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Long-term phytoplankton community dynamics in the Western English Channel

C. E. WIDDICOMBE[1]*, D. ELOIRE[1,2], D. HARBOUR[1], R. P. HARRIS[1] AND P. J. SOMERFIELD[1]

[1]PLYMOUTH MARINE LABORATORY, PROSPECT PLACE, WEST HOE, PLYMOUTH PL1 3DH, UK AND [2]LABORATOIRE ECOSYSTÈME LAGUNAIRE, UMR 5119, CNRS – UNIVERSITÉ MONTPELLIER II – IRD–IFREMER, CC093, PLACE EUGÈNE BATAILLON, 34095 MONTPELLIER CEDEX 05, FRANCE

*CORRESPONDING AUTHOR: clst@pml.ac.uk

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Over a 15-year period (1992–2007), weekly water samples were collected from the L4 time-series station in the Western English Channel and analysed for phytoplankton community structure and abundance. The data produced have been analysed to identify seasonal patterns, inter-annual variability and long-term trends in the composition of the seven main functional phytoplankton groups. Phyto-flagellates numerically dominated accounting for on average ca. 87% of the phytoplankton abundance while diatoms, *Phaeocystis*, coccolithophorids, dinoflagellates and ciliates contributed 13% of abundance. Distinct seasonal and inter-annual changes in the abundance and floristic composition of the functional groups were observed. Significant long-term changes in abundance showed that, over the study period, diatoms and *Phaeocystis* decreased while coccolithophorids, the dinoflagellate *Prorocentrum minimum* and some heterotrophic dinoflagellate and ciliates increased in abundance. These changes highlight the importance of long-term observations for the understanding of natural temporal variability in plankton communities. Such shifts in the community composition at L4 could have important consequences for ecosystem function.

INTRODUCTION

The worlds oceans are changing at an unprecedented rate with current estimates suggesting that they have warmed by ca. 0.6°C over the past 100 years (IPCC, 2007) and have absorbed almost 50% of all the anthropogenic CO_2 emitted over the last 250 years (Sabine *et al.*, 2004). Plankton not only play a central and critical role in the health and productivity of the oceans, but have also been shown to be sensitive indicators of climate change (Reid *et al.*, 1998; Cermeño *et al.*, 2008; Edwards *et al.*, 2008). Consequently, long-term studies of planktonic organisms can help illustrate the speed and severity of climate change impacts on the structure and function of marine ecosystems.

Phytoplankton are a diverse group of microscopic organisms comprising several functional groups, including diatoms, dinoflagellates, prymnesiophytes and flagellates. Although traditionally regarded as obligate photoautotrophs, some species are known to be mixotrophic or heterotrophic including ciliated protozoa and some dinoflagellates. Since phytoplankton growth is controlled by a combination of temperature and the availability of light and nutrients (nitrogen, phosphate, silicate and iron), which are in-turn controlled by physical processes such as ocean circulation, mixed layer dynamics and the solar cycle (Behrenfield *et al.*, 2006), the potential effects of climate change on plankton communities and consequences for marine food webs and ecosystem function are considerable, yet remain largely unknown. However, in order to identify the biological signals generated by human-induced environmental change, it is imperative to collect and analyse long-term data sets so as to describe the underlying patterns due

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to natural seasonal and inter-annual variability. Only then can the effects of climate change be clearly distinguished from the natural variability.

Since 1992, samples for phytoplankton community structure have been collected weekly (weather permitting) from the L4 time-series site in the Western English Channel. These samples provide a comprehensive temporal and seasonal data set of the abundance and floristic composition. Station L4 is characteristic of temperate coastal waters which are well mixed during the autumn and winter months when sea surface temperatures (SST) are ca. 8°C and nutrients are relatively abundant. During spring and summer, weak stratification of the water column is accompanied by a decline in nutrient concentrations and an increase in SST which typically peaks at ca. 18°C (www.westernchannelobservatory.org.uk/data). Given that climate warming is expected to reduce nutrient availability and enhance water column stratification thus favouring species better able to maintain their position in the euphotic zone (Falkowski and Oliver, 2007; Winder *et al.*, 2009), this paper aims to quantify and describe the seasonal and inter-annual phytoplankton dynamics in order to address the hypothesis that phytoplankton communities at L4, which have historically been dominated by diatoms, are gradually changing to those dominated by other phytoplankton groups.

METHOD

Sampling and enumeration of phytoplankton

Weekly phytoplankton samples were collected from the Western Channel Observatory (WCO) (www.westernchannelobservatory.org.uk) long-term monitoring station L4 (50° 15.00′N, 4° 13.02′W) between October 1992 and December 2007. Water was sampled from a depth of 10 m using a 10 L Niskin bottle. A 200 mL subsample was then removed from the bottle and immediately fixed with 2% (final concentration) Lugol's iodine solution (Throndsen, 1978). A second 200 mL sub-sample was then taken and preserved with neutral formaldehyde for the enumeration of coccolithophores. Samples were returned to Plymouth Marine Laboratory and stored in cool, dark conditions until analysis using light microscopy and the Utermöhl counting technique (Utermöhl, 1958). Samples were gently homogenized before settling a 50 mL subsample from the Lugol's-preserved sample, and a 100 mL subsample from the formaldehyde-preserved sample. Subsamples were settled for >48 h and all cells >2 μm were identified, where possible to species level, and enumerated at either ×200 or ×400 magnification using a Leica DM IRB inverted microscope. Cells with a mean diameter of between 2 and 10 μm and that had recognizable flagellae and/or plastids (excluding diatoms and dinoflagellates) were categorized as "phyto-flagellates" (Holligan and Harbour, 1977; Boalch *et al.*, 1978). Cells were divided into seven functional groups; phytoflagellates, diatoms, *Phaeocystis*, coccolithophorids, dinoflagellates, heterotrophic dinoflagellates and ciliates. Further details on the Western Channel Observatory and the time-series station L4 are provided by Smyth *et al.* (Smyth *et al.*, 2010) for the environmental parameters and Eloire *et al.* (Eloire *et al.*, 2010) for the mesozooplankton.

Data analysis

Weekly abundances from the whole time-series (Fig. 1) were averaged to elucidate the average seasonal cycle of each functional group and SST (Fig. 2). The overall average abundance and standard deviation of each species/genus and group over the time-series were calculated from monthly averages, including interpolated values for missing dates between October 1994 and May 1995. The relative contribution of each species/genus to its group, calculated for the entire time-series, was used to determine its ranking and the cumulative sum of the percentage of the total abundance at each rank (Table I).

Variation in species composition was analysed using non-parametric multivariate methods (Clarke, 1993; Clarke and Warwick, 1994, 2001). Abundances of three groups (total phytoplankton, diatoms and dinoflagellates) were averaged within months within years, and the resulting averages were $\log(n + 1)$ transformed to down-weight contributions to inter-sample similarities from numerically dominant species. Inter-sample similarities were calculated using the Bray–Curtis coefficient. Tests for differences between years and between months were conducted using analysis of similarities (ANOSIM) test for two-way crossed design with no replication (Clarke and Warwick, 1994, 2001) (Table II). Inter-sample similarities were visualized using non-metric multidimensional scaling ordination (NMDS) (Fig. 3), a technique which aims to produce a "map" in a predefined number of dimensions (two in this case) in which samples are represented by points and distances between points in the map retain the rank order of similarities between samples in the similarity matrix. How well the technique succeeded was assessed using Kruskal's stress formula 1 (Clarke, 1993).

