data was to test for normality. The results of the test of normality and a comparison between logarithmic and square root normalization methods on some selected variables are shown in Table 2. All the physical variables were normally distributed but the diatom counts were not. Diatom counts were normalized by logarithmic transformation (based 10) which gives a better approximation of normality than square root transformation.

Variables such as sea surface and air temperatures undergo seasonal cycles the long-term averages of which define the climatic normals. Any deviation from the normal constitutes an anomaly. The January anomaly of a variable, for example, is the difference between that January value and the average of all other Januaries. The use

Table 2. Correlations between 7 time series and their normal scores. NOTRS designates no transformation on the original data set have been performed prior to correlation and SQRT and LOG10 designate correlations obtained after the original time series have been converted by taking the square root and logarithm of each data point. N represents number of samples (weekly averages in this case). This analysis measures the 'straightness' of the normal probability plot where higher correlation indicates that samples are from a normal population. For these samples 1% level of significance is when $r = 0.98$.

	NOTRS	SQRT	LOG10	N
Sea-surface temp.	0.99			520
Wind stress	0.99			520
Chaetoceros compressus	0.62	0.88	0.99	468
Chaetoceros radicans	0.56	0.99	0.99	468
Chaetoceros socialis	0.56	0.81	0.99	468
Nitzschia seriata	0.44	0.74	0.97	468
Total diatoms	0.33	0.67	0.99	468

of anomalies makes it easier to detect climatic changes such as El Niño, but more importantly, their use is essential to prevent significant but spurious correlation between two variables which may lack a causal connection but undergo similar seasonal cycles. It is important to emphasize that magnitude of an anomaly depends on the length of the record and when correlating two variables one should use anomalies based on data acquired during the same time period.

Proxy variables are often used in climatic research; care should be exercised, however, in both the usage and interpretation of these variables. First, a proxy variable has to be related to the variable it is to replace, even though such relationships are often indirect. For example, off the coast of southern California, strong northwesterly winds will result in upwelling and increased flow of the coastal currents. Both of these effects lead to the formation of cooler than normal surface temperatures and lower than normal sea level heights. Considering the significant correlation between air temperature and sea-surface temperature (Roden, 1960), among the several possible combinations, one may choose sea level as proxy indicator of air temperature (Tont, 1978). Second, there is an important distinction between a logical connection such as : if A > B and B > C then A > C, and an expected relationship based on statistical correlations: If A is correlated with B and if B is correlated with C then it is expected that A is correlated with C. The later relationship will hold only if the first two correlations are reasonably high. (For an example where this relationship fails see below.)

In this study principal component analysis was used primarily to compare the variability of diatom abundances at two locations and, most importantly, to create an index (principal components) which represents a significant fraction of the total variance objectively on the basis of the covariability of the species. This index in turn was used to test the hypothesis that variability of diatom populations are correlated with physical variables. Briefly described, this technique consists of deriving a correlation matrix from all possible pairs of variables included for analysis; from this

matrix eigenvalues (percent of total variance) and their associated eigenvectors (also known as loadings) are calculated. Principal components are then determined from the eigenvectors and the original time series of variables. The eigenvectors form the "weights" which each variable contributes to the total variance, the higher the weight the higher its relative importance. Alternately, these eigenvectors represent the correlation between the original time series and the principal components. Each subsequent principal component explains a smaller part of the total variance than the previous component.

To avoid biasing the results, only the species which were most abundant were included in the analysis to identify a group of single species which is representative of the entire group. There is no established criteria for choosing the number of species which can be classified as 'abundant' or 'rare'. In this paper 23 species (three of which have been identified only to genus) which account for 95% of the total abundance at Scripps Pier, are considered as 'abundant' and the rest of the species are classified as 'rare'. Such classifications are also of utmost importance in calculating anomalies. For example, during the periods of 1930–1939 at Scripps Pier and 1930–1938 at Pt. Hueneme Pier when we have the weekly records of 98 species of diatoms, the occurrence of species range from 1 to 343 times. Thus, it would be misleading and illogical to calculate the anomalies of a diatom species which has occurred only 4 times during the entire period and attempt to correlate them with the anomalies of one or all of the climatic variables. Such occurrences should be treated as 'events'. Conversely, a species which occurs frequently and is present in most or every seasonal anomaly, can be treated as a 'continuous' variable of a system fluctuating between two limits and can be correlated with climatic variables.

Such considerations resulted in the construction of several different correlation matrices chosen from the original subset of 98 time series from which a set of eigenvalues, eigenvectors, cumulative explained variances and principal components were calculated. The first set (a set is a pair of matrices, one for each location, based on identical species and identical time scales) was calculated from the 23 most abundant species found at Scripps Pier and the corresponding matrix for Pt. Hueneme calculated from the counts of the same species. (It is important to point out that 3 of 23 species ranked by abundance at Scripps pier were not in the top 23 at Pt. Hueneme, but were still present.) The second set consisted of the same species but the elements of the matrices were correlations obtained from anomalies of counts. Anomalies in this sense are times series of counts where the seasonal cycles have been removed.

Another set of four matrices based on all 65 species of diatom common to both locations was also analyzed by identical techniques. This approach removes the difficulty of choosing which species to include in the analysis when one needs to compare two sites but may introduce a different bias because of the very low abundances of some species, thus violating the aforementioned recommendation of including only 'major variables' in the analysis.

