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Temporal variations among planktonic diatom assemblages in a turbulent environment of the southern Strait of Georgia, British Columbia, Canada

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ABSTRACT: We examined the species composition and concentration of planktonic algae as well as irradiance and near-surface temperature and salinity 3 times per week for 1 yr in a turbulent marine environment with continuously high nutrient concentrations. Seasonal variations in temperature and salinity were small, and diatoms composed the largest percentage of phytoplankton (≥5 µm) cell numbers throughout the year. We observed at least 96 diatom species, of which some were present throughout most of the year while others were observed for periods as short as 1 to 2 wk. Diatom species diversity reached minimum and maximum values during winter and summer months, respectively, and was positively correlated to temperature and daylength and negatively correlated to salinity. Winter and spring blooms occurred and were numerically dominated by small and large cells of *Skeletonema costatum*, respectively, and *Pseudo-nitzschia delicatissima*, resulting in minimum seasonal values of species evenness, which peaked during summer months. The first 4 axes of a canonical correspondence analysis (CCA) explained 76% of the variance in the diatom data; the measured environmental variables explained 90% of this variation, of which temperature had a dominant role. We discuss possible environmental optima of 44 diatom species based on results of CCA and make suggestions regarding altered measures of diversity.

KEY WORDS: Seasonal succession · Planktonic diatoms · Turbulent marine water

INTRODUCTION

Temporal changes in species composition of planktonic algae have long fascinated biological oceanographers because some seasonal patterns in the taxonomic composition of marine phytoplankton are predictable, and thus provoke searches for cause and effect. Potential causes have been discussed (Smayda 1980, Harris 1986) and may include variations in temperature, light, salinity, advection and turbulence, nutrients, production of resting stages, ectocrines, and predation, as well as water mass movement. Given these 9 variables and their potential interactions as well as our paucity of information about critical parameters relating most of them to division rates of species, we can conclude that prediction of temporal changes in species assemblages is currently not possible. This appears to be true when assemblage compositions occurring in different parts of the ocean are compared (e.g. Smayda 1980), but certain regularities appear when sufficient data from one region, such as the northern European seas (Lange et al. 1992), Narragansett Bay (Karentz & Smayda 1984), the Southern California Bight (Reid et al. 1985) or Saanich Inlet, a fjord in Vancouver Island, British Columbia (Takahashi et al. 1977, 1978, Huntley & Hobson 1978, Hobson 1981, 1983, Sancetta & Calvert 1988, Sancetta 1989, Smith & Hobson 1994) have been collected.

Saanich Inlet stratifies during late spring and summer months and vertical nutrient fluxes at these times are uncertain (Hobson 1985) sometimes resulting in ap-

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parent shifts from a diatom- to a flagellate-dominated flora (Hobson 1983). The inlet is part of the Strait of Georgia, and many regions of the strait are tidally well mixed throughout the year (Thomson 1981) causing nutrient fluxes to remain relatively high at all times (Hobson 1985). Stratified waters are separated from tidally well-mixed waters by frontal zones (Parsons et al. 1983) and spatial variations in diatom composition across fronts can be large, particularly during summer months (Haigh & Taylor 1991). This observation suggests that differences in species compositions of phytoplankton across fronts can be caused by variations in nutrient fluxes.

No seasonal studies of phytoplankton species composition in tidally well-mixed, nutrient-rich waters of the Strait of Georgia are known to us, and they would provide valuable information about changes in composition in the apparent absence of nutrient effects. Such regions in which strong tidal currents occur that are contiguous to the southern Strait of Georgia include Sidney Channel and Haro Strait (Thomson 1981). These 2 regions have near-surface concentrations of inorganic nitrogen generally ≥5 µM, although a value as low as 2.7 µM has been observed in early August (Hobson 1985). This coupled to an unknown but almost certainly large vertical flux of NO_3-N into the euphotic zone supports the assumption that division rates of cells are not nutrient limited in either Haro Strait or Sidney Channel. As in other regions, the diatoms *Skeletonema costatum* and *Thalassiosira nordenskiöldii* are important components of the spring bloom in these waters (Parsons et al. 1969, Hobson 1988). Information about other species is available at bimonthly intervals (Hobson unpubl.), but no coherent examination based on frequent sampling has been carried out. We therefore initiated a year-long study of species composition of phytoplankton based on frequent sample collection in Sidney Channel. We reasoned that the resulting information would allow us to qualitatively and quantitatively describe temporal changes in composition as well as resting spore production by species. The importance of resting spores in species succession is not well known (McQuoid & Hobson 1996) possibly because of poor temporal resolution in most data sets (Garrison 1981). Furthermore, an extensive data set with a high degree of temporal control would allow us to obtain correlations between species composition and their cell concentrations and environmental variables in the absence of nutrient effects.

METHODS AND MATERIALS

We began in September 1993, by sampling Sidney Channel 3 times per week for most of 1 yr. No research vessel was available and use of a small boat was impossible during winter months; therefore we took bucket samples of near-surface seawater from the end of a pier off Sidney, British Columbia, in Sidney Channel (Fig. 1). The most likely source of error introduced by using this sampling platform was the inclusion of benthic species with pelagic ones, particularly during storms. Samples were always taken during the highest phase of the daytime tide to minimize contamination of temporal variations in cell numbers and crop composition by their spatial variations.

Water temperature (bucket thermometer) was measured and seawater samples were placed in glass bottles with impervious caps for salinity measurements. Seawater (250 ml) was placed in glass bottles with sufficient Lugol's acid-iodine solution (10 ml) to