A monthly abundance anomaly for each month of the time series was obtained using the following

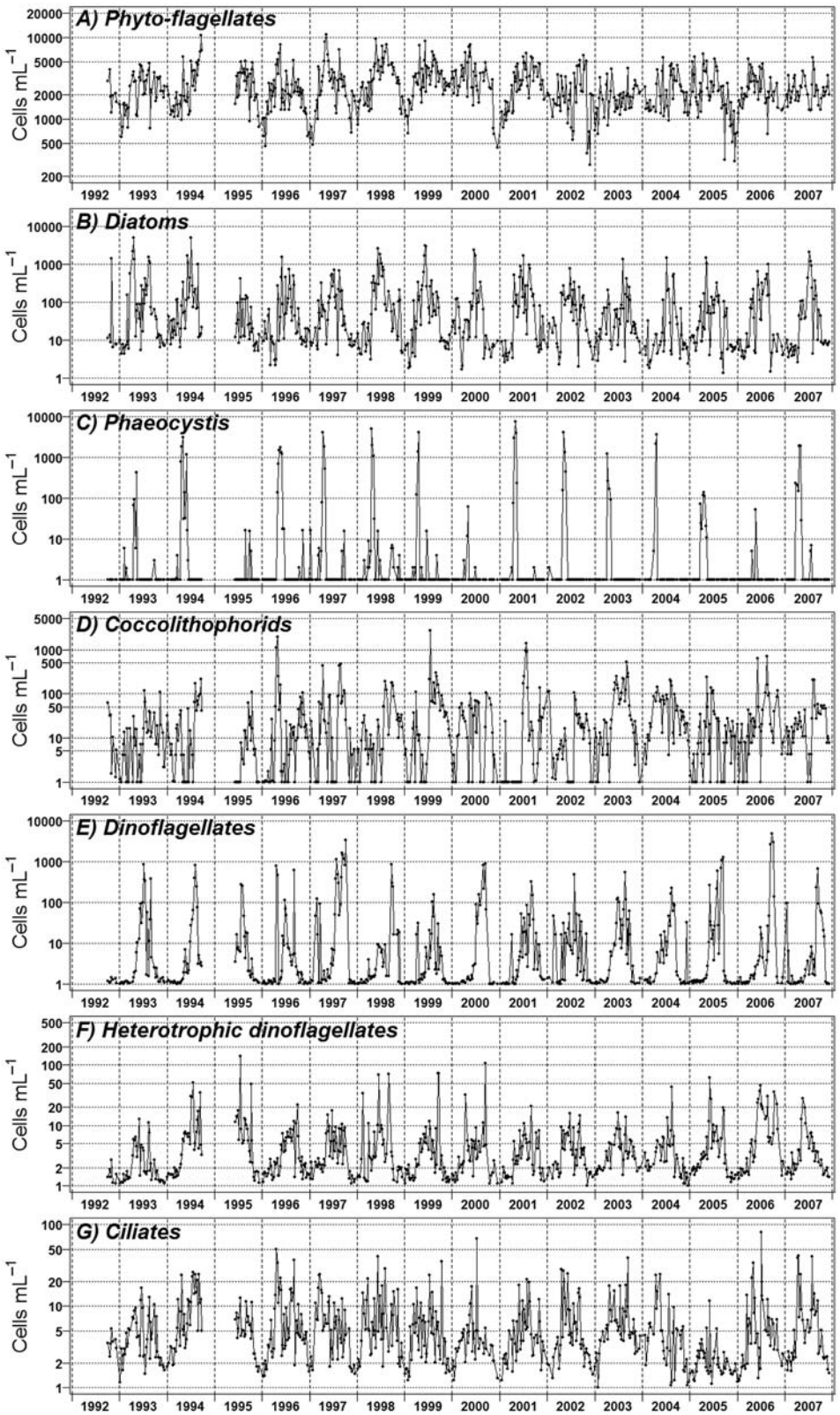

Fig. 1. Abundance (log scale cells mL^{-1}) of (**A**) phyto-flagellates, (**B**) diatoms, (**C**) *Phaeocystis*, (**D**) coccolithophorids, (**E**) dinoflagellates, (**F**) heterotrophic dinoflagellates and (**G**) ciliates recorded between 1992 and 2007.

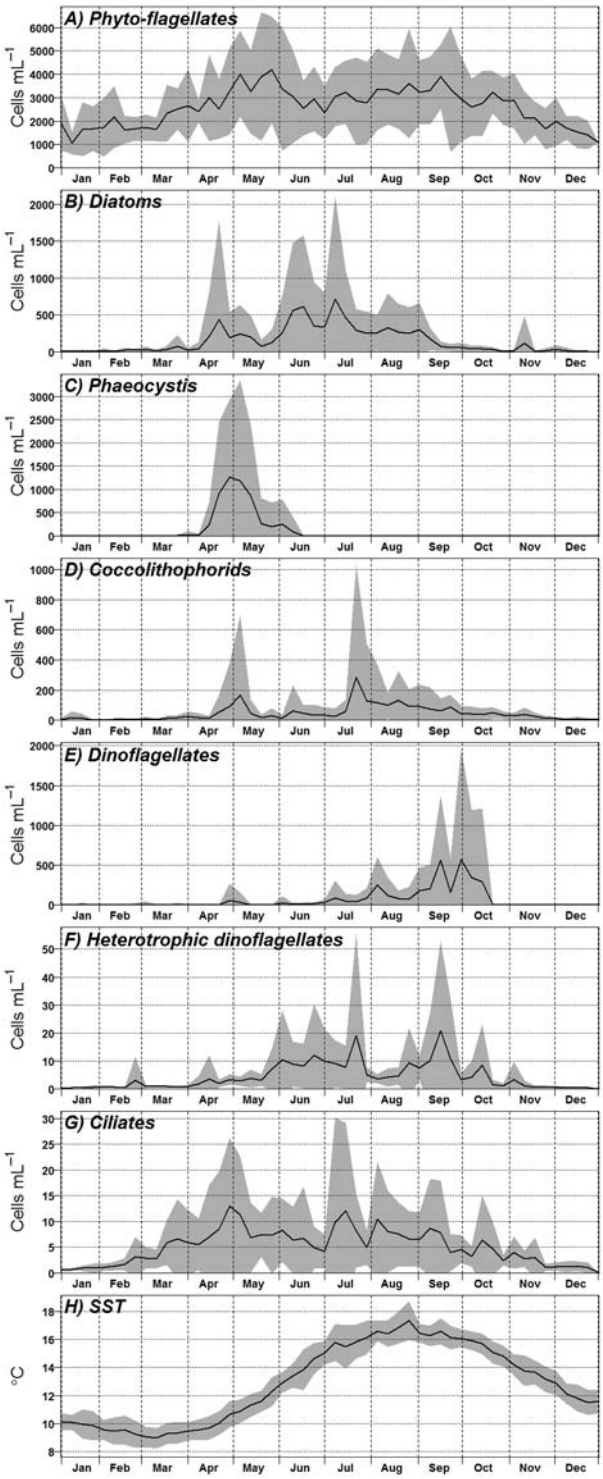

Fig. 2. Seasonal patterns in mean monthly abundance (cells mL^{-1}) of (**A**) phyto-flagellates, (**B**) diatoms, (**C**) *Phaeocystis*, (**D**) coccolithophorids, (**E**) dinoflagellates, (**F**) heterotrophic dinoflagellates, (**G**) ciliates and (**H**) weekly average of SST. Black line and shaded area represents average and standard deviation in abundance, respectively, over the 15-year time-series.

formula:

$$x'_{m,y} = \frac{x_{m,y} - \bar{x}_m}{\sigma(x_m)}$$

where m corresponds to the month (m: 1 = January, 2 = February, ..., 12 = December) and y the year; $x'_{m,y}$ is the monthly anomaly of the month m of the year y; $x_{m,y}$ is the monthly average abundance of the month m of the year y; $\bar{x}_m$ is the average abundance and $\sigma(x_m)$ the standard deviation for the month m over the entire time series. Thus, a positive anomaly means that the observed value was higher than the overall average for that month, and vice versa (Fig. 5).

Trends for the monthly anomalies and $\log_{10}$-transformed monthly averages were obtained by applying a type I linear model. Prior to testing the significance of the trend slope, a Durbin–Watson test to detect autocorrelation in the residuals of the regression analysis was performed (MacKenzie and Köster, 2004). When autocorrelation was present, the effective number of independent values used in the significance testing was adjusted using the following formula:

$$n_{\text{eff}} \approx n_t \frac{1 - r_1}{1 + r_1}$$

where n_{eff} is the effective number of independent values, n_t is the total number of values and R_1 is the lag-1 temporal autocorrelation coefficient (Quenouille, 1952; Hays *et al.*, 1993; Pyper and Peterman, 1998, Santer *et al.*, 2000). A Student's *t*-test was used to determine whether the slope of the linear model was significantly different from 0 and for each significant trend (P-value < 0.1), the overall change in abundance over the 15 years was estimated in term of abundance (cells mL^{-1}) and in term of percentage of the overall average abundance, using the slope from the regression analysis of the $\log_{10}$-transformed monthly averages (Table I).