Another possible bias with major ecological implications is that we could not determine how many species have been lumped together under one name when species were identified only to genus. Exclusion of these species in any analysis may bias the results; by the same token, one introduces a different bias by treating them as a single species. These considerations necessitated another analysis based on 20 most abundant species (23 most abundant species minus 3 species identified to genus).

3. Results and discussion

a. Short-period (days, weeks) changes.

Eigenvectors of 23 abundant species and the eigenvectors calculated for the same species but from a matrix of 65 species common to both locations are presented in Table 3. Eigenvectors for the remaining 42 species are shown in Table 4. (Since the analysis of the eigenvectors calculated from a matrix of 20 species were nearly identical to those obtained from 23 species, they are not shown in these tables.) The removal of seasonal cycles does not seem to influence the eigenvectors which suggests that most species do not undergo well-defined seasonal cycles. From a practical point of view, this means that diatom time series from which seasonal cycles cannot be removed because the record is too short can be used with some confidence to determine eigenvectors. Eigenvectors are remarkably similar regardless of location and the type of matrix used. Some exceptions to this rule are the eigenvectors for *Eucampia zoodiacus* (EUZO) and *Nitzschia longissima* (NILO) (Table 3). Since the same patterns occur at both locations, such discrepancies may be attributed to a combination of analysis, sampling error, and possibly, ecological interactions which cannot be resolved with the available data. In summary, most diatom species tend to vary similarly with respect to each other regardless of location and addition of 42 more species to a matrix of 23 which already accounts for over 95% of the abundances does not significantly change the eigenvectors.

A limited number of species contribute to the variance defined by principal component 2 which account only 6% to 8% of the total variance (Table 3). The most important species in this component include *Navicula* spp. (NAOO) (Table 3), *Stephanopyxis* spp. (STOO), *Detonula pumila* (DUPU), *Grammatophora marina* (GRMA), *Thalassiosira rotulla* (THRO), *Thalassiosira subtilis* (THSU), *Rhizosolenia styliformis* (RHST) and *Streptotheca thamensis* (SRTH) (Table 4). It is difficult to explain these differences for species identified only to genus since we do not know how many species are 'lumped' together in those categories. In the case of *Detonula pumila* (DUPU), where its abundance and frequency of occurrence at both locations are remarkably similar (Table 1), large differences between the eigenvectors at Scripps Pier (0.85) and at Pt. Hueneme Pier (0.00) could very well be due to sampling differences, for it is difficult to find either biotic or environmentally induced forcing to explain this dichotomy. *Streptotheca thamensis* (SRTH) is one species

Table 3. Eigenvectors based on 23 (sp23) and 65 (sp65) species of diatoms at Scripps Pier (SIO) and Pt. Hueneme Pier (PTH). (an) refers to anomalies. Eigenvalues (Eval) are given at the end of eigenvector columns, percent of explained variance (var) is eigenvalues divided by the number of species included in the original correlation matrix. The rest of the eigenvectors based on 65 species are given in Table 4. Their eigenvalues and variances are given in this table for comparison.