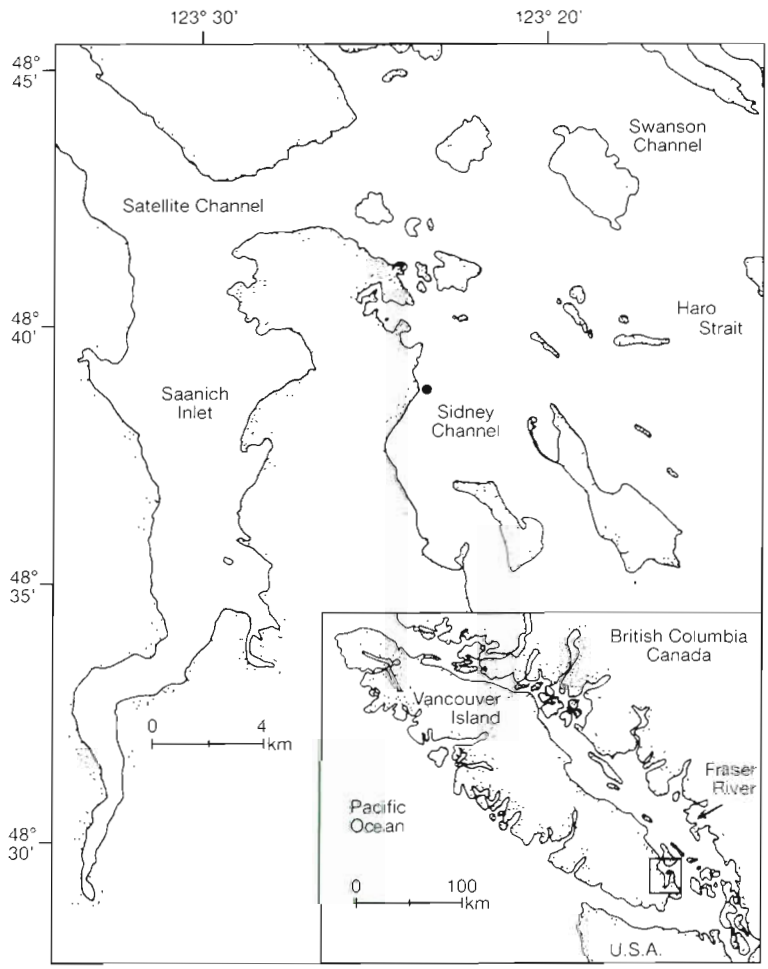

Fig. 1. Chart of the southern Strait of Georgia showing Sidney Channel, the sample site (●) and the complete strait and location of the Fraser River mouth (inset)

preserve cells (Throndsen 1978). Sea-surface irradiance was measured (Biospherical Instruments, QSP 170) at local apparent noon of each sampling day. Irradiance results are presented as percentages of the brightest sampled day of the year because of uncertainty in instrument calibration.

Salinity samples were stored for up to 2 mo before measurements were made (salinometer), while analysis of phytoplankton samples was carried out within 1 mo of sample collection, although most were done within a few days. Short storage time appears to be important because we found that some samples (n = 13) stored for about 1 yr had on average 40% (range = 5.3 to 100%) of the cell numbers counted just after collection, regardless of initial cell number, bottle hardness [varying between hard (Pyrex) and soft (Flint) glass] or pH (range = 4.4 to 7.0).

Particles in samples (50 ml) were allowed to settle for 24 h in split-ring chambers consisting of a short cylindrical well (3 × 26 mm) in a rectangular plastic support on which another removable cylinder rested. Supernatants were removed via gentle suction, the upper cylinder removed by sliding it off the base, the chamber covered by a glass slip and cells examined using an inverted biological microscope (Utermöhl 1931). One-third of the chamber was viewed (magnification = 140 or 280×) and up to 300 cells of each species having longest dimensions ≥5 µm were counted if that many or more were present. We used Cupp (1943), Rines & Hargraves (1988), Round et al. (1990) and Hasle & Syvertson (1996) as taxonomic references.

Species diversity and evenness were estimated by the number of species observed in 16.5 ml (S) and by diversity scaled on numbers of individuals of each species (H'), respectively. The latter was computed using the Shannon diversity index (Shannon & Weaver 1949, discussed by Pielou 1969):

$$H' = -C \sum_n p_j \log_2 p_j$$

where H' is diversity (bits/individual), C is set equal to 1, n is the number of species in a sample, and p_j is the ratio of the number of individuals of species j to the total number of individuals of all species in a sample.

Species composition of phytoplankton, primarily diatoms, in Sidney Channel was compared to that in Haro Strait, Swanson and Satellite Channels and Saanich Inlet (Fig. 1) using a similarity index consisting of the number of matches between species observed at each pair of stations divided by the largest number of species found at either of the 2 stations (Rohlf 1990). Species composition and cell numbers were determined using techniques outlined above, except that samples were taken by Niskin bottles lowered from the deck of the MSSV 'John Strickland' in 1983 and 1984. Spatial variation in cell numbers of each species in an ensemble was estimated using the the Bray-Curtis dissimilarity coefficient (Odum 1950), discussed by Legendre & Legendre (1983):

$$d_{ij} = \sum_{k=1}^{n} |x_{ki} - x_{kj}| / \sum_{k=1}^{n} (x_{ki} + x_{kj})$$

where d_{ij} is the coefficient, and x is the number of individuals of a species (k) in each of 2 samples, i and j, consisting of n species.

Correlations between untransformed cell numbers of each species and values of environmental variables were computed using canonical correspondence analysis (CCA) (ter Braak 1986), CANOCO version 3.1 (ter Braak 1990), which is an ordination technique for multivariate data. Cell numbers were transformed by logarithms and by square root with no noticeable effect on results of CCA. Therefore only the untransformed data are shown. The significance of the first of 4 axes was tested using a Monte Carlo analysis with 99 permutations. CCA has been used successfully to correlate fossil diatom species composition to environmental variables in lakes (Dixit et al. 1991, Fritz et al. 1991) and in Saanich Inlet (McQuoid & Hobson 1996) and to infer conditions leading to seasonal succession of phytoplankton (Bakker et al. 1990). Variables included were temperature, irradiance, daylength, salinity, tide height and tide range, and time of day when samples were collected. Tide height was the height of the sea surface above a reference level of lowest normal tide when samples were taken; tide range was the difference in heights of the highest and lowest tide during a 24.83 h period, which included the time when samples were taken. We had environmental and phytoplankton composition data for 122 sample dates, which were included in the analysis.

RESULTS

Environmental variables

Irradiance was highly variable, although fluxes during clear and overcast days temporally changed in parallel, reaching minimum and maximum values during winter and summer months, respectively (Fig 2A). A running average of irradiance was computed using a period of 1 wk offset by 2 d from nearest neighbors because of the scatter in the raw data (Fig 2A). The running average showed the seasonal trend more clearly than the raw data; nevertheless they were highly correlated (r = 0.99), and only raw data were used in subsequent analyses. Sea surface temperature averaged 8.1 ± 0.4°C (n = 37) from mid December to early March, after which it increased during the spring and early summer months to a plateau of 13.7 ± 1.3°C (n = 20) during most of July and August, then de-