RESULTS

Total phytoplankton abundance averaged 3196 cells mL^{-1} (SD 2186 cells mL^{-1}) during the time-series. There were significant seasonal and inter-annual changes in phytoplankton abundance and composition (Table II). However, the values of the R-statistic demonstrate that the patterns of seasonal change were greater than the inter-annual variability in the phytoplankton community. The tight clustering of winter samples (March to November) in the NMDS plot (Fig. 3A) shows that the winter community was relatively stable. During the

Table I: Statistics of the different functional groups and corresponding dominant species most responsible for patterns of abundance observed throughout the 15-year time-series

						Monthly anomalies				Monthly averages [$\log_{10}(N+1)$]					
Time series (1993–2007)	Average abundance (cell mL^{-1})	SD (cell mL^{-1})	Relative contribution (%)	Cumulative contribution (%)	Month(s) of maximum abundance	DW statistic	DW *P*-value	Trend *P*-value	Trend slope	DW statistic	DW *P*-value	Trend *P*-value	Trend slope	Change over 15 years (cells mL^{-1})	Change over 15 years as percentage of the average abundance (%)
A) Phyto-flagellates	2593.65	1238.60	86.98	–	4–10	2.18	0.233	0.339	−0.0013	2.11	0.481	0.367	−0.0003		
B) Diatoms	150.39	345.33	5.04	–	4–8	1.94	0.699	0.014	−0.0034	1.80	0.174	0.070	−0.0018	−30.86	−20.5
Pseudo-nitzschia delicatissima	29.48	135.70	19.61	19.61	6	2.01	0.957	0.287	0.0015	1.97	0.822	0.475	0.0007		
Chaetoceros socialis	20.46	205.31	13.60	33.21	4	1.98	0.909	0.052	−0.0028	1.93	0.599	0.033	−0.0016	−1.19	−5.8
Chaetoceros similis	16.32	134.27	10.85	44.06	7	2.01	0.945	<0.001	−0.0052	1.77	0.114	0.021	−0.0017	−1.15	−7.1
Leptocylindrus minimus	16.26	87.19	10.81	54.87	6	1.98	0.916	0.176	0.0022	1.91	0.530	0.381	0.0008		
Leptocylindrus danicus	9.18	29.74	6.10	60.97	7–8	1.98	0.871	0.349	0.0013	1.80	0.169	0.921	−0.0001		
Thalassiosira spp. (4 μm)	4.89	12.71	3.25	64.22	Irregular	2.05	0.750	0.158	−0.0020	2.00	0.986	0.024	−0.0017	−1.41	−28.9
Chaetoceros debilis	5.49	48.79	3.65	67.87	7	1.97	0.838	0.001	0.0046	2.00	0.983	0.020	0.0014	0.90	16.5
Skeletonema costatum	5.65	38.27	3.76	71.63	5	2.01	0.970	0.993	−0.00001	2.03	0.855	0.292	−0.0007		
Guinardia delicatula	4.34	10.16	2.88	74.51	4–5	1.99	0.917	0.868	−0.0002	1.86	0.341	0.348	−0.0006		
Chaetoceros simplex	3.91	20.84	2.60	77.12	8	2.04	0.789	0.158	−0.0020	2.07	0.660	0.001	−0.0020	−1.19	−30.5
C) Phaeocystis	101.83	352.99	3.41	–	4–5	1.84	0.310	0.039	−0.0030	1.84	0.267	0.091	−0.0022	−2.59	−2.5
D) Coccolithophorids	44.21	98.40	1.48	–	4–9	1.98	0.872	0.125	0.0021	1.92	0.593	0.041	0.0019	12.32	27.9
E) Dinoflagellates	81.91	338.09	2.75	–	8–10	2.00	0.975	0.719	−0.0005	1.88	0.396	0.877	−0.0002		
Prorocentrum minimum	32.65	208.08	39.86	39.86	9	1.98	0.867	0.012	0.0035	1.82	0.212	0.013	0.0023	1.72	5.3
Prorocentrum balticum	25.36	257.58	30.97	70.82	9–10	2.01	0.993	0.173	−0.0030	1.85	0.298	0.137	−0.0008		
Karenia mikimotoi	12.87	51.26	15.71	86.53	7–8	1.97	0.861	0.234	−0.0017	1.78	0.130	0.465	−0.0006		
Heterocapsa minuta	6.81	39.95	8.32	94.85	4/8	1.97	0.840	0.270	−0.0015	1.98	0.854	0.031	−0.0014	−0.88	−12.9
Scripsiella trochoidea	1.57	5.29	1.92	96.77	6	1.97	0.850	0.537	0.0009	1.95	0.721	0.542	−0.0003		
Heterocapsa niei	0.89	4.48	1.08	97.85	8	2.08	0.639	0.253	0.0017	2.10	0.530	0.411	0.0003		
Prorocentrum dentatum	0.48	4.76	0.59	98.43	9–10	1.72	0.299	0.200	−0.0036	1.82	0.204	0.172	−0.0003		
Mesoporous perforatus	0.42	2.39	0.52	98.95	6	1.93	0.615	0.222	−0.0017	1.96	0.784	0.938	−0.00002		
Prorocentrum micans	0.34	1.16	0.42	99.37	6	2.04	0.821	0.121	0.0023	1.96	0.740	0.123	0.0004		
Gymnodinium pygmaeum	0.26	2.25	0.32	99.69	7	2.05	0.762	0.196	0.0020	2.00	0.990	0.560	0.0001		
F) Heterotrophic dinoflagellates	4.56	7.24	0.15	–	6–9	2.01	0.966	0.058	0.0026	2.01	0.996	0.447	0.0004		
Gyrodinium spp.	1.40	3.27	30.71	30.71	9	1.99	0.949	0.004	0.0039	2.03	0.873	0.088	0.0006	0.47	33.5
Gymnodinium spp.	0.82	3.70	18.08	48.79	6–7	2.00	0.976	0.236	0.0016	2.04	0.797	0.595	−0.0002		
Katodinium spp.	0.82	1.96	17.90	66.69	5–8	2.02	0.928	0.001	0.0045	1.97	0.821	0.076	0.0006	0.34	42.0
Torodinium robustum	0.12	0.14	2.62	69.30	4–9	2.09	0.542	<0.001	0.0068	2.07	0.674	<0.001	0.0003	0.14	121.3
Torodinium teredo	0.07	0.10	1.58	70.89	5–8	2.06	0.717	0.001	−0.0047	2.06	0.690	0.023	−0.0001	−0.05	−72.7
Protoperidinium bipes	0.07	0.19	1.54	72.43	4–6	2.04	0.816	0.603	−0.0007	2.06	0.704	0.029	−0.0002	−0.07	−102.9
Protoperidinium steinii	0.07	0.25	1.52	73.95	5–6	1.92	0.569	0.001	0.0049	1.87	0.377	0.043	0.0002	0.07	106.2
Oxytoxum spp.	0.07	0.71	1.46	75.41	8	1.95	0.786	0.415	0.0015	2.00	0.978	0.846	0.00002		
Pronoctiluca pelagica	0.05	0.50	1.09	76.50	6	2.08	0.593	<0.001	0.0086	2.00	0.989	0.012	0.0003	0.11	218.6
Diplopsalis spp.	0.04	0.17	0.77	77.27	7	2.04	0.790	0.155	−0.0020	2.01	0.926	0.119	−0.0001		
G) Ciliates	5.18	5.09	0.17	–	4–9	2.02	0.934	0.087	−0.0024	1.93	0.611	0.112	−0.0007		
Strombidium spp.	3.52	3.81	67.82	67.82	4/7	2.04	0.806	0.008	−0.0037	2.04	0.810	0.008	−0.0011	−1.62	−46.1
Myrionecta spp.	1.40	2.15	27.03	94.85	4–5	2.01	0.968	0.007	−0.0038	1.94	0.647	0.079	−0.0006	−0.52	−36.9
Uronema spp.	0.04	0.38	0.83	95.69	4	2.10	0.525	<0.001	0.0087	2.00	0.978	0.005	0.0002	0.10	238.3
Balanian spp.	0.03	0.10	0.53	96.21	7–9	2.43[a]	0.004[a]	<0.001[a]	0.0101	2.19	0.210	<0.001	0.0003	0.12	435.3
Favella spp.	0.03	0.20	0.51	96.72	7	2.12	0.638	<0.001	0.0092	2.00	0.974	0.007	0.0002	0.08	299.8
Salpingella spp.	0.02	0.12	0.46	97.18	6	2.18	0.244	<0.001	0.0096	2.07	0.648	<0.001	0.0002	0.09	397.0
Askenasia stellaris	0.01	0.08	0.27	97.46	7	2.05	0.863	<0.001	0.0087	1.87	0.359	<0.001	0.0001	0.06	434.6
Laboea strobila	0.01	0.09	0.25	97.71	7	2.29[a]	0.096[a]	<0.001[a]	0.0090	2.03	0.858	0.001	0.0001	0.05	408.4
Tontonia spp.	0.01	0.11	0.25	97.96	8	2.22	0.179	<0.001	0.0080	1.66[a]	0.021[a]	0.107[a]	0.0001		