| | Eigenvector I | | | | | | | | Eigenvector II | | | | | | | |
| | SIO | | | | PTH | | | | SIO | | | | PTH | | | |
	sp23	sp65	(an) sp23	(an) sp65	sp23	sp65	(an) sp23	(an) sp65	sp23	sp65	(an) sp23	(an) sp65	sp23	sp65	(an) sp23	(an) sp65
ASGL	0.59	0.61	0.57	0.58	0.51	0.49	0.46	0.46	0.23	0.06	0.23	0.03	0.13	0.07	0.15	0.11
BAOO	0.52	0.52	0.55	0.55	0.56	0.60	0.54	0.51	-0.14	-0.04	-0.12	0.10	0.15	0.17	0.17	0.10
CHAF	0.59	0.34	0.62	0.58	0.48	0.43	0.37	0.35	-0.41	-0.04	-0.37	-0.16	-0.29	0.37	-0.37	-0.17
CHCN	0.52	0.50	0.50	0.51	0.58	0.47	0.53	0.55	0.05	-0.20	0.03	-0.16	0.43	-0.10	0.46	0.38
CHCO	0.76	0.70	0.76	0.72	0.74	0.69	0.71	0.65	-0.25	-0.26	-0.24	-0.23	-0.05	-0.05	-0.09	-0.10
CHCS	0.59	0.57	0.58	0.57	0.74	0.72	0.67	0.62	-0.47	-0.25	-0.47	-0.20	-0.12	-0.16	-0.21	-0.23
CHCU	0.68	0.64	0.67	0.65	0.50	0.62	0.56	0.56	0.04	-0.24	0.01	-0.24	-0.22	0.01	-0.18	-0.07
CHDE	0.77	0.79	0.78	0.77	0.74	0.49	0.72	0.70	0.06	-0.01	0.04	-0.07	-0.21	-0.12	-0.23	-0.32
CHDI	0.78	0.65	0.77	0.78	0.69	0.68	0.68	0.65	-0.07	-0.01	-0.06	-0.03	-0.29	-0.26	-0.27	-0.18
CHLA	0.77	0.77	0.76	0.75	0.72	0.67	0.66	0.62	-0.25	-0.07	-0.27	-0.24	-0.14	-0.15	-0.16	-0.25
CHOO	0.76	0.47	0.75	0.72	0.81	0.65	0.78	0.74	0.08	-0.20	0.09	0.10	-0.13	-0.26	-0.12	-0.22
CHRA	0.81	0.79	0.80	0.79	0.74	0.69	0.73	0.67	-0.11	-0.04	-0.09	0.01	-0.23	-0.20	-0.23	-0.22
CHSO	0.81	0.77	0.80	0.79	0.80	0.79	0.74	0.73	-0.03	-0.16	-0.02	-0.17	0.06	-0.00	0.09	-0.01
CHVA	0.55	0.57	0.52	0.51	0.21	0.47	0.15	0.12	-0.31	-0.22	-0.34	-0.15	-0.58	-0.16	-0.56	-0.34
EUZO	0.63	0.17	0.61	0.62	0.71	0.33	0.58	0.61	0.04	-0.04	0.06	0.09	0.22	-0.00	0.29	-0.01
LPDA	0.55	0.56	0.53	0.53	0.47	0.40	0.41	0.46	0.22	0.22	0.26	0.30	0.25	0.23	0.21	0.22
NAOO	0.31	0.55	0.29	0.29	0.27	0.45	0.18	0.23	0.45	0.01	0.49	0.17	0.59	-0.04	0.57	0.54
NILO	0.54	-0.02	0.50	0.49	0.56	0.16	0.46	0.46	0.47	0.02	0.50	0.24	0.20	0.42	0.25	0.03
NISE	0.68	0.52	0.66	0.65	0.76	0.54	0.69	0.67	0.30	0.18	0.30	0.10	0.01	0.01	0.04	-0.20
RHAL	0.49	0.52	0.44	0.47	0.51	0.53	0.38	0.41	0.12	0.25	0.12	0.28	0.45	0.27	0.52	0.33
RHDA	0.65	0.64	0.63	0.62	0.52	0.46	0.45	0.45	-0.09	-0.20	-0.13	-0.18	0.13	-0.05	0.13	0.11
SKCS	0.76	0.75	0.75	0.74	0.68	0.67	0.59	0.59	0.19	0.02	0.17	0.02	-0.04	-0.19	-0.02	-0.17
TNNI	0.51	0.59	0.51	0.49	0.50	0.10	0.50	0.51	0.27	-0.11	0.29	0.04	-0.04	-0.19	0.07	-0.10
Eval	9.73	16.03	9.49	13.07	9.00	13.04	7.60	10.08	1.45	5.43	1.53	5.54	1.68	3.69	1.88	4.37
Var.	0.42	0.25	0.41	0.20	0.39	0.20	0.33	0.15	0.06	0.08	0.07	0.08	0.07	0.06	0.08	0.07

Table 4. Eigenvectors for the remaining 42 diatom species not included in Table 3.

| | Eigenvector I | | | | Eigenvector II | | | |
| | SIO | | PTH | | SIO | | PTH | |
CODE		(an)		(an)		(an)		(an)
AMOO	0.13	0.11	0.18	0.15	0.61	0.56	0.27	0.37
CEPE	0.10	0.37	0.09	0.37	0.58	−0.10	0.16	0.43
CHDC	0.66	0.56	0.50	0.33	−0.09	0.10	−0.06	−0.01
CHLO	0.75	0.44	0.68	0.61	−0.26	−0.12	−0.21	−0.28
CHPE	0.72	0.16	0.76	0.32	0.04	0.04	−0.20	0.38
COOO	0.59	0.45	0.29	0.51	−0.27	−0.24	−0.29	−0.25
CYCL	0.28	−0.04	0.29	0.10	0.13	0.04	0.47	0.32
DIBR	0.08	0.16	0.07	0.31	0.03	−0.04	0.02	−0.07
DUPU	0.21	0.45	0.00	0.06	0.85	−0.14	−0.00	−0.30
FROO	0.63	0.04	0.73	0.19	0.07	0.63	−0.01	0.32
GRMA	0.11	0.02	0.15	−0.03	0.60	0.11	0.30	0.19
GUFL	0.02	0.07	0.03	0.10	0.10	0.30	0.19	0.02
HEHA	0.54	0.49	0.35	0.26	0.23	0.26	0.54	0.53
LCLY	0.25	0.19	−0.02	0.11	0.17	0.15	0.01	0.17
LPME	0.64	0.12	0.55	0.00	0.05	0.00	−0.21	0.03
LTUN	0.46	0.27	0.48	0.33	0.17	−0.15	0.24	−0.06
ODAU	0.46	0.11	0.42	0.00	0.33	−0.08	0.16	0.03
ODLO	0.36	0.40	0.00	0.19	−0.06	−0.07	0.03	0.02
ODMO	0.42	−0.04	0.24	0.01	−0.11	0.01	−0.00	0.25
ODOO	−0.01	0.07	0.03	0.10	0.00	0.65	0.24	0.19
PLOO	0.64	0.22	0.74	0.12	0.06	0.21	−0.17	0.19
PSDO	0.19	0.15	0.18	0.02	0.15	−0.10	0.18	0.26
RHCV	−0.00	0.01	−0.01	−0.02	0.01	0.03	0.09	0.09
RHFR	0.71	0.54	0.47	0.12	−0.21	−0.21	0.15	−0.12
RHIM	0.58	0.06	0.21	−0.01	−0.18	0.07	−0.09	−0.01
RHOO	0.04	0.12	−0.04	−0.07	0.04	0.44	−0.00	0.04
RHSE	0.16	0.37	−0.05	0.43	0.44	0.23	0.02	0.16
RHST	0.40	0.69	0.36	0.49	0.17	0.09	0.20	−0.03
RHSY	0.73	0.18	0.60	0.05	0.08	0.87	−0.00	0.02
SRTH	0.07	0.07	0.06	−0.00	0.47	0.39	0.43	0.33
STOO	0.15	0.16	0.27	0.23	0.67	0.80	0.51	0.55
SUOO	0.16	−0.01	0.28	0.09	0.75	0.32	0.59	0.27
THCD	0.15	0.36	0.09	0.55	0.39	−0.10	0.25	0.46
THDC	0.38	0.30	0.60	0.25	−0.06	−0.07	0.38	−0.00
THGR	0.30	0.38	0.29	0.14	−0.08	−0.11	−0.08	−0.11
THOO	0.39	0.13	0.25	0.14	−0.05	0.89	−0.14	0.28
THRO	0.19	0.47	0.15	0.43	0.86	−0.14	0.27	−0.46
THSU	0.53	0.09	0.51	0.14	−0.13	0.67	−0.43	0.33
TLAC	0.43	0.40	0.50	0.43	0.05	0.01	0.37	0.43
TLHE	0.42	0.40	0.23	0.16	−0.19	−0.13	−0.26	−0.36
TLLO	0.10	0.09	0.09	0.04	−0.05	−0.03	−0.18	−0.13
TROO	0.75	0.24	0.48	0.10	0.18	−0.08	−0.10	0.27