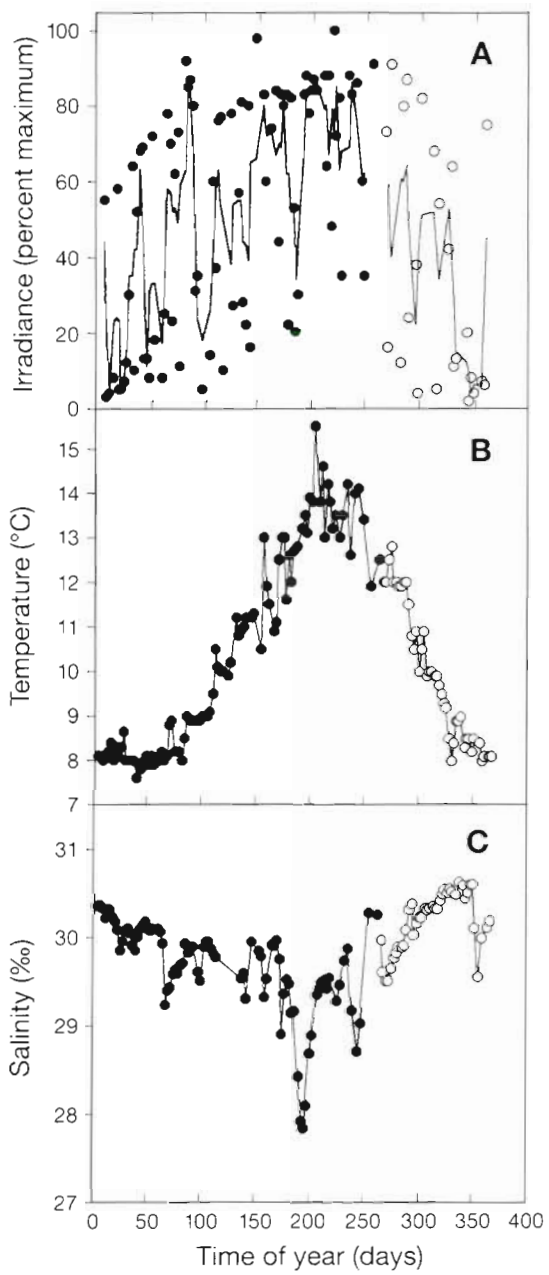

Fig. 2. (A) Irradiance at the sea surface of Sidney Channel, and (B) temperature and (C) salinity of near-surface waters of Sidney Channel during 1993 (○) and 1994 (●). A running average of irradiance, calculated using a period of 1 wk offset from its nearest neighbor by 2 d, is shown by the line in (A)

creased in late summer and fall months (Fig 2B). Surface salinity increased to a maximum of 30.5‰ in late November although frequent short-lived and small decreases occurred during heavy rainfall events (Fig 2C). A coherent decrease occurred from mid June to early July that resulted in a minimum salinity of 27.7‰ (Fig. 2C), probably due to the spring flood of the Fraser River (Fig. 1).

Many of the measured variables were significantly ($p \leq 0.05$) correlated (Table 1). For example, temperature was positively and negatively correlated to daylength ($r^2 = 0.54$) and salinity ($r^2 = 0.40$), respectively. Daylength was negatively correlated to salinity ($r^2 = 0.27$), and tide range and tide height were positively correlated ($r^2 = 0.60$). Only irradiance was not correlated to any other measured variable.

Cell concentrations and diversity

The seasonal cycle of cell concentrations was typical of temperate waters except that a winter bloom occurred (Fig. 3A). Cell numbers were at a minimum ($5.0 \times 10^3 \pm 4.5 \times 10^3$ cells l^{-1}, n = 25) during December and January. In February a winter bloom began, reaching a maximum of 2×10^5 cells l^{-1} on 7 February, then declined, reaching a second minimum ($5.8 \times 10^3 \pm 4.4 \times 10^3$ cells l^{-1}, n = 10) in March. A spring bloom occurred in April and May, ultimately reaching 3×10^6 cells l^{-1} on 20 May, followed by a decline that reached an apparent steady state ($1.8 \times 10^5 \pm 1.6 \times 10^5$ cells l^{-1}, n = 19) from June to mid July. Later in July, the concentration declined to a second apparent steady state ($4.8 \times 10^4 \pm 4.1 \times 10^4$ cells l^{-1}, n = 23) during most of August and September. Thereafter, a further decline to winter levels occurred in November.

Diatoms composed the largest percentage of phytoplankton cell numbers (≥5 µm in longest dimension) throughout the year In winter, 90 ± 15% (n = 24) of these cells were diatoms prior to the winter bloom and 84 ± 10% (n = 10) were present after the bloom until the advent of the spring bloom. During the 2 blooms, mean values were 97 ± 5% (n = 15) and 97 ± 8% (n = 22) in winter and spring. Phytoplankton during June and July, and August and September were composed of 95 ± 10 (n = 19) and 85 ± 28% (n = 25) diatoms, respectively. Only diatom species were considered in subsequent analyses.

During the year, we observed 96 identifiable diatom species. Species diversity (S) followed a regular sea-

Table 1. Matrix (n = 122) of product-moment correlation coefficients among environmental variables in Sidney Channel, British Columbia, September 1993 to September 1994

	Temp.	Irrad.	Salinity	Tide height	Day-length	Tide range
Temp.	1.00					
Irrad.	0.25	1.00				
Salinity	−0.63	−0.05	1.00			
Tide height	−0.11	0.38	0.21	1.00		
Daylength	0.73	0.06	−0.52	−0.31	1.00	
Tide range	0.23	0.37	0.05	0.78	0.17	1.00

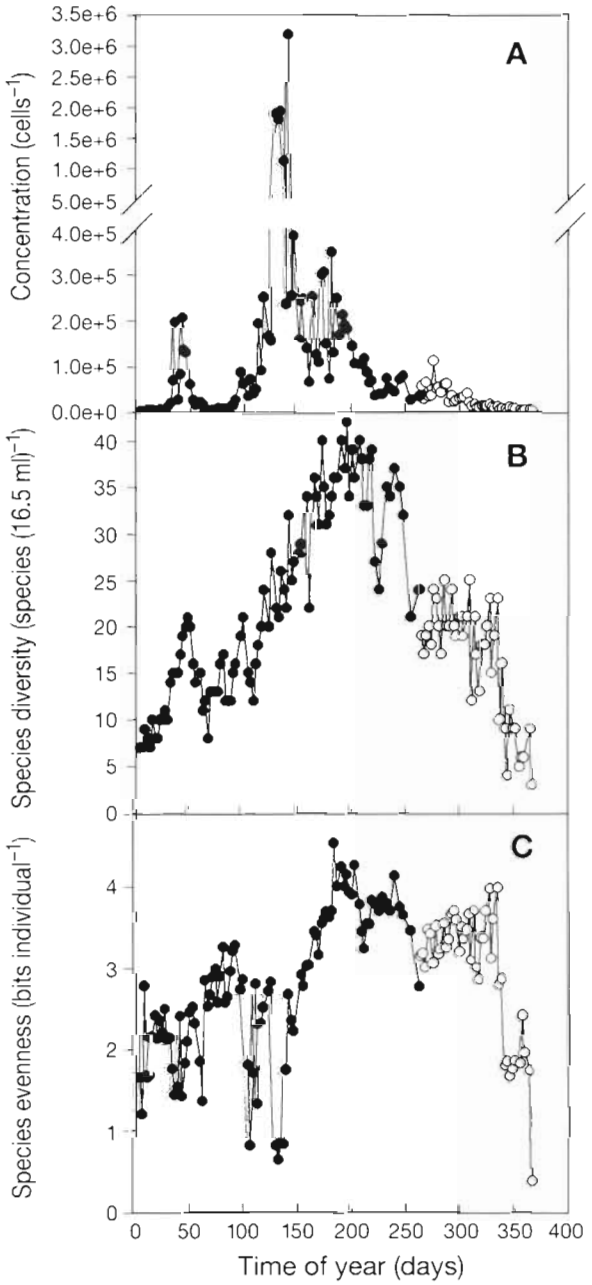

Fig. 3. (A) Concentration of phytoplankton cells, and (B) species diversity and (C) evenness of planktonic diatoms in near-surface waters of Sidney Channel during 1993 (○) and 1994 (●)