Continued

Table I: Continued

Time series (1993–2007)	Average abundance (cell mL^{-1})	SD (cell mL^{-1})	Relative contribution (%)	Cumulative contribution (%)	Month(s) of maximum abundance	Monthly anomalies				Monthly averages [$\log_{10}(N+1)$]				Change over 15 years (cells mL^{-1})	Change over 15 years as percentage of the average abundance (%)
						DW statistic	DW *P*-value	Trend *P*-value	Trend slope	DW statistic	DW *P*-value	Trend *P*-value	Trend slope		
Rhabdoaskenasia spp.	0.01	0.04	0.19	98.15	8–10	2.12	0.420	<0.001	0.0083	2.14	0.353	<0.001	0.0001	0.04	442.1

The average abundance, standard deviation and relative contribution were estimated over the period 1993–2007. The cumulative contributions of the 10 dominant species were estimated within each functional group. The month(s) corresponding to the maximum abundance were determined by visual examination of the seasonal cycle (where 1 = January, …, 12 = December). DW statistic and DW *P*-value correspond to the results of the Durbin–Watson test (a indicates a significant autocorrelation in which case the effective number of independent values has been adjusted). Trend *P*-value gives the significance of the slope (Trend slope) of the regression analysis (highlighted in grey are the non-significant trend with *P*-value > 0.1). Change in abundance over the 15 years was calculated for each significant trend using the slope from the regression analysis of the monthly averages, and this value was compared with the overall average abundance.

Table II: Results from two-way crossed ANOSIM tests for differences among years (between months) and months (between years) on Bray–Curtis similarities calculated from log(n + 1) transformed average abundance of total phytoplankton, diatoms, dinoflagellates

	Difference between years		Difference between months	
	R	*P*-value	R	*P*-value
Total phytoplankton	0.181	<0.001	0.557	<0.001
Diatoms	0.057	0.007	0.447	<0.001
Dinoflagellates	0.079	<0.001	0.354	<0.001

spring (April to May), there was an abrupt change in the species composition, which was relatively varied during the summer months (June to September) until it returned to the winter composition in October (Fig. 3A).

Phyto-flagellates, excluding *Phaeocystis*, were numerically dominant throughout the time-series, averaging 2785 cells mL^{-1} (SD 1720 cells mL^{-1}) and accounting for, on average, 87% of the total phytoplankton abundance. These small cells were recorded throughout the year (Fig. 1A) and were generally more abundant between April and November (Fig. 2A). Due to the difficulties of accurate identification of flagellates in Lugol's-preserved samples, this group was classified according to size and it was the small cells, typically between 2 and 4 μm in size, which were most numerous (average of 63%). Between 1993 and 1996, phyto-flagellates averaged 2668 cells mL^{-1} (SD 1702 cells mL^{-1}) (Fig. 4A) with few, short-lived intense peaks >3000 cells mL^{-1} between April and October (Fig. 1A). A change was observed in 1997 when the intensity and duration of phyto-flagellates increased, resulting in a shift towards more positive anomalies (Fig. 5A). This pattern continued between 1997 and 2001 when cell concentrations >3000 cells mL^{-1} were recorded as early as January and persisted into November (Fig. 1A), resulting in an annual average of 3379 cells mL^{-1} (SD 2020 cells mL^{-1}) (Fig. 4A) and few negative anomalies during winter months (Fig. 5A). In comparison, the duration and intensity of peaks in abundance were lower in 2002 and this continued into 2007 (Fig. 1A). The average annual abundance for this period was therefore lower than the period between 1997 and 2001, with a mean concentration of 2268 cells mL^{-1} (SD 155 cells mL^{-1}) (Fig. 4A), and resulted in fewer positive anomalies (Fig. 5A). Despite these

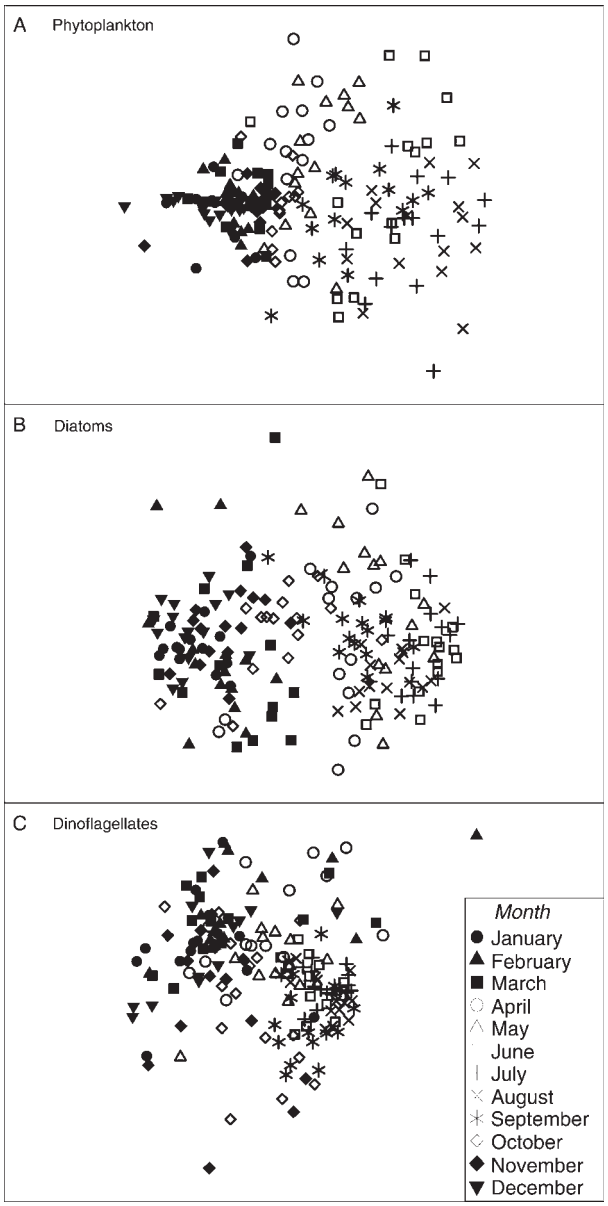

Fig. 3. Non-metric multidimensional scaling ordinations based on Bray–Curtis similarities calculated from log $(n+1)$ transformed monthly averaged densities of taxa. (**A**) Total phytoplankton, (**B**) diatoms and (**C**) dinoflagellates. Sample locations are coded with symbols denoting the months they represent. Stress = 0.2.