where the eigenvectors for the second principal component are similar in all 4 categories. Cupp (1943) describes this species as 'never common' for this region (see also Table 1), which may explain the discrepancy. Considering that the maximum variance contributed by the second eigenvector is 0.08, such differences play only a minor role in total variability of diatoms, and the absence of concurrent relevant data makes it difficult to find ecological explanations.

Goodman *et al.* (1984) applied principal component analysis to phytoplankton data collected at weekly intervals for 21 weeks at 3 offshore stations in the Southern California Bight. Because of different sampling strategies and locations, and their use of a data matrix which included both diatoms and dinoflagellates, the two studies are not directly comparable. Some of their results, however, concur with this study. For example, they also found that the first component was dominated by a large number of positive contributions; important contributors in both studies were *Skeletonema costatum* (SKCS), *Chaetoceros debilis* (CHDE), and *Rhizosolenia delicatula* (RHDA). Eigenvectors for the second component of some *Chaetoceros* species were also negative. In Goodman's study, however, the second component eigenvectors for *Chaetoceros radicans* and *Eucampia zoodiacus* were nearly double of the first component and both positive. These results are opposite our findings. Several other diatom species in Goodman's analysis had much higher contributions to the second component than in the present analysis.

Estrada and Blasco (1979) applied principal component analysis to phytoplankton data collected off the coast of Baja California which also included measurements of several physical and chemical variables. They found that diatom dominance was related to upwelling of deeper saline and nutrient water from the California Undercurrent whereas dinoflagellate dominance was associated with upwelling water of relatively low salinity and lower nutrients from below the minimum salinity core of the California Current.

Percent of explained variances do not change when anomalies (seasonal cycles removed) are used; however, there are marked differences between variances based on 65 and 23 species at both locations. The inclusion of species which occur very infrequently contributes to lower variance calculated from 65 species. However, it is very important to note that despite such differences, first principal components calculated from these eigenvectors based on weekly anomalies are correlated with anomalies of sea-surface temperatures (Table 5). The negative sea-surface temperature anomaly on the order of days and weeks is probably caused by upwelling events (Tont, 1981). The inverse correlation between diatom and sea-surface temperature is probably the result of such events. The anomalies of salinity and wind stress are not correlated with diatom anomalies based on weekly averages, but they become significant when seasonal averages are used (for a discussion of seasonal changes see below).

Table 5. Correlation coefficients between first principal components and the anomalies of sea-surface temperature (SST), salinity (SAL) and alongshore wind stress (WS) for Scripps Pier (SIO) and Pt. Hueneme Pier (PTH). Southward alongshore wind stress is positive and wind data was not available for Pt. Hueneme Pier. Principal components (PRC) have been calculated from the anomalies of 20, 23, and 65 species of diatoms. Principal components based on 20 species sampled at Scripps Pier have also been correlated with the physical variables at various lags (not shown). Maximum correlations, when significant, have been obtained at 0 lags.

		SST	SAL	WS
		WEEKS		
	PRC23	−0.30	0.03	
PT.H	PRC20	−0.31	0.04	
	PRC65	−0.31	0.03	
	PRC23	−0.39	−0.04	0.08
SIO	PRC20	−0.39	−0.05	0.05
	PRC65	−0.41	−0.06	0.08
		SEASONS		
SIO	PRC20	−0.54	−0.36	0.46

b. Long-period (months, seasons, years) changes.

i. Abundant species. The idea that certain marine organisms are indicators of the origin and characteristic of water masses is an old one (e.g., Cleve, 1900), and a growing body of evidence has linked the changes in the circulation patterns of these water masses to climatic change. The 1957–1958 El Niño which was also observed along the North American coast instigated several studies comparing the abundance and distribution of several organisms observed during this period with other periods. Balech (1960) found significant differences in diatom and dinoflagellate counts between 1957–58 and 1938–39 periods. According to Berner (1960) the distribution of some species of pelagic tunicates were shifted several kilometers northward and Brinton (1960) reached similar conclusion for euphausiids collected in the same region.