sonal cycle with a minimum [10 ± 8 species (16.5 ml)$^{-1}$, n = 36] during winter months, although an increase occurred during the winter bloom, and a maximum [37 ± 6 species (16.5 ml)$^{-1}$, n = 15] in July (Fig. 3B). Minimum values of species evenness (H') (1.9 ± 0.5 bits ind.$^{-1}$, n = 20) were observed during winter months and at the times of the winter (2.0 ± 0.4 bits ind.$^{-1}$, n = 14) and spring (2.2 ± 0.9 bits ind.$^{-1}$, n = 24) blooms when only a few species provided most of the cells (Fig. 3C). Maximum levels occurred during July (4.1 ± 0.2 bits ind.$^{-1}$, n = 8), while lower values were recorded for the latter half of June (3.3 ± 0.3 bits ind.$^{-1}$, n = 12) and August (3.7 ± 0.2 bits ind.$^{-1}$, n = 13).

Temporal variations in numbers of cells, S and H' were significantly ($p \leq 0.05$) correlated to some of the measured environmental variables (Table 2). However, correlation indices between S and temperature ($r^2 = 0.69$), S and salinity ($r^2 = 0.41$), S and daylength ($r^2 = 0.64$) and H' and temperature ($r^2 = 0.37$) were relatively high.

Temporal variations of species assemblages

Forty-four of the 96 species we observed formed distinct blooms in well-defined time intervals while the other species were only sporadically seen in small numbers; many of the latter were benthic species and could have been contaminants from bottom and pier surfaces at the sampling site. A few of the former group including *Cylindrotheca closterium* (Rabenhorst) Reimann & Lewin, *Pseudo-nitzschia delicatissima* (Cleve) Heiden, *Paralia sulcata* (Ehrenberg) Cleve, *Pleurosigma nicobaricum* Grunow, *Skeletonema costatum* (Grunow) Cleve and *Thalassionema nitzschioides* Grunow were present throughout the year However, their temporal distributions were not uniform; *P. delicatissima* and *S. costatum* (Fig. 4A) were most abundant during winter and spring blooms, *P. nicobaricum* during the spring bloom, *C. closterium* (Fig. 4B) and *T. nitzschioides* during summer and *P. sulcata* (Fig. 4C) in winter months.

Numerically, *Pseudo-nitzschia delicatissima* and *Skeletonema costatum* dominated the winter bloom. In addition, *Thalassiosira pacifica* Gran & Angst and a small diatom, about 5 µm in valve diameter, which appeared to be a species of *Thalassiosira*, were only seen during this bloom. Unfortunately the small diatom disappeared from samples, presumably by dissolving, before we could

Table 2. Matrix (n = 122) of product-moment correlation coefficients between environmental variables and diatom descriptors in Sidney Channel, British Columbia, September 1993 to September 1994

	Temp.	Irrad.	Salin.	Day-length	Tide height	Tide range
Cell numbers	0.15	0.02	−0.22	0.34	−0.17	0.02
Species diversity (S)	0.83	0.46	−0.64	0.80	−0.27	0.19
Species evenness (H')	0.61	0.36	−0.37	0.34	−0.02	0.18

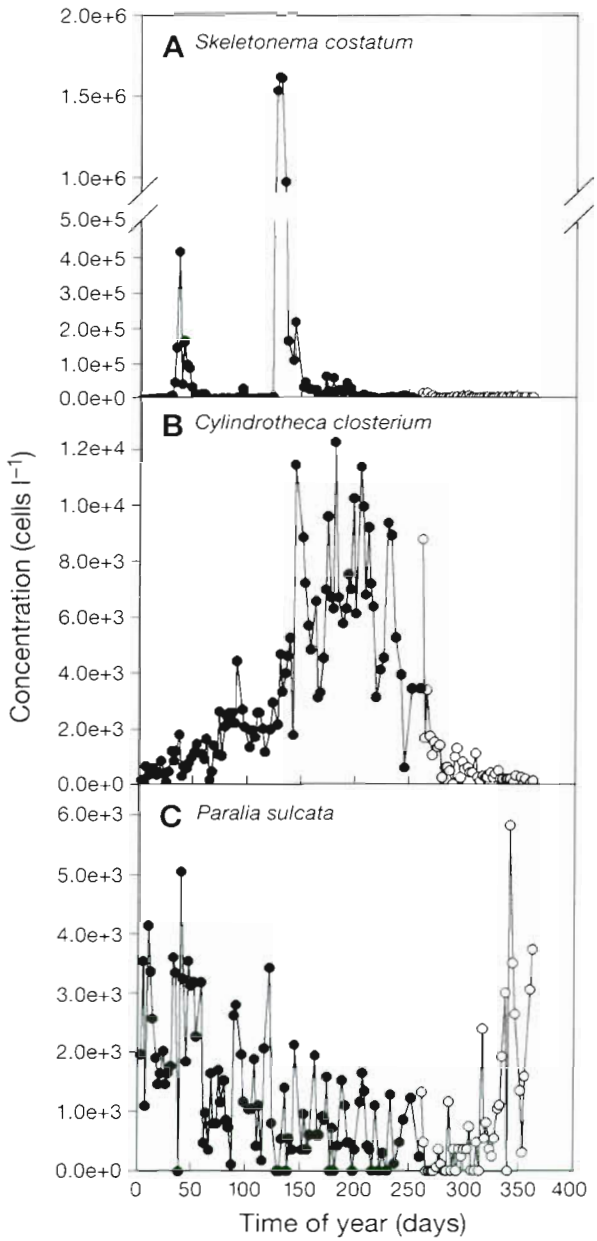

Fig. 4. Cell concentrations of (A) *Skeletonema costatum*, (B) *Cylindrotheca closterium* and (C) *Paralia sulcata* in near-surface waters of Sidney Channel during 1993 (○) and 1994 (●). These species were present throughout the year but reached maximum cell concentrations at different times