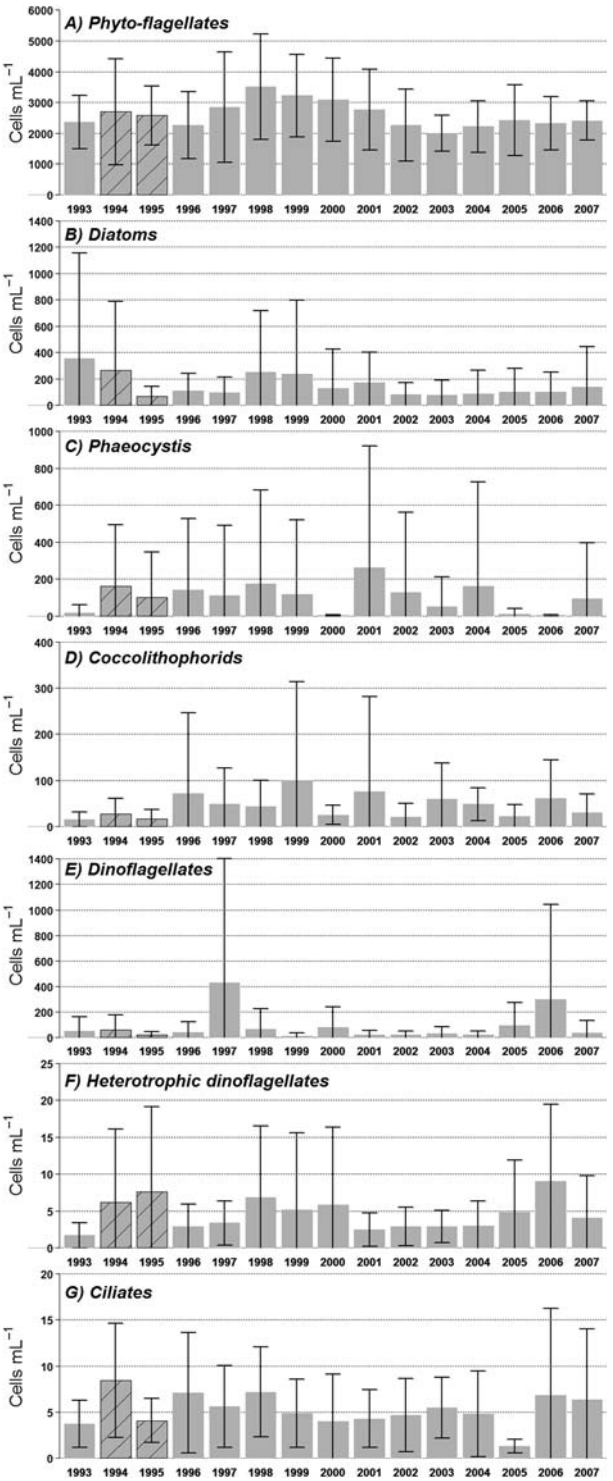

Fig. 4. Annual average abundance (cells mL^{-1}), calculated from monthly averages for the different functional groups over the period 1993–2007 (hatched areas indicates years for which some of the monthly averages were interpolated).

distinct periods of variability, there was no significant trend in phyto-flagellate abundance during the time-series.

Abundance of diatoms averaged 167 cells mL^{-1} (SD 456 cells mL^{-1}) throughout the time-series, which was equivalent to ca. 5% of the total phytoplankton abundance. Diatoms exhibited seasonal and inter-annual

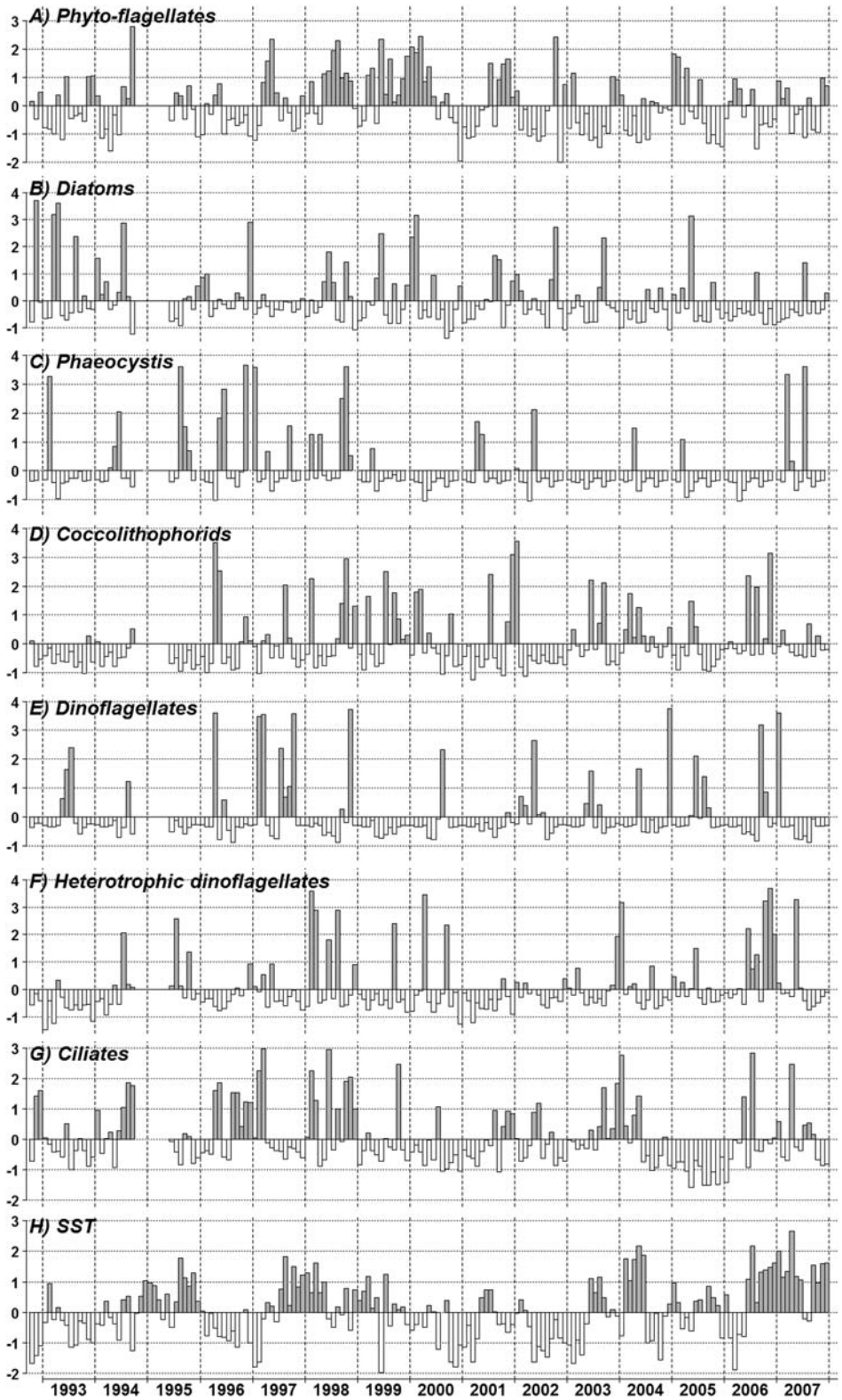

Fig. 5. Monthly anomalies (standardized units) of the different functional groups and SST over the time series.