The climate of a particular region is defined by long-term averages of variables such as air temperature and solar irradiance. In coastal zones air-sea interactions, on both global and local scales, are essential ingredients of climate. One of the most useful indicators of coastal climate change is change in sea-surface temperatures. Indeed, two of the best known methods of climate prediction use sea-surface temperatures as their starting points (Namias, 1975; Barnett and Hasselmann, 1979). Sea-surface temperatures have also been used as indicators of nutrient concentration (Zentara and Kamykowski, 1977), as tracers of circulation patterns of major water masses (Reid *et*

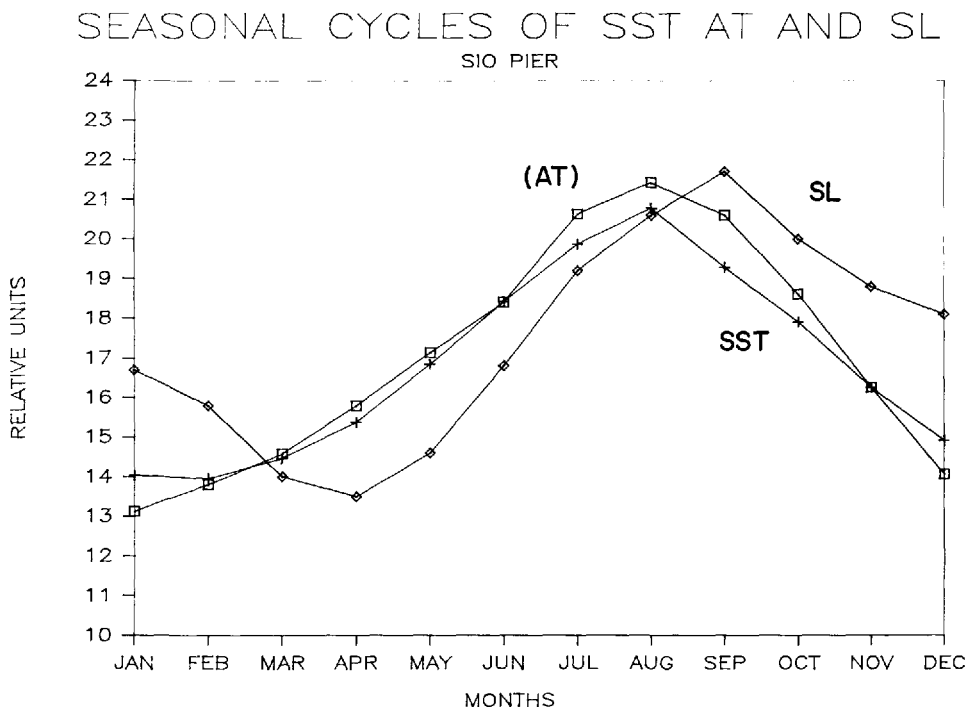## SEASONAL CYCLES OF SST AT AND SL
SIO PIER

Figure 2. Seasonal cycles of air temperature (AT), sea level (SL) and sea-surface temperatures (SST). Air and sea-surface temperatures are based on monthly averages of 1920–1973, and sea levels of 1928–1973 periods. Sea-surface temperatures are from Scripps Pier, air temperature and sea level sites are located approximately 20 kilometers south of the pier.

al., 1958), and as signatures of upwelling events (Tont, 1981). Furthermore, large-scale atmosphere-ocean phenomena such as El Niño events or their opposites (see below) are often defined and delineated by sea-surface temperature fields (Namias, 1975). The high correlation between air and sea-surface temperature near San Diego first noted by Hubbs (1948) and later verified by Roden (1960) for the western coast of North America, makes it possible to use either variable as a proxy indicator of the other.

Long-term averages of sea level, air temperature and sea-surface temperatures are shown in Figure 2. These averages are climatic normals and deviations from these normals constitute anomalies. Similarly, seasonal averages of 23 abundant species of diatoms have been calculated for Scripps and Pt. Hueneme piers and some examples are illustrated in Figure 3. Average of all the seasonal cycles for the 23 species verifies the 'classic' picture of diatom variability for the year: highest counts in spring when blooms dominate, followed by winter and summer, and the least abundance in the fall. A 'complete' reversal of this pattern (e.g., fall season being highest of the four) is never observed; however, there are significant differences between the seasonal cycles of