examine it using electron microscopy. Cell numbers declined during the late phase of the winter bloom and some species disappeared, while cell concentrations of *Licmophora abbreviata* Agardh and *Pleurosigma nicobaricum* increased. The spring bloom was numerically dominated by *S. costatum* and *P. delicatissima* and marked by the appearance of large cell numbers of *Lauderia annulata* Cleve (Fig. 5A) as well as other species, such as *Chaetoceros curvisetus* Cleve, *C. decipiens* Cleve and *Thalassiosira eccentrica* (Ehrenberg) Cleve. After the peak of the bloom, assemblages continued to change with the appearance of *Leptocylindrus danicus* Cleve (Fig 5B) and a suite of *Chaetoceros* species, *aequatorialis* Cleve, *affinis* Lauder, *debilis* Cleve, *didymus* Ehrenberg, *laciniosus* Schüt and *radicans* Schüt, as well as *Odontella pulchella* (Gray) Agardh, *Rhizosolenia setigera* Brightwell, and *Thalassiosira nordenskiöldii* Cleve. A late spring early summer assemblage characterized by *Chaetoceros cinctus* Gran, *diadema* (Ehrenberg) Gran (Fig. 5C) and *similis* Cleve, *Guinardia delicatula* (Cleve) Hasle, *Membraneis challengeri* Grunow, *Thalassiosira aestivalis* Gran & Angst, *angulata* (Gregory) Hasle and *rotula* Meunier then appeared. During summer months, *Asterionellopsis glacialis* (Castracane) Round, *Chaetoceros danicus* Cleve and *Eucampia zodiacus* Ehrenberg (Fig. 5D) were prominent. Then in late summer and fall, *Ditylum brightwellii* (West) Grunow (Fig 6A), *Proboscia alata* (Brightwell) Sundström and *Thalassiosira anguste-lineata* (A. Schmidt) Fryxell & Hasle became abundant and *A. glacialis* (Fig. 6B), *C. debilis*, *C. decipiens*, *C. didymus* and *G. delicatula* re-appeared in large numbers. We also recorded the presence of many small cells of the genera *Chaetoceros* and *Thalassiosira* but were unable to identify them using electron microscopy, presumably because of dissolution, which we noted above.

Species composition of phytoplankton at the sample site in Sidney Channel was similar to those in the adjoining well-mixed waters of Haro Strait and Swanson Channel (Fig 1) at any time from mid April to late September (Table 3). It was also similar to those in the

Table 3. Matching coefficients for the presence and absence of all identified phytoplankton species, and Bray-Curtis dissimilarity coefficients (in parentheses) comparing cell numbers of each species of a species ensemble at various locations in the southern Strait of Georgia (Fig. 1) to those at the sampling site during 1983 and 1984

Date	Haro Strait	Swanson Channel	Satellite Channel	Saanich Inlet
20 Apr	0.71 (0.84) 0.59 (0.84)	0.71 (0.81)	0.29 (0.78)	0.29 (0.56)
12 May	0.87 (0.80)	0.67 (0.50)	0.87 (0.49) 0.67 (0.58)	0.60 (0.63)
30 May			0.80 (0.78)	0.80 (0.35) 1.0 (0.49) 0.10 (1.0)
16 Jun	0.71 (0.52)	0.64 (0.64) 0.71 (0.80)		0.57 (0.31)
5 Jul			0.64 (0.62)	0.57 (0.97)
24 Aug			0.82 (0.51) 0.71 (0.78)	0.65 (0.52) 0.65 (0.82)
29 Sep			0.78 (0.11)	0.67 (0.39) 0.67 (0.41)
18 Apr		0.78 (0.38)	0.56 (0.71)	0.56 (0.85)

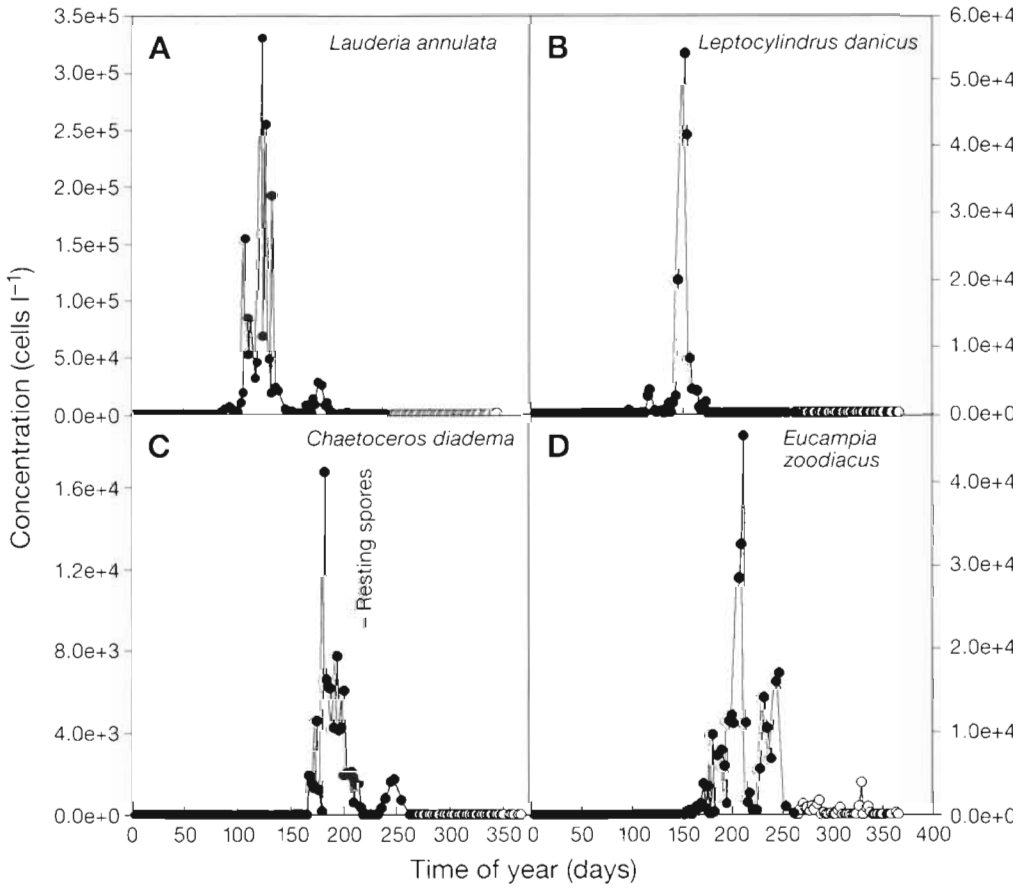

Fig. 5. Cell concentrations of (A) *Lauderia annulata*, (B) *Leptocylindrus danicus*, (C) *Chaetoceros diadema* and (D) *Eucampia zodiacus* in near-surface waters of Sidney Channel during 1993 (o) and 1994 (●). These species formed distinct blooms at different times during spring and summer months

frontal zone of Satellite Channel and the more stratified waters of Saanich Inlet (Fig. 1) except in April and in May at one location in the inlet (Table 3). Spatial variability of cell numbers of all enumerated species was generally large throughout this area with a few exceptions (Table 3).