variability (Fig. 1B). Results from the ANOSIM tests showed significant differences in community structure associated with seasonal patterns and a significant, albeit much lesser, difference between years (Table II). Changes in abundance were most pronounced during the development of the spring bloom between late March and early May (Fig. 2B) when the composition shifted from the winter community (Fig. 3B) dominated by large centric diatoms (*Odontella mobiliensis* and *Coscinodiscus* spp.) and benthic diatoms (*Paralia sulcata* and *Podosira stelligera*) towards a community numerically dominated by either *Chaetoceros* spp., *Thalassiosira* spp. or *Skeletonema costatum* (Table I). A further change in the diatom community occurred during the summer months when a second, more intense bloom of smaller pennate and centric diatoms such as *Pseudo-nitzschia* spp. and *Leptocylindrus* spp. exceeded concentrations of 1000 cells mL^{-1} (Fig. 1B). A gradual decline in the abundance of these species during the autumn reduced overall diatom concentrations back to low abundances typical of winter conditions (Fig. 2B). The differences and variability between winter and spring/summer diatom composition are clearly demonstrated in Fig. 3B. Of the 125 diatom taxa recorded at L4, the pennate *Pseudo-nitzschia delicatissima* was, on average, the most dominant contributing almost 20% of the average abundance and is indicative of the intensity of diatom blooms (Table I). The other dominant species were all chain-forming centric diatoms of the genera *Chaetoceros, Leptocylindrus, Guinardia, Thalassiosira* and *Skeletonema*. These "top 10" species accounted for almost 80% of the cumulative abundance of diatoms during the 15-year study (Table I). Despite these seasonal patterns in abundance and taxonomic composition being evident every year, inter-annual variability was considerable (Fig. 4B) as variations in the timing and intensity of spring or summer blooms caused distinct patterns in anomalies (Fig. 5B). Diatoms were most abundant (average 342 cells mL^{-1} and SD 872 cells mL^{-1}) at the beginning of the study giving rise to strong positive anomalies (Fig. 5B). This was partly due to an intense spring bloom of *Chaetoceros socialis* in 1993 and summer bloom of *Chaetoceros similis* in 1994 when concentrations exceeded 4000 cells mL^{-1} (Fig. 1B). A break in sampling unfortunately missed the spring peak in 1995, but diatoms were also abundant in 1996 (115 cells mL^{-1} and SD 261 cells mL^{-1}), albeit at lower concentrations than previously recorded (Fig. 4B). Concentrations in 1997 were consistently low (<700 cells mL^{-1}) with no distinct spring or summer maxima (Fig. 1B). However, blooms were regularly detected, although later in the spring or early summer, between 1998 and 2002, as represented by positive monthly anomalies (Fig. 5B) when annual abundance averaged 193 cells mL^{-1} (SD 460 cells mL^{-1}). In contrast, the spring bloom of 2003 was minor and brief and abundance did not peak until the late summer and was short-lived. This variable pattern continued for the remainder of the study as shown by a period of negative anomalies (Fig. 5B). The one exception during this time was an intense, but brief, spring bloom of *Skeletonema costatum* in 2005 (average 686 cells mL^{-1} and SD 542 cells mL^{-1}). Regardless of the seasonal and inter-annual variability, diatoms decreased significantly ($P < 0.05$) over the time-series (Table I).

Occurrence of the prymnesiophyte *Phaeocystis* was restricted to the spring when "blooms" typically occurred during May (Fig. 2C) when concentrations often exceeded 1000 cells mL^{-1} (Fig. 1C). On average, *Phaeocystis* contributed 4% of the total phytoplankton abundance during the time-series, with a mean concentration of 113 cells mL^{-1} (SD 593 cells mL^{-1}). During the first 7 years of the study, *Phaeocystis* blooms were reported each year when concentrations averaged 126 cells mL^{-1} (SD 558 cells mL^{-1}) and persisted for between 4 and 7 weeks (Fig. 1C) as demonstrated by several months of positive anomalies in abundance between 1994 and 1998 (Fig. 5C). However, since 1999, blooms only lasted for brief periods of 2 or 3 weeks, and in some cases were barely detected (Fig. 1C). This phase was marked by a period of few small positive anomalies which were interrupted in 2007 when an intense bloom persisted between March and May (Fig. 5C). These patterns of decreasing intensity were supported by an overall decrease in *Phaeocystis* abundance over the time series (Table I).

Coccolithophorids, dominated almost exclusively by *Emiliania huxleyi* (93%), were recorded in low numbers throughout the study (<10 cells mL^{-1}) (Fig. 1D) and typically bloomed (ca. 100 cells mL^{-1}) for a short time in May with a second and more pronounced bloom (>200 cells mL^{-1}) often occurring in late July or August (Fig. 2D). Despite seasonal periods of intense blooms, coccolithophorids accounted for less than 2% of the phytoplankton abundance, averaging 50 cells mL^{-1} (SD 173 cells mL^{-1}) over the time-series (Fig. 4D). Nevertheless, inter-annual variability was substantial (Fig. 1D). Between 1992 and 1995, coccolithophorid blooms were modest (up to 200 cells mL^{-1}). However, an early bloom in 1996 reached concentrations in excess of 1900 cells mL^{-1} and persisted for several weeks resulting in a switch to strong positive anomalies (Fig. 5D). By comparison, the bloom in 1997 was weak (<500 cells mL^{-1}) and short-lived (Fig. 1D). Persistent and relatively intense blooms were again recorded between 1998 and 2001, such as a maximum abundance of 2700 cells mL^{-1}

which was observed in July 1999, resulting in positive anomalies (Fig. 5D). Coccolithophorid abundance in 2002 (<105 cells mL^{-1}) was similar to the low levels found in 1997 (Fig. 1D) resulting in negative anomalies (Fig. 5D). However, the summer of 2003 was characterized by persistent abundances (May to September average 146 cells mL^{-1} and SD 121 cells mL^{-1}) which continued through 2004 (April to September average 80 cells mL^{-1} and SD 54 cells mL^{-1}) (Fig. 1D) resulting in positive anomalies in abundance (Fig. 5D). The remaining 3 years of the study were variable with moderate abundance in 2005 and 2007 (<200 cells mL^{-1}), separated by distinct but brief blooms in 2006 (Fig. 1D). Despite these periods of variability, analysis of the data set suggests an overall trend of increasing coccolithophorid abundance at L4 (Table I).

Dinoflagellate abundance was generally low during the winter and spring when concentrations were typically less than 1 cell mL^{-1} (Fig. 1E). During the summer months, as sea surface temperatures increased (Fig. 2H) dinoflagellates increased in abundance, culminating in intense but brief blooms (>500 cells mL^{-1}) of either *Karenia mikimotoi* or *Prorocentrum* spp. in late summer, before a sharp decline back to pre-bloom levels (Fig. 2E). Summer and winter communities differed in composition but this was less prominent than observed for the total phytoplankton and diatoms (Fig. 3C), as supported by the lower R value for testing differences between months (Table II). *Prorocentrum minimum* and *P. balticum* were, on average, the most dominant species contributing 70%, while *Karenia mikimotoi* accounted for 16% of the average dinoflagellate abundance, respectively (Table I). The remaining "top 10" species belonged to the genera *Prorocentrum, Heterocapsa, Scrippsiella, Mesoporous* and *Gymnodinium* and collectively accounted for more than 99% of the average dinoflagellate abundance. The remaining 29 species contributed less than 1% of the dinoflagellate abundance and this emphasizes the dominance of a few taxa and the intensity of their blooms. Despite these notable bloom events, dinoflagellates accounted for less than 3% of the total phytoplankton abundance, averaging 70 cells mL^{-1} (SD 330 cells mL^{-1}) during the time-series. Inter-annual variability in dinoflagellate abundance was considerable (Fig. 1E) with little or no distinct patterns (Fig. 4E) except for several prominent positive anomalies in 1997 (Fig. 5E) on account of an intense *Prorocentrum balticum* bloom (up to 3360 cells mL^{-1}) and noticeable absence of any positive anomalies in 1999 due to a small summer peak of *Heterocapsa* (155 cells mL^{-1}) with no blooms of either *Karenia mikimotoi* or *Prorocentrum*. Overall, no significant changes in dinoflagellate abundance were observed over the time-series (Table I).

Heterotrophic dinoflagellates are a minor component of the phytoplankton (0.15%) and were, on average, 7-fold lower in abundance than the main group of dinoflagellates, averaging 4.8 cells mL^{-1} (SD 10.9 cells mL^{-1}) (Fig. 1F). Nevertheless, heterotrophic dinoflagellates were more abundant (ca. 40 cells mL^{-1}) between spring and autumn and scarce during the winter with a gradual transition between the two (Fig. 2F). Their seasonal patterns in abundance were similar to those of SST (Fig. 2H). Naked species belonging to the genus *Gyrodinium* and *Gymnodinium* dominated, accounting for nearly 50% of the abundance (Table I). A combination of naked and armoured species made up the remainder of the "top 10" contributing ca. 77% of the cumulative abundance. As with the dinoflagellate group, inter-annual variability was high with alternating periods of positive and negative anomalies (Fig. 5F) and no evidence of long-term changes in abundance (Table I).