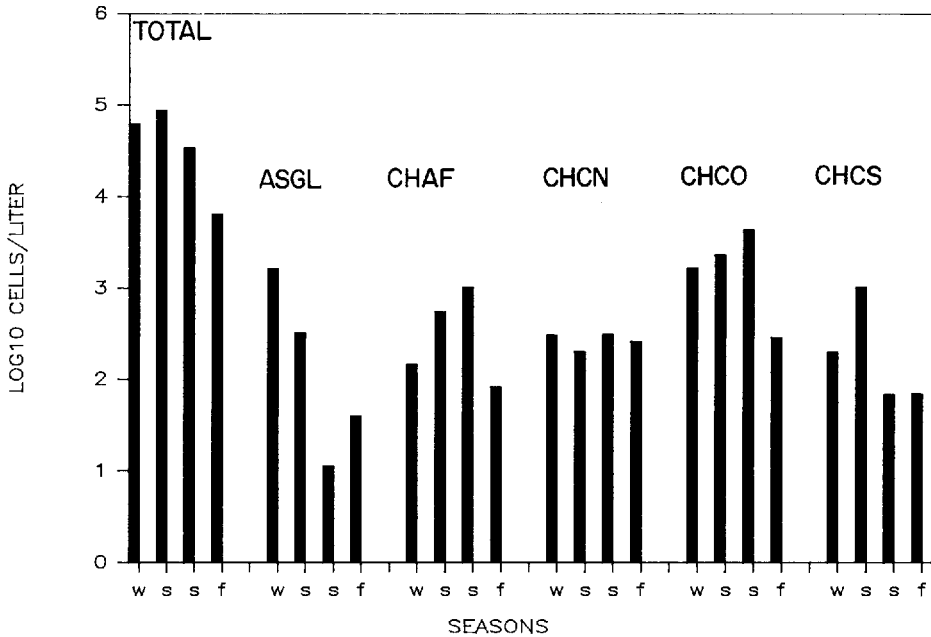## Seasonal cycles of diatoms Scripps pier

Figure 3. Seasonal cycles of combined totals of 23 abundant species of diatoms (extreme left) and 5 species of diatoms at Scripps Pier, 1930–1938. For abbreviation of diatom species consult Table 1. Seasons are labeled as w for winter, s for Spring, s for Summer, and f for Fall.

several species of diatoms. These cycles are the 'normals' from which anomalies for each abundant species are calculated. The significant correlations obtained between principal components and 3 environmental variables averaged over seasons (Table 5) strongly suggests the possibility of similar correlations when individual species of diatoms are considered. Table 6 represents the results of correlation analysis between seasonal anomalies of abundant species of diatoms and anomalies of several oceanic and atmospheric variables for the Scripps Pier. Figure 4 shows some examples of time series on which these correlations have been based (whenever possible, a species has been plotted with the variable with which it had the highest correlation). The best predictor of abundance for several species of diatoms is sea-surface temperature, followed by air temperature, wind stress and sea level. But considering that $r = 0.38$ corresponds to a 1% level of significance, a large number of correlations are too small to have a predictive value. The correlations between diatom counts and solar irradiance are too low to be of use but those with alongshore wind stress are of significance. Namias and Cayan (1984) have already shown that the northward component of large-scale wind systems (calculated from pressure maps) which effect the coast of

Table 6. Correlation coefficients between seasonal anomalies of 23 most abundant species of diatoms and sea-surface temperature (SST), wind stress (WS), sea level (SL), air temperature (AT), salinity (SAL), and solar irradiance (SOL) at Scripps Pier.

CODE	SST	WS	SL	AT	SAL	SOL
CHDE	−0.69	0.39	−0.53	−0.57	−0.38	−0.12
EUZO	−0.50	0.56	−0.39	−0.45	−0.33	0.10
CHSO	−0.48	0.43	−0.44	−0.44	−0.42	0.23
NISE	−0.48	0.43	−0.36	−0.36	−0.25	0.06
NILO	−0.41	0.29	−0.17	−0.41	−0.25	0.08
CHCN	−0.40	0.23	−0.41	−0.40	−0.23	−0.22
CHOO	−0.39	0.38	−0.22	−0.36	−0.35	0.20
RHDA	−0.39	0.37	−0.21	−0.34	−0.33	0.15
SKCS	−0.35	0.33	−0.28	−0.28	−0.27	0.05
CHDI	−0.34	0.19	−0.26	−0.38	−0.25	−0.12
CHCO	−0.33	0.35	−0.21	−0.32	−0.21	0.25
CHAF	−0.32	0.36	−0.32	−0.30	−0.23	0.29
CHCS	−0.31	0.33	−0.31	−0.26	−0.25	0.37
CHRA	−0.31	0.26	−0.13	−0.29	−0.31	0.02
CHLA	−0.30	0.30	−0.33	−0.32	−0.35	0.09
TNNI	−0.27	0.46	−0.19	−0.27	−0.25	0.13
RHAL	−0.25	0.11	−0.04	−0.18	0.14	−0.22
CHVA	−0.21	0.30	−0.21	−0.16	−0.26	0.38
CHCU	−0.19	0.39	−0.14	−0.12	−0.31	0.38
BAOO	−0.14	0.37	0.02	−0.15	−0.03	0.14
ASGL	−0.10	0.18	−0.02	−0.20	0.00	0.06
NAOO	−0.07	0.07	0.15	0.01	0.40	0.06
LPDA	−0.03	0.19	0.09	0.00	0.25	0.12

California, were anomalously high during 1982–1983 El Niño. Reliable weather maps do not exist prior to 1947, but winds measured locally should be representative of large-scale circulation when averaged over long periods. To the best of my knowledge this is the first time the fluctuation of a species of diatom over a 10 year period has been directly correlated with atmospheric circulation.