Resting stages of *Chaetoceros affinis*, *C. diadema* and *C. radicans* were observed free floating and within vegetative cells during the decline of vegetative cell numbers (Fig. 5C). Those of *Ditylum brightwellii* were also observed within vegetative cells during the declining phase of their cell numbers (Fig. 6A).

Species assemblages and environmental variables

Seventy-six percent of the temporal variation in cells per species was described by 4 canonical axes, while the chosen environmental variables explained 90% of this variation (Table 4). Interset correlations of environmental variables showed that, in decreasing order, variations in temperature, salinity, daylength and irradiance were most highly correlated to the canonical axes (Table 5). The first axis was primarily composed of temperature, while axis 2 was dominated by salinity and daylength (Table 5, Fig. 7). Sampling time-of-day, while not an environmental variable, was also correlated to cell concentrations of species (Table 5) because concentrations were generally larger during early morning than afternoon hours.

Positions of diatom species relative to the first 2 canonical axes gave a qualitative indication of their environmental optima (Fig. 7). A group of species, *Asterionellopsis glacialis*, *Chaetoceros cinctus*, *C. danicus*, *C. diadema*, *C. laciniosus*, *C. radicans*, *C. similis*, *Thalassiosira aestivalis* and *T. rotula*, were abundant in warm water on long days with lower than average salinity. However, within this group there were differences in abundance along the irradiance gradient; *A.*

Table 4. Summary statistics for the first 4 axes of a canonical correspondence analysis carried out with the species-environment data (n = 122) in Sidney Channel, British Columbia, from September 1993 to September 1994

Axes:	1	2	3	4
Fraction of variance explained	0.46	0.24	0.12	0.08
Eigenvalues	0.39	0.20	0.10	0.07
Species-environment correlations	0.86	0.79	0.62	0.56

Table 5. Interset correlations of environmental variables with the first 4 axes of the canonical correspondence analysis (n = 122) for Sidney Channel, British Columbia, from September 1993 to September 1994

Axes:	1	2	3	4
Temperature	+0.42	−0.47	−0.03	−0.16
Irradiance	+0.28	+0.07	+0.42	−0.21
Salinity	−0.17	+0.66	+0.06	−0.14
Tidal height	+0.03	+0.36	+0.37	+0.23
Daylength	−0.16	−0.58	−0.01	−0.26
Tidal range	−0.03	+0.20	+0.26	+0.01
Time of day	−0.27	+0.05	+0.19	+0.06

glacialis and *C. danicus* were most frequently observed at times of moderately high irradiance, while the other species had optima at intermediate light levels. Another group composed of *Eucampia zodiacus*, *Guinardia delicatula*, *Membraneis challengeri*, *Odontella longicruris*, *Stephanopyxis turris*, *Thalassiosira angulata* and *T. anguste-lineata* were found when irradiance was high, but temperature and daylength were near their annual means. *Chaetoceros concavicornis* Mangin, *C. decipiens*, *Ditylum brightwellii*, *Guinardia striata* (Stolterfoth) Hasle and *Proboscia alata* were often observed when irradiance was high but daylength short. *Chaetoceros pelagicus*, *Paralia sulcata*, *Licmophora abbreviata*, *Thalassiosira eccentrica* and *T. pacifica* were most abundant in cooler than average conditions at times of short daylengths. Also, the latter 3 species were generally found in lower light levels than the first 2. Many species (19) had positions near the origin of the ordination diagram (Fig. 7) and thus were either most abundant under average environmental conditions [e.g. *Lauderia annulata*, *Leptocylindrus danicus*, *Odontella aurita*, *Melosira moniliformis* (Müller) Agardh] or found thoughout most of the year (e.g. *Chaetoceros curvisetus*, *Pseudo-nitzschia delicatissima*, *Skeletonema costatum*).

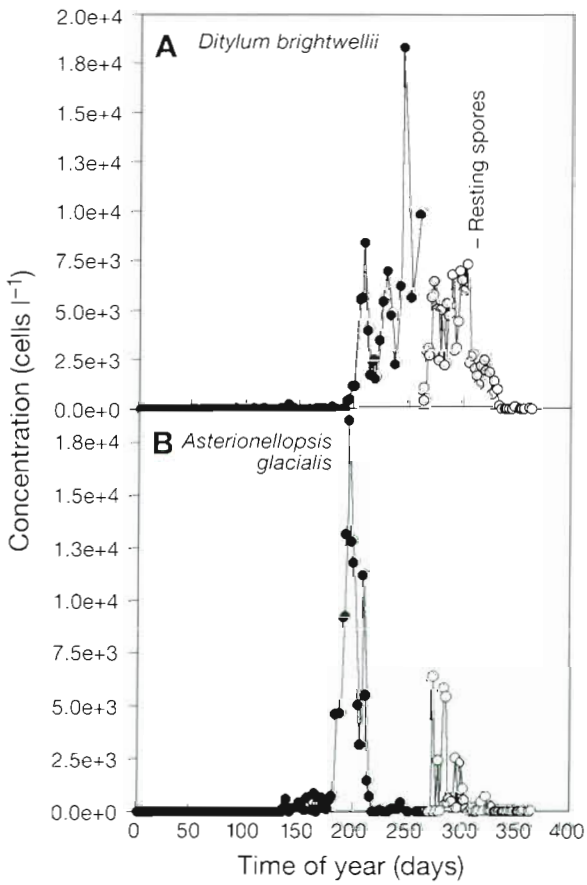

Fig. 6. Cell concentrations of (A) *Ditylum brightwellii* and (B) *Asterionellopsis glacialis* in near-surface waters of Sidney Channel during 1993 (○) and 1994 (●). These species formed distinct blooms in summer and fall months

DISCUSSION

Planktonic diatoms flourish in turbulent, nutrient-rich water (Margalef 1978), and accordingly dominate spring blooms in temperate coastal waters. Our results show that diatoms were the principal component of cells with longest dimensions ≥5 µm throughout the year in a turbulent coastal environment, even during winter months. The taxonomic composition, species-specific cell numbers, diversity and evenness of planktonic diatoms appeared to undergo temporal changes even though environmental variations were small, suggesting that the physiological poise of each species is set by a narrow subset of interacting environmental variables.