Ciliates also constituted a minor component of the phytoplankton (0.17%) and averaged 5.4 cells mL^{-1} (SD 7.7 cells mL^{-1}) (Fig. 1G). The transition in their abundance from low levels during winter to higher levels in spring was gradual with peaks in May and July followed by a decline in winter (Fig. 2G). The genus *Strombidium* dominated the ciliates throughout, accounting for more than 68% of the ciliate abundance, with *Myrionecta* contributing a further 26% (Table I). The remaining eight most common species contributed only 3% (Table I). Ciliate abundance was low throughout 1993 (3.9 cells mL^{-1} and SD 3.5 cells mL^{-1}) (Fig. 4G) as demonstrated by a number of negative anomalies (Fig. 5G). However, ciliates were, on average, twice as abundant in the period between 1994 and 1998 (6.8 cells mL^{-1} and SD 7.6 cells mL^{-1}) (Fig. 4G) highlighting, with one exception in 1995, a period of positive anomalies when ciliates were more numerous and for a longer period each year (Fig. 1G). A third distinct period followed between 1999 and 2002 when ciliates were comparatively rare during the winter months and peaks in abundance during spring or summer were less intense; as such the annual average abundance was lower (4.9 cells mL^{-1} and SD 7.3 cells mL^{-1}) (Fig. 4G) and marked by a period of negative anomalies (Fig. 5G). The abundance of ciliates during the remainder of the time-series was variable. Ciliate concentrations during autumn and winter of 2003 and spring of 2004 were relatively high (Fig. 1G) giving rise to positive anomalies (Fig. 5G) and average concentrations of 5.2 cells mL^{-1} (SD 6.1 cells mL^{-1}) (Fig. 4G). In contrast, ciliates were particularly scarce during 2005 (average 1.3 cells mL^{-1} and SD 1.7 cells mL^{-1}), as demonstrated by a period of strong negative anomalies (Fig. 5G). Numbers of ciliates recovered in 2006 and

2007 (average 7 cells mL^{-1} and SD 12 cells mL^{-1}) with highest abundances recorded during spring and summer (Fig. 1G). No significant changes in the abundance of ciliates were detected across the time-series, although the two most dominant genera, *Strombidium* and *Myrionecta*, were found to be declining while rarer species appeared to be increasing significantly (Table I). These changes may, however, be attributed to the expansion of the number of ciliate species identified during the latter 3 years of the time-series.

DISCUSSION

Analysis of the L4 phytoplankton time-series data set presented in this paper has identified three important elements of community change between 1992 and 2007. First, distinct seasonal patterns have been identified in the abundance of all of the seven phytoplankton groups. Secondly, substantial inter-annual variability in the floristic composition of the phytoplankton community was observed. Thirdly, significant long-term trends were found with the average abundance of diatoms and *Phaeocystis* decreasing and the average abundances of coccolithophorids and the dinoflagellate *Prorocentrum minimum* increasing over the study period.

The strong seasonal succession observed in the composition of the phytoplankton community between 1992 and 2007 is in-keeping with previous findings made over the past ca. 100 years from samples collected from stations L4 or E1 in the Western English Channel (e.g. Lebour, 1917; Harvey *et al.*, 1935; Holligan and Harbour, 1977; Boalch *et al.*, 1987; Maddock *et al.*, 1989). Consistent with the findings of Holligan and Harbour (Holligan and Harbour, 1977) and Boalch *et al.* (Boalch *et al.*, 1978), the phyto-flagellates in the current study were numerically the most dominant phytoplankton and showed relatively little seasonal variability. This is likely to be due to tight grazing control (Holligan and Harbour, 1977; Stelfox-Widdicombe *et al.*, 2004), e.g. ciliates are known to prey upon the nanoplankton ($<20\,\mu m$ in size) (Rassoulzadegan *et al.*, 1988). In the current study, the seasonal patterns of ciliate abundance were similar to the phyto-flagellates with slightly higher concentrations recorded between April and November and are comparable to the patterns observed by Lebour (Lebour, 1917). The most pronounced shift in the phytoplankton community occurred between March and May when day length and light intensity increased and by virtue of high maximum growth rates diatoms such as *Chaetoceros* and *Thalassiosira* flourished. Diatoms have regularly dominated the spring period in the Western English Channel (e.g. Lebour, 1917; Harvey *et al.*, 1935; Holligan and Harbour, 1977; Boalch *et al.*, 1978), but, as was seen in the current and previous (e.g. Harvey *et al.*, 1935) studies, the dominant "typical" spring species varied considerably from site to site and year to year. For example, *Skeletonema costatum* was recorded in abundance (>30 cells mL^{-1}) during the spring of 1916 and 1933 at station L4 (Lebour, 1917; Harvey *et al.*, 1935) and commonly found in waters close to Plymouth (Boalch *et al.*, 1978) yet during the current study *Skeletonema* was only recorded in concentrations >30 cells mL^{-1} during the spring of 1995. Diatoms belonging to the genus *Chaetoceros* and *Thalassiosira* have, however, frequently been observed to be abundant during spring in both the past (e.g. Lebour, 1917; Harvey *et al.*, 1935; Holligan and Harbour, 1977) and the present study.

After the initial outburst of diatoms, and in line with the findings reported by Lebour (Lebour, 1917), *Phaeocystis* co-occurred or followed the spring diatom peak in May when single flagellate forms, typically ca. 5 μm in size, developed into colonies up to 10 mm in diameter (e.g. Gieskes and Kraay, 1975). Colonies are commonly found in net samples but less frequently in the water samples (Lebour, 1917) and as such, *Phaeocystis* is likely to be under-represented in the current study. During the summer months a second more pronounced diatom bloom, dominated by smaller species of the genus *Rhizosolenia* and *Pseudo-Nitzschia*, occurred between June and July. This is contrary to previous findings (e.g. Lebour, 1917; Harvey *et al.*, 1935; Holligan and Harbour, 1977; Boalch *et al.*, 1978). Although a second diatom bloom is well documented at L4 and E1, these were reported to occur during the autumn when phytoplankton production was lower than the spring (Boalch *et al.*, 1978). In addition, the community composition of the late summer blooms observed during the current study and that of the autumn blooms described in previous studies also appears to be different.

During the summer months, thermal stratification and increased irradiance resulted in an increase in coccolithophorid abundance, of which *Emiliania huxleyi* accounted for ca. 90%, which supports the findings of Lebour (Lebour, 1917). Coccolithophorids rapidly rose to dominance relative to the diatoms (Cermeño *et al.*, 2008) with a pronounced *E. huxleyi* bloom occurring in late summer. In the current study, the autumn was dominated by a bloom of dinoflagellates, in particular potentially harmful species of the genus *Prorocentrum*, *Karenia* and *Dinophysis* which favoured the warm, stratified conditions following the summer months. At the beginning of the time-series, *Karenia mikimotoi* (formerly classified as *Gyrodinium aureolum*) regularly dominated these blooms but latterly *Prorocentrum balticum* and *P. minimum* were most numerous during the late summer/early autumn at L4. These findings are

surprising as blooms of dinoflagellates were previously observed during the summer (e.g. Harvey *et al.*, 1935; Holligan and Harbour, 1977; Maddock *et al.*, 1981) and not the autumn, when instead diatoms were the dominant phytoplankton group. This change in the seasonal succession of the phytoplankton community might be attributed in part to the observed 0.5°C warming in the Western English Channel over the past 50 years (Smyth *et al.*, 2010). Certainly, heterotrophic dinoflagellates were, like their autotrophic counterparts, most prominent during the summer and autumn months, albeit at much lower concentrations. The occurrence of species such as *Protoperidinium* spp. and *Gyrodinium* spp. in spring and summer months is expected to be a response to the increase in diatoms, since diatoms are a good food source for some dinoflagellates (e.g. Stelfox-Widdicombe *et al.*, 2004). Renewed mixing and cooler temperatures in the autumn were responsible for driving total phytoplankton abundance back to low winter levels when vigorous physical mixing of the water column allows larger diatoms, as found by Lebour (Lebour, 1917), including benthic species, to be maintained in surface waters.