These findings suggest the following: A lessening of southward wind stress results in positive sea-surface temperature anomalies due to both slackening of the California Current and decreased upwelling (opposite is true for increased southward wind stress). Sea-surface temperatures observed in this region are inversely correlated with nitrate concentration (Kamykowski, 1974; Eppley *et al.,* 1978) and if diatoms abundances are related to nutrient input, then they would be expected to be inversely correlated with sea-surface temperatures. Significant correlations between diatom abundances and air temperature, and to a lesser degree with sea level and salinity, are also expected because of the aforementioned proxy relationships. More importantly, the reconstruction of the past history of certain species of diatoms is feasible from historical climatological data. It is difficult to explain the differences in diatom species response to climatic fluctuations. Climate is only one of several agents affecting plant
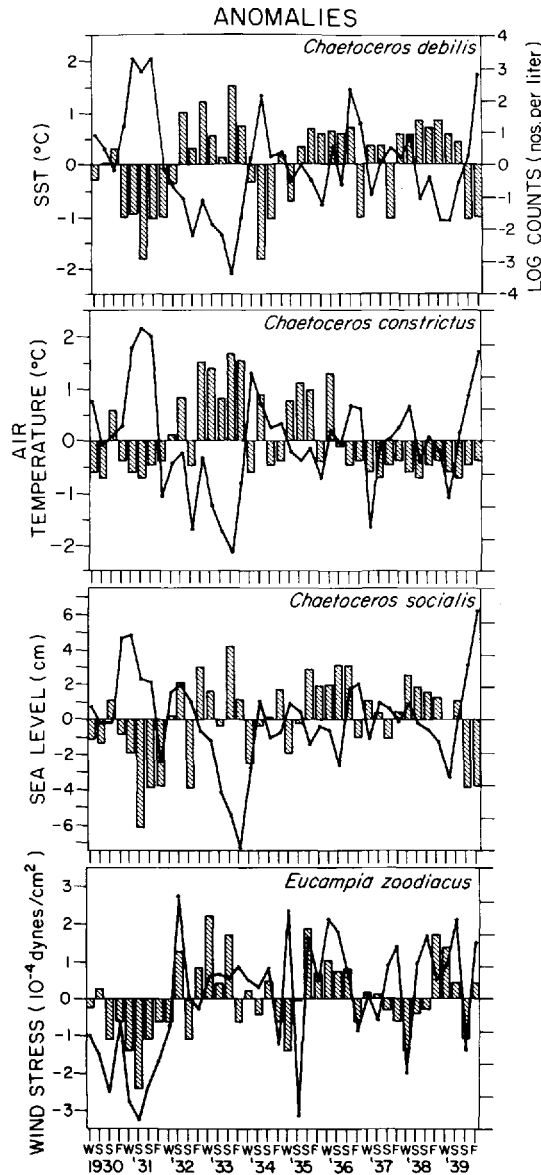
Figure 4. Seasonal anomalies of sea-surface temperatures (SST), air temperature (AT), sea level (SL), alongshore wind stress (WS), and 4 species of diatoms. Southward wind stress is considered positive.

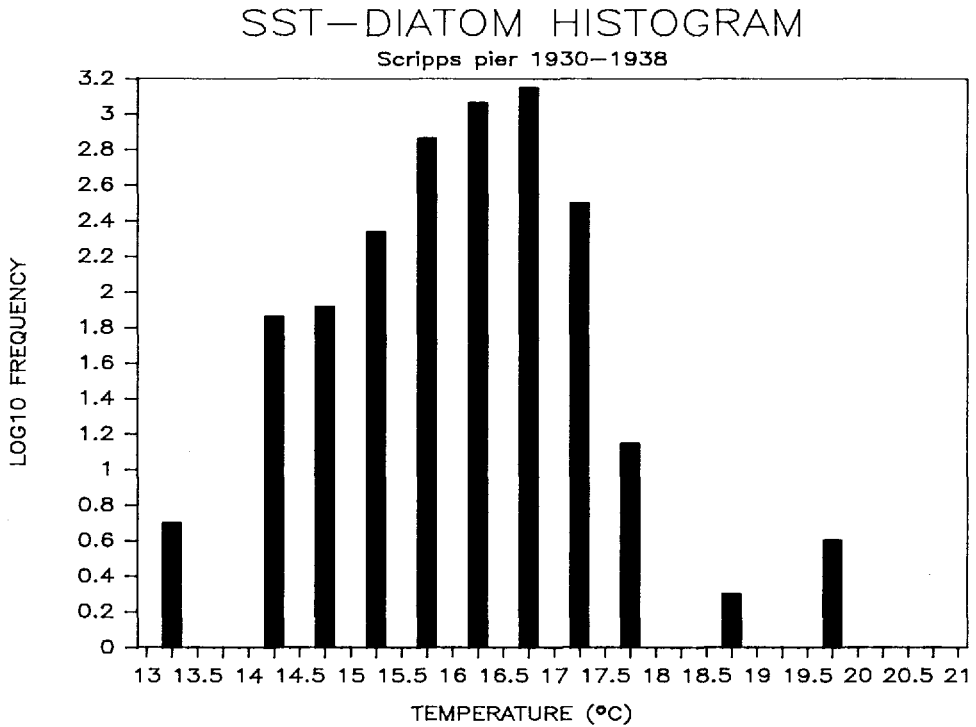# SST—DIATOM HISTOGRAM
Scripps pier 1930—1938