Variations in species composition at the sampling site were characteristic of most of the phytoplankton in the southern Strait of Georgia (Table 3) except in highly stratified water in Saanich Inlet (Fig. 1) when near-surface nutrient concentrations were undetectable (Hobson 1985). Thus, changes in species composition at the sampling site were unlikely to have been caused by spatial variations in species composition and current flow. Furthermore, results of other studies show that many of the same species as those observed at the sampling site occur in other regions at about the same time. For example, the spring bloom in the Strait of Georgia is often initially composed of the genus *Thalassiosira*, including the species *pacifica*, *eccentrica*, *gravida*, *nordenskiöldii* and *rotula* (Parsons et al. 1969, Huntly & Hobson 1978, Takahashi et al. 1978, Hobson 1981, Sancetta & Calvert 1988, Sancetta 1989, Haigh et al. 1992, McQuoid & Hobson 1997), and in some cases, a small form of *Skeletonema costatum* (Sancetta 1989) and *Lauderia annulata* (Hobson 1988). Later during the

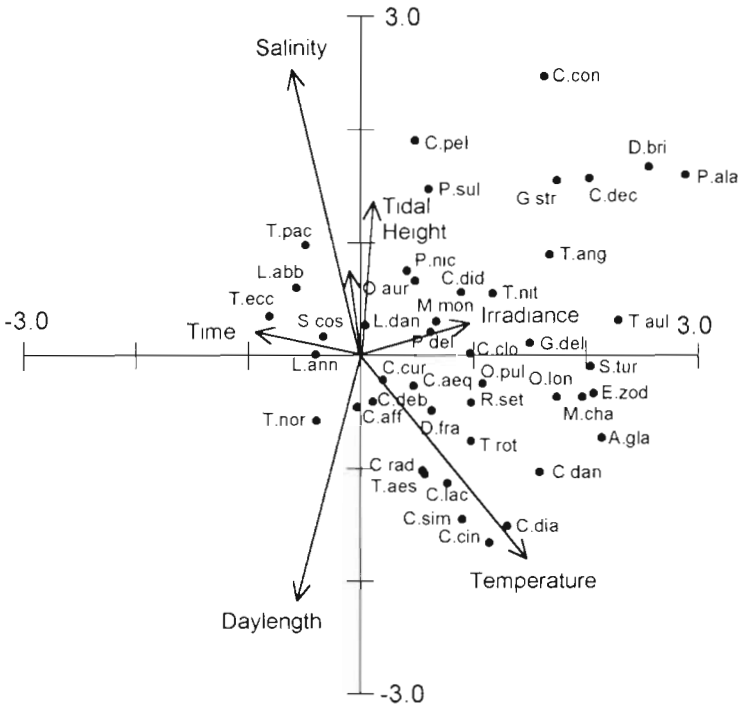

Fig. 7. Distributions of 44 diatom species (●) and environmental variables (arrows) in near surface waters of Sidney Channel during 1993 and 1994 relative to the first 2 canonical axes. Lengths of arrows and their angles to the axes give a qualitative indication of their relative importance to the ordination. Average values of environmental gradients are at the origin and only above-average vectors are displayed to increase presentation clarity. The arrow depicting tidal range is not labeled, and 'Time' refers to the time of day samples were taken and is not an environmental variable, although it was included in the analysis. Abbreviations are: A.gla = *Asterionellopsis glacialis*, C.aeq = *Chaetoceros aequatorialis*, C.aff = *C. affinis*, C.cin = *C. cinctus*, C.con = *C. concavicornis*, C.cur = *C. curvisetus*, C.dan = *C. danicus*, C.deb = *C. debilis*, C.dec = *C. decipiens*, C.dia = *C. diadema*, C.did = *C. didymus*, C.lac = *C. laciniosus*, C.pel = *C. pelagicus*, C.rad = *C. radicans*, C.sim = *C. similis*, C.clo = *Cylindrotheca closterium*, D.fra = *Dactyliosolen fragilissimus*, D.bri = *Ditylum brightwellii*, E.zod = *Eucampia zodiacus*, G.del = *Guinardia delicatula*, G.str = *G. striata*, L.ann = *Lauderia annulata*, L.dan = *Leptocylindrus danicus*, L.abb = *Licmophora abbreviata*, M.mon = *Melosira moniliformis*, M.cha = *Membraneis challengeri*, O.aur = *Odontella aurita*, O.lon = *O. longicruris*, O.pul = *O. pulchella*, P.ala = *Proboscia alata*, P.del = *Pseudo-nitzschia delicatissima*, P.sul = *Paralia sulcata*, P.nic = *Pleurosigma nicobaricum*, R.set = *Rhizosolenia setigera*, S.cos = *Skeletonema costatum*, S.tur = *Stephanopyxis turris*, T.nit = *Thalassionema nitzschioides*, T.aes = *Thalassiosira aestivalis*, T.ang = *T. angulata*, T.aul = *T. anguste-lineata*, T.ecc = *T. eccentrica*, T.nor = *T. nordenskioldii*, T.pac = *T. pacifica*, T.rot = *T. rotula*

bloom, the early assemblage is replaced by a number of *Chaetoceros* species, including *radicans*, and a large form of *S. costatum* (Parsons et al. 1969, Takahashi et al. 1977, Hobson 1981, 1983, Sancetta & Calvert 1988, Sancetta 1989, Haigh et al. 1992, McQuoid & Hobson 1997). During summer, if nutrient fluxes increase in stratified waters, short-lived blooms of *Chaetoceros debilis*, *Ditylum brightwellii*, *Eucampia zodiacus*, *Leptocylindrus danicus* and *S. costatum* occur (Parsons et al. 1967, Takahashi et al. 1977, Parsons et al. 1983, McQuoid & Hobson 1997). Fall blooms of *Chaetoceros* species, including *concavicornis*, *debilis*, *diadema* and *didymus*, and *Rhizosolenia setigera*, *S. costatum* and *Thalassionema nitzschioides* occur (Sancetta 1989, Haigh et al. 1992). *Ditylum brightwellii* may also persist into the fall months (Takahashi et al. 1977, Sancetta & Calvert 1988, Sancetta 1989, McQuoid & Hobson 1997) and *Paralia sulcata* is present during winter months (Sancetta 1989). *Chaetoceros radicans* has been observed during spring and summer (Sancetta 1989, McQuoid & Hobson 1997) and fall (Sancetta 1989) in Saanich Inlet and in the fall in the Strait of Georgia (Haigh et al. 1992). We saw all of the foregoing species at about the same time in Sydney Channel indicating that temporal variations are similar throughout the southern Strait of Georgia; however, we found some species at times other than those reported in the literature, and also observed some species for the first time in this region.