While the analysis of the current time-series shows that the patterns of seasonal succession were generally, but not always, consistent year-on-year, the inter-annual variability in species composition and in the magnitude of the phytoplankton "blooms" was considerable. This lends support to the findings from previous studies quantifying the phytoplankton communities in the Western English Channel (Lebour, 1917; Harvey *et al.*, 1935; Boalch *et al.*, 1978; Maddock *et al.*, 1989). Of all the years in the current study, 1999 appears to be something of an anomaly as the dinoflagellates *Karenia mikimotoi* and *Prorocentrum minimum* did not bloom, yet this year also saw the highest recorded abundance of coccolithophorids and the third highest recorded abundances of diatoms and phyto-flagellates (Figs 1 and 4). This coincided with a period of transition from low to high zooplankton abundance (Eloire *et al.*, 2010). Taken as a single year, the phytoplankton community is markedly different from other years in the study. This demonstrates the potential pitfalls inherent in some previous studies (e.g. Lebour, 1917, Harvey *et al*, 1935) which have compared data from a limited number of years. In such studies, the impact of an "unusual" year sampled by chance can have a large and erroneous impact on the study's conclusion. This further emphasizes the importance of continuous, long-term data collections when attempting to differentiate progressive changes in community structure due to environmental change from the underlying patterns of natural, temporal variability.

Analysis of the entire 15-year time-series (1992–2007) demonstrates that some elements of the composition of the phytoplankton community have changed significantly. This would seem to provide support for the hypothesis that in the English Channel phytoplankton, communities traditionally dominated by diatoms are gradually changing to those dominated by other groups. These long-term trends in phytoplankton community composition and patterns of species dominance may have important ecological consequences. Phytoplankton represent the basis of the marine food web providing nutrition for higher trophic levels and as such have an essential ecological function for all aquatic life (Doney, 2006). The abundance, composition and seasonality of phytoplankton communities can ultimately determine the structure and function of marine ecosystems (Edwards and Richardson, 2004). As zooplankton rely on the occurrence and magnitude of phytoplankton bloom events, particularly during the spring, a change from diatoms to a potentially harmful dinoflagellate species, such as *Prorocentrum minimum*, as identified in the current time-series, could directly influence higher trophic levels (Landsberg, 2002). Many meroplanktonic larvae are released in response to phytoplankton blooms (Highfield *et al.*, 2010), so changes in phytoplankton communities could alter benthic-pelagic coupling and disrupt life-cycles of key benthic species. In addition, any increase in these potentially nuisance species in coastal areas could have societal implications with respect to the viability of fisheries and impacts on human health.

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REFERENCES

Behrenfield, M. J., O'Malley, R. T., Siegel, D. A. *et al.* (2006) Climate-driven trends in contemporary ocean productivity. *Nature*, **444**, 752–755.

Boalch, G. T., Harbour, D. S. and Butler, E. I. (1978) Seasonal phytoplankton production in the western English Channel 1964–1974. *J. Mar. Biol. Assoc. UK*, **58**, 943–953.

Cermeño, P., Dutkiewicz, S., Harris, R. P. *et al.* (2008) The role of the nutricline in regulating the ocean carbon cycle. *PNAS* **105**, 20344–20349.

Clarke, K. R. (1993) Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.*, **18**, 117–143.

Clarke, K. R. and Warwick, R. (1994) Similarity-based testing for community pattern: the 2-way layout with no replication. *Mar. Biol.*, **118**, 167–176.

Clarke, K. R. and Warwick, R. (2001) *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation*, 2nd edn. Primer-E Ltd, Plymouth, UK.

Doney, S. C. (2006) Plankton in a warmer world. *Nature*, **444**, 695–696.

Edwards, M. and Richardson, A. (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, **430**, 881–884.

Edwards, M., Johns, D. G., Beaugrand, G. *et al.* (2008) Ecological Status Report: results from the CPR survey 2006/2007. *SAHFOS Tech. Rep.*, **5**, 1–8.

Eloire, D., Somerfield, P. J., Conway, D. V. P. *et al.* (2010) Temporal variability and community composition of zooplankton at Station L4 in the Western Channel: twenty years of sampling. *J. Plankton Res.*, **32**, 657–679.

Falkowski, P. G. and Oliver, M. J. (2007) Mix and match: how climate selects phytoplankton. *Nat. Rev. Microbiol.*, **5**, 813–819.

Gieskes, W. W. C. and Kraay, G. W. (1975) The phytoplankton spring bloom in Dutch coastal waters of the North Sea. *J. Sea Res.*, **9**, 166–196.

Harvey, H. W., Cooper, L. H. N., Lebour, M. V. *et al.* (1935) Plankton production and its control. *J. Mar. Biol. Assoc. UK*, **20**, 407–441.

Hays, G. C., Carr, M. R. and Taylor, A. H. (1993) The relationship between Gulf Stream position and copepod abundance derived from the Continuous Plankton Recorder Survey: separating biological signal from sampling noise. *J. Plankton Res.*, **15**, 1359–1373.

Highfield, J. M., Eloire, D., Conway, D. V. P. *et al.* (2010) Seasonal dynamics of meroplankton assemblages at Station L4. *J. Plankton Res.*, **32**, 681–691.

Holligan, P. M. and Harbour, D. S. (1977) The vertical distribution and succession of phytoplankton in the western English Channel in 1975 and 1976. *J. Mar. Biol. Assoc. UK*, **57**, 1075–1093.

IPCC (Intergovernmental Panel on Climate Change). (2007) Climate change 2007—the physical science basis. Contribution of working group I to the fourth assessment report of the IPCC. In Solomon, S., Quin, D., Manning, M., Marquis, M., Averyt, K., Tognor, M. M. B., Miller, H. L., Chen, Z. *et al.* (eds), *IPCC*. Cambridge University Press, Cambridge.

Landsberg, J. H. (2002) The effects of harmful algal blooms on aquatic organisms. *Rev. Fish. Sci.*, **10**, 113–390.

Lebour, M. V. (1917) The microplankton of Plymouth Sound from the region beyond the breakwater. *J. Mar. Biol. Assoc. UK*, **11**, 133–182.

MacKenzie, B. R. and Köster, F. W. (2004) Fish production and climate: sprat in the Baltic Sea. *Ecology*, **85**, 784–794.

Maddock, L., Boalch, G. T. and Harbour, D. S. (1981) Populations of phytoplankton in the western English Channel between 1964 and 1974. *J. Mar. Biol. Assoc. UK*, **61**, 565–583.

Maddock, L., Harbour, D. S. and Boalch, G. T. (1989) Seasonal and year-to-year changes in the phytoplankton from the Plymouth area, 1963–1986. *J. Mar. Biol. Assoc. UK*, **69**, 229–224.

Pyper, B. J. and Peterman, R. M. (1998) Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Can. J. Fish. Aquat. Sci.*, **55**, 2127–2140.

Quenouille, N. H. (1952) *Associated Measurements*. Butterworths, 241 pp.

Rassoulzadegan, F., Laval-Peuto, M. and Sheldon, R. W. (1988) Partitioning the food ration of marine ciliates between pico- and nanoplankton. *Hydrobiologia*, **159**, 75–88.

Reid, P. C., Edwards, M., Hunt, H. G. *et al.* (1998) Phytoplankton change in the North Atlantic. *Nature*, **391**, 546.

Sabine, C. L., Feely, R. A., Gruber, N. *et al.* (2004) The oceanic sink for anthropogenic CO_2. *Science*, **305**, 367–371.

Santer, B. D., Wigley, T. M. L., Boyle, J. S. *et al.* (2000) Statistical significance of trends and trend differences in layer-average atmospheric temperature time series. *J. Geophys. Res.*, **105**, 7337–7356.

Smyth, T. J., Fishwick, J. R., Al-Moosawi, L. *et al.* (2010) L4 in context: a broad spatio-temporal view in the Western English Channel Observatory. *J. Plankton Res.*, **32**, 585–601.

Stelfox-Widdicombe, C. E., Archer, S. D., Burkill, P. H. *et al.* (2004) Microzooplankton grazing in *Phaeocystis* and diatom-dominated waters in the southern North Sea in spring. *J. Sea Res.*, **51**, 37–51.

Throndsen, J. (1978) Preservation and storage. In Sournia, A. (ed.), *Phytoplankton Manual*. UNESCO, Paris, pp. 69–74.

Utermöhl, H. (1958) Zur vervollkommnung der quantitativen Phytoplankton Methodik. *Mitteil. Int. Verein. Theor. Angew. Limnol.*, **9**, 1–38.

Winder, M., Reuter, J. E. and Schladow, S. G. (2009) Lake warming favours small-sized planktonic diatom species. *Proc. Royal Soc. B*, **276**, 427–435.