Figure 5. Number of occurrences of diatom species and the corresponding average sea-surface temperatures at Scripps Pier, 1930–1938. Each bar represents accumulated frequency of any number of species which have occurred during that particular temperature range. For example, the second bar from the left indicates 72 occurrences (log 10 transformed) by 5 species (not shown) at temperatures between 14.00 and 14.5°C.

and animal populations and for some species of diatoms other factors, e.g., competition for available nutrients, predation, may override climatic effects.

ii. Rare species. Rare species, as defined above, account for 5% of the total diatom abundance. The important question is how the abundance and occurrences of these species not treated above are related to climatic change. Figure 5 shows the distribution of occurrence of all the species observed at Scripps Pier at temperature intervals within which such occurrences have been recorded. It is obvious that most of the occurrences are confined to a narrow limit between 14 and 18 degrees centigrade. The important question then is whether those occurrences which fall outside this range are due to appearance of rare species. Table 7 lists several species of diatom which occurred infrequently at Scripps and Pt. Hueneme piers along with averaged sea-surface temperatures and salinities. *Thalassiosira decipiens* (THDC) and *Ditylum brightwellii* (DIBR) occur at both locations at low temperature and salinities and can be used as indicators of what one may call as 'Anti El Niño' events. As Table 7 shows, it

Table 7. Species code (CODE), average sea-surface temperature (SST), salinity (SAL), and number of occurrences of diatoms (OCC) at Scripps and Pt. Hueneme piers, 1930–1938.

	Scripps Pier			Pt. Hueneme Pier		
CODE	SST	SAL	OCC	SST	SAL	OCC
PASU	20.56	33.71	1	—	—	0
CYCL	19.86	33.67	2	14.20	33.73	5
CHNE	19.73	33.69	1	—	—	0
ODMO	18.77	33.63	1	14.78	33.60	73
RHCV	17.96	33.74	1	17.10	33.66	5
CEOO	17.87	33.64	2	—	—	0
RHIM	17.38	33.67	3	15.52	33.41	1
THSU	16.96	33.59	5	12.87	33.77	2
STOO	16.62	33.61	7	14.69	33.69	21
HESI	16.59	33.62	10	—	—	0
SRTH	16.32	33.65	4	16.42	33.79	6
GUFL	16.29	33.55	1	13.17	33.59	4
DIOO	16.24	33.61	6	—	—	0
BAVA	16.08	33.58	8	—	—	0
TLLO	15.95	33.63	8	14.30	33.56	11
AMOO	15.37	33.56	2	13.65	33.75	6
BAEL	15.03	33.58	3	—	—	0
SPME	15.02	33.66	1	—	—	0
BADL	14.80	33.60	2	—	—	0
DIBR	14.78	33.51	9	14.05	33.60	83
TROO	14.09	33.62	3	13.35	33.71	6
THDC	13.02	33.55	4	13.13	33.60	33

is difficult to find species which may be considered as the harbingers of El Niño events. A case in point is *Odontella mobiliensis* (ODMO) which was found at 18.8 degrees centigrade at Scripps pier but at 14.8 at Pt. Hueneme, even though Pt. Hueneme (because of its more northerly location) is generally cooler than Scripps pier. It is surprising that several rare species appear when the conditions are normal (average) as, for example, is the case with *Streptotheca thamensis* (SRTH). Such occurrences are difficult to explain on the basis of circulation patterns of major water masses which result in large-scale temperature and salinity anomalies. However, smaller scale circulation features, such as eddies (Haury *et al.,* 1978) could be the cause. Reid *et al.,* (1985) stated that phytoplankton species composition was not "unusual" at Scripps Pier during 1983 El Niño, which is the opposite of the findings by Balech (1960) who reported significant differences in phytoplankton species composition during the 1957–1958 El Niño compared to previous periods. Indeed, there is growing evidence that both in terms of physical structure and related biological indicators, El Niño events may differ significantly from each other. Simpson (1984), for example, has argued that unusual warming in the California Bight in 1982–1983 El Niño, was caused by the movement of water from the subarctic by way of California Current and

not from the south as generally reported for previous El Niño events (Sette and Isaacs, 1960).

In summary, based on the data set it is difficult to establish a direct link between climatic change and the presence or absence of rare species, although some leads presented here show some promise. As has been shown in the preceding section, the climatic changes are best reflected in the abundances of major species, e.g., *Chaetoceros debilis* (CHDE), *Eucampia zoodiacus* (EUZO) (Fig. 4., Table 6), and in the total number of diatoms (Tont, 1981).

4. Conclusions

The response of diatom species to climatic fluctuations are varied and highly complex. Correlations between diatom abundances and climatic variables are significant at certain time scales but further research is needed to ascertain whether such correlations will lead to the ability to predict. An important result of this study is that measurements made at a single site over a relatively long period of time provide useful information about interactions between biological and physical variables and such interactions may be generalized to other locations. The results also suggest that historical records should not be ignored simply because measurements of parameters important to describe bioclimatological events are lacking. This work is respectfully dedicated to Prof. W. E. Allen and his co-workers.

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