We found *Rhizosolenia setigera* and *Thalassionema nitzschioides* during late spring, summer and fall months in Sidney Channel whereas they previously have only been reported in the fall phytoplankton of Saanich Inlet (Sancetta 1989, McQuoid & Hobson 1997) It seems likely that these species are eliminated from fjord phytoplankton during summer months either by excessive temperature, nutrient deficiency or both. However, we found *Chaetoceros diadema* between June and the end of September in Sidney Channel, whereas it is usually a spring form in Saanich Inlet (McQuoid & Hobson 1997). Species that have generally not been reported include *Chaetoceros affinis*, *curvisetus*, *aequitorialis*, *decipiens*, *laciniosus*, and *similis*, *Cylindrotheca closterium* and *Odontella pulchella* between May and the end of August, although some of these were also found later in the year. We observed *Guinardia delicatula* primarily between June and the end of September and *Chaetoceros cinctus* only in July. Until additional data are available, we cannot be certain whether or not variations in the foregoing species were temporal.

The winter bloom, which we observed, was unexpected because critical depth is generally shallower than mixed depth during this season (Hobson 1981), although irradiance during the bloom was above average (Fig 2A). However, later in the winter, irradiance was also above average and higher than that observed during the winter bloom (Fig 2A), but cell concentrations remained low. Some species that were present during the winter bloom were also present in the pre-

vious fall season. One explanation for the appearance of 'fall' species is that winter mixing transported viable cells from the surface sediments back into the water column. Whatever the mechanism, cells had normal-appearing chloroplasts, suggesting that they were actively photosynthesizing. Clearly, the dynamics of winter blooms and whether or not they are a general phenomenon in the Strait of Georgia remain to be explored. When winter blooms occur, they must contribute to the annual primary production of an area, but the quantity is unknown because winter measurements are not usually carried out.

Spatial variations in species-specific cell concentrations can be large in the southern Strait of Georgia (Table 3) and thus probably contributed to apparent daily variations in cell concentrations of individual species at the sampling site (Figs. 4 to 6). The impact of these variations on results of CCA analysis is unknown, although 76% of the temporal variation in cells per species was described by the 4 canonical axes we used. Results suggest that temperature variation at the sea surface was the principal cause of temporal variations in species-specific cell numbers, even though temperature variation was small, about 7°C throughout the year at the sampling site (Fig. 2B). In addition, changes in irradiance, salinity and daylength were also important factors. Irradiance and daylength are probably manifested by their roles in determining daily irradiation, although daylength per se may also be important (Hobson 1974, Hobson et al. 1979, Hobson 1981, McQuoid & Hobson 1995). Bakker et al. (1990) and Karentz & Smayda (1984) observed similar correlations between variations in temperature, irradiance and species successions in the Osterschelde and Narragansett Bay, respectively, although seasonal variations of temperature in Narragansett Bay are larger than those in Sidney Channel. However, because of the eurythermal characteristics of observed species, Karentz & Smayda (1984) concluded that variables other than temperature must play a major role in determining succession. These could include nutrients and turbulence, salinity, anthropogenic substances and water quality, life cycle, ectocrines and predation (Smayda 1980).

Our study was carried out in a continuously turbulent environment in which nutrient concentrations are large throughout the year (Hobson 1985) to reduce nutrient effects. However, variables other than nutrients may or may not impact on temporal changes in species composition in Sidney Channel. Salinity was negatively correlated to temperature (Table 1) because flood of freshwater from the Fraser River (Fig. 1) occurs in late spring and early summer when near-surface temperature is near the maximum (Herlinveaux 1962). Whether or not salinity variations (Fig. 2C) altered species composition is not known but the annual range, 2.5‰, was small and we suspect of little consequence. Furthermore, no freshwater species typical of the Fraser River were observed. Anthropogenic substances such as waste water input and chemicals from residents on land and on boats probably were of minimal importance because there are no reasons to expect major seasonal shifts in input rates to Sidney Channel. We were unable to add much information about life history effects because we saw no identifiable resting stages in the water prior to blooms and only observed resting cell production by 3 species of *Chaetoceros* and *Ditylum brightwellii* among the 44 species that we frequently encountered. Resting cells appeared during the declining phase of cell concentrations of each of the 4 species, a timing which appears to be typical of diatom blooms (McQuoid & Hobson 1996). We are unable to comment on effects of ectocrine production and grazing rate, except to state that if either variable strongly co-varied with temperature, daylength or both, then they might have important but undiscovered effects on our measurements of succession.

Based on our results and others' (e.g. Karentz & Smayda 1984, Bakker et al. 1990), we suggest that variations in temperature, irradiance and daylength and their interactions play an important role in shaping temporal variations in species composition. For example, in Sidney Channel only a few species, *Licmophora abbreviata*, *Skeletonema costatum*, and *Thalassiosira eccentrica* and *pacifica*, were abundant when temperature and irradiance were low and daylength was short (Fig. 7), conditions typical of winter at temperate and more polar latitudes. This was reflected in minima of species diversity (Fig. 3B) and evenness (Fig. 3C) during winter months. Some species, including *Ditylum brightwellii* and *Paralia sulcata*, the most abundant diatoms found by us during fall and winter months in Sidney Channel and by others in Saanich Inlet (Takahashi et al. 1977, 1978, Sancetta 1989), and *Chaetoceros concavicornis* appear capable of increasing rates of cell division if irradiance increases to above average levels even though temperature and daylength remain low and short, respectively (Fig. 7). As temperature and daylength increased in the presence of above average levels of irradiance, more species reached their maximum numerical abundance. Their cell numbers began to decrease as temperature and daylength continued to increase and they were replaced by species, including *Chaetoceros cinctus*, *diadema* and *similis*, which produced maximum abundances at elevated temperature and long daylength (Fig. 7). When temperature and daylength were above average and irradiance was below average, a set of conditions which must reduce net photosynthetic rates, only 1 species, *Thalassiosira nordenskiöldii*, was found

to produce maximum cell numbers (Fig. 7). *T nordenskiöldii* is a common diatom in Strait of Georgia waters in spring and early summer (Huntley & Hobson 1978, Hobson 1983, Sancetta 1989, Haigh et al. 1992).

The validity of the foregoing results depends on a major assumption in the use of CCA. This analysis is based on the presumed gaussian distribution of the metabolic activity of individuals of a species in multidimensional space and the direct relationship of numbers of individuals to activity (ter Braak 1986). However, in our study, it is uncertain that this relationship is direct because cell concentration may be a complex function of cellular division rate and cell removal through processes such as herbivore grazing; these relationships are under investigation. At any given time the species assemblage composing phytoplankton must consist of species in varying stages of their life history. This variability needs to be incorporated into other ecological measurements such as species diversity and evenness, which necessarily consider all species and their cell numbers to be equivalent. Metabolically normalized diversity and evenness measures might give more insight into ecological processes than appears to be provided by classical measures.

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